BIOL 22: ANIMAL BIOLOGY



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1: BIOLOGY & THE PROCESS OF SCIENCE

1.1: The Study of Life
1.2: The Process of Science

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1.1: The Study of Life

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

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

Properties of Life

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

Order

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



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

Sensitivity or Response to Stimuli

Organisms respond to diverse stimuli. For example, plants can bend toward a source of light or respond to touch (Figure 1.1.2). Even tiny bacteria can move toward or away from chemicals (a process called chemotaxis) or light (phototaxis). Movement toward

a stimulus is considered a positive response, while movement away from a stimulus is considered a negative response.



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

CONCEPT IN ACTION

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

Reproduction

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

Adaptation

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

Growth and Development

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



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

Regulation

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

Homeostasis

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



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

Energy Processing

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



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

Levels of Organization of Living Things

Living things are highly organized and structured, following a hierarchy on a scale from small to large. The atom is the smallest and most fundamental unit of matter. It consists of a nucleus surrounded by electrons. Atoms form molecules. A molecule is a chemical structure consisting of at least two atoms held together by a chemical bond. Many molecules that are biologically important are macromolecules, large molecules that are typically formed by combining smaller units called monomers. An

example of a macromolecule is deoxyribonucleic acid (DNA) (Figure 1.1.6), which contains the instructions for the functioning of the organism that contains it.

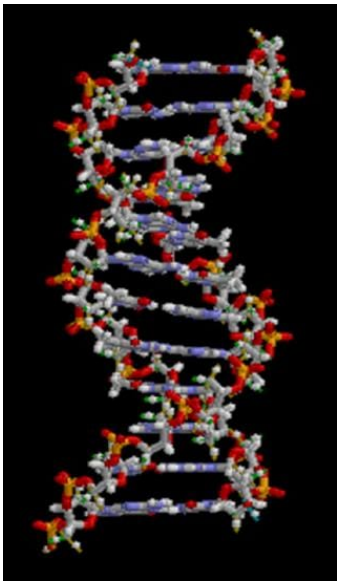


Figure 1.1.6: A molecule, like this large DNA molecule, is composed of atoms. (credit: "Brian0918"/Wikimedia Commons)

CONCEPT IN ACTION

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

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

In most multicellular organisms, cells combine to make tissues, which are groups of similar cells carrying out the same function. Organs are collections of tissues grouped together based on a common function. Organs are present not only in animals but also

in plants. An organ system is a higher level of organization that consists of functionally related organs. For example vertebrate animals have many organ systems, such as the circulatory system that transports blood throughout the body and to and from the lungs; it includes organs such as the heart and blood vessels. Organisms are individual living entities. For example, each tree in a forest is an organism. Single-celled prokaryotes and single-celled eukaryotes are also considered organisms and are typically referred to as microorganisms.

ART CONNECTION

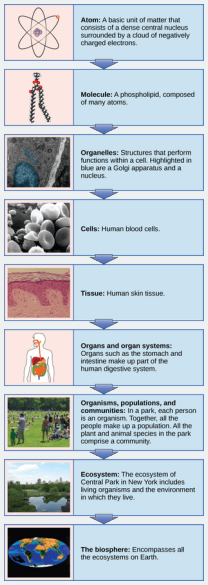


Figure 1.1.7**:** From an atom to the entire Earth, biology examines all aspects of life. (credit "molecule": modification of work by Jane Whitney; credit "organelles": modification of work by Louisa Howard; credit "cells": modification of work by Bruce Wetzel, Harry Schaefer, National Cancer Institute;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

Which of the following statements is false?

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

Answer available at the end of this section.

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

The Diversity of Life

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

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

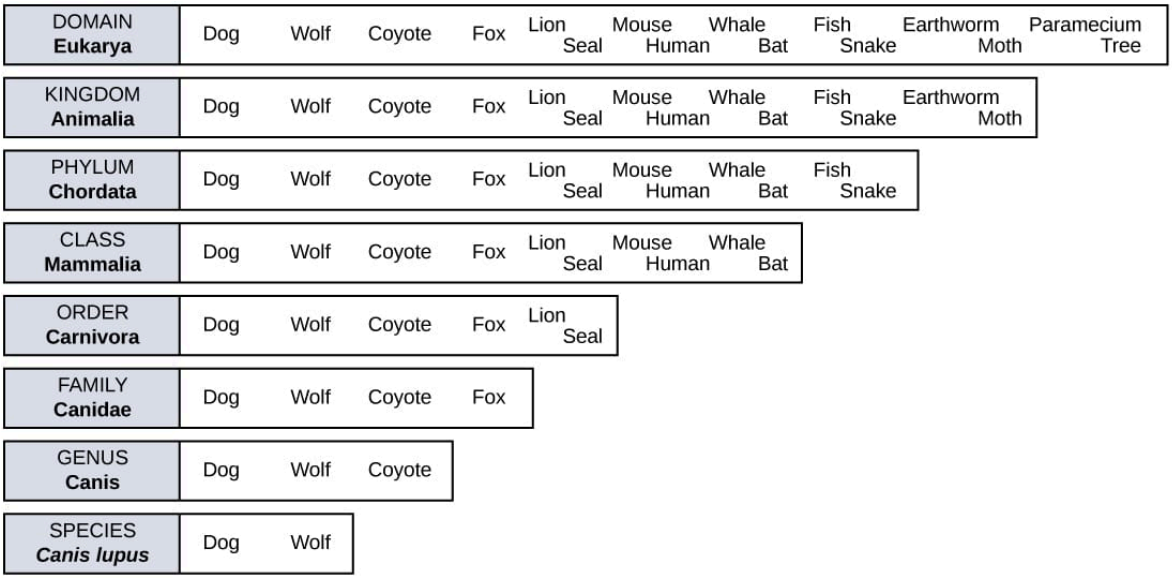


Figure 1.1.8**:** This diagram shows the levels of taxonomic hierarchy for a dog, from the broadest category—domain—to the most specific—species.

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

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



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

EVOLUTION IN ACTION: Carl Woese and the Phylogenetic Tree

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

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

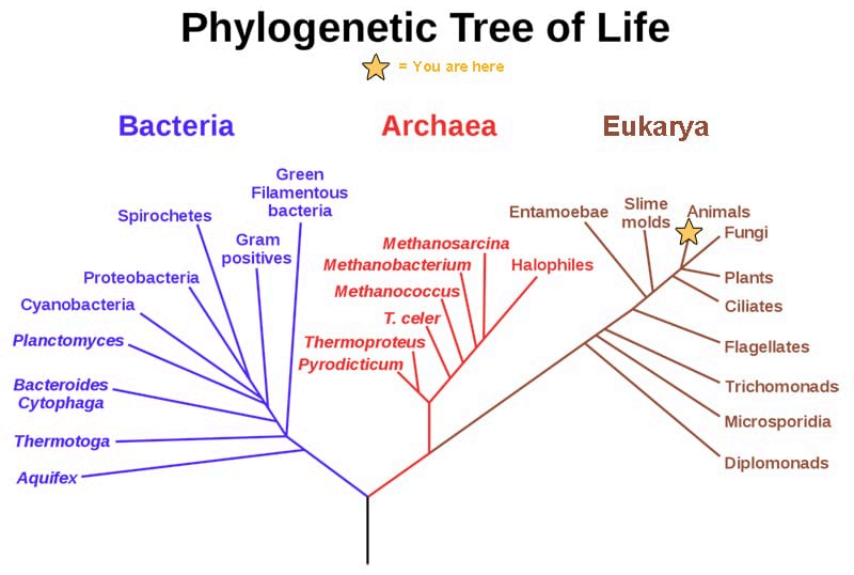


Figure 1.1.10**:** This phylogenetic tree was constructed by microbiologist Carl Woese using genetic relationships. The tree shows the separation of living organisms into three domains: Bacteria, Archaea, and Eukarya. Bacteria and Archaea are organisms without a nucleus or other organelles surrounded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

Branches of Biological Study

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

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



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

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

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

CAREERS IN ACTION: Forensic Scientist

Forensic science is the application of science to answer questions related to the law. Biologists as well as chemists and biochemists can be forensic scientists. Forensic scientists provide scientific evidence for use in courts, and their job involves examining trace material associated with crimes. Interest in forensic science has increased in the last few years, possibly because of popular television shows that feature forensic scientists on the job. Also, the development of molecular techniques and the establishment of DNA databases have updated the types of work that forensic scientists can do. Their job activities

are primarily related to crimes against people such as murder, rape, and assault. Their work involves analyzing samples such as hair, blood, and other body fluids and also processing DNA (Figure 1.1.12) found in many different environments and materials. Forensic scientists also analyze other biological evidence left at crime scenes, such as insect parts or pollen grains. Students who want to pursue careers in forensic science will most likely be required to take chemistry and biology courses as well as some intensive math courses.



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

Summary

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

Glossary

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

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

biosphere
: a collection of all ecosystems on Earth

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

community
: a set of populations inhabiting a particular area

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

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

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

homeostasis
the ability of an organism to maintain constant internal conditions

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

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

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

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

organelle
a membrane-bound compartment or sac within a cell

organism
an individual living entity

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

population
all individuals within a species living within a specific area

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

tissue
a group of similar cells carrying out the same function

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Answers

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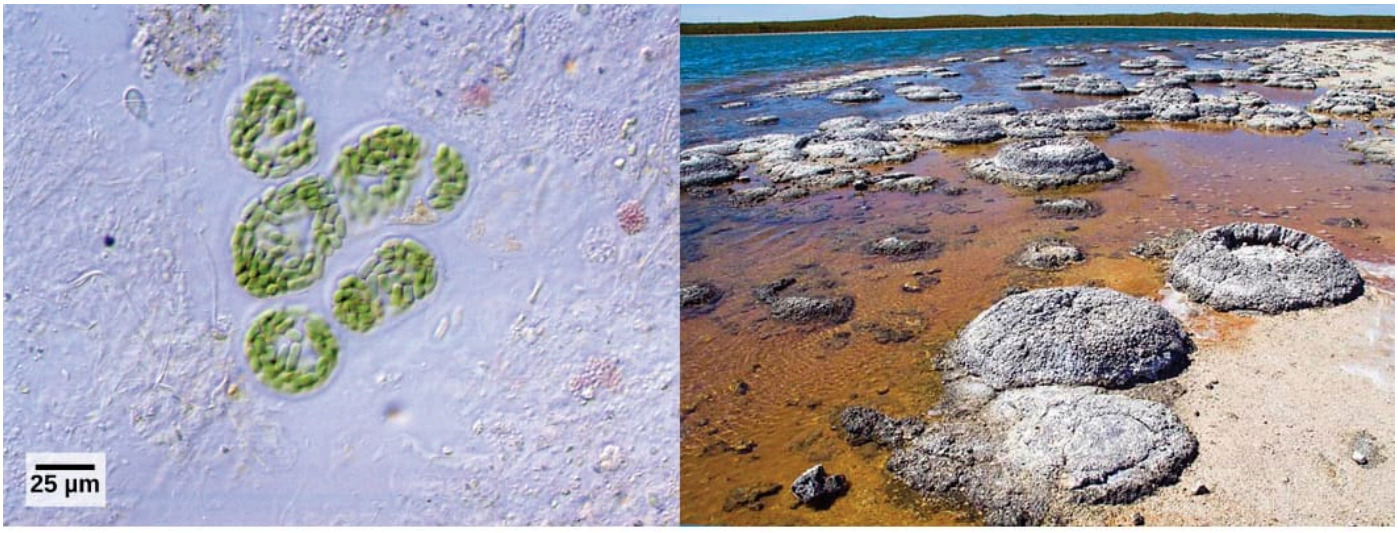
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1.2: The Process of Science

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



(a) (b)

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

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

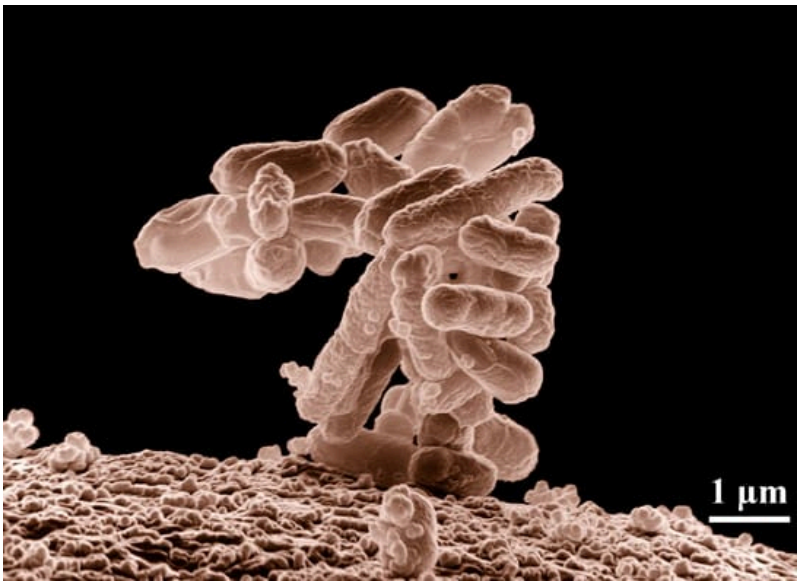


Figure 1.2.2**:** Biologists may choose to study *Escherichia coli* (*E. coli*), a bacterium that is a normal resident of our digestive tracts but which is also sometimes responsible for disease outbreaks. In this micrograph, the bacterium is visualized using a scanning electron microscope and digital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

The Nature of Science

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

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

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

Natural Sciences

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

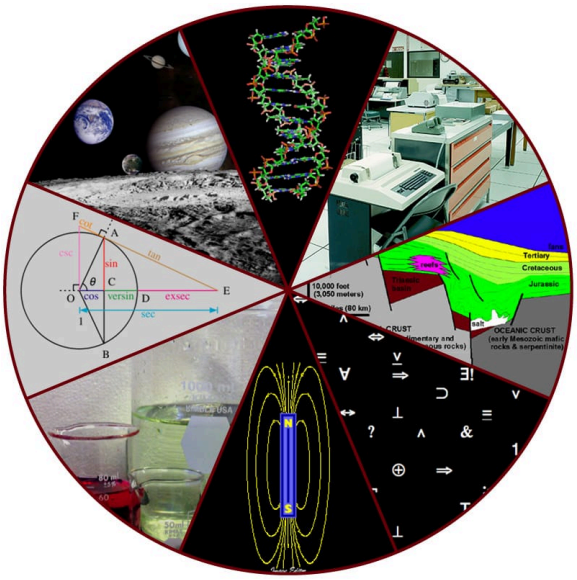


Figure 1.2.3**:** Some fields of science include astronomy, biology, computer science, geology, logic, physics, chemistry, and mathematics. (credit: "Image Editor"/Flickr)

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

Scientific Inquiry

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

Inductive reasoning is a form of logical thinking that uses related observations to arrive at a general conclusion. This type of reasoning is common in descriptive science. A life scientist such as a biologist makes observations and records them. These data can be qualitative (descriptive) or quantitative (consisting of numbers), and the raw data can be supplemented with drawings, pictures, photos, or videos. From many observations, the scientist can infer conclusions (inductions) based on evidence. Inductive reasoning involves formulating generalizations inferred from careful observation and the analysis of a large amount of data. Brain studies often work this way. Many brains are observed while people are doing a task. The part of the brain that lights up, indicating activity, is then demonstrated to be the part controlling the response to that task.

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

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

Hypothesis Testing

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



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

The scientific process typically starts with an observation (often a problem to be solved) that leads to a question. Let's think about a simple problem that starts with an observation and apply the scientific method to solve the problem. One Monday morning, a student arrives at class and quickly discovers that the classroom is too warm. That is an observation that also describes a problem: the classroom is too warm. The student then asks a question: "Why is the classroom so warm?"

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

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

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

Each experiment will have one or more variables and one or more controls. A variable is any part of the experiment that can vary or change during the experiment. A control is a part of the experiment that does not change. Look for the variables and controls in the example that follows. As a simple example, an experiment might be conducted to test the hypothesis that phosphate limits the growth of algae in freshwater ponds. A series of artificial ponds are filled with water and half of them are treated by adding phosphate each week, while the other half are treated by adding a salt that is known not to be used by algae. The variable here is the phosphate (or lack of phosphate), the experimental or treatment cases are the ponds with added phosphate and the control

ponds are those with something inert added, such as the salt. Just adding something is also a control against the possibility that adding extra matter to the pond has an effect. If the treated ponds show lesser growth of algae, then we have found support for our hypothesis. If they do not, then we reject our hypothesis. Be aware that rejecting one hypothesis does not determine whether or not the other hypotheses can be accepted; it simply eliminates one hypothesis that is not valid (Figure 1.2.5). Using the scientific method, the hypotheses that are inconsistent with experimental data are rejected.

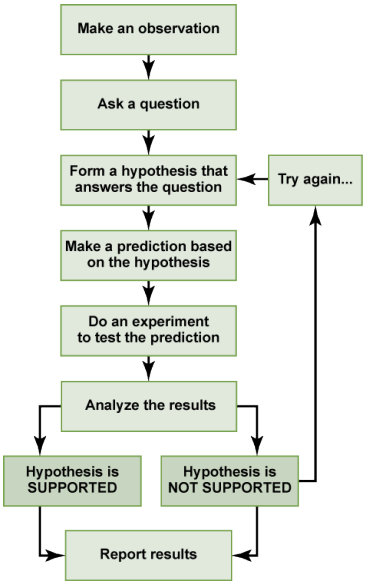


Figure 1.2.5: The scientific method is a series of defined steps that include experiments and careful observation. If a hypothesis is not supported by data, a new hypothesis can be proposed.

Example 1.2.1

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

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

Solution

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

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

Basic and Applied Science

The scientific community has been debating for the last few decades about the value of different types of science. Is it valuable to pursue science for the sake of simply gaining knowledge, or does scientific knowledge only have worth if we can apply it to

solving a specific problem or bettering our lives? This question focuses on the differences between two types of science: basic science and applied science.

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

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

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

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

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

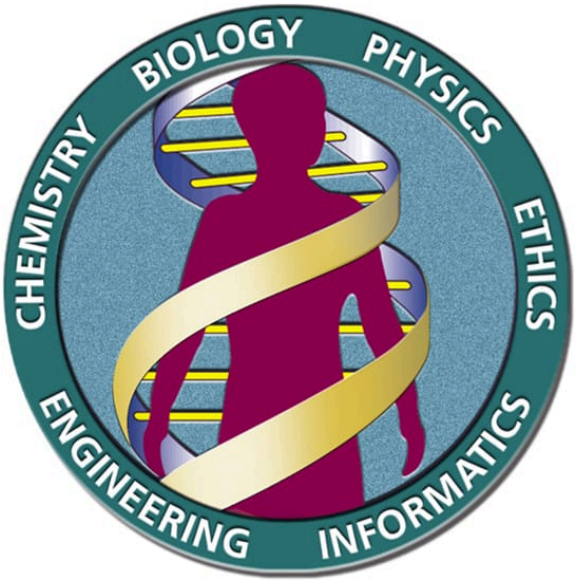


Figure 1.2.6: The Human Genome Project was a 13-year collaborative effort among researchers working in several different fields of science. The project was completed in 2003. (credit: the U.S. Department of Energy Genome Programs)

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

science, luck—when combined with an observant, curious mind—can lead to unexpected breakthroughs.

Reporting Scientific Work

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

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

Summary

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

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

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

Glossary

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

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

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

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

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

falsifiable
: able to be disproven by experimental results

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

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

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

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

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

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

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

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

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

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

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

variable
a part of an experiment that can vary or change

Contributors and Attributions

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2: ANIMAL CELLS & CELLULAR PROCESSES

2.1: How Cells Are Studied
2.2: Eukaryotic Cells
2.3: The Cell Membrane
2.4: Passive Transport
2.5: Active Transport

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2.1: How Cells Are Studied

A cell is the smallest unit of a living thing. A living thing, like you, is called an organism. Thus, cells are the basic building blocks of all organisms.

In multicellular organisms, several cells of one particular kind interconnect with each other and perform shared functions to form tissues (for example, muscle tissue, connective tissue, and nervous tissue), several tissues combine to form an organ (for example, stomach, heart, or brain), and several organs make up an organ system (such as the digestive system, circulatory system, or nervous system). Several systems functioning together form an organism (such as an elephant, for example).

There are many types of cells, and all are grouped into one of two broad categories: prokaryotic and eukaryotic. Animal cells, plant cells, fungal cells, and protist cells are classified as eukaryotic, whereas bacteria and archaea cells are classified as prokaryotic. Before discussing the criteria for determining whether a cell is prokaryotic or eukaryotic, let us first examine how biologists study cells.

Microscopy

Cells vary in size. With few exceptions, individual cells are too small to be seen with the naked eye, so scientists use microscopes to study them. A microscope is an instrument that magnifies an object. Most images of cells are taken with a microscope and are called micrographs.

Light Microscopes

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

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

Most student microscopes are classified as light microscopes (Figure 2.1.1**a**). Visible light both passes through and is bent by the lens system to enable the user to see the specimen. Light microscopes are advantageous for viewing living organisms, but since individual cells are generally transparent, their components are not distinguishable unless they are colored with special stains. Staining, however, usually kills the cells.

Light microscopes commonly used in the undergraduate college laboratory magnify up to approximately 400 times. Two parameters that are important in microscopy are magnification and resolving power. Magnification is the degree of enlargement of an object. Resolving power is the ability of a microscope to allow the eye to distinguish two adjacent structures as separate; the higher the resolution, the closer those two objects can be, and the better the clarity and detail of the image. When oil immersion lenses are used, magnification is usually increased to 1,000 times for the study of smaller cells, like most prokaryotic cells. Because light entering a specimen from below is focused onto the eye of an observer, the specimen can be viewed using light microscopy. For this reason, for light to pass through a specimen, the sample must be thin or translucent.

CONCEPT IN ACTION

For another perspective on cell size, try the HowBig interactive.

A second type of microscope used in laboratories is the dissecting microscope (Figure 2.1.1**b**). These microscopes have a lower magnification (20 to 80 times the object size) than light microscopes and can provide a three-dimensional view of the specimen. Thick objects can be examined with many components in focus at the same time. These microscopes are designed to give a magnified and clear view of tissue structure as well as the anatomy of the whole organism. Like light microscopes, most modern dissecting microscopes are also binocular, meaning that they have two separate lens systems, one for each eye. The lens systems are separated by a certain distance, and therefore provide a sense of depth in the view of their subject to make manipulations by hand easier. Dissecting microscopes also have optics that correct the image so that it appears as if being seen by the naked eye and not as an inverted image. The light illuminating a sample under a dissecting microscope typically comes from above the sample, but may also be directed from below.

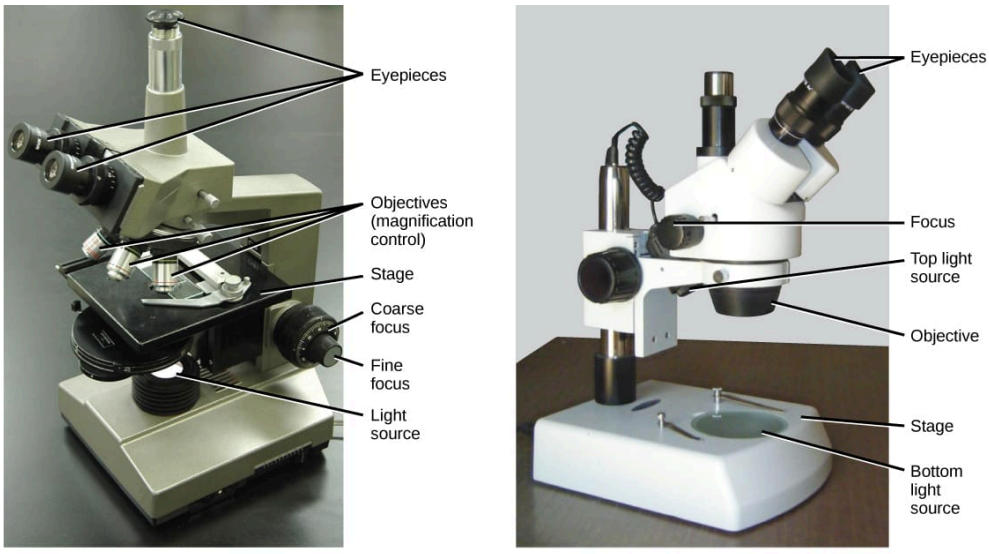


Figure 2.1.1**:** (a) Most light microscopes used in a college biology lab can magnify cells up to approximately 400 times. (b) Dissecting microscopes have a lower magnification than light microscopes and are used to examine larger objects, such as tissues.

Electron Microscopes

In contrast to light microscopes, electron microscopes use a beam of electrons instead of a beam of light. Not only does this allow for higher magnification and, thus, more detail (Figure 2.1.2), it also provides higher resolving power. Preparation of a specimen for viewing under an electron microscope will kill it; therefore, live cells cannot be viewed using this type of microscopy. In addition, the electron beam moves best in a vacuum, making it impossible to view living materials.

In a scanning electron microscope, a beam of electrons moves back and forth across a cell's surface, rendering the details of cell surface characteristics by reflection. Cells and other structures are usually coated with a metal like gold. In a transmission electron microscope, the electron beam is transmitted through the cell and provides details of a cell's internal structures. As you might imagine, electron microscopes are significantly more bulky and expensive than are light microscopes.

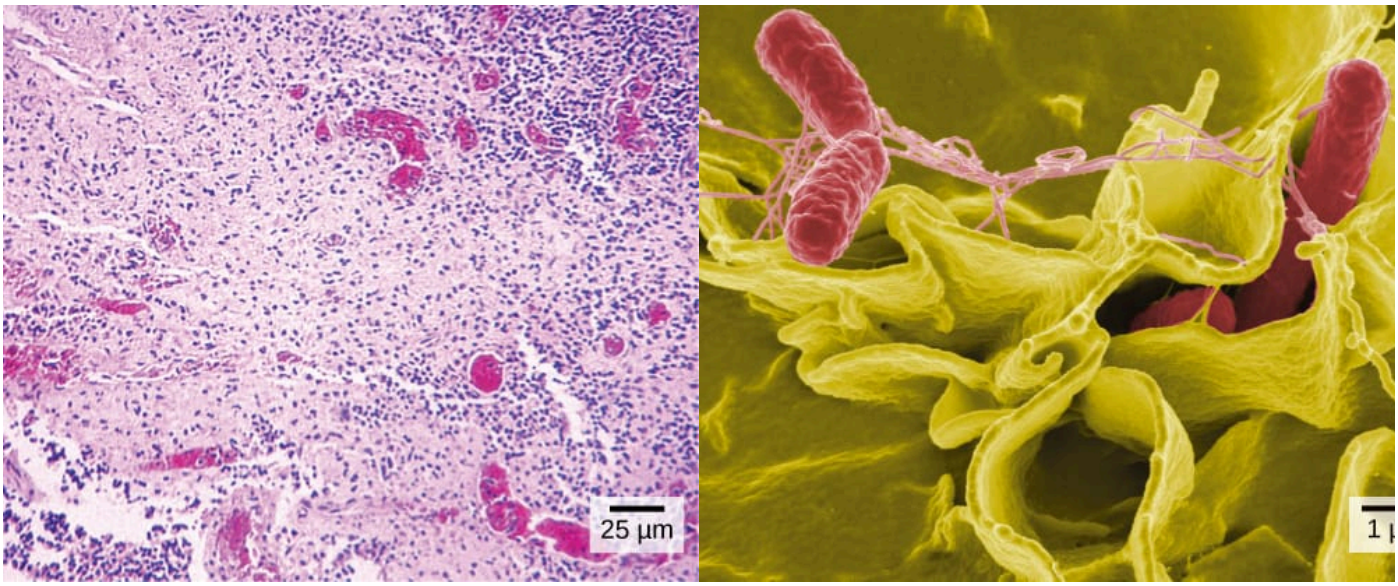


Figure 2.1.2**:** (a) *Salmonella* bacteria are viewed with a light microscope. (b) This scanning electron micrograph shows *Salmonella* bacteria (in red) invading human cells. (credit a: modification of work by CDC, Armed Forces Institute of Pathology, Charles N. Farmer; credit b: modification of work by Rocky Mountain Laboratories, NIAID, NIH; scale-bar data from Matt Russell)

CAREERS IN ACTION: Cytotechnologist

Have you ever heard of a medical test called a Pap smear (Figure 2.1.3)? In this test, a doctor takes a small sample of cells from the uterine cervix of a patient and sends it to a medical lab where a cytotechnologist stains the cells and examines them for any changes that could indicate cervical cancer or a microbial infection.

Cytotechnologists (*cyto-* = cell) are professionals who study cells through microscopic examinations and other laboratory tests. They are trained to determine which cellular changes are within normal limits or are abnormal. Their focus is not limited to cervical cells; they study cellular specimens that come from all organs. When they notice abnormalities, they consult a pathologist, who is a medical doctor who can make a clinical diagnosis.

Cytotechnologists play vital roles in saving people's lives. When abnormalities are discovered early, a patient's treatment can begin sooner, which usually increases the chances of successful treatment.

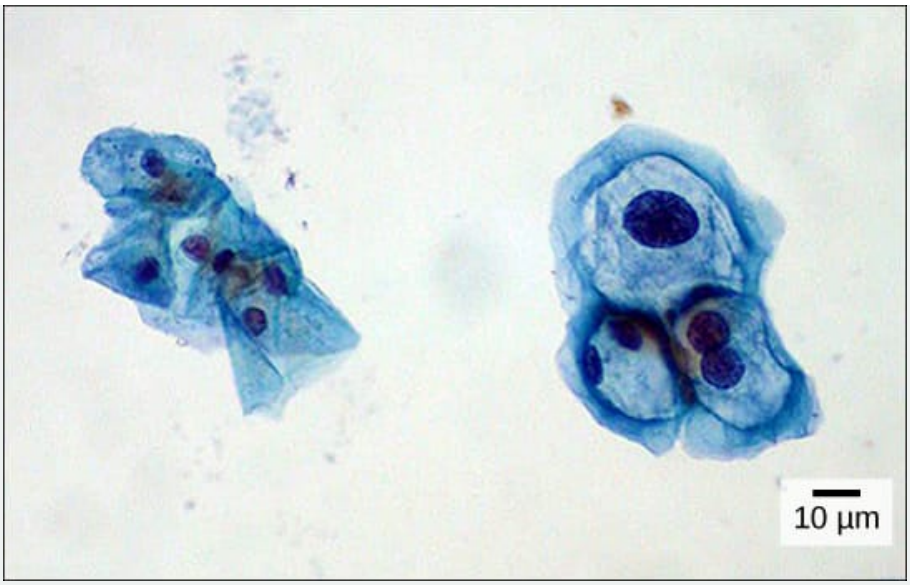


Figure 2.1.3**:** These uterine cervix cells, viewed through a light microscope, were obtained from a Pap smear. Normal cells are on the left. The cells on the right are infected with human papillomavirus. (credit: modification of work by Ed Uthman; scale-bar data from Matt Russell)

Cell Theory

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

In a 1665 publication called *Micrographia*, experimental scientist Robert Hooke coined the term "cell" (from the Latin *cella*, meaning "small room") for the box-like structures he observed when viewing cork tissue through a lens. In the 1670s, van Leeuwenhoek discovered bacteria and protozoa. Later advances in lenses and microscope construction enabled other scientists to see different components inside cells.

By the late 1830s, botanist Matthias Schleiden and zoologist Theodor Schwann were studying tissues and proposed the unified cell theory, which states that all living things are composed of one or more cells, that the cell is the basic unit of life, and that all new cells arise from existing cells. These principles still stand today.

Section Summary

A cell is the smallest unit of life. Most cells are so small that they cannot be viewed with the naked eye. Therefore, scientists must use microscopes to study cells. Electron microscopes provide higher magnification, higher resolution, and more detail than light microscopes. The unified cell theory states that all organisms are composed of one or more cells, the cell is the basic unit of life, and new cells arise from existing cells.

Glossary

microscope
: the instrument that magnifies an object

unified cell theory
: the biological concept that states that all organisms are composed of one or more cells, the cell is the basic unit of life, and new cells arise from existing cells

Contributors and Attributions

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2.2: Eukaryotic Cells

At this point, it should be clear that eukaryotic cells have a more complex structure than do prokaryotic cells. Organelles allow for various functions to occur in the cell at the same time. Before discussing the functions of organelles within a eukaryotic cell, let us first examine two important components of the cell: the plasma membrane and the cytoplasm.

ART CONNECTION

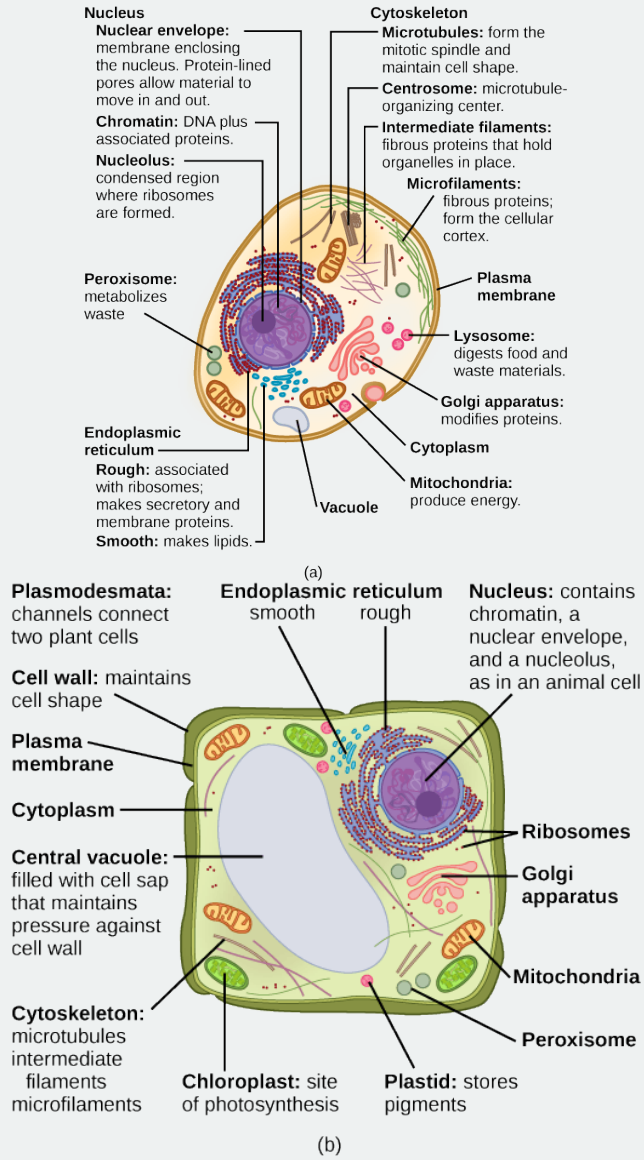


Figure 2.2.1**:** This figure shows (a) a typical animal cell and (b) a typical plant cell.

What structures does a plant cell have that an animal cell does not have? What structures does an animal cell have that a plant cell does not have?

The Plasma Membrane

Like prokaryotes, eukaryotic cells have a plasma membrane (Figure 2.2.2) made up of a phospholipid bilayer with embedded

proteins that separates the internal contents of the cell from its surrounding environment. A phospholipid is a lipid molecule composed of two fatty acid chains, a glycerol backbone, and a phosphate group. The plasma membrane regulates the passage of some substances, such as organic molecules, ions, and water, preventing the passage of some to maintain internal conditions, while actively bringing in or removing others. Other compounds move passively across the membrane.

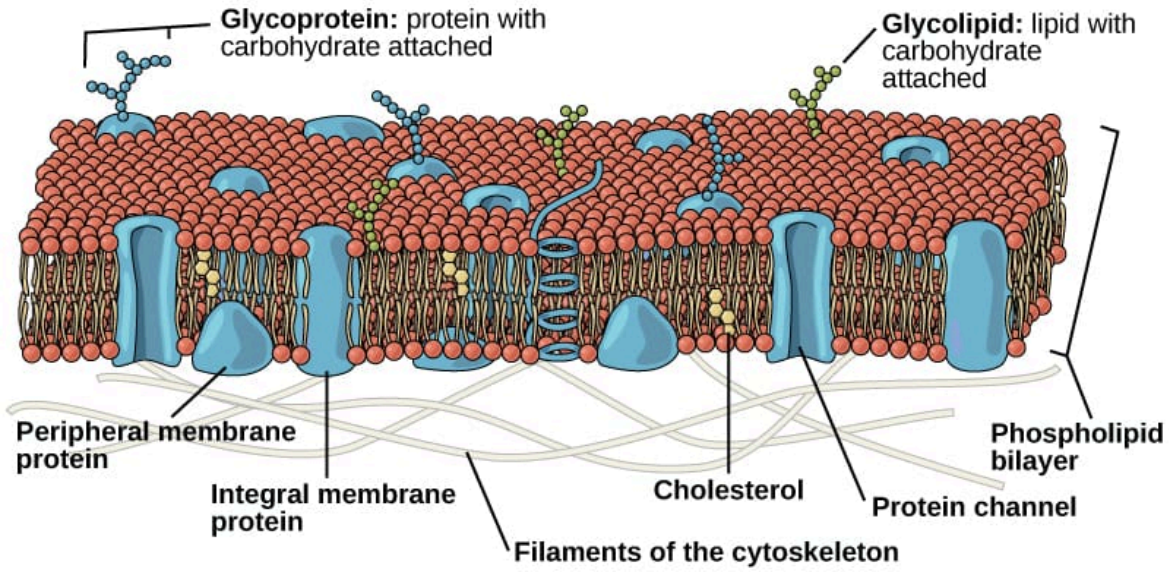


Figure 2.2.2**:** The plasma membrane is a phospholipid bilayer with embedded proteins. There are other components, such as cholesterol and carbohydrates, which can be found in the membrane in addition to phospholipids and protein.

The plasma membranes of cells that specialize in absorption are folded into fingerlike projections called microvilli (singular = microvillus). This folding increases the surface area of the plasma membrane. Such cells are typically found lining the small intestine, the organ that absorbs nutrients from digested food. This is an excellent example of form matching the function of a structure.

People with celiac disease have an immune response to gluten, which is a protein found in wheat, barley, and rye. The immune response damages microvilli, and thus, afflicted individuals cannot absorb nutrients. This leads to malnutrition, cramping, and diarrhea. Patients suffering from celiac disease must follow a gluten-free diet.

The Cytoplasm

The cytoplasm comprises the contents of a cell between the plasma membrane and the nuclear envelope (a structure to be discussed shortly). It is made up of organelles suspended in the gel-like cytosol, the cytoskeleton, and various chemicals (Figure 2.2.1). Even though the cytoplasm consists of 70 to 80 percent water, it has a semi-solid consistency, which comes from the proteins within it. However, proteins are not the only organic molecules found in the cytoplasm. Glucose and other simple sugars, polysaccharides, amino acids, nucleic acids, fatty acids, and derivatives of glycerol are found there too. Ions of sodium, potassium, calcium, and many other elements are also dissolved in the cytoplasm. Many metabolic reactions, including protein synthesis, take place in the cytoplasm.

The Cytoskeleton

If you were to remove all the organelles from a cell, would the plasma membrane and the cytoplasm be the only components left? No. Within the cytoplasm, there would still be ions and organic molecules, plus a network of protein fibers that helps to maintain the shape of the cell, secures certain organelles in specific positions, allows cytoplasm and vesicles to move within the cell, and enables unicellular organisms to move independently. Collectively, this network of protein fibers is known as the cytoskeleton. There are three types of fibers within the cytoskeleton: microfilaments, also known as actin filaments, intermediate filaments, and microtubules (Figure 2.2.3).

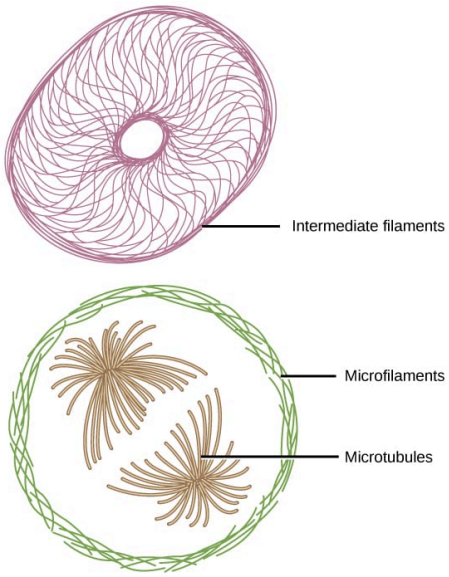


Figure 2.2.3**:** Microfilaments, intermediate filaments, and microtubules compose a cell's cytoskeleton.

Microfilaments are the thinnest of the cytoskeletal fibers and function in moving cellular components, for example, during cell division. They also maintain the structure of microvilli, the extensive folding of the plasma membrane found in cells dedicated to absorption. These components are also common in muscle cells and are responsible for muscle cell contraction. Intermediate filaments are of intermediate diameter and have structural functions, such as maintaining the shape of the cell and anchoring organelles. Keratin, the compound that strengthens hair and nails, forms one type of intermediate filament. Microtubules are the thickest of the cytoskeletal fibers. These are hollow tubes that can dissolve and reform quickly. Microtubules guide organelle movement and are the structures that pull chromosomes to their poles during cell division. They are also the structural components of flagella and cilia. In cilia and flagella, the microtubules are organized as a circle of nine double microtubules on the outside and two microtubules in the center.

The centrosome is a region near the nucleus of animal cells that functions as a microtubule-organizing center. It contains a pair of centrioles, two structures that lie perpendicular to each other. Each centriole is a cylinder of nine triplets of microtubules.

The centrosome replicates itself before a cell divides, and the centrioles play a role in pulling the duplicated chromosomes to opposite ends of the dividing cell. However, the exact function of the centrioles in cell division is not clear, since cells that have the centrioles removed can still divide, and plant cells, which lack centrioles, are capable of cell division.

Flagella and Cilia

Flagella (singular = flagellum) are long, hair-like structures that extend from the plasma membrane and are used to move an entire cell, (for example, sperm, *Euglena*). When present, the cell has just one flagellum or a few flagella. When cilia (singular = cilium) are present, however, they are many in number and extend along the entire surface of the plasma membrane. They are short, hair-like structures that are used to move entire cells (such as paramecium) or move substances along the outer surface of the cell (for example, the cilia of cells lining the fallopian tubes that move the ovum toward the uterus, or cilia lining the cells of the respiratory tract that move particulate matter toward the throat that mucus has trapped).

The Endomembrane System

The endomembrane system (*endo* = within) is a group of membranes and organelles (Figure 2.2.3) in eukaryotic cells that work together to modify, package, and transport lipids and proteins. It includes the nuclear envelope, lysosomes, and vesicles, the endoplasmic reticulum and Golgi apparatus, which we will cover shortly. Although not technically *within* the cell, the plasma membrane is included in the endomembrane system because, as you will see, it interacts with the other endomembranous organelles.

The Nucleus

Typically, the nucleus is the most prominent organelle in a cell (Figure 2.2.1). The nucleus (plural = nuclei) houses the cell's DNA in the form of chromatin and directs the synthesis of ribosomes and proteins. Let us look at it in more detail (Figure 2.2.4).

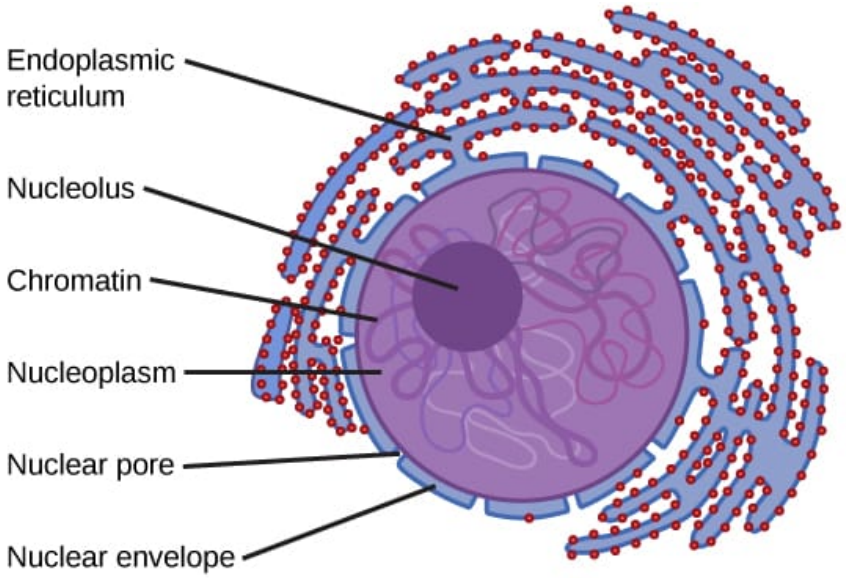


Figure 2.2.4: The outermost boundary of the nucleus is the nuclear envelope. Notice that the nuclear envelope consists of two phospholipid bilayers (membranes)—an outer membrane and an inner membrane—in contrast to the plasma membrane (Figure 2.2.2), which consists of only one phospholipid bilayer. (credit: modification of work by NIGMS, NIH)

The nuclear envelope is a double-membrane structure that constitutes the outermost portion of the nucleus (Figure 2.2.4). Both the inner and outer membranes of the nuclear envelope are phospholipid bilayers.

The nuclear envelope is punctuated with pores that control the passage of ions, molecules, and RNA between the nucleoplasm and the cytoplasm.

To understand chromatin, it is helpful to first consider chromosomes. Chromosomes are structures within the nucleus that are made up of DNA, the hereditary material, and proteins. This combination of DNA and proteins is called chromatin. In eukaryotes, chromosomes are linear structures. Every species has a specific number of chromosomes in the nucleus of its body cells. For example, in humans, the chromosome number is 46, whereas in fruit flies, the chromosome number is eight.

Chromosomes are only visible and distinguishable from one another when the cell is getting ready to divide. When the cell is in the growth and maintenance phases of its life cycle, the chromosomes resemble an unwound, jumbled bunch of threads.

We already know that the nucleus directs the synthesis of ribosomes, but how does it do this? Some chromosomes have sections of DNA that encode ribosomal RNA. A darkly staining area within the nucleus, called the nucleolus (plural = nucleoli), aggregates the ribosomal RNA with associated proteins to assemble the ribosomal subunits that are then transported through the nuclear pores into the cytoplasm.

The Endoplasmic Reticulum

The endoplasmic reticulum (ER) (Figure 2.2.7) is a series of interconnected membranous tubules that collectively modify proteins and synthesize lipids. However, these two functions are performed in separate areas of the endoplasmic reticulum: the rough endoplasmic reticulum and the smooth endoplasmic reticulum, respectively.

The hollow portion of the ER tubules is called the lumen or cisternal space. The membrane of the ER, which is a phospholipid bilayer embedded with proteins, is continuous with the nuclear envelope.

The rough endoplasmic reticulum (RER) is so named because the ribosomes attached to its cytoplasmic surface give it a studded appearance when viewed through an electron microscope.

The ribosomes synthesize proteins while attached to the ER, resulting in transfer of their newly synthesized proteins into the lumen of the RER where they undergo modifications such as folding or addition of sugars. The RER also makes phospholipids for cell membranes.

If the phospholipids or modified proteins are not destined to stay in the RER, they will be packaged within vesicles and transported from the RER by budding from the membrane (Figure 2.2.7). Since the RER is engaged in modifying proteins that will be secreted from the cell, it is abundant in cells that secrete proteins, such as the liver.

The smooth endoplasmic reticulum (SER) is continuous with the RER but has few or no ribosomes on its cytoplasmic surface (see Figure 2.2.1). The SER's functions include synthesis of carbohydrates, lipids (including phospholipids), and steroid hormones; detoxification of medications and poisons; alcohol metabolism; and storage of calcium ions.

The Golgi Apparatus

We have already mentioned that vesicles can bud from the ER, but where do the vesicles go? Before reaching their final destination, the lipids or proteins within the transport vesicles need to be sorted, packaged, and tagged so that they wind up in the right place. The sorting, tagging, packaging, and distribution of lipids and proteins take place in the Golgi apparatus (also called the Golgi body), a series of flattened membranous sacs (Figure 2.2.5).

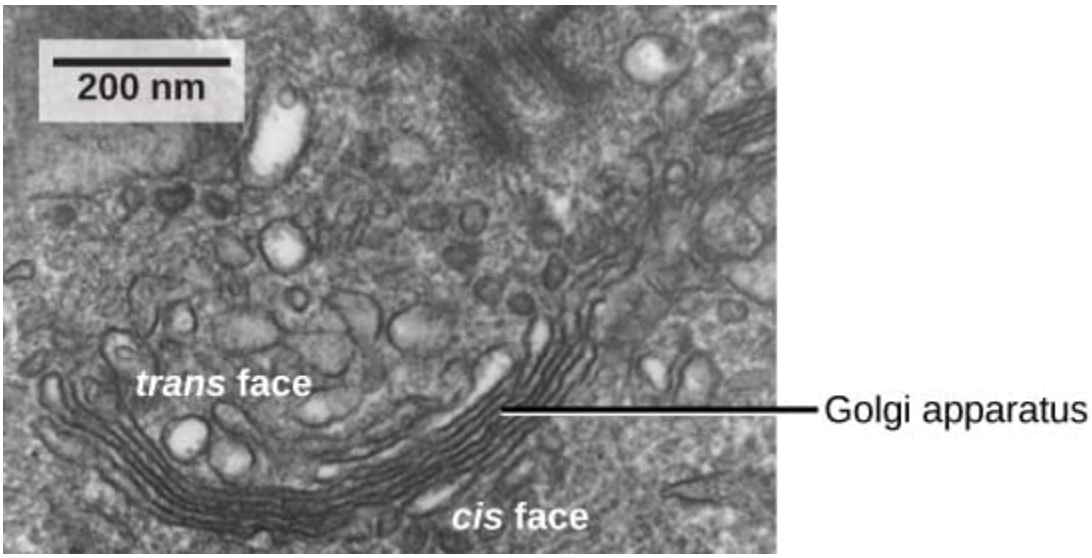


Figure 2.2.5: The Golgi apparatus in this transmission electron micrograph of a white blood cell is visible as a stack of semicircular flattened rings in the lower portion of this image. Several vesicles can be seen near the Golgi apparatus. (credit: modification of work by Louisa Howard; scale-bar data from Matt Russell)

The Golgi apparatus has a receiving face near the endoplasmic reticulum and a releasing face on the side away from the ER, toward the cell membrane. The transport vesicles that form from the ER travel to the receiving face, fuse with it, and empty their contents into the lumen of the Golgi apparatus. As the proteins and lipids travel through the Golgi, they undergo further modifications. The most frequent modification is the addition of short chains of sugar molecules. The newly modified proteins and lipids are then tagged with small molecular groups to enable them to be routed to their proper destinations.

Finally, the modified and tagged proteins are packaged into vesicles that bud from the opposite face of the Golgi. While some of these vesicles, transport vesicles, deposit their contents into other parts of the cell where they will be used, others, secretory vesicles, fuse with the plasma membrane and release their contents outside the cell.

The amount of Golgi in different cell types again illustrates that form follows function within cells. Cells that engage in a great deal of secretory activity (such as cells of the salivary glands that secrete digestive enzymes or cells of the immune system that secrete antibodies) have an abundant number of Golgi.

In plant cells, the Golgi has an additional role of synthesizing polysaccharides, some of which are incorporated into the cell wall and some of which are used in other parts of the cell.

Lysosomes

In animal cells, the lysosomes are the cell's "garbage disposal." Digestive enzymes within the lysosomes aid the breakdown of proteins, polysaccharides, lipids, nucleic acids, and even worn-out organelles. In single-celled eukaryotes, lysosomes are important for digestion of the food they ingest and the recycling of organelles. These enzymes are active at a much lower pH (more acidic) than those located in the cytoplasm. Many reactions that take place in the cytoplasm could not occur at a low pH, thus the advantage of compartmentalizing the eukaryotic cell into organelles is apparent.

Lysosomes also use their hydrolytic enzymes to destroy disease-causing organisms that might enter the cell. A good example of this occurs in a group of white blood cells called macrophages, which are part of your body's immune system. In a process known as phagocytosis, a section of the plasma membrane of the macrophage invaginates (folds in) and engulfs a pathogen. The invaginated section, with the pathogen inside, then pinches itself off from the plasma membrane and becomes a vesicle. The vesicle fuses with a lysosome. The lysosome's hydrolytic enzymes then destroy the pathogen (Figure 2.2.6).

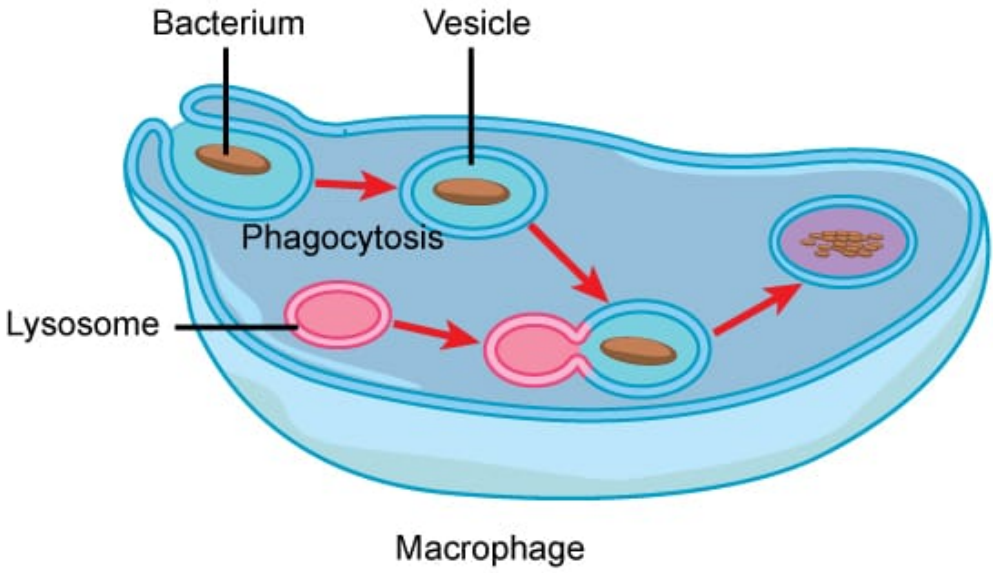


Figure 2.2.6: A macrophage has phagocytized a potentially pathogenic bacterium into a vesicle, which then fuses with a lysosome within the cell so that the pathogen can be destroyed. Other organelles are present in the cell, but for simplicity, are not shown.

Vesicles and Vacuoles

Vesicles and vacuoles are membrane-bound sacs that function in storage and transport. Vacuoles are somewhat larger than vesicles, and the membrane of a vacuole does not fuse with the membranes of other cellular components. Vesicles can fuse with other membranes within the cell system. Additionally, enzymes within plant vacuoles can break down macromolecules.

ART CONNECTION

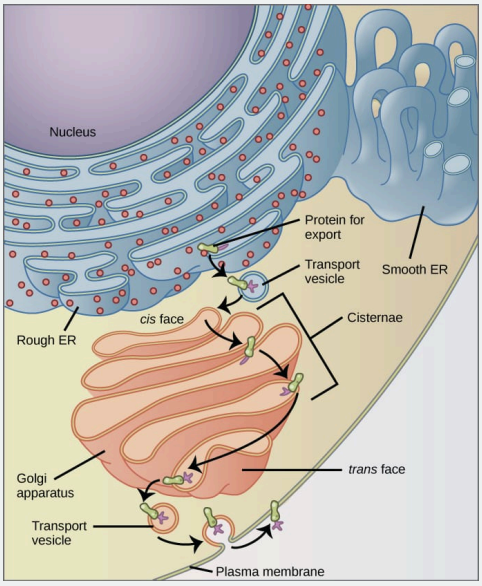


Figure 2.2.7**:** The endomembrane system works to modify, package, and transport lipids and proteins. (credit: modification of work by Magnus Manske)

Why does the *cis* face of the Golgi not face the plasma membrane?

Ribosomes

Ribosomes are the cellular structures responsible for protein synthesis. When viewed through an electron microscope, free ribosomes appear as either clusters or single tiny dots floating freely in the cytoplasm. Ribosomes may be attached to either the cytoplasmic side of the plasma membrane or the cytoplasmic side of the endoplasmic reticulum (Figure 2.2.7). Electron microscopy has shown that ribosomes consist of large and small subunits. Ribosomes are enzyme complexes that are responsible for protein synthesis.

Because protein synthesis is essential for all cells, ribosomes are found in practically every cell, although they are smaller in prokaryotic cells. They are particularly abundant in immature red blood cells for the synthesis of hemoglobin, which functions in the transport of oxygen throughout the body.

Mitochondria

Mitochondria (singular = mitochondrion) are often called the “powerhouses” or “energy factories” of a cell because they are responsible for making adenosine triphosphate (ATP), the cell’s main energy-carrying molecule. The formation of ATP from the breakdown of glucose is known as cellular respiration. Mitochondria are oval-shaped, double-membrane organelles (Figure 2.2.8) that have their own ribosomes and DNA. Each membrane is a phospholipid bilayer embedded with proteins. The inner layer has folds called cristae, which increase the surface area of the inner membrane. The area surrounded by the folds is called the mitochondrial matrix. The cristae and the matrix have different roles in cellular respiration.

In keeping with our theme of form following function, it is important to point out that muscle cells have a very high concentration of mitochondria because muscle cells need a lot of energy to contract.

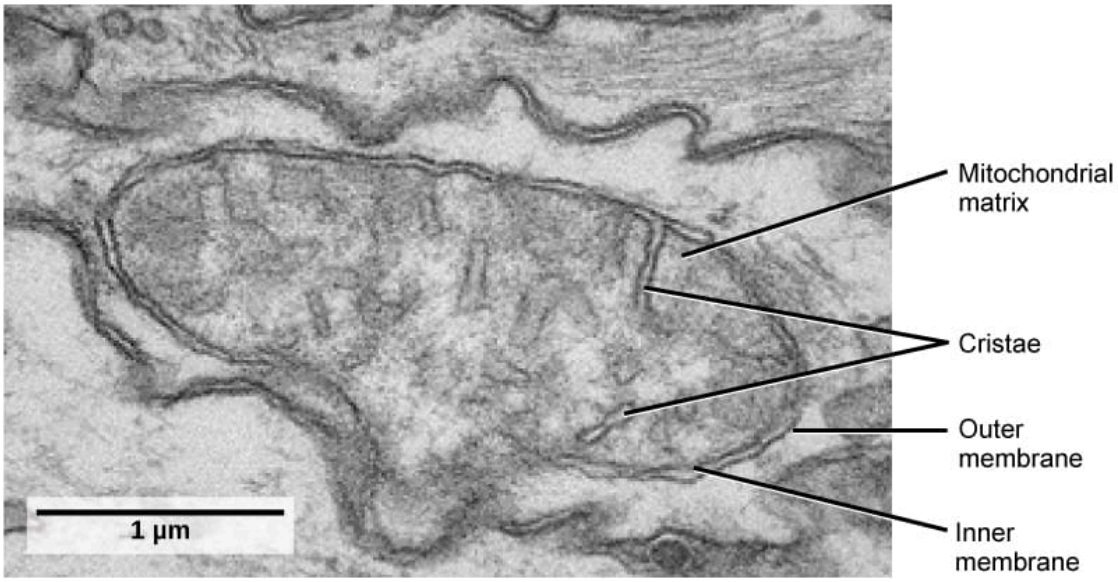


Figure 2.2.8**:** This transmission electron micrograph shows a mitochondrion as viewed with an electron microscope. Notice the inner and outer membranes, the cristae, and the mitochondrial matrix. (credit: modification of work by Matthew Britton; scale-bar data from Matt Russell)

Peroxisomes

Peroxisomes are small, round organelles enclosed by single membranes. They carry out oxidation reactions that break down fatty acids and amino acids. They also detoxify many poisons that may enter the body. Alcohol is detoxified by peroxisomes in liver cells. A byproduct of these oxidation reactions is hydrogen peroxide, H_2O_2, which is contained within the peroxisomes to prevent the chemical from causing damage to cellular components outside of the organelle. Hydrogen peroxide is safely broken down by peroxisomal enzymes into water and oxygen.

Animal Cells versus Plant Cells

Despite their fundamental similarities, there are some striking differences between animal and plant cells (see Table 2.2.1). Animal cells have centrioles, centrosomes (discussed under the cytoskeleton), and lysosomes, whereas plant cells do not. Plant cells have a cell wall, chloroplasts, plasmodesmata, and plastids used for storage, and a large central vacuole, whereas animal cells do not.

The Cell Wall

In Figure 2.2.1**b**, the diagram of a plant cell, you see a structure external to the plasma membrane called the cell wall. The cell wall is a rigid covering that protects the cell, provides structural support, and gives shape to the cell. Fungal and protist cells also have cell walls.

While the chief component of prokaryotic cell walls is peptidoglycan, the major organic molecule in the plant cell wall is cellulose, a polysaccharide made up of long, straight chains of glucose units. When nutritional information refers to dietary fiber, it is referring to the cellulose content of food.

Chloroplasts

Like mitochondria, chloroplasts also have their own DNA and ribosomes. Chloroplasts function in photosynthesis and can be found in eukaryotic cells such as plants and algae. In photosynthesis, carbon dioxide, water, and light energy are used to make glucose and oxygen. This is the major difference between plants and animals: Plants (autotrophs) are able to make their own food, like glucose, whereas animals (heterotrophs) must rely on other organisms for their organic compounds or food source.

Like mitochondria, chloroplasts have outer and inner membranes, but within the space enclosed by a chloroplast's inner membrane is a set of interconnected and stacked, fluid-filled membrane sacs called thylakoids (Figure 2.2.9). Each stack of thylakoids is called a granum (plural = grana). The fluid enclosed by the inner membrane and surrounding the grana is called the

stroma.

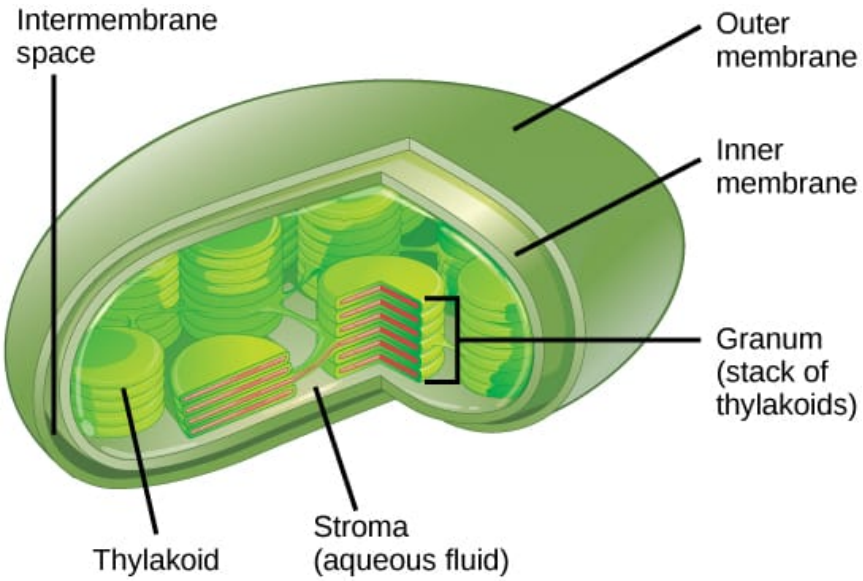


Figure 2.2.9**:** This simplified diagram of a chloroplast shows the outer membrane, inner membrane, thylakoids, grana, and stroma.

The chloroplasts contain a green pigment called chlorophyll, which captures the energy of sunlight for photosynthesis. Like plant cells, photosynthetic protists also have chloroplasts. Some bacteria also perform photosynthesis, but they do not have chloroplasts. Their photosynthetic pigments are located in the thylakoid membrane within the cell itself.

EVOLUTION IN ACTION: Endosymbiosis

We have mentioned that both mitochondria and chloroplasts contain DNA and ribosomes. Have you wondered why? Strong evidence points to endosymbiosis as the explanation.

Symbiosis is a relationship in which organisms from two separate species live in close association and typically exhibit specific adaptations to each other. Endosymbiosis (*endo*-= within) is a relationship in which one organism lives inside the other. Endosymbiotic relationships abound in nature. Microbes that produce vitamin K live inside the human gut. This relationship is beneficial for us because we are unable to synthesize vitamin K. It is also beneficial for the microbes because they are protected from other organisms and are provided a stable habitat and abundant food by living within the large intestine.

Scientists have long noticed that bacteria, mitochondria, and chloroplasts are similar in size. We also know that mitochondria and chloroplasts have DNA and ribosomes, just as bacteria do. Scientists believe that host cells and bacteria formed a mutually beneficial endosymbiotic relationship when the host cells ingested aerobic bacteria and cyanobacteria but did not destroy them. Through evolution, these ingested bacteria became more specialized in their functions, with the aerobic bacteria becoming mitochondria and the photosynthetic bacteria becoming chloroplasts.

The Central Vacuole

Previously, we mentioned vacuoles as essential components of plant cells. If you look at Figure 2.2.1, you will see that plant cells each have a large, central vacuole that occupies most of the cell. The central vacuole plays a key role in regulating the cell's concentration of water in changing environmental conditions. In plant cells, the liquid inside the central vacuole provides turgor pressure, which is the outward pressure caused by the fluid inside the cell. Have you ever noticed that if you forget to water a plant for a few days, it wilts? That is because as the water concentration in the soil becomes lower than the water concentration in the plant, water moves out of the central vacuoles and cytoplasm and into the soil. As the central vacuole shrinks, it leaves the cell wall unsupported. This loss of support to the cell walls of a plant results in the wilted appearance. Additionally, this fluid has a very bitter taste, which discourages consumption by insects and animals. The central vacuole also functions to store proteins in developing seed cells.

Extracellular Matrix of Animal Cells

Most animal cells release materials into the extracellular space. The primary components of these materials are glycoproteins and the protein collagen. Collectively, these materials are called the extracellular matrix (Figure 2.2.10). Not only does the extracellular matrix hold the cells together to form a tissue, but it also allows the cells within the tissue to communicate with each other.

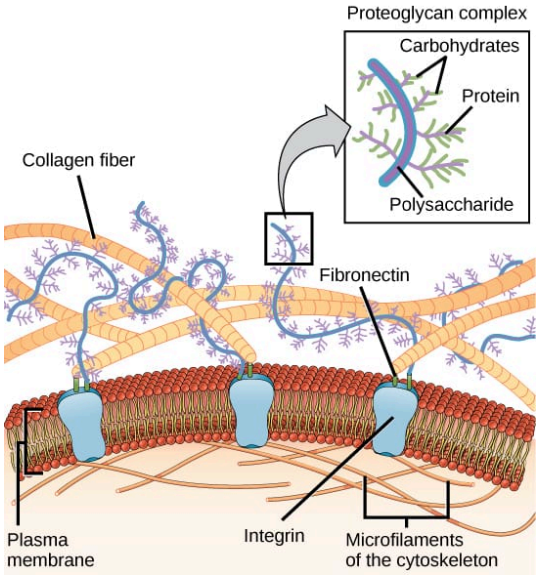


Figure 2.2.10: The extracellular matrix consists of a network of substances secreted by cells.

Blood clotting provides an example of the role of the extracellular matrix in cell communication. When the cells lining a blood vessel are damaged, they display a protein receptor called tissue factor. When tissue factor binds with another factor in the extracellular matrix, it causes platelets to adhere to the wall of the damaged blood vessel, stimulates adjacent smooth muscle cells in the blood vessel to contract (thus constricting the blood vessel), and initiates a series of steps that stimulate the platelets to produce clotting factors.

Intercellular Junctions

Cells can also communicate with each other by direct contact, referred to as intercellular junctions. There are some differences in the ways that plant and animal cells do this. Plasmodesmata (singular = plasmodesma) are junctions between plant cells, whereas animal cell contacts include tight and gap junctions, and desmosomes.

In general, long stretches of the plasma membranes of neighboring plant cells cannot touch one another because they are separated by the cell walls surrounding each cell. Plasmodesmata are numerous channels that pass between the cell walls of adjacent plant cells, connecting their cytoplasm and enabling signal molecules and nutrients to be transported from cell to cell (Figure 2.2.11**a**).

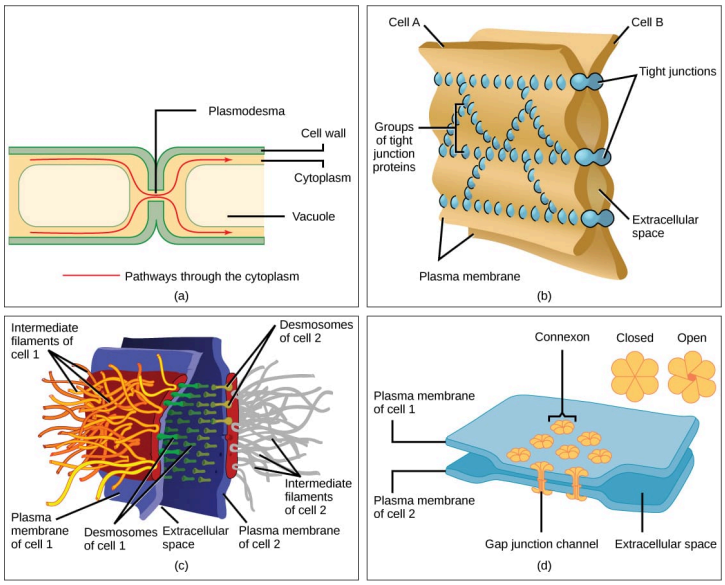


Figure 2.2.11**:** There are four kinds of connections between cells. (a) A plasmodesma is a channel between the cell walls of two adjacent plant cells. (b) Tight junctions join adjacent animal cells. (c) Desmosomes join two animal cells together. (d) Gap junctions act as channels between animal cells. (credit b, c, d: modification of work by Mariana Ruiz Villareal)

A tight junction is a watertight seal between two adjacent animal cells (Figure 2.2.11**b**). Proteins hold the cells tightly against each other. This tight adhesion prevents materials from leaking between the cells. Tight junctions are typically found in the epithelial tissue that lines internal organs and cavities, and composes most of the skin. For example, the tight junctions of the epithelial cells lining the urinary bladder prevent urine from leaking into the extracellular space.

Also found only in animal cells are desmosomes, which act like spot welds between adjacent epithelial cells (Figure 2.2.11**c**). They keep cells together in a sheet-like formation in organs and tissues that stretch, like the skin, heart, and muscles.

Gap junctions in animal cells are like plasmodesmata in plant cells in that they are channels between adjacent cells that allow for the transport of ions, nutrients, and other substances that enable cells to communicate (Figure 2.2.11**d**). Structurally, however, gap junctions and plasmodesmata differ.

Table 2.2.1***:*** *This table provides the components of prokaryotic and eukaryotic cells and their respective functions.*

Cell Component	Function	Present in Prokaryotes?	Present in Animal Cells?	Present in Plant Cells?
Plasma membrane	Separates cell from external environment; controls passage of organic molecules, ions, water, oxygen, and wastes into and out of the cell	Yes	Yes	Yes
Cytoplasm	Provides structure to cell; site of many metabolic reactions; medium in which organelles are found	Yes	Yes	Yes
Nucleoid	Location of DNA	Yes	No	No
Nucleus	Cell organelle that houses DNA and directs synthesis of ribosomes and proteins	No	Yes	Yes
Ribosomes	Protein synthesis	Yes	Yes	Yes
Mitochondria	ATP production/cellular respiration	No	Yes	Yes
Peroxisomes	Oxidizes and breaks down fatty acids and amino acids, and detoxifies poisons	No	Yes	Yes
Vesicles and vacuoles	Storage and transport; digestive function in plant cells	No	Yes	Yes

Cell Component	Function	Present in Prokaryotes?	Present in Animal Cells?	Present in Plant Cells?
Centrosome	Unspecified role in cell division in animal cells; organizing center of microtubules in animal cells	No	Yes	No
Lysosomes	Digestion of macromolecules; recycling of worn-out organelles	No	Yes	No
Cell wall	Protection, structural support and maintenance of cell shape	Yes, primarily peptidoglycan in bacteria but not Archaea	No	Yes, primarily cellulose
Chloroplasts	Photosynthesis	No	No	Yes
Endoplasmic reticulum	Modifies proteins and synthesizes lipids	No	Yes	Yes
Golgi apparatus	Modifies, sorts, tags, packages, and distributes lipids and proteins	No	Yes	Yes
Cytoskeleton	Maintains cell's shape, secures organelles in specific positions, allows cytoplasm and vesicles to move within the cell, and enables unicellular organisms to move independently	Yes	Yes	Yes
Flagella	Cellular locomotion	Some	Some	No, except for some plant sperm
Cilia	Cellular locomotion, movement of particles along extracellular surface of plasma membrane, and filtration	No	Some	No

Summary

Like a prokaryotic cell, a eukaryotic cell has a plasma membrane, cytoplasm, and ribosomes, but a eukaryotic cell is typically larger than a prokaryotic cell, has a true nucleus (meaning its DNA is surrounded by a membrane), and has other membrane-bound organelles that allow for compartmentalization of functions. The plasma membrane is a phospholipid bilayer embedded with proteins. The nucleolus within the nucleus is the site for ribosome assembly. Ribosomes are found in the cytoplasm or are attached to the cytoplasmic side of the plasma membrane or endoplasmic reticulum. They perform protein synthesis. Mitochondria perform cellular respiration and produce ATP. Peroxisomes break down fatty acids, amino acids, and some toxins. Vesicles and vacuoles are storage and transport compartments. In plant cells, vacuoles also help break down macromolecules.

Animal cells also have a centrosome and lysosomes. The centrosome has two bodies, the centrioles, with an unknown role in cell division. Lysosomes are the digestive organelles of animal cells.

Plant cells have a cell wall, chloroplasts, and a central vacuole. The plant cell wall, whose primary component is cellulose, protects the cell, provides structural support, and gives shape to the cell. Photosynthesis takes place in chloroplasts. The central vacuole expands, enlarging the cell without the need to produce more cytoplasm.

The endomembrane system includes the nuclear envelope, the endoplasmic reticulum, Golgi apparatus, lysosomes, vesicles, as well as the plasma membrane. These cellular components work together to modify, package, tag, and transport membrane lipids and proteins.

The cytoskeleton has three different types of protein elements. Microfilaments provide rigidity and shape to the cell, and facilitate cellular movements. Intermediate filaments bear tension and anchor the nucleus and other organelles in place. Microtubules help the cell resist compression, serve as tracks for motor proteins that move vesicles through the cell, and pull replicated chromosomes to opposite ends of a dividing cell. They are also the structural elements of centrioles, flagella, and cilia.

Animal cells communicate through their extracellular matrices and are connected to each other by tight junctions, desmosomes,

and gap junctions. Plant cells are connected and communicate with each other by plasmodesmata.

Art Connections

Figure 2.2.1: What structures does a plant cell have that an animal cell does not have? What structures does an animal cell have that a plant cell does not have?

Answer

Plant cells have plasmodesmata, a cell wall, a large central vacuole, chloroplasts, and plastids. Animal cells have lysosomes and centrosomes.

Figure 2.2.7: Why does the *cis* face of the Golgi not face the plasma membrane?

Answer

Because that face receives chemicals from the ER, which is toward the center of the cell.

Glossary

cell wall
a rigid cell covering made of cellulose in plants, peptidoglycan in bacteria, non-peptidoglycan compounds in Archaea, and chitin in fungi that protects the cell, provides structural support, and gives shape to the cell

central vacuole
a large plant cell organelle that acts as a storage compartment, water reservoir, and site of macromolecule degradation

chloroplast
a plant cell organelle that carries out photosynthesis

cilium
(plural: cilia) a short, hair-like structure that extends from the plasma membrane in large numbers and is used to move an entire cell or move substances along the outer surface of the cell

cytoplasm
the entire region between the plasma membrane and the nuclear envelope, consisting of organelles suspended in the gel-like cytosol, the cytoskeleton, and various chemicals

cytoskeleton
the network of protein fibers that collectively maintains the shape of the cell, secures some organelles in specific positions, allows cytoplasm and vesicles to move within the cell, and enables unicellular organisms to move

cytosol
the gel-like material of the cytoplasm in which cell structures are suspended

desmosome
a linkage between adjacent epithelial cells that forms when cadherins in the plasma membrane attach to intermediate filaments

endomembrane system
the group of organelles and membranes in eukaryotic cells that work together to modify, package, and transport lipids and proteins

endoplasmic reticulum (ER)
a series of interconnected membranous structures within eukaryotic cells that collectively modify proteins and synthesize lipids

extracellular matrix
the material, primarily collagen, glycoproteins, and proteoglycans, secreted from animal cells that holds cells

together as a tissue, allows cells to communicate with each other, and provides mechanical protection and anchoring for cells in the tissue

flagellum
(plural: flagella) the long, hair-like structure that extends from the plasma membrane and is used to move the cell

gap junction
a channel between two adjacent animal cells that allows ions, nutrients, and other low-molecular weight substances to pass between the cells, enabling the cells to communicate

Golgi apparatus
a eukaryotic organelle made up of a series of stacked membranes that sorts, tags, and packages lipids and proteins for distribution

lysosome
an organelle in an animal cell that functions as the cell's digestive component; it breaks down proteins, polysaccharides, lipids, nucleic acids, and even worn-out organelles

mitochondria
(singular: mitochondrion) the cellular organelles responsible for carrying out cellular respiration, resulting in the production of ATP, the cell's main energy-carrying molecule

nuclear envelope
the double-membrane structure that constitutes the outermost portion of the nucleus

nucleolus
the darkly staining body within the nucleus that is responsible for assembling ribosomal subunits

nucleus
the cell organelle that houses the cell's DNA and directs the synthesis of ribosomes and proteins

peroxisome
a small, round organelle that contains hydrogen peroxide, oxidizes fatty acids and amino acids, and detoxifies many poisons

plasma membrane
a phospholipid bilayer with embedded (integral) or attached (peripheral) proteins that separates the internal contents of the cell from its surrounding environment

plasmodesma
(plural: plasmodesmata) a channel that passes between the cell walls of adjacent plant cells, connects their cytoplasm, and allows materials to be transported from cell to cell

ribosome
a cellular structure that carries out protein synthesis

rough endoplasmic reticulum (RER)
the region of the endoplasmic reticulum that is studded with ribosomes and engages in protein modification

smooth endoplasmic reticulum (SER)
the region of the endoplasmic reticulum that has few or no ribosomes on its cytoplasmic surface and synthesizes carbohydrates, lipids, and steroid hormones; detoxifies chemicals like pesticides, preservatives, medications, and environmental pollutants, and stores calcium ions

tight junction
a firm seal between two adjacent animal cells created by protein adherence

vacuole
a membrane-bound sac, somewhat larger than a vesicle, that functions in cellular storage and transport

vesicle
: a small, membrane-bound sac that functions in cellular storage and transport; its membrane is capable of fusing with the plasma membrane and the membranes of the endoplasmic reticulum and Golgi apparatus

Contributors and Attributions

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2.3: The Cell Membrane

A cell's plasma membrane defines the boundary of the cell and determines the nature of its contact with the environment. Cells exclude some substances, take in others, and excrete still others, all in controlled quantities. Plasma membranes enclose the borders of cells, but rather than being a static bag, they are dynamic and constantly in flux. The plasma membrane must be sufficiently flexible to allow certain cells, such as red blood cells and white blood cells, to change shape as they pass through narrow capillaries. These are the more obvious functions of a plasma membrane. In addition, the surface of the plasma membrane carries markers that allow cells to recognize one another, which is vital as tissues and organs form during early development, and which later plays a role in the "self" versus "non-self" distinction of the immune response.

The plasma membrane also carries receptors, which are attachment sites for specific substances that interact with the cell. Each receptor is structured to bind with a specific substance. For example, surface receptors of the membrane create changes in the interior, such as changes in enzymes of metabolic pathways. These metabolic pathways might be vital for providing the cell with energy, making specific substances for the cell, or breaking down cellular waste or toxins for disposal. Receptors on the plasma membrane's exterior surface interact with hormones or neurotransmitters, and allow their messages to be transmitted into the cell. Some recognition sites are used by viruses as attachment points. Although they are highly specific, pathogens like viruses may evolve to exploit receptors to gain entry to a cell by mimicking the specific substance that the receptor is meant to bind. This specificity helps to explain why human immunodeficiency virus (HIV) or any of the five types of hepatitis viruses invade only specific cells.

Fluid Mosaic Model

In 1972, S. J. Singer and Garth L. Nicolson proposed a new model of the plasma membrane that, compared to earlier understanding, better explained both microscopic observations and the function of the plasma membrane. This was called the fluid mosaic model. The model has evolved somewhat over time, but still best accounts for the structure and functions of the plasma membrane as we now understand them. The fluid mosaic model describes the structure of the plasma membrane as a mosaic of components—including phospholipids, cholesterol, proteins, and carbohydrates—in which the components are able to flow and change position, while maintaining the basic integrity of the membrane. Both phospholipid molecules and embedded proteins are able to diffuse rapidly and laterally in the membrane. The fluidity of the plasma membrane is necessary for the activities of certain enzymes and transport molecules within the membrane. Plasma membranes range from 5–10 nm thick. As a comparison, human red blood cells, visible via light microscopy, are approximately 8 µm thick, or approximately 1,000 times thicker than a plasma membrane. (Figure 2.3.1)

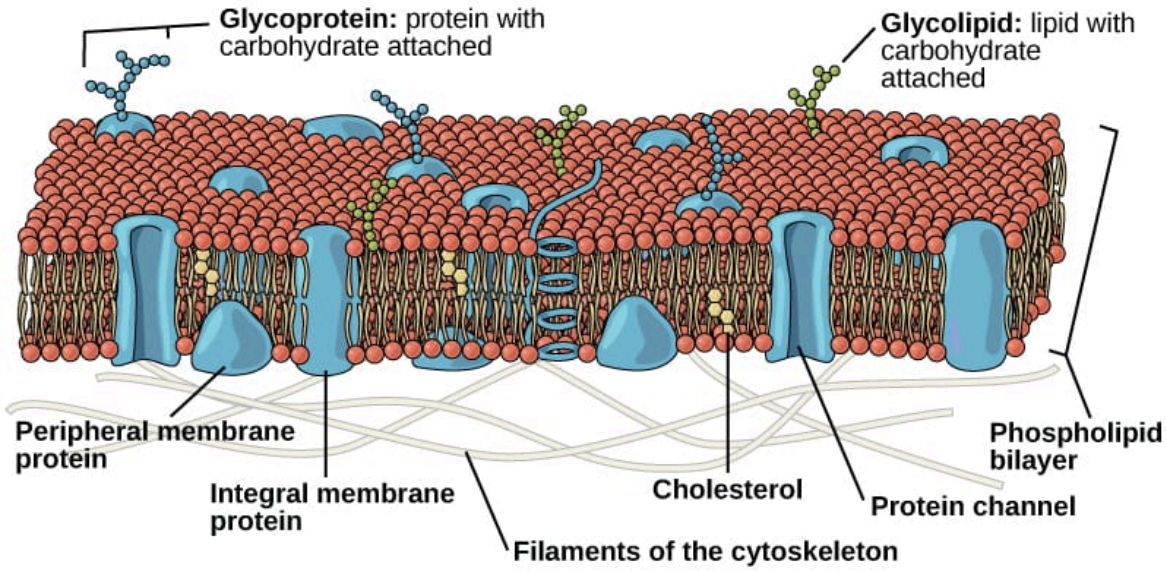


Figure 2.3.1**:** The fluid mosaic model of the plasma membrane structure describes the plasma membrane as a fluid combination of phospholipids, cholesterol, proteins, and carbohydrates.

The plasma membrane is made up primarily of a bilayer of phospholipids with embedded proteins, carbohydrates, glycolipids, and glycoproteins, and, in animal cells, cholesterol. The amount of cholesterol in animal plasma membranes regulates the fluidity of the membrane and changes based on the temperature of the cell's environment. In other words, cholesterol acts as antifreeze in the cell membrane and is more abundant in animals that live in cold climates.

The main fabric of the membrane is composed of two layers of phospholipid molecules, and the polar ends of these molecules (which look like a collection of balls in an artist's rendition of the model) (Figure 2.3.1) are in contact with aqueous fluid both inside and outside the cell. Thus, both surfaces of the plasma membrane are hydrophilic. In contrast, the interior of the membrane, between its two surfaces, is a hydrophobic or nonpolar region because of the fatty acid tails. This region has no attraction for water or other polar molecules.

Proteins make up the second major chemical component of plasma membranes. Integral proteins are embedded in the plasma membrane and may span all or part of the membrane. Integral proteins may serve as channels or pumps to move materials into or out of the cell. Peripheral proteins are found on the exterior or interior surfaces of membranes, attached either to integral proteins or to phospholipid molecules. Both integral and peripheral proteins may serve as enzymes, as structural attachments for the fibers of the cytoskeleton, or as part of the cell's recognition sites.

Carbohydrates are the third major component of plasma membranes. They are always found on the exterior surface of cells and are bound either to proteins (forming glycoproteins) or to lipids (forming glycolipids). These carbohydrate chains may consist of 2–60 monosaccharide units and may be either straight or branched. Along with peripheral proteins, carbohydrates form specialized sites on the cell surface that allow cells to recognize each other.

EVOLUTION IN ACTION: How Viruses Infect Specific Organs

Specific glycoprotein molecules exposed on the surface of the cell membranes of host cells are exploited by many viruses to infect specific organs. For example, HIV is able to penetrate the plasma membranes of specific kinds of white blood cells called T-helper cells and monocytes, as well as some cells of the central nervous system. The hepatitis virus attacks only liver cells.

These viruses are able to invade these cells, because the cells have binding sites on their surfaces that the viruses have exploited with equally specific glycoproteins in their coats (Figure 2.3.2). The cell is tricked by the mimicry of the virus coat molecules, and the virus is able to enter the cell. Other recognition sites on the virus's surface interact with the human immune system, prompting the body to produce antibodies. Antibodies are made in response to the antigens (or proteins associated with invasive pathogens). These same sites serve as places for antibodies to attach, and either destroy or inhibit the activity of the virus. Unfortunately, these sites on HIV are encoded by genes that change quickly, making the production of an effective vaccine against the virus very difficult. The virus population within an infected individual quickly evolves through mutation into different populations, or variants, distinguished by differences in these recognition sites. This rapid change of viral surface markers decreases the effectiveness of the person's immune system in attacking the virus, because the antibodies will not recognize the new variations of the surface patterns.

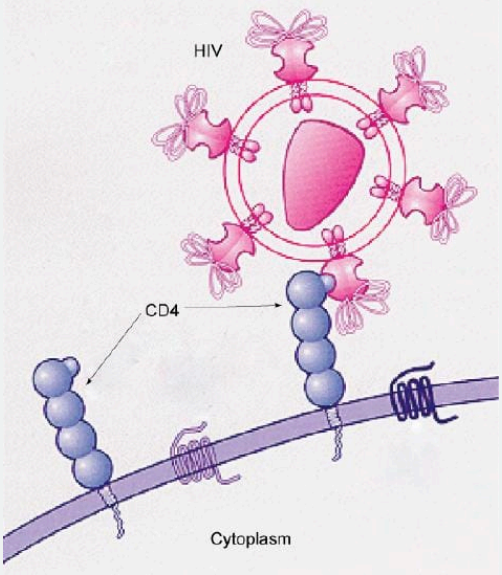


Figure 2.3.2**:** HIV docks at and binds to the CD4 receptor, a glycoprotein on the surface of T cells, before entering, or infecting, the cell. (credit: modification of work by US National Institutes of Health/National Institute of Allergy and Infectious Diseases).

Summary

The modern understanding of the plasma membrane is referred to as the fluid mosaic model. The plasma membrane is composed of a bilayer of phospholipids, with their hydrophobic, fatty acid tails in contact with each other. The landscape of the membrane is studded with proteins, some of which span the membrane. Some of these proteins serve to transport materials into or out of the cell. Carbohydrates are attached to some of the proteins and lipids on the outward-facing surface of the membrane. These form complexes that function to identify the cell to other cells. The fluid nature of the membrane owes itself to the configuration of the fatty acid tails, the presence of cholesterol embedded in the membrane (in animal cells), and the mosaic nature of the proteins and protein-carbohydrate complexes, which are not firmly fixed in place. Plasma membranes enclose the borders of cells, but rather than being a static bag, they are dynamic and constantly in flux.

Glossary

fluid mosaic model
: a model of the structure of the plasma membrane as a mosaic of components, including phospholipids, cholesterol, proteins, and glycolipids, resulting in a fluid rather than static character

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2.4: Passive Transport

Plasma membranes must allow certain substances to enter and leave a cell, while preventing harmful material from entering and essential material from leaving. In other words, plasma membranes are selectively permeable—they allow some substances through but not others. If they were to lose this selectivity, the cell would no longer be able to sustain itself, and it would be destroyed. Some cells require larger amounts of specific substances than do other cells; they must have a way of obtaining these materials from the extracellular fluids. This may happen passively, as certain materials move back and forth, or the cell may have special mechanisms that ensure transport. Most cells expend most of their energy, in the form of adenosine triphosphate (ATP), to create and maintain an uneven distribution of ions on the opposite sides of their membranes. The structure of the plasma membrane contributes to these functions, but it also presents some problems.

The most direct forms of membrane transport are passive. Passive transport is a naturally occurring phenomenon and does not require the cell to expend energy to accomplish the movement. In passive transport, substances move from an area of higher concentration to an area of lower concentration in a process called diffusion. A physical space in which there is a different concentration of a single substance is said to have a concentration gradient.

Selective Permeability

Plasma membranes are asymmetric, meaning that despite the mirror image formed by the phospholipids, the interior of the membrane is not identical to the exterior of the membrane. Integral proteins that act as channels or pumps work in one direction. Carbohydrates, attached to lipids or proteins, are also found on the exterior surface of the plasma membrane. These carbohydrate complexes help the cell bind substances that the cell needs in the extracellular fluid. This adds considerably to the selective nature of plasma membranes.

Recall that plasma membranes have hydrophilic and hydrophobic regions. This characteristic helps the movement of certain materials through the membrane and hinders the movement of others. Lipid-soluble material can easily slip through the hydrophobic lipid core of the membrane. Substances such as the fat-soluble vitamins A, D, E, and K readily pass through the plasma membranes in the digestive tract and other tissues. Fat-soluble drugs also gain easy entry into cells and are readily transported into the body's tissues and organs. Molecules of oxygen and carbon dioxide have no charge and pass through by simple diffusion.

Polar substances, with the exception of water, present problems for the membrane. While some polar molecules connect easily with the outside of a cell, they cannot readily pass through the lipid core of the plasma membrane. Additionally, whereas small ions could easily slip through the spaces in the mosaic of the membrane, their charge prevents them from doing so. Ions such as sodium, potassium, calcium, and chloride must have a special means of penetrating plasma membranes. Simple sugars and amino acids also need help with transport across plasma membranes.

Diffusion

Diffusion is a passive process of transport. A single substance tends to move from an area of high concentration to an area of low concentration until the concentration is equal across the space. You are familiar with diffusion of substances through the air. For example, think about someone opening a bottle of perfume in a room filled with people. The perfume is at its highest concentration in the bottle and is at its lowest at the edges of the room. The perfume vapor will diffuse, or spread away, from the bottle, and gradually, more and more people will smell the perfume as it spreads. Materials move within the cell's cytosol by diffusion, and certain materials move through the plasma membrane by diffusion (Figure 2.4.1). Diffusion expends no energy. Rather the different concentrations of materials in different areas are a form of potential energy, and diffusion is the dissipation of that potential energy as materials move down their concentration gradients, from high to low.

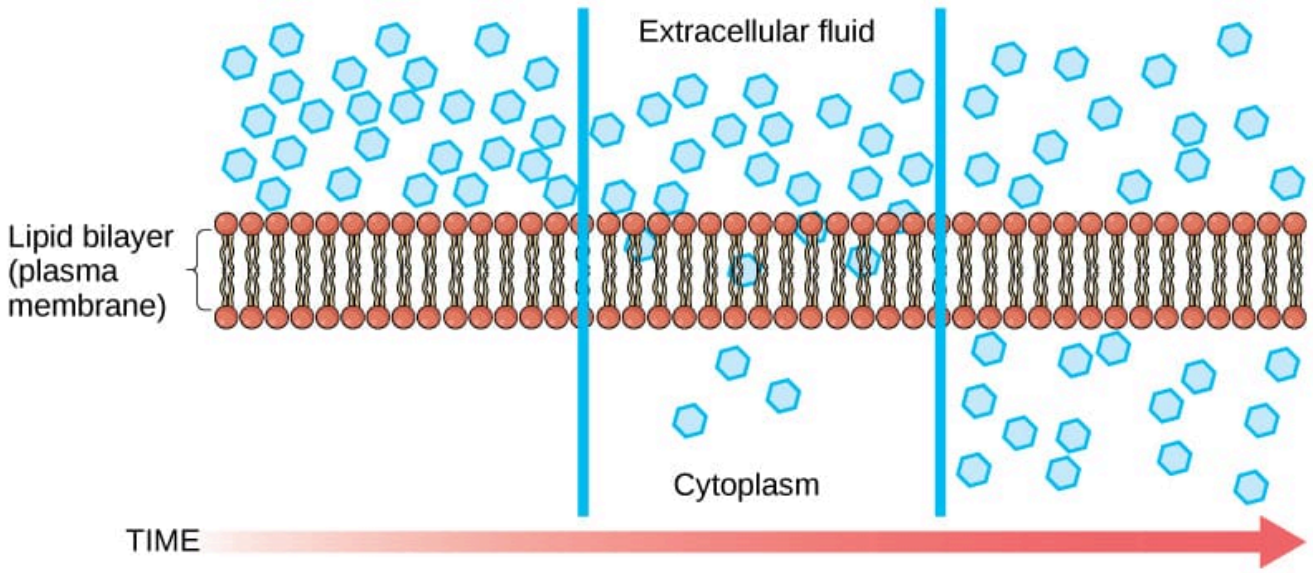


Figure 2.4.1**:** Diffusion through a permeable membrane follows the concentration gradient of a substance, moving the substance from an area of high concentration to one of low concentration. (credit: modification of work by Mariana Ruiz Villarreal)

Each separate substance in a medium, such as the extracellular fluid, has its own concentration gradient, independent of the concentration gradients of other materials. Additionally, each substance will diffuse according to that gradient.

Several factors affect the rate of diffusion.

- Extent of the concentration gradient: The greater the difference in concentration, the more rapid the diffusion. The closer the distribution of the material gets to equilibrium, the slower the rate of diffusion becomes.
- Mass of the molecules diffusing: More massive molecules move more slowly, because it is more difficult for them to move between the molecules of the substance they are moving through; therefore, they diffuse more slowly.
- Temperature: Higher temperatures increase the energy and therefore the movement of the molecules, increasing the rate of diffusion.
- Solvent density: As the density of the solvent increases, the rate of diffusion decreases. The molecules slow down because they have a more difficult time getting through the denser medium.

CONCEPT IN ACTION

This interactive element is not available in this format. Visit the link or scan the QR code to access it online.

View this YouTube Video online

For an animation of the diffusion process in action, view this short video on cell membrane transport.

Facilitated transport

In facilitated transport, also called facilitated diffusion, material moves across the plasma membrane with the assistance of transmembrane proteins down a concentration gradient (from high to low concentration) without the expenditure of cellular energy. However, the substances that undergo facilitated transport would otherwise not diffuse easily or quickly across the plasma membrane. The solution to moving polar substances and other substances across the plasma membrane rests in the proteins that span its surface. The material being transported is first attached to protein or glycoprotein receptors on the exterior surface of the plasma membrane. This allows the material that is needed by the cell to be removed from the extracellular fluid. The substances

are then passed to specific integral proteins that facilitate their passage, because they form channels or pores that allow certain substances to pass through the membrane. The integral proteins involved in facilitated transport are collectively referred to as transport proteins, and they function as either channels for the material or carriers.

Osmosis

Osmosis is the diffusion of water through a semipermeable membrane according to the concentration gradient of water across the membrane. Whereas diffusion transports material across membranes and within cells, osmosis transports *only water* across a membrane and the membrane limits the diffusion of solutes in the water. Osmosis is a special case of diffusion. Water, like other substances, moves from an area of higher concentration to one of lower concentration. Imagine a beaker with a semipermeable membrane, separating the two sides or halves (Figure 2.4.2). On both sides of the membrane, the water level is the same, but there are different concentrations on each side of a dissolved substance, or solute, that cannot cross the membrane. If the volume of the water is the same, but the concentrations of solute are different, then there are also different concentrations of water, the solvent, on either side of the membrane.

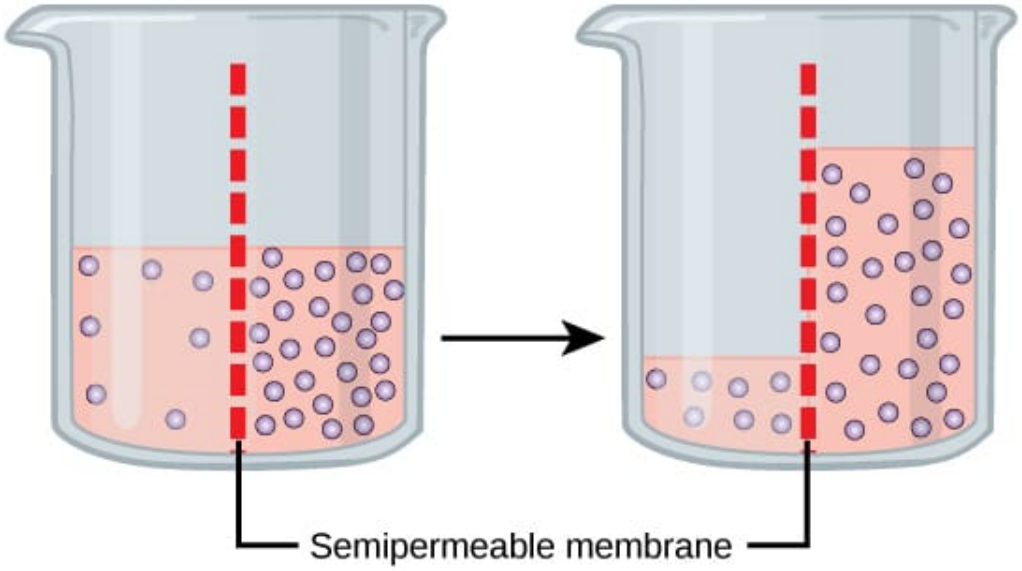


Figure 2.4.2**:** In osmosis, water always moves from an area of higher concentration (of water) to one of lower concentration (of water). In this system, the solute cannot pass through the selectively permeable membrane.

A principle of diffusion is that the molecules move around and will spread evenly throughout the medium if they can. However, only the material capable of getting through the membrane will diffuse through it. In this example, the solute cannot diffuse through the membrane, but the water can. Water has a concentration gradient in this system. Therefore, water will diffuse down its concentration gradient, crossing the membrane to the side where it is less concentrated. This diffusion of water through the membrane—osmosis—will continue until the concentration gradient of water goes to zero. Osmosis proceeds constantly in living systems.

Tonicity

Tonicity describes the amount of solute in a solution. The measure of the tonicity of a solution, or the total amount of solutes dissolved in a specific amount of solution, is called its osmolarity. Three terms—hypotonic, isotonic, and hypertonic—are used to relate the osmolarity of a cell to the osmolarity of the extracellular fluid that contains the cells. In a hypotonic solution, such as tap water, the extracellular fluid has a lower concentration of solutes than the fluid inside the cell, and water enters the cell. (In living systems, the point of reference is always the cytoplasm, so the prefix *hypo-* means that the extracellular fluid has a lower concentration of solutes, or a lower osmolarity, than the cell cytoplasm.) It also means that the extracellular fluid has a higher concentration of water than does the cell. In this situation, water will follow its concentration gradient and enter the cell. This may cause an animal cell to burst, or lyse.

In a hypertonic solution (the prefix *hyper-* refers to the extracellular fluid having a higher concentration of solutes than the cell's cytoplasm), the fluid contains less water than the cell does, such as seawater. Because the cell has a lower concentration of

solutes, the water will leave the cell. In effect, the solute is drawing the water out of the cell. This may cause an animal cell to shrivel, or crenate.

In an isotonic solution, the extracellular fluid has the same osmolarity as the cell. If the concentration of solutes of the cell matches that of the extracellular fluid, there will be no net movement of water into or out of the cell. Blood cells in hypertonic, isotonic, and hypotonic solutions take on characteristic appearances (Figure 2.4.3).

ART CONNECTION

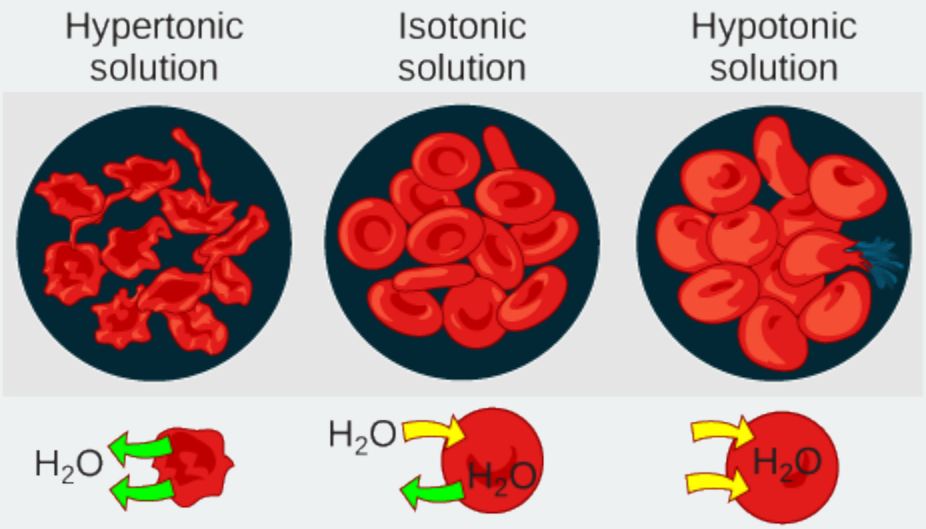


Figure 2.4.3: Osmotic pressure changes the shape of red blood cells in hypertonic, isotonic, and hypotonic solutions. (credit: modification of work by Mariana Ruiz Villarreal)

A doctor injects a patient with what the doctor thinks is isotonic saline solution. The patient dies, and autopsy reveals that many red blood cells have been destroyed. Do you think the solution the doctor injected was really isotonic?

Some organisms, such as plants, fungi, bacteria, and some protists, have cell walls that surround the plasma membrane and prevent cell lysis. The plasma membrane can only expand to the limit of the cell wall, so the cell will not lyse. In fact, the cytoplasm in plants is always slightly hypertonic compared to the cellular environment, and water will always enter a cell if water is available. This influx of water produces turgor pressure, which stiffens the cell walls of the plant (Figure 2.4.4). In nonwoody plants, turgor pressure supports the plant. If the plant cells become hypertonic, as occurs in drought or if a plant is not watered adequately, water will leave the cell. Plants lose turgor pressure in this condition and wilt.

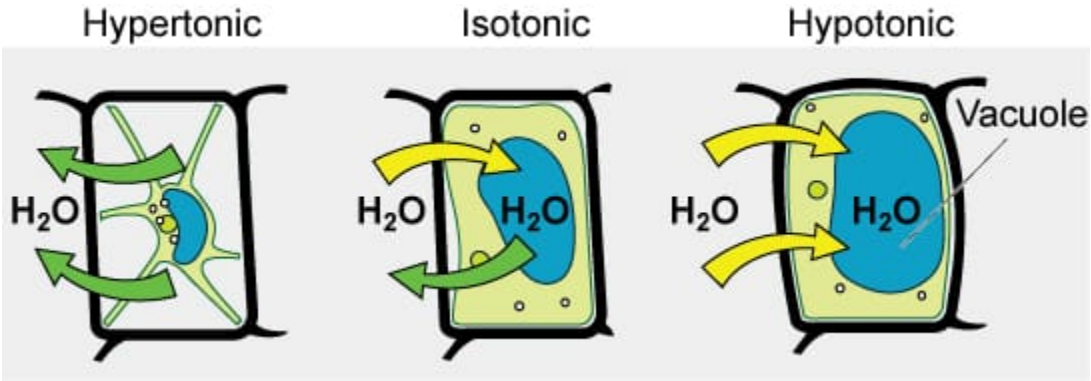


Figure 2.4.4: The turgor pressure within a plant cell depends on the tonicity of the solution that it is bathed in. (credit: modification of work by Mariana Ruiz Villarreal)

Section Summary

The passive forms of transport, diffusion and osmosis, move material of small molecular weight. Substances diffuse from areas of high concentration to areas of low concentration, and this process continues until the substance is evenly distributed in a system. In solutions of more than one substance, each type of molecule diffuses according to its own concentration gradient. Many factors can affect the rate of diffusion, including concentration gradient, the sizes of the particles that are diffusing, and the temperature of the system.

In living systems, diffusion of substances into and out of cells is mediated by the plasma membrane. Some materials diffuse readily through the membrane, but others are hindered, and their passage is only made possible by protein channels and carriers. The chemistry of living things occurs in aqueous solutions, and balancing the concentrations of those solutions is an ongoing problem. In living systems, diffusion of some substances would be slow or difficult without membrane proteins.

Art Connections

Figure 2.4.3: A doctor injects a patient with what he thinks is isotonic saline solution. The patient dies, and autopsy reveals that many red blood cells have been destroyed. Do you think the solution the doctor injected was really isotonic?

Answer

No, it must have been hypotonic, as a hypotonic solution would cause water to enter the cells, thereby making them burst.

Glossary

concentration gradient
an area of high concentration across from an area of low concentration

diffusion
a passive process of transport of low-molecular weight material down its concentration gradient

facilitated transport
a process by which material moves down a concentration gradient (from high to low concentration) using integral membrane proteins

hypertonic
describes a solution in which extracellular fluid has higher osmolarity than the fluid inside the cell

hypotonic
describes a solution in which extracellular fluid has lower osmolarity than the fluid inside the cell

isotonic
describes a solution in which the extracellular fluid has the same osmolarity as the fluid inside the cell

osmolarity
the total amount of substances dissolved in a specific amount of solution

osmosis
the transport of water through a semipermeable membrane from an area of high water concentration to an area of low water concentration across a membrane

passive transport
a method of transporting material that does not require energy

selectively permeable
the characteristic of a membrane that allows some substances through but not others

solute
a substance dissolved in another to form a solution

tonicity
: the amount of solute in a solution.

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2.5: Active Transport

Active transport mechanisms require the use of the cell's energy, usually in the form of adenosine triphosphate (ATP). If a substance must move into the cell against its concentration gradient, that is, if the concentration of the substance inside the cell must be greater than its concentration in the extracellular fluid, the cell must use energy to move the substance. Some active transport mechanisms move small-molecular weight material, such as ions, through the membrane.

In addition to moving small ions and molecules through the membrane, cells also need to remove and take in larger molecules and particles. Some cells are even capable of engulfing entire unicellular microorganisms. You might have correctly hypothesized that the uptake and release of large particles by the cell requires energy. A large particle, however, cannot pass through the membrane, even with energy supplied by the cell.

Electrochemical Gradient

We have discussed simple concentration gradients—differential concentrations of a substance across a space or a membrane—but in living systems, gradients are more complex. Because cells contain proteins, most of which are negatively charged, and because ions move into and out of cells, there is an electrical gradient, a difference of charge, across the plasma membrane. The interior of living cells is electrically negative with respect to the extracellular fluid in which they are bathed; at the same time, cells have higher concentrations of potassium (K^+) and lower concentrations of sodium (Na^+) than does the extracellular fluid. Thus, in a living cell, the concentration gradient and electrical gradient of Na^+ promotes diffusion of the ion into the cell, and the electrical gradient of Na^+ (a positive ion) tends to drive it inward to the negatively charged interior. The situation is more complex, however, for other elements such as potassium. The electrical gradient of K^+ promotes diffusion of the ion *into* the cell, but the concentration gradient of K^+ promotes diffusion *out* of the cell (Figure 2.5.1). The combined gradient that affects an ion is called its electrochemical gradient, and it is especially important to muscle and nerve cells.

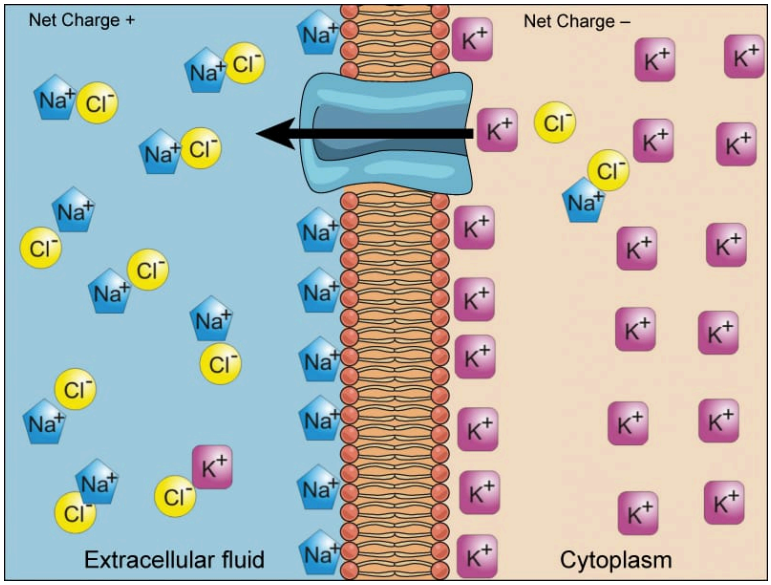


Figure 2.5.1: Electrochemical gradients arise from the combined effects of concentration gradients and electrical gradients. (credit: modification of work by "Synaptitude"/Wikimedia Commons)

Moving Against a Gradient

To move substances against a concentration or an electrochemical gradient, the cell must use energy. This energy is harvested from ATP that is generated through cellular metabolism. Active transport mechanisms, collectively called pumps or carrier proteins, work against electrochemical gradients. With the exception of ions, small substances constantly pass through plasma membranes. Active transport maintains concentrations of ions and other substances needed by living cells in the face of these

passive changes. Much of a cell's supply of metabolic energy may be spent maintaining these processes. Because active transport mechanisms depend on cellular metabolism for energy, they are sensitive to many metabolic poisons that interfere with the supply of ATP.

Two mechanisms exist for the transport of small-molecular weight material and macromolecules. Primary active transport moves ions across a membrane and creates a difference in charge across that membrane. The primary active transport system uses ATP to move a substance, such as an ion, into the cell, and often at the same time, a second substance is moved out of the cell. The sodium-potassium pump, an important pump in animal cells, expends energy to move potassium ions into the cell and a different number of sodium ions out of the cell (Figure 2.5.2). The action of this pump results in a concentration and charge difference across the membrane.

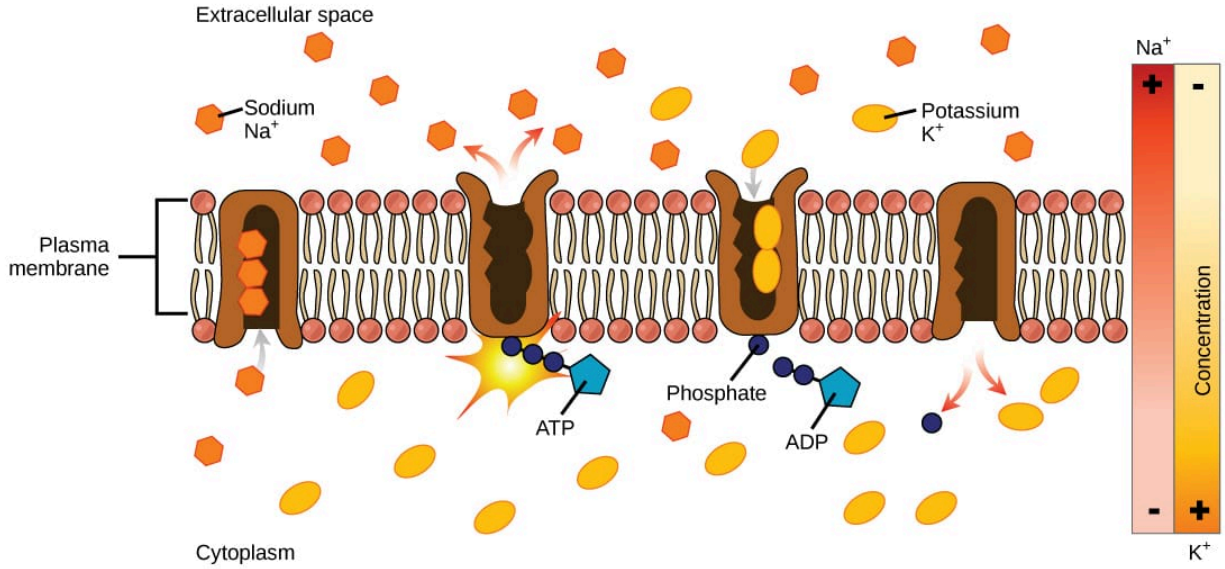


Figure 2.5.2: The sodium-potassium pump moves potassium and sodium ions across the plasma membrane. (credit: modification of work by Mariana Ruiz Villarreal)

Secondary active transport describes the movement of material using the energy of the electrochemical gradient established by primary active transport. Using the energy of the electrochemical gradient created by the primary active transport system, other substances such as amino acids and glucose can be brought into the cell through membrane channels. ATP itself is formed through secondary active transport using a hydrogen ion gradient in the mitochondrion.

Endocytosis

Endocytosis is a type of active transport that moves particles, such as large molecules, parts of cells, and even whole cells, into a cell. There are different variations of endocytosis, but all share a common characteristic: The plasma membrane of the cell invaginates, forming a pocket around the target particle. The pocket pinches off, resulting in the particle being contained in a newly created vacuole that is formed from the plasma membrane.

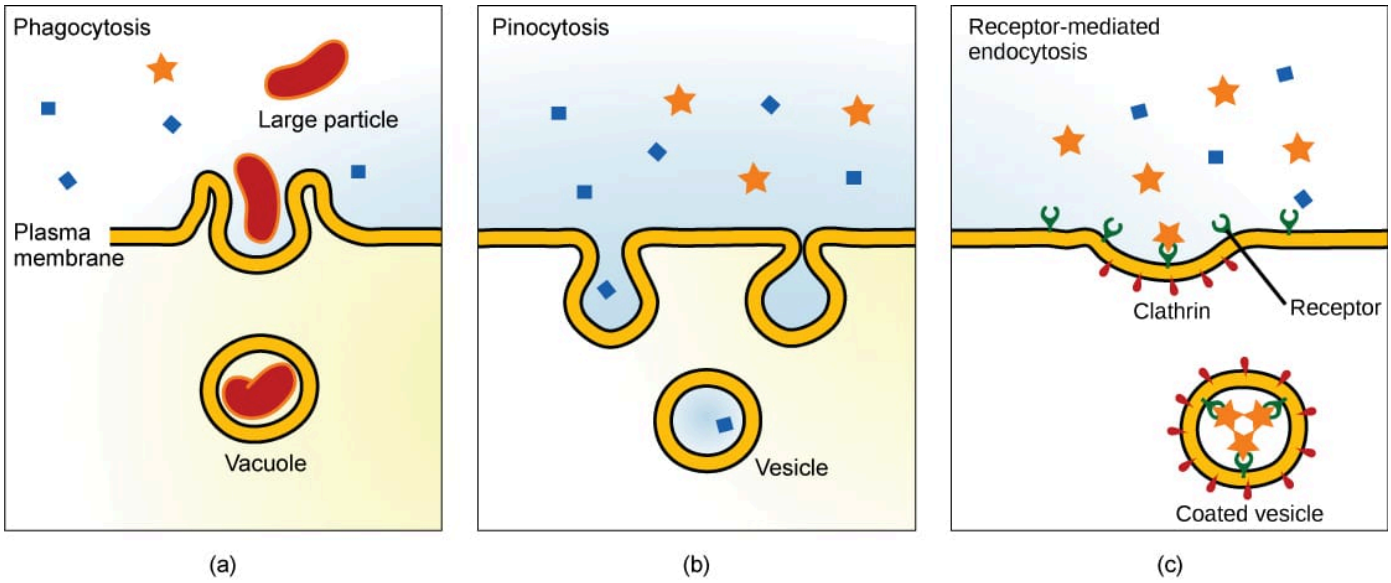


Figure 2.5.3: Three variations of endocytosis are shown. (a) In one form of endocytosis, phagocytosis, the cell membrane surrounds the particle and pinches off to form an intracellular vacuole. (b) In another type of endocytosis, pinocytosis, the cell membrane surrounds a small volume of fluid and pinches off, forming a vesicle. (c) In receptor-mediated endocytosis, uptake of substances by the cell is targeted to a single type of substance that binds at the receptor on the external cell membrane. (credit: modification of work by Mariana Ruiz Villarreal)

Phagocytosis is the process by which large particles, such as cells, are taken in by a cell. For example, when microorganisms invade the human body, a type of white blood cell called a neutrophil removes the invader through this process, surrounding and engulfing the microorganism, which is then destroyed by the neutrophil (Figure 2.5.3).

A variation of endocytosis is called pinocytosis. This literally means “cell drinking” and was named at a time when the assumption was that the cell was purposefully taking in extracellular fluid. In reality, this process takes in solutes that the cell needs from the extracellular fluid (Figure 2.5.3).

A targeted variation of endocytosis employs binding proteins in the plasma membrane that are specific for certain substances (Figure 2.5.3). The particles bind to the proteins and the plasma membrane invaginates, bringing the substance and the proteins into the cell. If passage across the membrane of the target of receptor-mediated endocytosis is ineffective, it will not be removed from the tissue fluids or blood. Instead, it will stay in those fluids and increase in concentration. Some human diseases are caused by a failure of receptor-mediated endocytosis. For example, the form of cholesterol termed low-density lipoprotein or LDL (also referred to as “bad” cholesterol) is removed from the blood by receptor-mediated endocytosis. In the human genetic disease familial hypercholesterolemia, the LDL receptors are defective or missing entirely. People with this condition have life-threatening levels of cholesterol in their blood, because their cells cannot clear the chemical from their blood.

CONCEPT IN ACTION

This interactive element is not available in this format. Visit the link or scan the QR code to access it online.

View this YouTube Video online

See receptor-mediated endocytosis animation in action.

Exocytosis

In contrast to these methods of moving material into a cell is the process of exocytosis. Exocytosis is the opposite of the processes discussed above in that its purpose is to expel material from the cell into the extracellular fluid. A particle enveloped

in membrane fuses with the interior of the plasma membrane. This fusion opens the membranous envelope to the exterior of the cell, and the particle is expelled into the extracellular space (Figure 2.5.4).

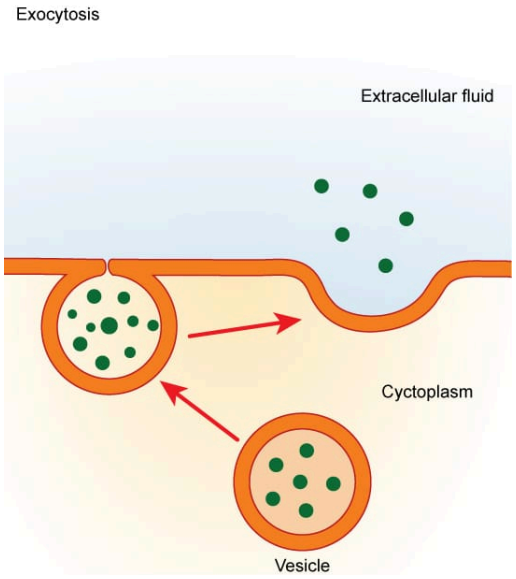


Figure 2.5.4: In exocytosis, a vesicle migrates to the plasma membrane, binds, and releases its contents to the outside of the cell. (credit: modification of work by Mariana Ruiz Villarreal)

Section Summary

The combined gradient that affects an ion includes its concentration gradient and its electrical gradient. Living cells need certain substances in concentrations greater than they exist in the extracellular space. Moving substances up their electrochemical gradients requires energy from the cell. Active transport uses energy stored in ATP to fuel the transport. Active transport of small molecular-size material uses integral proteins in the cell membrane to move the material—these proteins are analogous to pumps. Some pumps, which carry out primary active transport, couple directly with ATP to drive their action. In secondary transport, energy from primary transport can be used to move another substance into the cell and up its concentration gradient.

Endocytosis methods require the direct use of ATP to fuel the transport of large particles such as macromolecules; parts of cells or whole cells can be engulfed by other cells in a process called phagocytosis. In phagocytosis, a portion of the membrane invaginates and flows around the particle, eventually pinching off and leaving the particle wholly enclosed by an envelope of plasma membrane. Vacuoles are broken down by the cell, with the particles used as food or dispatched in some other way. Pinocytosis is a similar process on a smaller scale. The cell expels waste and other particles through the reverse process, exocytosis. Wastes are moved outside the cell, pushing a membranous vesicle to the plasma membrane, allowing the vesicle to fuse with the membrane and incorporating itself into the membrane structure, releasing its contents to the exterior of the cell.

Glossary

active transport
: the method of transporting material that requires energy

electrochemical gradient
: a gradient produced by the combined forces of the electrical gradient and the chemical gradient

endocytosis
: a type of active transport that moves substances, including fluids and particles, into a cell

exocytosis
: a process of passing material out of a cell

phagocytosis
: a process that takes macromolecules that the cell needs from the extracellular fluid; a variation of endocytosis

pinocytosis
: a process that takes solutes that the cell needs from the extracellular fluid; a variation of endocytosis

receptor-mediated endocytosis
: a variant of endocytosis that involves the use of specific binding proteins in the plasma membrane for specific molecules or particles

Contributors and Attributions

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3: CELLULAR ENERGY & METABOLISM

3.1: Energy and Metabolism
3.2: Glycolysis
3.3: Cellular Respiration and ATP Production
3.4: Fermentation

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3.1: Energy and Metabolism

Scientists use the term bioenergetics to describe the concept of energy flow (Figure 3.1.1) through living systems, such as cells. Cellular processes such as the building and breaking down of complex molecules occur through stepwise chemical reactions. Some of these chemical reactions are spontaneous and release energy, whereas others require energy to proceed. Just as living things must continually consume food to replenish their energy supplies, cells must continually produce more energy to replenish that used by the many energy-requiring chemical reactions that constantly take place. Together, all of the chemical reactions that take place inside cells, including those that consume or generate energy, are referred to as the cell's metabolism.

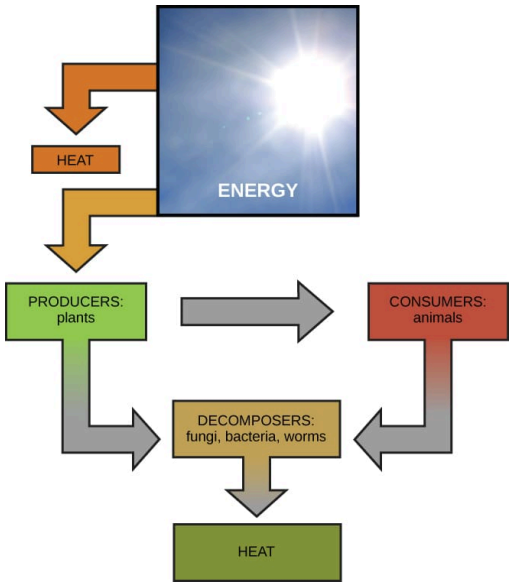


Figure 3.1.1**:** Ultimately, most life forms get their energy from the sun. Plants use photosynthesis to capture sunlight, and herbivores eat the plants to obtain energy. Carnivores eat the herbivores, and eventual decomposition of plant and animal material contributes to the nutrient pool.

Metabolic Pathways

Consider the metabolism of sugar. This is a classic example of one of the many cellular processes that use and produce energy. Living things consume sugars as a major energy source, because sugar molecules have a great deal of energy stored within their bonds. For the most part, photosynthesizing organisms like plants produce these sugars. During photosynthesis, plants use energy (originally from sunlight) to convert carbon dioxide gas (CO_2) into sugar molecules (like glucose: $C_6H_{12}O_6$). They consume carbon dioxide and produce oxygen as a waste product. This reaction is summarized as:

$$6\,CO_2 + 6\,H_2O \longrightarrow C_6H_{12}O_6 + 6\,O_2$$

Because this process involves synthesizing an energy-storing molecule, it requires energy input to proceed. During the light reactions of photosynthesis, energy is provided by a molecule called adenosine triphosphate (ATP), which is the primary energy currency of all cells. Just as the dollar is used as currency to buy goods, cells use molecules of ATP as energy currency to perform immediate work. In contrast, energy-storage molecules such as glucose are consumed only to be broken down to use their energy. The reaction that harvests the energy of a sugar molecule in cells requiring oxygen to survive can be summarized by the reverse reaction to photosynthesis. In this reaction, oxygen is consumed and carbon dioxide is released as a waste product. The reaction is summarized as:

$$C_6H_{12}O_6 + 6\,O_2 \longrightarrow 6\,H_2O + 6\,CO_2$$

Both of these reactions involve many steps.

The processes of making and breaking down sugar molecules illustrate two examples of metabolic pathways. A metabolic pathway is a series of chemical reactions that takes a starting molecule and modifies it, step-by-step, through a series of

metabolic intermediates, eventually yielding a final product. In the example of sugar metabolism, the first metabolic pathway synthesized sugar from smaller molecules, and the other pathway broke sugar down into smaller molecules. These two opposite processes—the first requiring energy and the second producing energy—are referred to as anabolic pathways (building polymers) and catabolic pathways (breaking down polymers into their monomers), respectively. Consequently, metabolism is composed of synthesis (anabolism) and degradation (catabolism) (Figure 3.1.2).

It is important to know that the chemical reactions of metabolic pathways do not take place on their own. Each reaction step is facilitated, or catalyzed, by a protein called an enzyme. Enzymes are important for catalyzing all types of biological reactions—those that require energy as well as those that release energy.

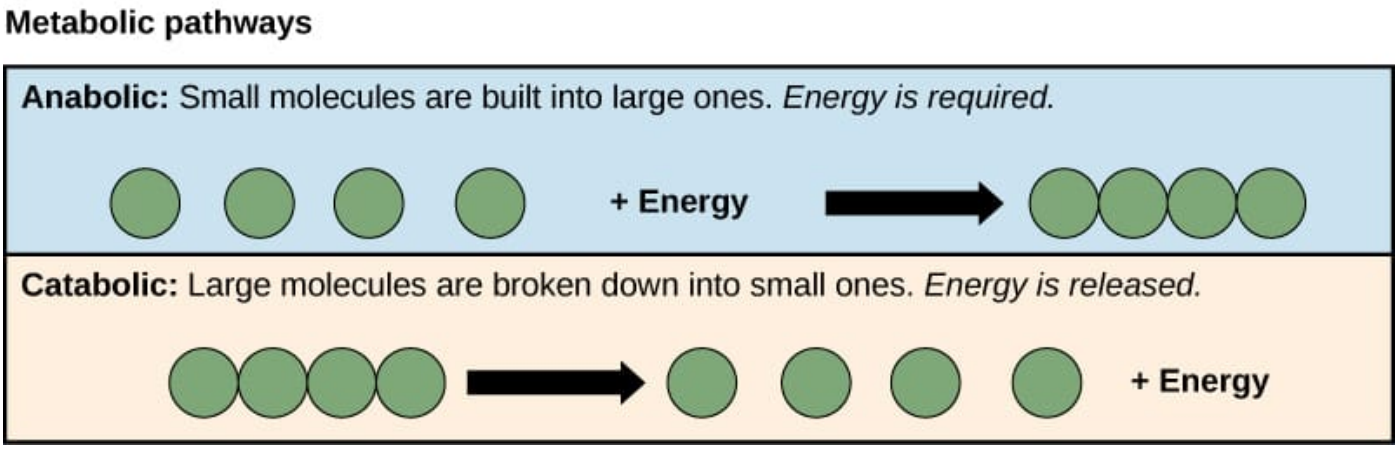


Figure 3.1.2**:** Catabolic pathways are those that generate energy by breaking down larger molecules. Anabolic pathways are those that require energy to synthesize larger molecules. Both types of pathways are required for maintaining the cell's energy balance.

Energy

Thermodynamics refers to the study of energy and energy transfer involving physical matter. The matter relevant to a particular case of energy transfer is called a system, and everything outside of that matter is called the surroundings. For instance, when heating a pot of water on the stove, the system includes the stove, the pot, and the water. Energy is transferred within the system (between the stove, pot, and water). There are two types of systems: open and closed. In an open system, energy can be exchanged with its surroundings. The stovetop system is open because heat can be lost to the air. A closed system cannot exchange energy with its surroundings.

Biological organisms are open systems. Energy is exchanged between them and their surroundings as they use energy from the sun to perform photosynthesis or consume energy-storing molecules and release energy to the environment by doing work and releasing heat. Like all things in the physical world, energy is subject to physical laws. The laws of thermodynamics govern the transfer of energy in and among all systems in the universe.

In general, energy is defined as the ability to do work, or to create some kind of change. Energy exists in different forms. For example, electrical energy, light energy, and heat energy are all different types of energy. To appreciate the way energy flows into and out of biological systems, it is important to understand two of the physical laws that govern energy.

Thermodynamics

The first law of thermodynamics states that the total amount of energy in the universe is constant and conserved. In other words, there has always been, and always will be, exactly the same amount of energy in the universe. Energy exists in many different forms. According to the first law of thermodynamics, energy may be transferred from place to place or transformed into different forms, but it cannot be created or destroyed. The transfers and transformations of energy take place around us all the time. Light bulbs transform electrical energy into light and heat energy. Gas stoves transform chemical energy from natural gas into heat energy. Plants perform one of the most biologically useful energy transformations on earth: that of converting the energy of sunlight to chemical energy stored within organic molecules (Figure 3.1.1). Some examples of energy transformations are shown in Figure 3.1.3.

The challenge for all living organisms is to obtain energy from their surroundings in forms that they can transfer or transform into usable energy to do work. Living cells have evolved to meet this challenge. Chemical energy stored within organic molecules such as sugars and fats is transferred and transformed through a series of cellular chemical reactions into energy within molecules of ATP. Energy in ATP molecules is easily accessible to do work. Examples of the types of work that cells need to do include building complex molecules, transporting materials, powering the motion of cilia or flagella, and contracting muscle fibers to create movement.

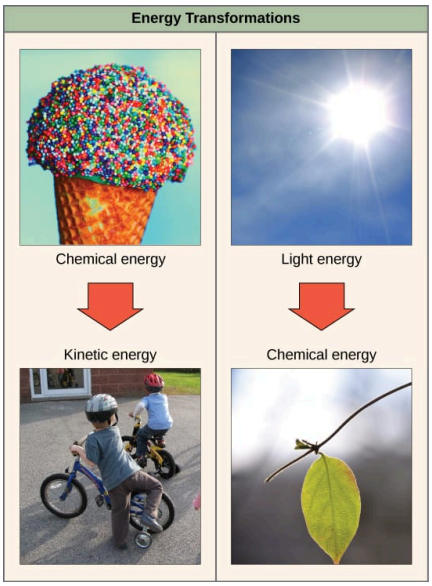


Figure 3.1.3**:** Shown are some examples of energy transferred and transformed from one system to another and from one form to another. The food we consume provides our cells with the energy required to carry out bodily functions, just as light energy provides plants with the means to create the chemical energy they need. (credit "ice cream": modification of work by D. Sharon Pruitt; credit "kids": modification of work by Max from Providence; credit "leaf": modification of work by Cory Zanker)

A living cell's primary tasks of obtaining, transforming, and using energy to do work may seem simple. However, the second law of thermodynamics explains why these tasks are harder than they appear. All energy transfers and transformations are never completely efficient. In every energy transfer, some amount of energy is lost in a form that is unusable. In most cases, this form is heat energy. Thermodynamically, heat energy is defined as the energy transferred from one system to another that is not work. For example, when a light bulb is turned on, some of the energy being converted from electrical energy into light energy is lost as heat energy. Likewise, some energy is lost as heat energy during cellular metabolic reactions.

An important concept in physical systems is that of order and disorder. The more energy that is lost by a system to its surroundings, the less ordered and more random the system is. Scientists refer to the measure of randomness or disorder within a system as entropy. High entropy means high disorder and low energy. Molecules and chemical reactions have varying entropy as well. For example, entropy increases as molecules at a high concentration in one place diffuse and spread out. The second law of thermodynamics says that energy will always be lost as heat in energy transfers or transformations.

Living things are highly ordered, requiring constant energy input to be maintained in a state of low entropy.

Potential and Kinetic Energy

When an object is in motion, there is energy associated with that object. Think of a wrecking ball. Even a slow-moving wrecking ball can do a great deal of damage to other objects. Energy associated with objects in motion is called kinetic energy (Figure 3.1.4). A speeding bullet, a walking person, and the rapid movement of molecules in the air (which produces heat) all have kinetic energy.

Now what if that same motionless wrecking ball is lifted two stories above ground with a crane? If the suspended wrecking ball is unmoving, is there energy associated with it? The answer is yes. The energy that was required to lift the wrecking ball did not disappear, but is now stored in the wrecking ball by virtue of its position and the force of gravity acting on it. This type of energy is called potential energy (Figure 3.1.4). If the ball were to fall, the potential energy would be transformed into kinetic energy until all of the potential energy was exhausted when the ball rested on the ground. Wrecking balls also swing like a pendulum; through

the swing, there is a constant change of potential energy (highest at the top of the swing) to kinetic energy (highest at the bottom of the swing). Other examples of potential energy include the energy of water held behind a dam or a person about to skydive out of an airplane.



Figure 3.1.4**:** Still water has potential energy; moving water, such as in a waterfall or a rapidly flowing river, has kinetic energy. (credit "dam": modification of work by "Pascal"/Flickr; credit "waterfall": modification of work by Frank Gualtieri)

Potential energy is not only associated with the location of matter, but also with the structure of matter. Even a spring on the ground has potential energy if it is compressed; so does a rubber band that is pulled taut. On a molecular level, the bonds that hold the atoms of molecules together exist in a particular structure that has potential energy. Remember that anabolic cellular pathways require energy to synthesize complex molecules from simpler ones and catabolic pathways release energy when complex molecules are broken down. The fact that energy can be released by the breakdown of certain chemical bonds implies that those bonds have potential energy. In fact, there is potential energy stored within the bonds of all the food molecules we eat, which is eventually harnessed for use. This is because these bonds can release energy when broken. The type of potential energy that exists within chemical bonds, and is released when those bonds are broken, is called chemical energy. Chemical energy is responsible for providing living cells with energy from food. The release of energy occurs when the molecular bonds within food molecules are broken.

CONCEPT IN ACTION

Visit the site and select “Pendulum” from the “Work and Energy” menu to see the shifting kinetic and potential energy of a pendulum in motion.

Free and Activation Energy

After learning that chemical reactions release energy when energy-storing bonds are broken, an important next question is the following: How is the energy associated with these chemical reactions quantified and expressed? How can the energy released from one reaction be compared to that of another reaction? A measurement of free energy is used to quantify these energy transfers. Recall that according to the second law of thermodynamics, all energy transfers involve the loss of some amount of energy in an unusable form such as heat. Free energy specifically refers to the energy associated with a chemical reaction that is available after the losses are accounted for. In other words, free energy is usable energy, or energy that is available to do work.

If energy is released during a chemical reaction, then the change in free energy, signified as ΔG (delta G) will be a negative number. A negative change in free energy also means that the products of the reaction have less free energy than the reactants, because they release some free energy during the reaction. Reactions that have a negative change in free energy and consequently release free energy are called exergonic reactions. Think: *ex*ergonic means energy is *ex*iting the system. These reactions are also referred to as spontaneous reactions, and their products have less stored energy than the reactants. An

important distinction must be drawn between the term spontaneous and the idea of a chemical reaction occurring immediately. Contrary to the everyday use of the term, a spontaneous reaction is not one that suddenly or quickly occurs. The rusting of iron is an example of a spontaneous reaction that occurs slowly, little by little, over time.

If a chemical reaction absorbs energy rather than releases energy on balance, then the ΔG for that reaction will be a positive value. In this case, the products have more free energy than the reactants. Thus, the products of these reactions can be thought of as energy-storing molecules. These chemical reactions are called endergonic reactions and they are non-spontaneous. An endergonic reaction will not take place on its own without the addition of free energy.

ART CONNECTION

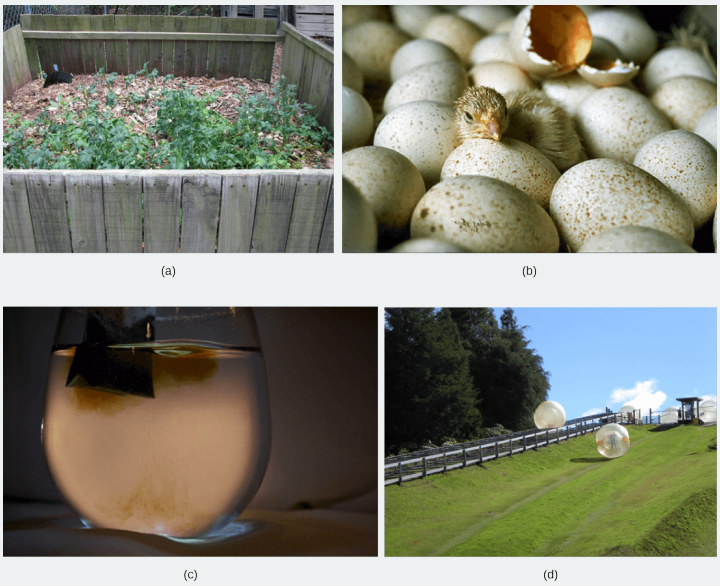


Figure 3.1.5**:** Shown are some examples of endergonic processes (ones that require energy) and exergonic processes (ones that release energy). (credit a: modification of work by Natalie Maynor; credit b: modification of work by USDA; credit c: modification of work by Cory Zanker; credit d: modification of work by Harry Malsch)

Look at each of the processes shown and decide if it is endergonic or exergonic.

There is another important concept that must be considered regarding endergonic and exergonic reactions. Exergonic reactions require a small amount of energy input to get going, before they can proceed with their energy-releasing steps. These reactions have a net release of energy, but still require some energy input in the beginning. This small amount of energy input necessary for all chemical reactions to occur is called the activation energy.

CONCEPT IN ACTION

This interactive element is not available in this format. Visit the link or scan the QR code to access it online.

View this YouTube Video online

Watch an animation of the move from free energy to transition state of the reaction.

Enzymes

A substance that helps a chemical reaction to occur is called a catalyst, and the molecules that catalyze biochemical reactions are

called enzymes. Most enzymes are proteins and perform the critical task of lowering the activation energies of chemical reactions inside the cell. Most of the reactions critical to a living cell happen too slowly at normal temperatures to be of any use to the cell. Without enzymes to speed up these reactions, life could not persist. Enzymes do this by binding to the reactant molecules and holding them in such a way as to make the chemical bond-breaking and -forming processes take place more easily. It is important to remember that enzymes do not change whether a reaction is exergonic (spontaneous) or endergonic. This is because they do not change the free energy of the reactants or products. They only reduce the activation energy required for the reaction to go forward (Figure 3.1.6). In addition, an enzyme itself is unchanged by the reaction it catalyzes. Once one reaction has been catalyzed, the enzyme is able to participate in other reactions.

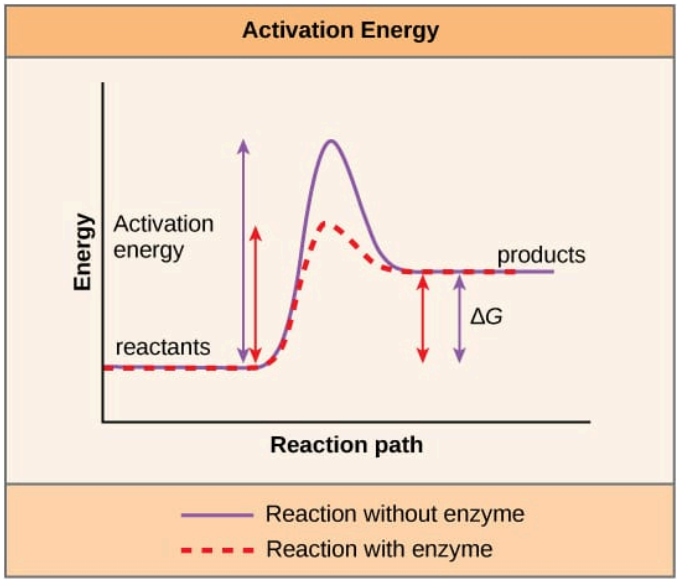


Figure 3.1.6**:** Enzymes lower the activation energy of the reaction but do not change the free energy of the reaction.

The chemical reactants to which an enzyme binds are called the enzyme's substrates. There may be one or more substrates, depending on the particular chemical reaction. In some reactions, a single reactant substrate is broken down into multiple products. In others, two substrates may come together to create one larger molecule. Two reactants might also enter a reaction and both become modified, but they leave the reaction as two products. The location within the enzyme where the substrate binds is called the enzyme's active site. The active site is where the "action" happens. Since enzymes are proteins, there is a unique combination of amino acid side chains within the active site. Each side chain is characterized by different properties. They can be large or small, weakly acidic or basic, hydrophilic or hydrophobic, positively or negatively charged, or neutral. The unique combination of side chains creates a very specific chemical environment within the active site. This specific environment is suited to bind to one specific chemical substrate (or substrates).

Active sites are subject to influences of the local environment. Increasing the environmental temperature generally increases reaction rates, enzyme-catalyzed or otherwise. However, temperatures outside of an optimal range reduce the rate at which an enzyme catalyzes a reaction. Hot temperatures will eventually cause enzymes to denature, an irreversible change in the three-dimensional shape and therefore the function of the enzyme. Enzymes are also suited to function best within a certain pH and salt concentration range, and, as with temperature, extreme pH, and salt concentrations can cause enzymes to denature.

For many years, scientists thought that enzyme-substrate binding took place in a simple "lock and key" fashion. This model asserted that the enzyme and substrate fit together perfectly in one instantaneous step. However, current research supports a model called induced fit (Figure 3.1.7). The induced-fit model expands on the lock-and-key model by describing a more dynamic binding between enzyme and substrate. As the enzyme and substrate come together, their interaction causes a mild shift in the enzyme's structure that forms an ideal binding arrangement between enzyme and substrate.

CONCEPT IN ACTION

This interactive element is not available in this format. Visit the link or scan the QR code to access it online.

View this YouTube Video online

View an animation of induced fit.

When an enzyme binds its substrate, an enzyme-substrate complex is formed. This complex lowers the activation energy of the reaction and promotes its rapid progression in one of multiple possible ways. On a basic level, enzymes promote chemical reactions that involve more than one substrate by bringing the substrates together in an optimal orientation for reaction. Another way in which enzymes promote the reaction of their substrates is by creating an optimal environment within the active site for the reaction to occur. The chemical properties that emerge from the particular arrangement of amino acid R groups within an active site create the perfect environment for an enzyme's specific substrates to react.

The enzyme-substrate complex can also lower activation energy by compromising the bond structure so that it is easier to break. Finally, enzymes can also lower activation energies by taking part in the chemical reaction itself. In these cases, it is important to remember that the enzyme will always return to its original state by the completion of the reaction. One of the hallmark properties of enzymes is that they remain ultimately unchanged by the reactions they catalyze. After an enzyme has catalyzed a reaction, it releases its product(s) and can catalyze a new reaction.

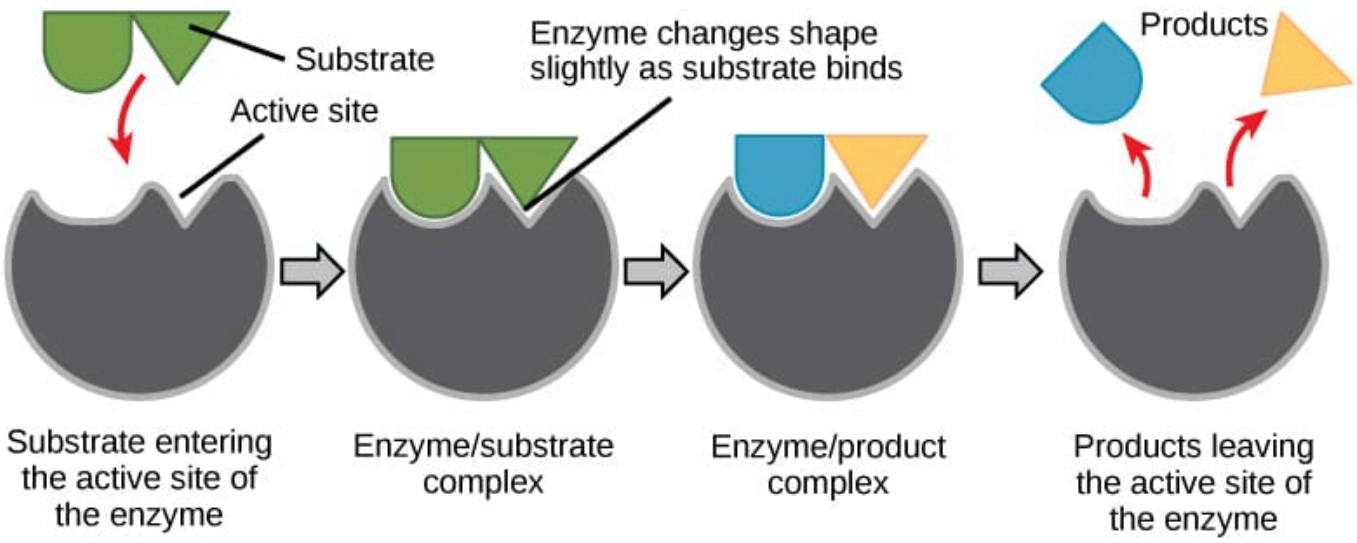


Figure 3.1.7**:** The induced-fit model is an adjustment to the lock-and-key model and explains how enzymes and substrates undergo dynamic modifications during the transition state to increase the affinity of the substrate for the active site.

It would seem ideal to have a scenario in which all of an organism's enzymes existed in abundant supply and functioned optimally under all cellular conditions, in all cells, at all times. However, a variety of mechanisms ensures that this does not happen. Cellular needs and conditions constantly vary from cell to cell, and change within individual cells over time. The required enzymes of stomach cells differ from those of fat storage cells, skin cells, blood cells, and nerve cells. Furthermore, a digestive organ cell works much harder to process and break down nutrients during the time that closely follows a meal compared with many hours after a meal. As these cellular demands and conditions vary, so must the amounts and functionality of different enzymes.

Since the rates of biochemical reactions are controlled by activation energy, and enzymes lower and determine activation energies for chemical reactions, the relative amounts and functioning of the variety of enzymes within a cell ultimately determine which reactions will proceed and at what rates. This determination is tightly controlled in cells. In certain cellular environments, enzyme activity is partly controlled by environmental factors like pH, temperature, salt concentration, and, in some cases, cofactors

or coenzymes.

Enzymes can also be regulated in ways that either promote or reduce enzyme activity. There are many kinds of molecules that inhibit or promote enzyme function, and various mechanisms by which they do so. In some cases of enzyme inhibition, an inhibitor molecule is similar enough to a substrate that it can bind to the active site and simply block the substrate from binding. When this happens, the enzyme is inhibited through competitive inhibition, because an inhibitor molecule competes with the substrate for binding to the active site.

On the other hand, in noncompetitive inhibition, an inhibitor molecule binds to the enzyme in a location other than the active site, called an allosteric site, but still manages to block substrate binding to the active site. Some inhibitor molecules bind to enzymes in a location where their binding induces a conformational change that reduces the affinity of the enzyme for its substrate. This type of inhibition is called allosteric inhibition(Figure 3.1.8). Most allosterically regulated enzymes are made up of more than one polypeptide, meaning that they have more than one protein subunit. When an allosteric inhibitor binds to a region on an enzyme, all active sites on the protein subunits are changed slightly such that they bind their substrates with less efficiency. There are allosteric activators as well as inhibitors. Allosteric activators bind to locations on an enzyme away from the active site, inducing a conformational change that increases the affinity of the enzyme's active site(s) for its substrate(s) (Figure 3.1.8).

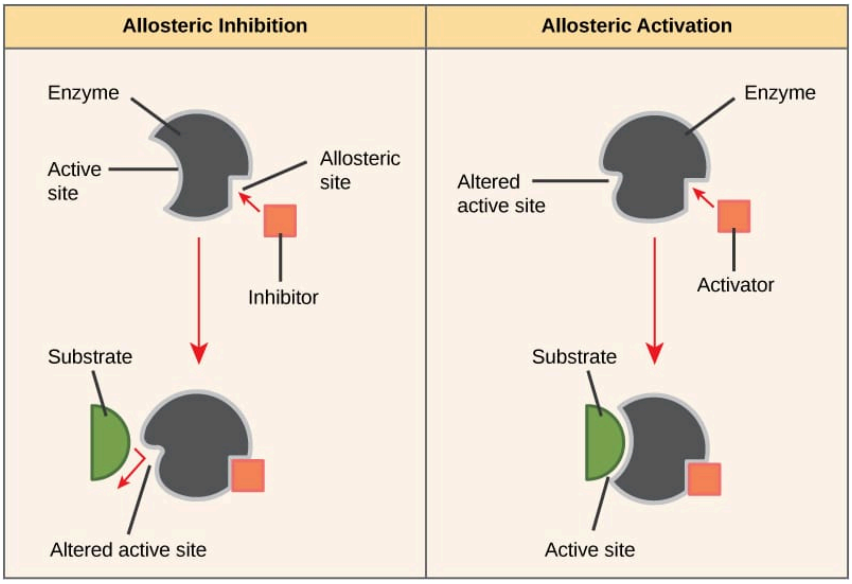


Figure 3.1.8**:** Allosteric inhibition works by indirectly inducing a conformational change to the active site such that the substrate no longer fits. In contrast, in allosteric activation, the activator molecule modifies the shape of the active site to allow a better fit of the substrate.

CAREERS IN ACTION: Pharmaceutical Drug Developer



Figure 3.1.9**:** Have you ever wondered how pharmaceutical drugs are developed? (credit: Deborah Austin)

Enzymes are key components of metabolic pathways. Understanding how enzymes work and how they can be regulated are key principles behind the development of many of the pharmaceutical drugs on the market today. Biologists working in this field collaborate with other scientists to design drugs (Figure 3.1.9).

Consider statins for example—statins is the name given to one class of drugs that can reduce cholesterol levels. These compounds are inhibitors of the enzyme HMG-CoA reductase, which is the enzyme that synthesizes cholesterol from lipids in the body. By inhibiting this enzyme, the level of cholesterol synthesized in the body can be reduced. Similarly, acetaminophen, popularly marketed under the brand name Tylenol, is an inhibitor of the enzyme cyclooxygenase. While it is used to provide relief from fever and inflammation (pain), its mechanism of action is still not completely understood.

How are drugs discovered? One of the biggest challenges in drug discovery is identifying a drug target. A drug target is a molecule that is literally the target of the drug. In the case of statins, HMG-CoA reductase is the drug target. Drug targets are identified through painstaking research in the laboratory. Identifying the target alone is not enough; scientists also need to know how the target acts inside the cell and which reactions go awry in the case of disease. Once the target and the pathway are identified, then the actual process of drug design begins. In this stage, chemists and biologists work together to design and synthesize molecules that can block or activate a particular reaction. However, this is only the beginning: If and when a drug prototype is successful in performing its function, then it is subjected to many tests from in vitro experiments to clinical trials before it can get approval from the U.S. Food and Drug Administration to be on the market.

Many enzymes do not work optimally, or even at all, unless bound to other specific non-protein helper molecules. They may bond either temporarily through ionic or hydrogen bonds, or permanently through stronger covalent bonds. Binding to these molecules promotes optimal shape and function of their respective enzymes. Two examples of these types of helper molecules are cofactors and coenzymes. Cofactors are inorganic ions such as ions of iron and magnesium. Coenzymes are organic helper molecules, those with a basic atomic structure made up of carbon and hydrogen. Like enzymes, these molecules participate in reactions without being changed themselves and are ultimately recycled and reused. Vitamins are the source of coenzymes. Some vitamins are the precursors of coenzymes and others act directly as coenzymes. Vitamin C is a direct coenzyme for multiple enzymes that take part in building the important connective tissue, collagen. Therefore, enzyme function is, in part, regulated by the abundance of various cofactors and coenzymes, which may be supplied by an organism's diet or, in some cases, produced by the organism.

Feedback Inhibition in Metabolic Pathways

Molecules can regulate enzyme function in many ways. The major question remains, however: What are these molecules and where do they come from? Some are cofactors and coenzymes, as you have learned. What other molecules in the cell provide enzymatic regulation such as allosteric modulation, and competitive and non-competitive inhibition? Perhaps the most relevant

sources of regulatory molecules, with respect to enzymatic cellular metabolism, are the products of the cellular metabolic reactions themselves. In a most efficient and elegant way, cells have evolved to use the products of their own reactions for feedback inhibition of enzyme activity. Feedback inhibition involves the use of a reaction product to regulate its own further production (Figure 3.1.10). The cell responds to an abundance of the products by slowing down production during anabolic or catabolic reactions. Such reaction products may inhibit the enzymes that catalyzed their production through the mechanisms described above.

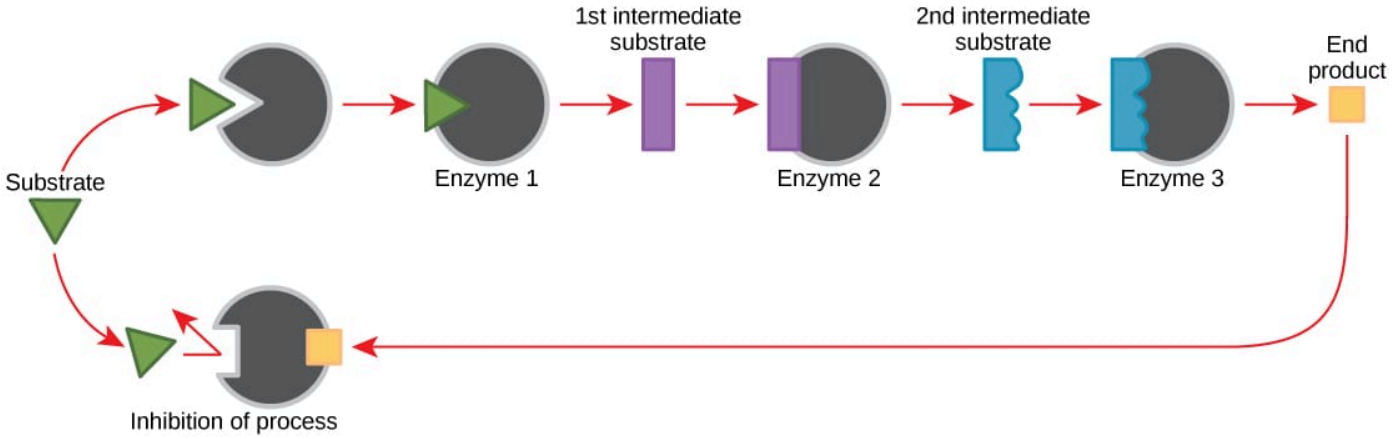


Figure 3.1.10**:** Metabolic pathways are a series of reactions catalyzed by multiple enzymes. Feedback inhibition, where the end product of the pathway inhibits an upstream process, is an important regulatory mechanism in cells.

The production of both amino acids and nucleotides is controlled through feedback inhibition. Additionally, ATP is an allosteric regulator of some of the enzymes involved in the catabolic breakdown of sugar, the process that creates ATP. In this way, when ATP is in abundant supply, the cell can prevent the production of ATP. On the other hand, ADP serves as a positive allosteric regulator (an allosteric activator) for some of the same enzymes that are inhibited by ATP. Thus, when relative levels of ADP are high compared to ATP, the cell is triggered to produce more ATP through sugar catabolism.

Section Summary

Cells perform the functions of life through various chemical reactions. A cell's metabolism refers to the combination of chemical reactions that take place within it. Catabolic reactions break down complex chemicals into simpler ones and are associated with energy release. Anabolic processes build complex molecules out of simpler ones and require energy.

In studying energy, the term system refers to the matter and environment involved in energy transfers. Entropy is a measure of the disorder of a system. The physical laws that describe the transfer of energy are the laws of thermodynamics. The first law states that the total amount of energy in the universe is constant. The second law of thermodynamics states that every energy transfer involves some loss of energy in an unusable form, such as heat energy. Energy comes in different forms: kinetic, potential, and free. The change in free energy of a reaction can be negative (releases energy, exergonic) or positive (consumes energy, endergonic). All reactions require an initial input of energy to proceed, called the activation energy.

Enzymes are chemical catalysts that speed up chemical reactions by lowering their activation energy. Enzymes have an active site with a unique chemical environment that fits particular chemical reactants for that enzyme, called substrates. Enzymes and substrates are thought to bind according to an induced-fit model. Enzyme action is regulated to conserve resources and respond optimally to the environment.

Art Connections

Figure 3.1.5: Look at each of the processes shown and decide if it is endergonic or exergonic.

Answer

A compost pile decomposing is an exergonic process. A baby developing from a fertilized egg is an endergonic process. Tea dissolving into water is an exergonic process. A ball rolling downhill is an exergonic process.

Glossary

activation energy
: the amount of initial energy necessary for reactions to occur

active site
: a specific region on the enzyme where the substrate binds

allosteric inhibition
: the mechanism for inhibiting enzyme action in which a regulatory molecule binds to a second site (not the active site) and initiates a conformation change in the active site, preventing binding with the substrate

anabolic
: describes the pathway that requires a net energy input to synthesize complex molecules from simpler ones

bioenergetics
: the concept of energy flow through living systems

catabolic
: describes the pathway in which complex molecules are broken down into simpler ones, yielding energy as an additional product of the reaction

competitive inhibition
: a general mechanism of enzyme activity regulation in which a molecule other than the enzyme's substrate is able to bind the active site and prevent the substrate itself from binding, thus inhibiting the overall rate of reaction for the enzyme

endergonic
: describes a chemical reaction that results in products that store more chemical potential energy than the reactants

enzyme
: a molecule that catalyzes a biochemical reaction

exergonic
: describes a chemical reaction that results in products with less chemical potential energy than the reactants, plus the release of free energy

feedback inhibition
: a mechanism of enzyme activity regulation in which the product of a reaction or the final product of a series of sequential reactions inhibits an enzyme for an earlier step in the reaction series

heat energy
: the energy transferred from one system to another that is not work

kinetic energy
: the type of energy associated with objects in motion

metabolism
: all the chemical reactions that take place inside cells, including those that use energy and those that release energy

noncompetitive inhibition
: a general mechanism of enzyme activity regulation in which a regulatory molecule binds to a site other than the active site and prevents the active site from binding the substrate; thus, the inhibitor molecule does not compete with the substrate for the active site; allosteric inhibition is a form of noncompetitive inhibition

potential energy
: the type of energy that refers to the potential to do work

substrate
: a molecule on which the enzyme acts

thermodynamics
: the science of the relationships between heat, energy, and work

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3.2: Glycolysis

Even exergonic, energy-releasing reactions require a small amount of activation energy to proceed. However, consider endergonic reactions, which require much more energy input because their products have more free energy than their reactants. Within the cell, where does energy to power such reactions come from? The answer lies with an energy-supplying molecule called adenosine triphosphate, or ATP. ATP is a small, relatively simple molecule, but within its bonds contains the potential for a quick burst of energy that can be harnessed to perform cellular work. This molecule can be thought of as the primary energy currency of cells in the same way that money is the currency that people exchange for things they need. ATP is used to power the majority of energy-requiring cellular reactions.

ATP in Living Systems

A living cell cannot store significant amounts of free energy. Excess free energy would result in an increase of heat in the cell, which would denature enzymes and other proteins, and thus destroy the cell. Rather, a cell must be able to store energy safely and release it for use only as needed. Living cells accomplish this using ATP, which can be used to fill any energy need of the cell. How? It functions as a rechargeable battery.

When ATP is broken down, usually by the removal of its terminal phosphate group, energy is released. This energy is used to do work by the cell, usually by the binding of the released phosphate to another molecule, thus activating it. For example, in the mechanical work of muscle contraction, ATP supplies energy to move the contractile muscle proteins.

ATP Structure and Function

At the heart of ATP is a molecule of adenosine monophosphate (AMP), which is composed of an adenine molecule bonded to both a ribose molecule and a single phosphate group (Figure 3.2.1). Ribose is a five-carbon sugar found in RNA and AMP is one of the nucleotides in RNA. The addition of a second phosphate group to this core molecule results in adenosine diphosphate (ADP); the addition of a third phosphate group forms adenosine triphosphate (ATP).

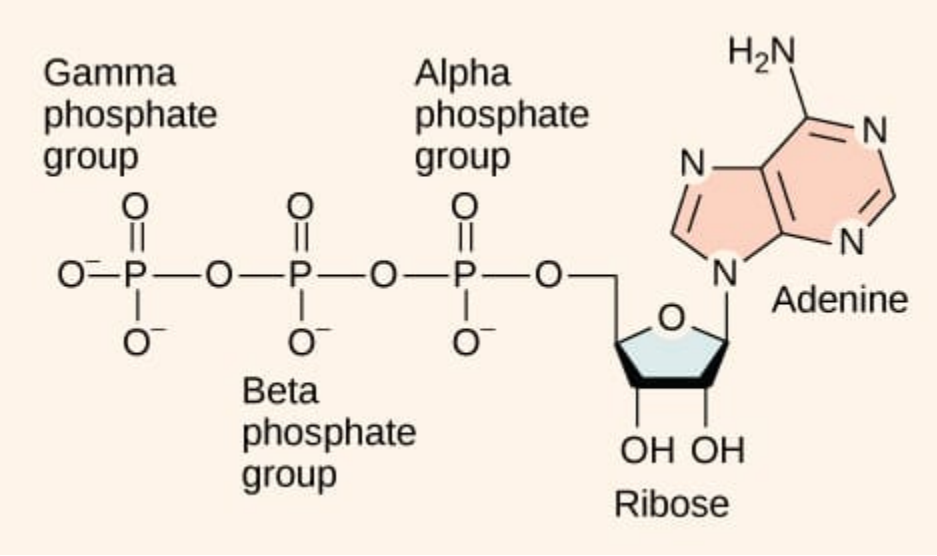


Figure 3.2.1**:** The structure of ATP shows the basic components of a two-ring adenine, five-carbon ribose, and three phosphate groups.

The addition of a phosphate group to a molecule requires a high amount of energy and results in a high-energy bond. Phosphate groups are negatively charged and thus repel one another when they are arranged in series, as they are in ADP and ATP. This repulsion makes the ADP and ATP molecules inherently unstable. The release of one or two phosphate groups from ATP, a process called hydrolysis, releases energy.

Glycolysis

You have read that nearly all of the energy used by living things comes to them in the bonds of the sugar, glucose. Glycolysis is the first step in the breakdown of glucose to extract energy for cell metabolism. Many living organisms carry out glycolysis as part of their metabolism. Glycolysis takes place in the cytoplasm of most prokaryotic and all eukaryotic cells.

Glycolysis begins with the six-carbon, ring-shaped structure of a single glucose molecule and ends with two molecules of a three-carbon sugar called pyruvate. Glycolysis consists of two distinct phases. In the first part of the glycolysis pathway, energy is used to make adjustments so that the six-carbon sugar molecule can be split evenly into two three-carbon pyruvate molecules. In the second part of glycolysis, ATP and nicotinamide-adenine dinucleotide (NADH) are produced (Figure 3.2.2).

If the cell cannot catabolize the pyruvate molecules further, it will harvest only two ATP molecules from one molecule of glucose. For example, mature mammalian red blood cells are only capable of glycolysis, which is their sole source of ATP. If glycolysis is interrupted, these cells would eventually die.

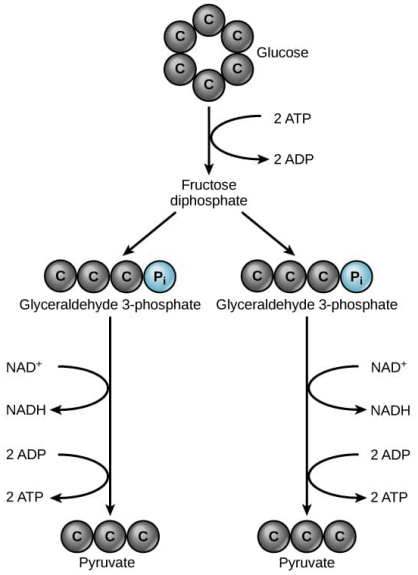


Figure 3.2.2: In glycolysis, a glucose molecule is converted into two pyruvate molecules.

Summary

ATP functions as the energy currency for cells. It allows cells to store energy briefly and transport it within itself to support endergonic chemical reactions. The structure of ATP is that of an RNA nucleotide with three phosphate groups attached. As ATP is used for energy, a phosphate group is detached, and ADP is produced. Energy derived from glucose catabolism is used to recharge ADP into ATP.

Glycolysis is the first pathway used in the breakdown of glucose to extract energy. Because it is used by nearly all organisms on earth, it must have evolved early in the history of life. Glycolysis consists of two parts: The first part prepares the six-carbon ring of glucose for separation into two three-carbon sugars. Energy from ATP is invested into the molecule during this step to energize the separation. The second half of glycolysis extracts ATP and high-energy electrons from hydrogen atoms and attaches them to NAD^+. Two ATP molecules are invested in the first half and four ATP molecules are formed during the second half. This produces a net gain of two ATP molecules per molecule of glucose for the cell.

Glossary

ATP
: (also, adenosine triphosphate) the cell's energy currency

glycolysis
: the process of breaking glucose into two three-carbon molecules with the production of ATP and NADH

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3.3: Cellular Respiration and ATP Production

The Citric Acid Cycle

In eukaryotic cells, the pyruvate molecules produced at the end of glycolysis are transported into mitochondria, which are sites of cellular respiration. If oxygen is available, aerobic respiration will go forward. In mitochondria, pyruvate will be transformed into a two-carbon acetyl group (by removing a molecule of carbon dioxide) that will be picked up by a carrier compound called coenzyme A (CoA), which is made from vitamin B_5. The resulting compound is called acetyl CoA. (Figure 3.3.1). Acetyl CoA can be used in a variety of ways by the cell, but its major function is to deliver the acetyl group derived from pyruvate to the next pathway in glucose catabolism.

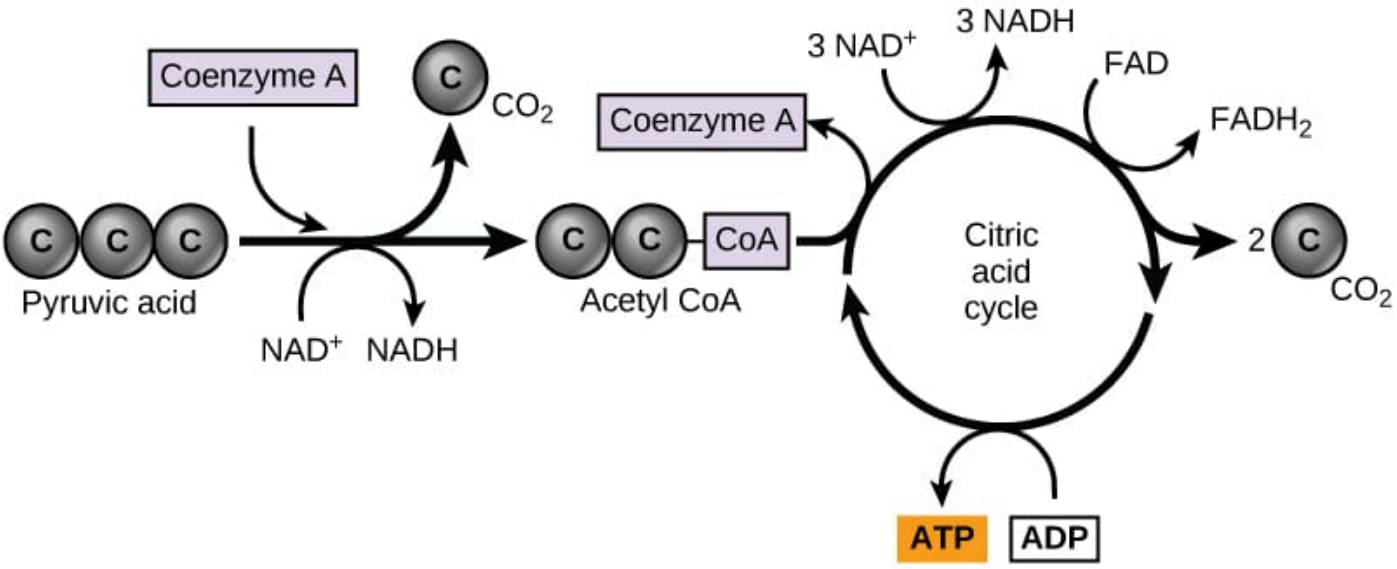


Figure 3.3.1**:** Pyruvate is converted into acetyl-CoA before entering the citric acid cycle.

Like the conversion of pyruvate to acetyl CoA, the citric acid cycle in eukaryotic cells takes place in the matrix of the mitochondria. Unlike glycolysis, the citric acid cycle is a closed loop: The last part of the pathway regenerates the compound used in the first step. The eight steps of the cycle are a series of chemical reactions that produces two carbon dioxide molecules, one ATP molecule (or an equivalent), and reduced forms (NADH and $FADH_2$) of NAD^+ and FAD^+, important coenzymes in the cell. Part of this is considered an aerobic pathway (oxygen-requiring) because the NADH and $FADH_2$ produced must transfer their electrons to the next pathway in the system, which will use oxygen. If oxygen is not present, this transfer does not occur.

Two carbon atoms come into the citric acid cycle from each acetyl group. Two carbon dioxide molecules are released on each turn of the cycle; however, these do not contain the same carbon atoms contributed by the acetyl group on that turn of the pathway. The two acetyl-carbon atoms will eventually be released on later turns of the cycle; in this way, all six carbon atoms from the original glucose molecule will be eventually released as carbon dioxide. It takes two turns of the cycle to process the equivalent of one glucose molecule. Each turn of the cycle forms three high-energy NADH molecules and one high-energy $FADH_2$ molecule. These high-energy carriers will connect with the last portion of aerobic respiration to produce ATP molecules. One ATP (or an equivalent) is also made in each cycle. Several of the intermediate compounds in the citric acid cycle can be used in synthesizing non-essential amino acids; therefore, the cycle is both anabolic and catabolic.

Oxidative Phosphorylation

You have just read about two pathways in glucose catabolism—glycolysis and the citric acid cycle—that generate ATP. Most of the ATP generated during the aerobic catabolism of glucose, however, is not generated directly from these pathways. Rather, it derives from a process that begins with passing electrons through a series of chemical reactions to a final electron acceptor, oxygen. These reactions take place in specialized protein complexes located in the inner membrane of the mitochondria of eukaryotic

organisms and on the inner part of the cell membrane of prokaryotic organisms. The energy of the electrons is harvested and used to generate a electrochemical gradient across the inner mitochondrial membrane. The potential energy of this gradient is used to generate ATP. The entirety of this process is called oxidative phosphorylation.

The electron transport chain (Figure 3.3.2**a**) is the last component of aerobic respiration and is the only part of metabolism that uses atmospheric oxygen. Oxygen continuously diffuses into plants for this purpose. In animals, oxygen enters the body through the respiratory system. Electron transport is a series of chemical reactions that resembles a bucket brigade in that electrons are passed rapidly from one component to the next, to the endpoint of the chain where oxygen is the final electron acceptor and water is produced. There are four complexes composed of proteins, labeled I through IV in Figure 3.3.2**c**, and the aggregation of these four complexes, together with associated mobile, accessory electron carriers, is called the electron transport chain. The electron transport chain is present in multiple copies in the inner mitochondrial membrane of eukaryotes and in the plasma membrane of prokaryotes. In each transfer of an electron through the electron transport chain, the electron loses energy, but with some transfers, the energy is stored as potential energy by using it to pump hydrogen ions across the inner mitochondrial membrane into the intermembrane space, creating an electrochemical gradient.

ART CONNECTION

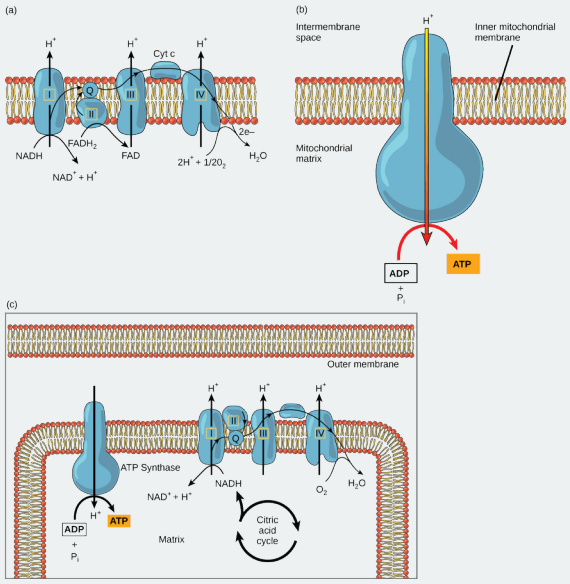


Figure 3.3.2**:** (a) The electron transport chain is a set of molecules that supports a series of oxidation-reduction reactions. (b) ATP synthase is a complex, molecular machine that uses an H^+ gradient to regenerate ATP from ADP. (c) Chemiosmosis relies on the potential energy provided by the H^+ gradient across the membrane.

Cyanide inhibits cytochrome c oxidase, a component of the electron transport chain. If cyanide poisoning occurs, would you expect the pH of the intermembrane space to increase or decrease? What affect would cyanide have on ATP synthesis?

Electrons from NADH and $FADH_2$ are passed to protein complexes in the electron transport chain. As they are passed from one complex to another (there are a total of four), the electrons lose energy, and some of that energy is used to pump hydrogen ions from the mitochondrial matrix into the intermembrane space. In the fourth protein complex, the electrons are accepted by oxygen, the terminal acceptor. The oxygen with its extra electrons then combines with two hydrogen ions, further enhancing the electrochemical gradient, to form water. If there were no oxygen present in the mitochondrion, the electrons could not be removed from the system, and the entire electron transport chain would back up and stop. The mitochondria would be unable to generate new ATP in this way, and the cell would ultimately die from lack of energy. This is the reason we must breathe to draw in new oxygen.

In the electron transport chain, the free energy from the series of reactions just described is used to pump hydrogen ions across the membrane. The uneven distribution of H^+ ions across the membrane establishes an electrochemical gradient, owing to the H^+ ions' positive charge and their higher concentration on one side of the membrane.

Hydrogen ions diffuse through the inner membrane through an integral membrane protein called ATP synthase (Figure 3.3.2

b). This complex protein acts as a tiny generator, turned by the force of the hydrogen ions diffusing through it, down their electrochemical gradient from the intermembrane space, where there are many mutually repelling hydrogen ions to the matrix, where there are few. The turning of the parts of this molecular machine regenerate ATP from ADP. This flow of hydrogen ions across the membrane through ATP synthase is called chemiosmosis.

Chemiosmosis (Figure 3.3.2**c**) is used to generate 90 percent of the ATP made during aerobic glucose catabolism. The result of the reactions is the production of ATP from the energy of the electrons removed from hydrogen atoms. These atoms were originally part of a glucose molecule. At the end of the electron transport system, the electrons are used to reduce an oxygen molecule to oxygen ions. The extra electrons on the oxygen ions attract hydrogen ions (protons) from the surrounding medium, and water is formed. The electron transport chain and the production of ATP through chemiosmosis are collectively called oxidative phosphorylation.

ATP Yield

The number of ATP molecules generated from the catabolism of glucose varies. For example, the number of hydrogen ions that the electron transport chain complexes can pump through the membrane varies between species. Another source of variance stems from the shuttle of electrons across the mitochondrial membrane. The NADH generated from glycolysis cannot easily enter mitochondria. Thus, electrons are picked up on the inside of the mitochondria by either NAD^+ or FAD^+. Fewer ATP molecules are generated when FAD^+ acts as a carrier. NAD^+ is used as the electron transporter in the liver and FAD^+ in the brain, so ATP yield depends on the tissue being considered.

Another factor that affects the yield of ATP molecules generated from glucose is that intermediate compounds in these pathways are used for other purposes. Glucose catabolism connects with the pathways that build or break down all other biochemical compounds in cells, and the result is somewhat messier than the ideal situations described thus far. For example, sugars other than glucose are fed into the glycolytic pathway for energy extraction. Other molecules that would otherwise be used to harvest energy in glycolysis or the citric acid cycle may be removed to form nucleic acids, amino acids, lipids, or other compounds. Overall, in living systems, these pathways of glucose catabolism extract about 34 percent of the energy contained in glucose.

CAREERS IN ACTION: Mitochondrial Disease Physician

What happens when the critical reactions of cellular respiration do not proceed correctly? Mitochondrial diseases are genetic disorders of metabolism. Mitochondrial disorders can arise from mutations in nuclear or mitochondrial DNA, and they result in the production of less energy than is normal in body cells. Symptoms of mitochondrial diseases can include muscle weakness, lack of coordination, stroke-like episodes, and loss of vision and hearing. Most affected people are diagnosed in childhood, although there are some adult-onset diseases. Identifying and treating mitochondrial disorders is a specialized medical field. The educational preparation for this profession requires a college education, followed by medical school with a specialization in medical genetics. Medical geneticists can be board certified by the American Board of Medical Genetics and go on to become associated with professional organizations devoted to the study of mitochondrial disease, such as the Mitochondrial Medicine Society and the Society for Inherited Metabolic Disease.

Summary

The citric acid cycle is a series of chemical reactions that removes high-energy electrons and uses them in the electron transport chain to generate ATP. One molecule of ATP (or an equivalent) is produced per each turn of the cycle.

The electron transport chain is the portion of aerobic respiration that uses free oxygen as the final electron acceptor for electrons removed from the intermediate compounds in glucose catabolism. The electrons are passed through a series of chemical reactions, with a small amount of free energy used at three points to transport hydrogen ions across the membrane. This contributes to the gradient used in chemiosmosis. As the electrons are passed from NADH or $FADH_2$ down the electron transport chain, they lose energy. The products of the electron transport chain are water and ATP. A number of intermediate compounds can be diverted into the anabolism of other biochemical molecules, such as nucleic acids, non-essential amino acids, sugars, and lipids. These same molecules, except nucleic acids, can serve as energy sources for the glucose pathway.

Art Connections

Figure 3.3.2: Cyanide inhibits cytochrome c oxidase, a component of the electron transport chain. If cyanide poisoning occurs, would you expect the pH of the intermembrane space to increase or decrease? What affect would cyanide have on ATP synthesis?

Answer

After cyanide poisoning, the electron transport chain can no longer pump electrons into the intermembrane space. The pH of the intermembrane space would increase, and ATP synthesis would stop.

Glossary

acetyl CoA
the combination of an acetyl group derived from pyruvic acid and coenzyme A which is made from pantothenic acid (a B-group vitamin)

ATP synthase
a membrane-embedded protein complex that regenerates ATP from ADP with energy from protons diffusing through it

chemiosmosis
the movement of hydrogen ions down their electrochemical gradient across a membrane through ATP synthase to generate ATP

citric acid cycle
a series of enzyme-catalyzed chemical reactions of central importance in all living cells that harvests the energy in carbon-carbon bonds of sugar molecules to generate ATP; the citric acid cycle is an aerobic metabolic pathway because it requires oxygen in later reactions to proceed

electron transport chain
a series of four large, multi-protein complexes embedded in the inner mitochondrial membrane that accepts electrons from donor compounds and harvests energy from a series of chemical reactions to generate a hydrogen ion gradient across the membrane

oxidative phosphorylation
the production of ATP by the transfer of electrons down the electron transport chain to create a proton gradient that is used by ATP synthase to add phosphate groups to ADP molecules

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3.4: Fermentation

In aerobic respiration, the final electron acceptor is an oxygen molecule, O_2. If aerobic respiration occurs, then ATP will be produced using the energy of the high-energy electrons carried by NADH or $FADH_2$ to the electron transport chain. If aerobic respiration does not occur, NADH must be reoxidized to NAD^+ for reuse as an electron carrier for glycolysis to continue. How is this done? Some living systems use an organic molecule as the final electron acceptor. Processes that use an organic molecule to regenerate NAD^+ from NADH are collectively referred to as fermentation. In contrast, some living systems use an inorganic molecule (other than oxygen) as a final electron acceptor to regenerate NAD^+; both methods are anaerobic (do not require oxygen) to achieve NAD^+ regeneration and enable organisms to convert energy for their use in the absence of oxygen.

Lactic Acid Fermentation

The fermentation method used by animals and some bacteria like those in yogurt is lactic acid fermentation (Figure 3.4.1). This occurs routinely in mammalian red blood cells and in skeletal muscle that has insufficient oxygen supply to allow aerobic respiration to continue (that is, in muscles used to the point of fatigue). In muscles, lactic acid produced by fermentation must be removed by the blood circulation and brought to the liver for further metabolism. The chemical reaction of lactic acid fermentation is the following:

$$\text{Pyruvic acid} + \text{NADH} \leftrightarrow \text{lactic acid} + \text{NAD}^+$$

The enzyme that catalyzes this reaction is lactate dehydrogenase. The reaction can proceed in either direction, but the left-to-right reaction is inhibited by acidic conditions. This lactic acid build-up causes muscle stiffness and fatigue. Once the lactic acid has been removed from the muscle and is circulated to the liver, it can be converted back to pyruvic acid and further catabolized for energy.

ART CONNECTION

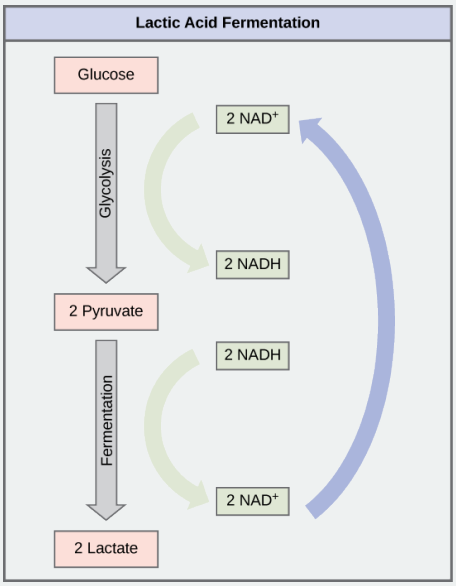


Figure 3.4.1: Lactic acid fermentation is common in muscles that have become exhausted by use.

Tremetol, a metabolic poison found in white snake root plant, prevents the metabolism of lactate. When cows eat this plant, Tremetol is concentrated in the milk. Humans who consume the milk become ill. Symptoms of this disease, which include vomiting, abdominal pain, and tremors, become worse after exercise. Why do you think this is the case?

Alcohol Fermentation

Another familiar fermentation process is alcohol fermentation (Figure 3.4.2), which produces ethanol, an alcohol. The alcohol fermentation reaction is the following:

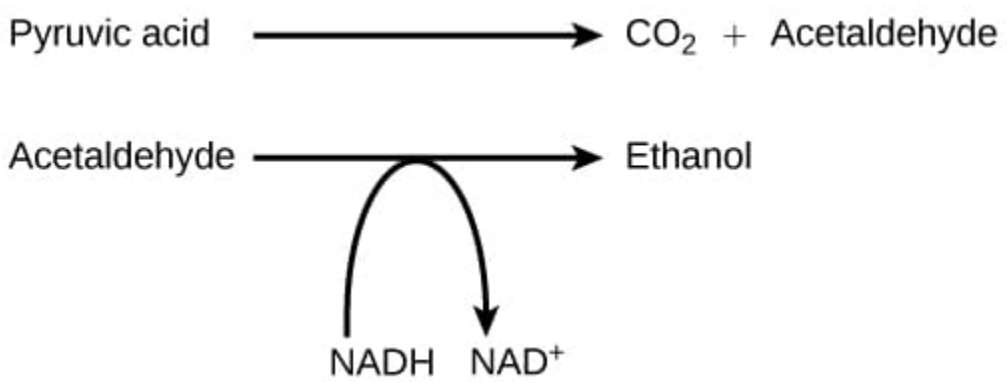


Figure 3.4.2**:** The reaction resulting in alcohol fermentation is shown.

In the first reaction, a carboxyl group is removed from pyruvic acid, releasing carbon dioxide as a gas. The loss of carbon dioxide reduces the molecule by one carbon atom, making acetaldehyde. The second reaction removes an electron from NADH, forming NAD^+ and producing ethanol from the acetaldehyde, which accepts the electron. The fermentation of pyruvic acid by yeast produces the ethanol found in alcoholic beverages (Figure 3.4.3). If the carbon dioxide produced by the reaction is not vented from the fermentation chamber, for example in beer and sparkling wines, it remains dissolved in the medium until the pressure is released. Ethanol above 12 percent is toxic to yeast, so natural levels of alcohol in wine occur at a maximum of 12 percent.



Figure 3.4.3**:** Fermentation of grape juice to make wine produces CO_2 as a byproduct. Fermentation tanks have valves so that pressure inside the tanks can be released.

Anaerobic Cellular Respiration

Certain prokaryotes, including some species of bacteria and Archaea, use anaerobic respiration. For example, the group of Archaea called methanogens reduces carbon dioxide to methane to oxidize NADH. These microorganisms are found in soil and in the digestive tracts of ruminants, such as cows and sheep. Similarly, sulfate-reducing bacteria and Archaea, most of which are anaerobic (Figure 3.4.4), reduce sulfate to hydrogen sulfide to regenerate NAD^+ from NADH.

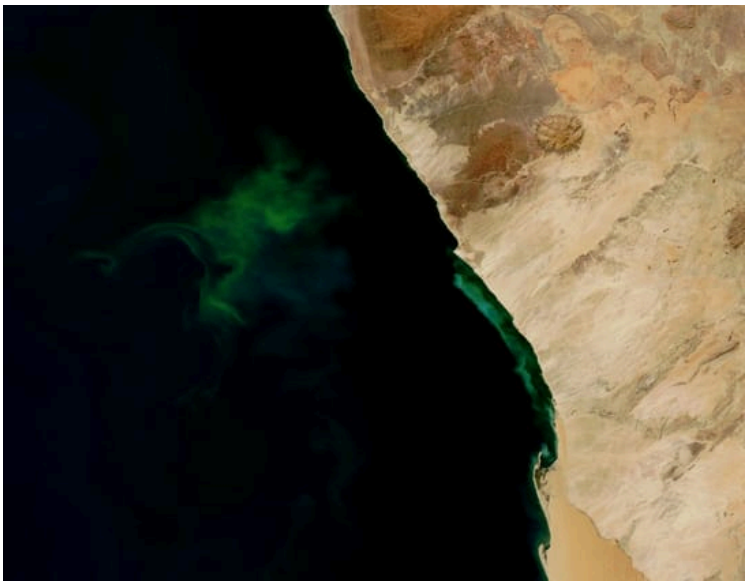


Figure 3.4.4**:** The green color seen in these coastal waters is from an eruption of hydrogen sulfide. Anaerobic, sulfate-reducing bacteria release hydrogen sulfide gas as they decompose algae in the water. (credit: NASA image courtesy Jeff Schmaltz, MODIS Land Rapid Response Team at NASA GSFC)

CONCEPT IN ACTION

This interactive element is not available in this format. Visit the link or scan the QR code to access it online.

View this YouTube Video online

Visit this site to see anaerobic cellular respiration in action.

Other fermentation methods occur in bacteria. Many prokaryotes are facultatively anaerobic. This means that they can switch between aerobic respiration and fermentation, depending on the availability of oxygen. Certain prokaryotes, like *Clostridia* bacteria, are obligate anaerobes. Obligate anaerobes live and grow in the absence of molecular oxygen. Oxygen is a poison to these microorganisms and kills them upon exposure. It should be noted that all forms of fermentation, except lactic acid fermentation, produce gas. The production of particular types of gas is used as an indicator of the fermentation of specific carbohydrates, which plays a role in the laboratory identification of the bacteria. The various methods of fermentation are used by different organisms to ensure an adequate supply of NAD^+ for the sixth step in glycolysis. Without these pathways, that step would not occur, and no ATP would be harvested from the breakdown of glucose.

Section Summary

If NADH cannot be metabolized through aerobic respiration, another electron acceptor is used. Most organisms will use some form of fermentation to accomplish the regeneration of NAD^+, ensuring the continuation of glycolysis. The regeneration of NAD^+ in fermentation is not accompanied by ATP production; therefore, the potential for NADH to produce ATP using an electron transport chain is not utilized.

Art Connections

Figure 3.4.1: Tremetol, a metabolic poison found in white snake root plant, prevents the metabolism of lactate. When cows eat this plant, Tremetol is concentrated in the milk. Humans who consume the milk become ill. Symptoms of this disease, which include

vomiting, abdominal pain, and tremors, become worse after exercise. Why do you think this is the case?

Answer

The illness is caused by lactic acid build-up. Lactic acid levels rise after exercise, making the symptoms worse. Milk sickness is rare today, but was common in the Midwestern United States in the early 1800s.

Glossary

anaerobic cellular respiration
the use of an electron acceptor other than oxygen to complete metabolism using electron transport-based chemiosmosis

fermentation
the steps that follow the partial oxidation of glucose via glycolysis to regenerate NAD^+; occurs in the absence of oxygen and uses an organic compound as the final electron acceptor

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4: CELL DIVISION & GENETICS

4.1: Chromosomes & the Genome
4.2: The Cell Cycle & Mitosis
4.3: Sexual Reproduction
4.4: Meiosis
4.5: Mendelian Genetics
4.6: Patterns of Inheritance

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4.1: Chromosomes & the Genome

The continuity of life from one cell to another has its foundation in the reproduction of cells by way of the cell cycle. The cell cycle is an orderly sequence of events in the life of a cell from the division of a single parent cell to produce two new daughter cells, to the subsequent division of those daughter cells. The mechanisms involved in the cell cycle are highly conserved across eukaryotes. Organisms as diverse as protists, plants, and animals employ similar steps.

Genomic DNA

Before discussing the steps a cell undertakes to replicate, a deeper understanding of the structure and function of a cell's genetic information is necessary. A cell's complete complement of DNA is called its genome. In prokaryotes, the genome is composed of a single, double-stranded DNA molecule in the form of a loop or circle. The region in the cell containing this genetic material is called a nucleoid. Some prokaryotes also have smaller loops of DNA called plasmids that are not essential for normal growth.

In eukaryotes, the genome comprises several double-stranded, linear DNA molecules (Figure 4.1.1) bound with proteins to form complexes called chromosomes. Each species of eukaryote has a characteristic number of chromosomes in the nuclei of its cells. Human body cells (somatic cells) have 46 chromosomes. A somatic cell contains two matched sets of chromosomes, a configuration known as diploid. The letter *n* is used to represent a single set of chromosomes; therefore a diploid organism is designated 2*n*. Human cells that contain one set of 23 chromosomes are called gametes, or sex cells; these eggs and sperm are designated *n*, or haploid.

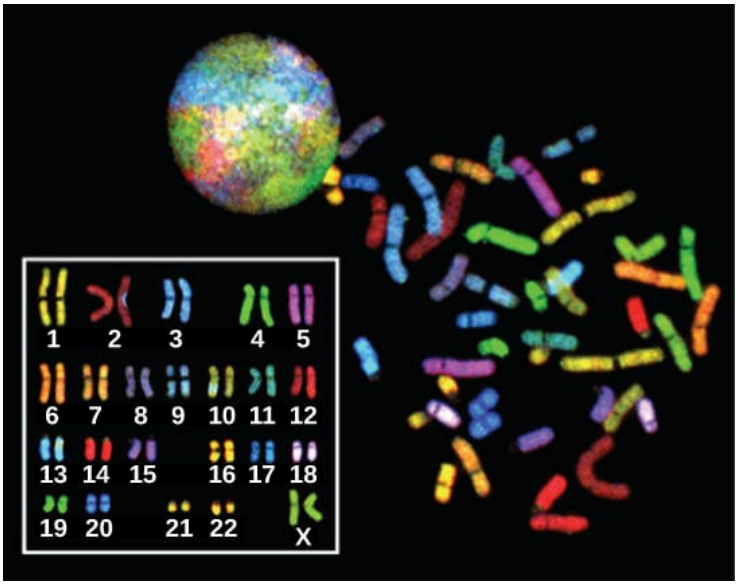


Figure 4.1.1**:** There are 23 pairs of homologous chromosomes in a female human somatic cell. These chromosomes are viewed within the nucleus (top), removed from a cell in mitosis (right), and arranged according to length (left) in an arrangement called a karyotype. In this image, the chromosomes were exposed to fluorescent stains to distinguish them. (credit: "718 Bot"/Wikimedia Commons, National Human Genome Research)

The matched pairs of chromosomes in a diploid organism are called homologous chromosomes. Homologous chromosomes are the same length and have specific nucleotide segments called genes in exactly the same location, or locus. Genes, the functional units of chromosomes, determine specific characteristics by coding for specific proteins. Traits are the different forms of a characteristic. For example, the shape of earlobes is a characteristic with traits of free or attached.

Each copy of the homologous pair of chromosomes originates from a different parent; therefore, the copies of each of the genes themselves may not be identical. The variation of individuals within a species is caused by the specific combination of the genes inherited from both parents. For example, there are three possible gene sequences on the human chromosome that codes for blood type: sequence A, sequence B, and sequence O. Because all diploid human cells have two copies of the chromosome that determines blood type, the blood type (the trait) is determined by which two versions of the marker gene are inherited. It is

possible to have two copies of the same gene sequence, one on each homologous chromosome (for example, AA, BB, or OO), or two different sequences, such as AB.

Minor variations in traits such as those for blood type, eye color, and height contribute to the natural variation found within a species. The sex chromosomes, X and Y, are the single exception to the rule of homologous chromosomes; other than a small amount of homology that is necessary to reliably produce gametes, the genes found on the X and Y chromosomes are not the same.

Summary

Prokaryotes have a single loop chromosome, whereas eukaryotes have multiple, linear chromosomes surrounded by a nuclear membrane. Human somatic cells have 46 chromosomes consisting of two sets of 22 homologous chromosomes and a pair of nonhomologous sex chromosomes. This is the *2n,* or diploid, state. Human gametes have 23 chromosomes or one complete set of chromosomes. This is the *n,* or haploid, state. Genes are segments of DNA that code for a specific protein or RNA molecule. An organism's traits are determined in large part by the genes inherited from each parent, but also by the environment that they experience. Genes are expressed as characteristics of the organism and each characteristic may have different variants called traits that are caused by differences in the DNA sequence for a gene.

Glossary

diploid
: describes a cell, nucleus, or organism containing two sets of chromosomes (*2n*)

gamete
: a haploid reproductive cell or sex cell (sperm or egg)

gene
: the physical and functional unit of heredity; a sequence of DNA that codes for a specific peptide or RNA molecule

genome
: the entire genetic complement (DNA) of an organism

haploid
: describes a cell, nucleus, or organism containing one set of chromosomes (*n*)

homologous chromosomes
: chromosomes of the same length with genes in the same location; diploid organisms have pairs of homologous chromosomes, and the members of each pair come from different parents

locus
: the position of a gene on a chromosome

Contributors and Attributions

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4.2: The Cell Cycle & Mitosis

The cell cycle is an ordered series of events involving cell growth and cell division that produces two new daughter cells. Cells on the path to cell division proceed through a series of precisely timed and carefully regulated stages of growth, DNA replication, and division that produce two genetically identical cells. The cell cycle has two major phases: interphase and the mitotic phase (Figure 4.2.1). During interphase, the cell grows and DNA is replicated. During the mitotic phase, the replicated DNA and cytoplasmic contents are separated and the cell divides.

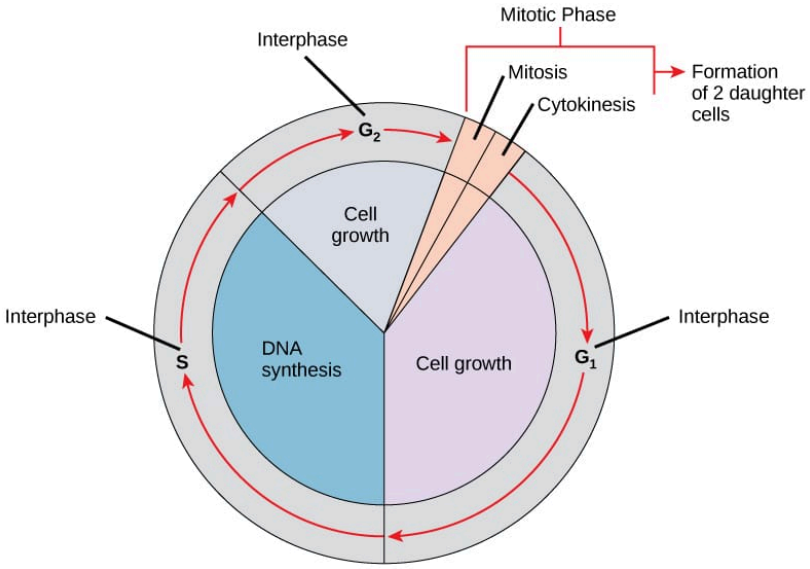


Figure 4.2.1**:** A cell moves through a series of phases in an orderly manner. During interphase, G_1 involves cell growth and protein synthesis, the S phase involves DNA replication and the replication of the centrosome, and G_2 involves further growth and protein synthesis. The mitotic phase follows interphase. Mitosis is nuclear division during which duplicated chromosomes are segregated and distributed into daughter nuclei. Usually the cell will divide after mitosis in a process called cytokinesis in which the cytoplasm is divided and two daughter cells are formed.

Interphase

During interphase, the cell undergoes normal processes while also preparing for cell division. For a cell to move from interphase to the mitotic phase, many internal and external conditions must be met. The three stages of interphase are called G_1, S, and G_2.

G_1 Phase

The first stage of interphase is called the G_1 phase, or first gap, because little change is visible. However, during the G_1 stage, the cell is quite active at the biochemical level. The cell is accumulating the building blocks of chromosomal DNA and the associated proteins, as well as accumulating enough energy reserves to complete the task of replicating each chromosome in the nucleus.

S Phase

Throughout interphase, nuclear DNA remains in a semi-condensed chromatin configuration. In the S phase (synthesis phase), DNA replication results in the formation of two identical copies of each chromosome—sister chromatids—that are firmly attached at the centromere region. At this stage, each chromosome is made of two sister chromatids and is a duplicated chromosome. The centrosome is duplicated during the S phase. The two centrosomes will give rise to the mitotic spindle, the apparatus that orchestrates the movement of chromosomes during mitosis. The centrosome consists of a pair of rod-like centrioles at right angles to each other. Centrioles help organize cell division. Centrioles are not present in the centrosomes of many eukaryotic species, such as plants and most fungi.

G_2 Phase

In the G_2 phase, or second gap, the cell replenishes its energy stores and synthesizes the proteins necessary for chromosome manipulation. Some cell organelles are duplicated, and the cytoskeleton is dismantled to provide resources for the mitotic spindle. There may be additional cell growth during G_2. The final preparations for the mitotic phase must be completed before the cell is able to enter the first stage of mitosis.

The Mitotic Phase

To make two daughter cells, the contents of the nucleus and the cytoplasm must be divided. The mitotic phase is a multistep process during which the duplicated chromosomes are aligned, separated, and moved to opposite poles of the cell, and then the cell is divided into two new identical daughter cells. The first portion of the mitotic phase, mitosis, is composed of five stages, which accomplish nuclear division. The second portion of the mitotic phase, called cytokinesis, is the physical separation of the cytoplasmic components into two daughter cells.

Mitosis

Mitosis is divided into a series of phases—prophase, prometaphase, metaphase, anaphase, and telophase—that result in the division of the cell nucleus (Figure 4.2.2).

ART CONNECTION

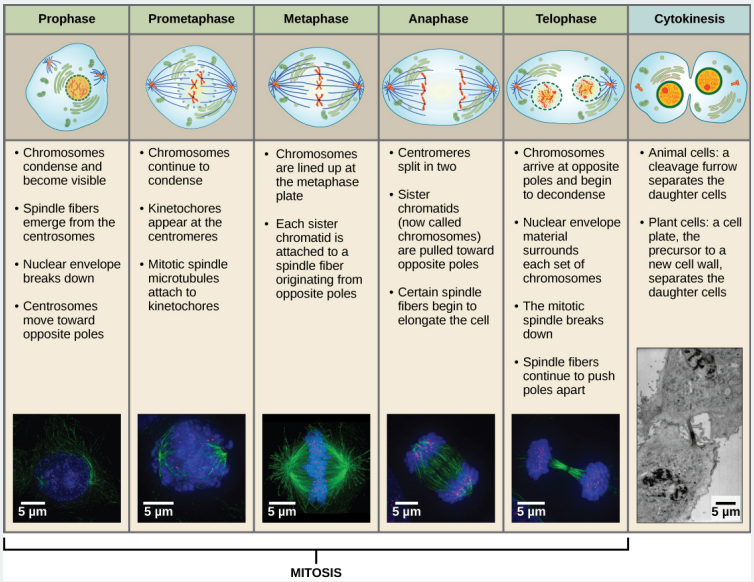


Figure 4.2.2: Animal cell mitosis is divided into five stages—prophase, prometaphase, metaphase, anaphase, and telophase—visualized here by light microscopy with fluorescence. Mitosis is usually accompanied by cytokinesis, shown here by a transmission electron microscope. (credit "diagrams": modification of work by Mariana Ruiz Villareal; credit "mitosis micrographs": modification of work by Roy van Heesbeen; credit "cytokinesis micrograph": modification of work by the Wadsworth Center, NY State Department of Health; donated to the Wikimedia foundation; scale-bar data from Matt Russell)

Which of the following is the correct order of events in mitosis?

A. Sister chromatids line up at the metaphase plate. The kinetochore becomes attached to the mitotic spindle. The nucleus re-forms and the cell divides. The sister chromatids separate.
B. The kinetochore becomes attached to the mitotic spindle. The sister chromatids separate. Sister chromatids line up at the metaphase plate. The nucleus re-forms and the cell divides.
C. The kinetochore becomes attached to metaphase plate. Sister chromatids line up at the metaphase plate. The kinetochore breaks down and the sister chromatids separate. The nucleus re-forms and the cell divides.

D. The kinetochore becomes attached to the mitotic spindle. Sister chromatids line up at the metaphase plate. The kinetochore breaks apart and the sister chromatids separate. The nucleus re-forms and the cell divides.

During prophase, the “first phase,” several events must occur to provide access to the chromosomes in the nucleus. The nuclear envelope starts to break into small vesicles, and the Golgi apparatus and endoplasmic reticulum fragment and disperse to the periphery of the cell. The nucleolus disappears. The centrosomes begin to move to opposite poles of the cell. The microtubules that form the basis of the mitotic spindle extend between the centrosomes, pushing them farther apart as the microtubule fibers lengthen. The sister chromatids begin to coil more tightly and become visible under a light microscope.

During prometaphase, many processes that were begun in prophase continue to advance and culminate in the formation of a connection between the chromosomes and cytoskeleton. The remnants of the nuclear envelope disappear. The mitotic spindle continues to develop as more microtubules assemble and stretch across the length of the former nuclear area. Chromosomes become more condensed and visually discrete. Each sister chromatid attaches to spindle microtubules at the centromere via a protein complex called the kinetochore.

During metaphase, all of the chromosomes are aligned in a plane called the metaphase plate, or the equatorial plane, midway between the two poles of the cell. The sister chromatids are still tightly attached to each other. At this time, the chromosomes are maximally condensed.

During anaphase, the sister chromatids at the equatorial plane are split apart at the centromere. Each chromatid, now called a chromosome, is pulled rapidly toward the centrosome to which its microtubule was attached. The cell becomes visibly elongated as the non-kinetochore microtubules slide against each other at the metaphase plate where they overlap.

During telophase, all of the events that set up the duplicated chromosomes for mitosis during the first three phases are reversed. The chromosomes reach the opposite poles and begin to decondense (unravel). The mitotic spindles are broken down into monomers that will be used to assemble cytoskeleton components for each daughter cell. Nuclear envelopes form around chromosomes.

CONCEPT IN ACTION

This page of movies illustrates different aspects of mitosis. Watch the movie entitled “DIC microscopy of cell division in a newt lung cell” and identify the phases of mitosis.

Cytokinesis

Cytokinesis is the second part of the mitotic phase during which cell division is completed by the physical separation of the cytoplasmic components into two daughter cells. Although the stages of mitosis are similar for most eukaryotes, the process of cytokinesis is quite different for eukaryotes that have cell walls, such as plant cells.

In cells such as animal cells that lack cell walls, cytokinesis begins following the onset of anaphase. A contractile ring composed of actin filaments forms just inside the plasma membrane at the former metaphase plate. The actin filaments pull the equator of the cell inward, forming a fissure. This fissure, or “crack,” is called the cleavage furrow. The furrow deepens as the actin ring contracts, and eventually the membrane and cell are cleaved in two (Figure 4.2.3).

In plant cells, a cleavage furrow is not possible because of the rigid cell walls surrounding the plasma membrane. A new cell wall must form between the daughter cells. During interphase, the Golgi apparatus accumulates enzymes, structural proteins, and glucose molecules prior to breaking up into vesicles and dispersing throughout the dividing cell. During telophase, these Golgi vesicles move on microtubules to collect at the metaphase plate. There, the vesicles fuse from the center toward the cell walls; this structure is called a cell plate. As more vesicles fuse, the cell plate enlarges until it merges with the cell wall at the periphery of the cell. Enzymes use the glucose that has accumulated between the membrane layers to build a new cell wall of cellulose. The Golgi membranes become the plasma membrane on either side of the new cell wall (Figure 4.2.3).

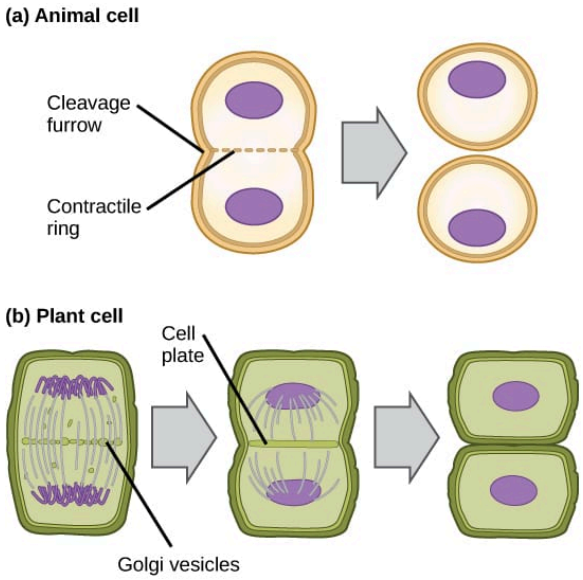


Figure 4.2.3**:** In part (a), a cleavage furrow forms at the former metaphase plate in the animal cell. The plasma membrane is drawn in by a ring of actin fibers contracting just inside the membrane. The cleavage furrow deepens until the cells are pinched in two. In part (b), Golgi vesicles coalesce at the former metaphase plate in a plant cell. The vesicles fuse and form the cell plate. The cell plate grows from the center toward the cell walls. New cell walls are made from the vesicle contents.

G_0 Phase

Not all cells adhere to the classic cell-cycle pattern in which a newly formed daughter cell immediately enters interphase, closely followed by the mitotic phase. Cells in the G_0 phase are not actively preparing to divide. The cell is in a quiescent (inactive) stage, having exited the cell cycle. Some cells enter G_0 temporarily until an external signal triggers the onset of G_1. Other cells that never or rarely divide, such as mature cardiac muscle and nerve cells, remain in G_0 permanently (Figure 4.2.4).

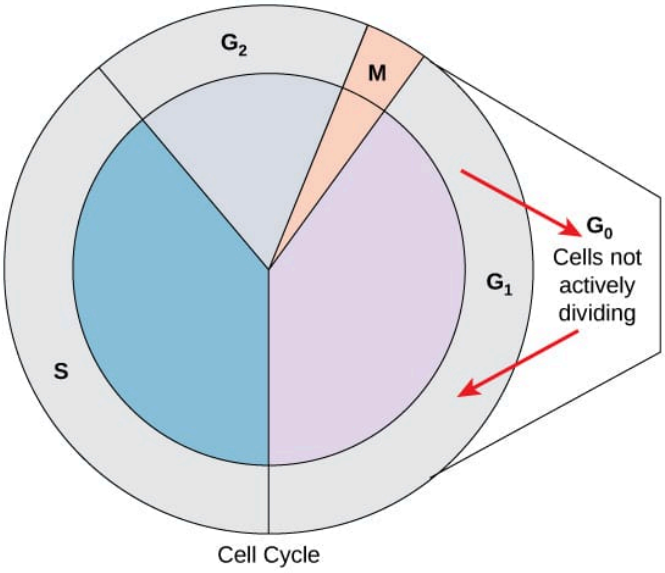


Figure 4.2.4: Cells that are not actively preparing to divide enter an alternate phase called G_0. In some cases, this is a temporary condition until triggered to enter G_1. In other cases, the cell will remain in G_0 permanently.

Control of the Cell Cycle

The length of the cell cycle is highly variable even within the cells of an individual organism. In humans, the frequency of cell turnover ranges from a few hours in early embryonic development to an average of two to five days for epithelial cells, or to an

entire human lifetime spent in G_0 by specialized cells such as cortical neurons or cardiac muscle cells. There is also variation in the time that a cell spends in each phase of the cell cycle. When fast-dividing mammalian cells are grown in culture (outside the body under optimal growing conditions), the length of the cycle is approximately 24 hours. In rapidly dividing human cells with a 24-hour cell cycle, the G_1 phase lasts approximately 11 hours. The timing of events in the cell cycle is controlled by mechanisms that are both internal and external to the cell.

Regulation at Internal Checkpoints

It is essential that daughter cells be exact duplicates of the parent cell. Mistakes in the duplication or distribution of the chromosomes lead to mutations that may be passed forward to every new cell produced from the abnormal cell. To prevent a compromised cell from continuing to divide, there are internal control mechanisms that operate at three main cell cycle checkpoints at which the cell cycle can be stopped until conditions are favorable. These checkpoints occur near the end of G_1, at the G_2–M transition, and during metaphase (Figure 4.2.5).

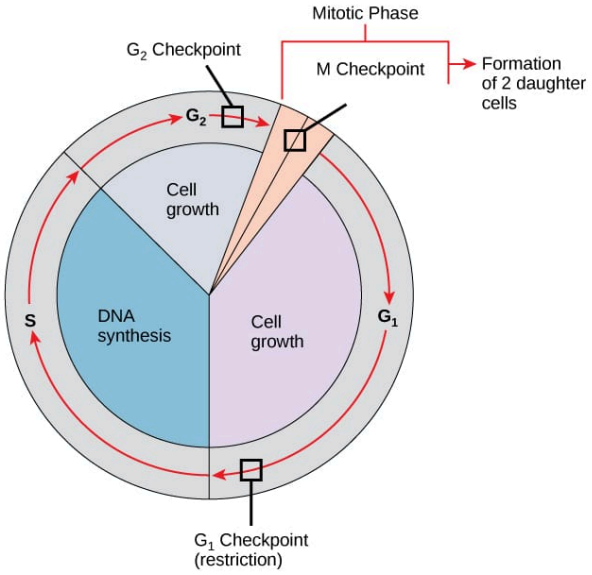


Figure 4.2.5: The cell cycle is controlled at three checkpoints. Integrity of the DNA is assessed at the G_1 checkpoint. Proper chromosome duplication is assessed at the G_2 checkpoint. Attachment of each kinetochore to a spindle fiber is assessed at the M checkpoint.

The G_1 Checkpoint

The G_1 checkpoint determines whether all conditions are favorable for cell division to proceed. The G_1 checkpoint, also called the restriction point, is the point at which the cell irreversibly commits to the cell-division process. In addition to adequate reserves and cell size, there is a check for damage to the genomic DNA at the G_1 checkpoint. A cell that does not meet all the requirements will not be released into the S phase.

The G_2 Checkpoint

The G_2 checkpoint bars the entry to the mitotic phase if certain conditions are not met. As in the G_1 checkpoint, cell size and protein reserves are assessed. However, the most important role of the G_2 checkpoint is to ensure that all of the chromosomes have been replicated and that the replicated DNA is not damaged.

The M Checkpoint

The M checkpoint occurs near the end of the metaphase stage of mitosis. The M checkpoint is also known as the spindle checkpoint because it determines if all the sister chromatids are correctly attached to the spindle microtubules. Because the separation of the sister chromatids during anaphase is an irreversible step, the cycle will not proceed until the kinetochores of each pair of sister chromatids are firmly anchored to spindle fibers arising from opposite poles of the cell.

CONCEPT IN ACTION

Watch what occurs at the G_1, G_2, and M checkpoints by visiting this animation of the cell cycle.

Summary

The cell cycle is an orderly sequence of events. Cells on the path to cell division proceed through a series of precisely timed and carefully regulated stages. In eukaryotes, the cell cycle consists of a long preparatory period, called interphase. Interphase is divided into G_1, S, and G_2 phases. Mitosis consists of five stages: prophase, prometaphase, metaphase, anaphase, and telophase. Mitosis is usually accompanied by cytokinesis, during which the cytoplasmic components of the daughter cells are separated either by an actin ring (animal cells) or by cell plate formation (plant cells).

Each step of the cell cycle is monitored by internal controls called checkpoints. There are three major checkpoints in the cell cycle: one near the end of G_1, a second at the G_2–M transition, and the third during metaphase.

Art Connections

Figure 4.2.2: Which of the following is the correct order of events in mitosis?

A. Sister chromatids line up at the metaphase plate. The kinetochore becomes attached to the mitotic spindle. The nucleus re-forms and the cell divides. The sister chromatids separate.
B. The kinetochore becomes attached to the mitotic spindle. The sister chromatids separate. Sister chromatids line up at the metaphase plate. The nucleus re-forms and the cell divides.
C. The kinetochore becomes attached to metaphase plate. Sister chromatids line up at the metaphase plate. The kinetochore breaks down and the sister chromatids separate. The nucleus re-forms and the cell divides.
D. The kinetochore becomes attached to the mitotic spindle. Sister chromatids line up at the metaphase plate. The kinetochore breaks apart and the sister chromatids separate. The nucleus re-forms and the cell divides.

Answer

D. The kinetochore becomes attached to the mitotic spindle. Sister chromatids line up at the metaphase plate. The kinetochore breaks apart and the sister chromatids separate. The nucleus reforms and the cell divides.

Glossary

anaphase
the stage of mitosis during which sister chromatids are separated from each other

cell cycle
the ordered sequence of events that a cell passes through between one cell division and the next

cell cycle checkpoints
mechanisms that monitor the preparedness of a eukaryotic cell to advance through the various cell cycle stages

cell plate
a structure formed during plant-cell cytokinesis by Golgi vesicles fusing at the metaphase plate; will ultimately lead to formation of a cell wall to separate the two daughter cells

centriole
a paired rod-like structure constructed of microtubules at the center of each animal cell centrosome

cleavage furrow
a constriction formed by the actin ring during animal-cell cytokinesis that leads to cytoplasmic division

cytokinesis
the division of the cytoplasm following mitosis to form two daughter cells

G_0 phase
: a cell-cycle phase distinct from the G_1 phase of interphase; a cell in G_0 is not preparing to divide

G_1 phase
: (also, first gap) a cell-cycle phase; first phase of interphase centered on cell growth during mitosis

G_2 phase
: (also, second gap) a cell-cycle phase; third phase of interphase where the cell undergoes the final preparations for mitosis

interphase
: the period of the cell cycle leading up to mitosis; includes G_1, S, and G_2 phases; the interim between two consecutive cell divisions

kinetochore
: a protein structure in the centromere of each sister chromatid that attracts and binds spindle microtubules during prometaphase

metaphase plate
: the equatorial plane midway between two poles of a cell where the chromosomes align during metaphase

metaphase
: the stage of mitosis during which chromosomes are lined up at the metaphase plate

mitosis
: the period of the cell cycle at which the duplicated chromosomes are separated into identical nuclei; includes prophase, prometaphase, metaphase, anaphase, and telophase

mitotic phase
: the period of the cell cycle when duplicated chromosomes are distributed into two nuclei and the cytoplasmic contents are divided; includes mitosis and cytokinesis

mitotic spindle
: the microtubule apparatus that orchestrates the movement of chromosomes during mitosis

prometaphase
: the stage of mitosis during which mitotic spindle fibers attach to kinetochores

prophase
: the stage of mitosis during which chromosomes condense and the mitotic spindle begins to form

quiescent
: describes a cell that is performing normal cell functions and has not initiated preparations for cell division

S phase
: the second, or synthesis phase, of interphase during which DNA replication occurs

telophase
: the stage of mitosis during which chromosomes arrive at opposite poles, decondense, and are surrounded by new nuclear envelopes

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4.3: Sexual Reproduction

Sexual reproduction was an early evolutionary innovation after the appearance of eukaryotic cells. The fact that most eukaryotes reproduce sexually is evidence of its evolutionary success. In many animals, it is the only mode of reproduction. And yet, scientists recognize some real disadvantages to sexual reproduction. On the surface, offspring that are genetically identical to the parent may appear to be more advantageous. If the parent organism is successfully occupying a habitat, offspring with the same traits would be similarly successful. There is also the obvious benefit to an organism that can produce offspring by asexual budding, fragmentation, or asexual eggs. These methods of reproduction do not require another organism of the opposite sex. There is no need to expend energy finding or attracting a mate. That energy can be spent on producing more offspring. Indeed, some organisms that lead a solitary lifestyle have retained the ability to reproduce asexually. In addition, asexual populations only have female individuals, so every individual is capable of reproduction. In contrast, the males in sexual populations (half the population) are not producing offspring themselves. Because of this, an asexual population can grow twice as fast as a sexual population in theory. This means that in competition, the asexual population would have the advantage. All of these advantages to asexual reproduction, which are also disadvantages to sexual reproduction, should mean that the number of species with asexual reproduction should be more common.

However, multicellular organisms that exclusively depend on asexual reproduction are exceedingly rare. Why is sexual reproduction so common? This is one of the important questions in biology and has been the focus of much research from the latter half of the twentieth century until now. A likely explanation is that the variation that sexual reproduction creates among offspring is very important to the survival and reproduction of those offspring. The only source of variation in asexual organisms is mutation. This is the ultimate source of variation in sexual organisms. In addition, those different mutations are continually reshuffled from one generation to the next when different parents combine their unique genomes, and the genes are mixed into different combinations by the process of meiosis. Meiosis is the division of the contents of the nucleus that divides the chromosomes among gametes. Variation is introduced during meiosis, as well as when the gametes combine in fertilization.

EVOLUTION IN ACTION: The Red Queen Hypothesis

There is no question that sexual reproduction provides evolutionary advantages to organisms that employ this mechanism to produce offspring. The problematic question is why, even in the face of fairly stable conditions, sexual reproduction persists when it is more difficult and produces fewer offspring for individual organisms? Variation is the outcome of sexual reproduction, but why are ongoing variations necessary? Enter the Red Queen hypothesis, first proposed by Leigh Van Valen in 1973.[1] The concept was named in reference to the Red Queen's race in Lewis Carroll's book, *Through the Looking-Glass,* in which the Red Queen says one must run at full speed just to stay where one is.

All species coevolve with other organisms. For example, predators coevolve with their prey, and parasites coevolve with their hosts. A remarkable example of coevolution between predators and their prey is the unique coadaptation of night flying bats and their moth prey. Bats find their prey by emitting high-pitched clicks, but moths have evolved simple ears to hear these clicks so they can avoid the bats. The moths have also adapted behaviors, such as flying away from the bat when they first hear it, or dropping suddenly to the ground when the bat is upon them. Bats have evolved “quiet” clicks in an attempt to evade the moth’s hearing. Some moths have evolved the ability to respond to the bats’ clicks with their own clicks as a strategy to confuse the bats echolocation abilities.

Each tiny advantage gained by favorable variation gives a species an edge over close competitors, predators, parasites, or even prey. The only method that will allow a coevolving species to keep its own share of the resources is also to continually improve its ability to survive and produce offspring. As one species gains an advantage, other species must also develop an advantage or they will be outcompeted. No single species progresses too far ahead because genetic variation among progeny of sexual reproduction provides all species with a mechanism to produce adapted individuals. Species whose individuals cannot keep up become extinct. The Red Queen’s catchphrase was, “It takes all the running you can do to stay in the same place.” This is an apt description of coevolution between competing species.

Life Cycles of Sexually Reproducing Organisms

Fertilization and meiosis alternate in sexual life cycles. What happens between these two events depends on the organism. The

process of meiosis reduces the resulting gamete's chromosome number by half. Fertilization, the joining of two haploid gametes, restores the diploid condition. There are three main categories of life cycles in multicellular organisms: diploid-dominant, in which the multicellular diploid stage is the most obvious life stage (and there is no multicellular haploid stage), as with most animals including humans; haploid-dominant, in which the multicellular haploid stage is the most obvious life stage (and there is no multicellular diploid stage), as with all fungi and some algae; and alternation of generations, in which the two stages, haploid and diploid, are apparent to one degree or another depending on the group, as with plants and some algae.

Nearly all animals employ a diploid-dominant life-cycle strategy in which the only haploid cells produced by the organism are the gametes. The gametes are produced from diploid germ cells, a special cell line that only produces gametes. Once the haploid gametes are formed, they lose the ability to divide again. There is no multicellular haploid life stage. Fertilization occurs with the fusion of two gametes, usually from different individuals, restoring the diploid state (Figure 4.3.1**a**).

ART CONNECTION

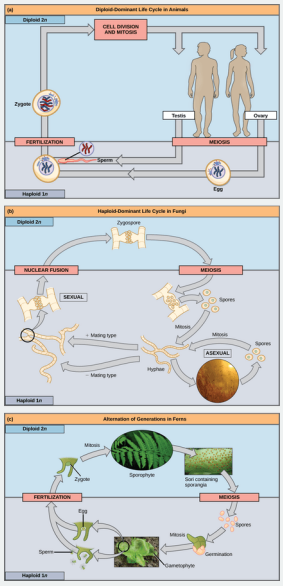


Figure 4.3.1**:** (a) In animals, sexually reproducing adults form haploid gametes from diploid germ cells. (b) Fungi, such as black bread mold (Rhizopus nigricans), have haploid-dominant life cycles. (c) Plants have a life cycle that alternates between a multicellular haploid organism and a multicellular diploid organism. (credit c "fern": modification of work by Cory Zanker; credit c "gametophyte": modification of work by "Vlmastra"/Wikimedia Commons)

If a mutation occurs so that a fungus is no longer able to produce a minus mating type, will it still be able to reproduce?

Most fungi and algae employ a life-cycle strategy in which the multicellular "body" of the organism is haploid. During sexual reproduction, specialized haploid cells from two individuals join to form a diploid zygote. The zygote immediately undergoes meiosis to form four haploid cells called spores (Figure 4.3.1**b**).

The third life-cycle type, employed by some algae and all plants, is called alternation of generations. These species have both haploid and diploid multicellular organisms as part of their life cycle. The haploid multicellular plants are called gametophytes because they produce gametes. Meiosis is not involved in the production of gametes in this case, as the organism that produces gametes is already haploid. Fertilization between the gametes forms a diploid zygote. The zygote will undergo many rounds of mitosis and give rise to a diploid multicellular plant called a sporophyte. Specialized cells of the sporophyte will undergo meiosis and produce haploid spores. The spores will develop into the gametophytes (Figure 4.3.1**c**).

Section Summary

Nearly all eukaryotes undergo sexual reproduction. The variation introduced into the reproductive cells by meiosis appears to be one of the advantages of sexual reproduction that has made it so successful. Meiosis and fertilization alternate in sexual life cycles. The process of meiosis produces genetically unique reproductive cells called gametes, which have half the number of chromosomes as the parent cell. Fertilization, the fusion of haploid gametes from two individuals, restores the diploid condition.

Thus, sexually reproducing organisms alternate between haploid and diploid stages. However, the ways in which reproductive cells are produced and the timing between meiosis and fertilization vary greatly. There are three main categories of life cycles: diploid-dominant, demonstrated by most animals; haploid-dominant, demonstrated by all fungi and some algae; and alternation of generations, demonstrated by plants and some algae.

Art Connections

Figure 4.3.1: If a mutation occurs so that a fungus is no longer able to produce a minus mating type, will it still be able to reproduce?

Answer

Yes, it will be able to reproduce asexually.

Footnotes

1. 1 Leigh Van Valen, "A new evolutionary law," Evolutionary Theory 1 (1973): 1–30.

Glossary

alternation of generations
a life-cycle type in which the diploid and haploid stages alternate

diploid-dominant
a life-cycle type in which the multicellular diploid stage is prevalent

haploid-dominant
a life-cycle type in which the multicellular haploid stage is prevalent

gametophyte
a multicellular haploid life-cycle stage that produces gametes

germ cell
a specialized cell that produces gametes, such as eggs or sperm

life cycle
the sequence of events in the development of an organism and the production of cells that produce offspring

meiosis
a nuclear division process that results in four haploid cells

sporophyte
a multicellular diploid life-cycle stage that produces spores

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4.4: Meiosis

Sexual reproduction requires fertilization, a union of two cells from two individual organisms. If those two cells each contain one set of chromosomes, then the resulting cell contains two sets of chromosomes. The number of sets of chromosomes in a cell is called its ploidy level. Haploid cells contain one set of chromosomes. Cells containing two sets of chromosomes are called diploid. If the reproductive cycle is to continue, the diploid cell must somehow reduce its number of chromosome sets before fertilization can occur again, or there will be a continual doubling in the number of chromosome sets in every generation. So, in addition to fertilization, sexual reproduction includes a nuclear division, known as meiosis, that reduces the number of chromosome sets.

Most animals and plants are diploid, containing two sets of chromosomes; in each somatic cell (the nonreproductive cells of a multicellular organism), the nucleus contains two copies of each chromosome that are referred to as homologous chromosomes. Somatic cells are sometimes referred to as “body” cells. Homologous chromosomes are matched pairs containing genes for the same traits in identical locations along their length. Diploid organisms inherit one copy of each homologous chromosome from each parent; all together, they are considered a full set of chromosomes. In animals, haploid cells containing a single copy of each homologous chromosome are found only within gametes. Gametes fuse with another haploid gamete to produce a diploid cell.

The nuclear division that forms haploid cells, which is called meiosis, is related to mitosis. As you have learned, mitosis is part of a cell reproduction cycle that results in identical daughter nuclei that are also genetically identical to the original parent nucleus. In mitosis, both the parent and the daughter nuclei contain the same number of chromosome sets—diploid for most plants and animals. Meiosis employs many of the same mechanisms as mitosis. However, the starting nucleus is always diploid and the nuclei that result at the end of a meiotic cell division are haploid. To achieve the reduction in chromosome number, meiosis consists of one round of chromosome duplication and two rounds of nuclear division. Because the events that occur during each of the division stages are analogous to the events of mitosis, the same stage names are assigned. However, because there are two rounds of division, the stages are designated with a “I” or “II.” Thus, meiosis I is the first round of meiotic division and consists of prophase I, prometaphase I, and so on. Meiosis I reduces the number of chromosome sets from two to one. The genetic information is also mixed during this division to create unique recombinant chromosomes. Meiosis II, in which the second round of meiotic division takes place in a way that is similar to mitosis, includes prophase II, prometaphase II, and so on.

Interphase

Meiosis is preceded by an interphase consisting of the G_1, S, and G_2 phases, which are nearly identical to the phases preceding mitosis. The G_1 phase is the first phase of interphase and is focused on cell growth. In the S phase, the DNA of the chromosomes is replicated. Finally, in the G_2 phase, the cell undergoes the final preparations for meiosis.

During DNA duplication of the S phase, each chromosome becomes composed of two identical copies (called sister chromatids) that are held together at the centromere until they are pulled apart during meiosis II. In an animal cell, the centrosomes that organize the microtubules of the meiotic spindle also replicate. This prepares the cell for the first meiotic phase.

Meiosis I

Early in prophase I, the chromosomes can be seen clearly microscopically. As the nuclear envelope begins to break down, the proteins associated with homologous chromosomes bring the pair close to each other. The tight pairing of the homologous chromosomes is called synapsis. In synapsis, the genes on the chromatids of the homologous chromosomes are precisely aligned with each other. An exchange of chromosome segments between non-sister homologous chromatids occurs and is called crossing over. This process is revealed visually after the exchange as chiasmata (singular = *chiasma*) (Figure $4.4.1$).

As prophase I progresses, the close association between homologous chromosomes begins to break down, and the chromosomes continue to condense, although the homologous chromosomes remain attached to each other at chiasmata. The number of chiasmata varies with the species and the length of the chromosome. At the end of prophase I, the pairs are held together only at chiasmata (Figure $4.4.1$) and are called tetrads because the four sister chromatids of each pair of homologous chromosomes are now visible.

The crossover events are the first source of genetic variation produced by meiosis. A single crossover event between homologous

non-sister chromatids leads to a reciprocal exchange of equivalent DNA between a maternal chromosome and a paternal chromosome. Now, when that sister chromatid is moved into a gamete, it will carry some DNA from one parent of the individual and some DNA from the other parent. The recombinant sister chromatid has a combination of maternal and paternal genes that did not exist before the crossover.

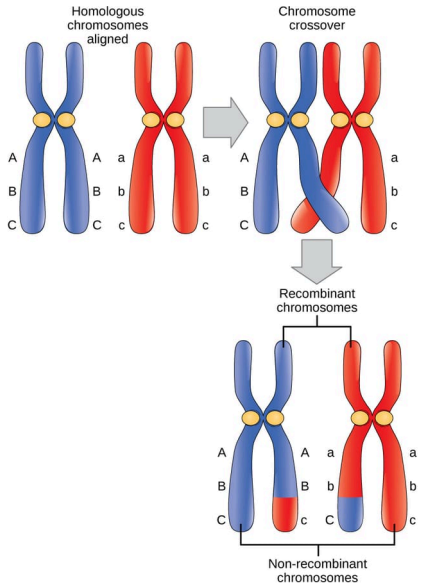


Figure 4.4.1**:** In this illustration of the effects of crossing over, the blue chromosome came from the individual's father and the red chromosome came from the individual's mother. Crossover occurs between non-sister chromatids of homologous chromosomes. The result is an exchange of genetic material between homologous chromosomes. The chromosomes that have a mixture of maternal and paternal sequence are called recombinant and the chromosomes that are completely paternal or maternal are called non-recombinant.

The key event in prometaphase I is the attachment of the spindle fiber microtubules to the kinetochore proteins at the centromeres. The microtubules assembled from centrosomes at opposite poles of the cell grow toward the middle of the cell. At the end of prometaphase I, each tetrad is attached to microtubules from both poles, with one homologous chromosome attached at one pole and the other homologous chromosome attached to the other pole. The homologous chromosomes are still held together at chiasmata. In addition, the nuclear membrane has broken down entirely.

During metaphase I, the homologous chromosomes are arranged in the center of the cell with the kinetochores facing opposite poles. The orientation of each pair of homologous chromosomes at the center of the cell is random.

This randomness, called independent assortment, is the physical basis for the generation of the second form of genetic variation in offspring. Consider that the homologous chromosomes of a sexually reproducing organism are originally inherited as two separate sets, one from each parent. Using humans as an example, one set of 23 chromosomes is present in the egg donated by the mother. The father provides the other set of 23 chromosomes in the sperm that fertilizes the egg. In metaphase I, these pairs line up at the midway point between the two poles of the cell. Because there is an equal chance that a microtubule fiber will encounter a maternally or paternally inherited chromosome, the arrangement of the tetrads at the metaphase plate is random. Any maternally inherited chromosome may face either pole. Any paternally inherited chromosome may also face either pole. The orientation of each tetrad is independent of the orientation of the other 22 tetrads.

In each cell that undergoes meiosis, the arrangement of the tetrads is different. The number of variations depends on the number of chromosomes making up a set. There are two possibilities for orientation (for each tetrad); thus, the possible number of alignments equals 2^n where n is the number of chromosomes per set. Humans have 23 chromosome pairs, which results in over eight million (2^{23}) possibilities. This number does not include the variability previously created in the sister chromatids by crossover. Given these two mechanisms, it is highly unlikely that any two haploid cells resulting from meiosis will have the same genetic composition (Figure 4.4.2).

To summarize the genetic consequences of meiosis I: the maternal and paternal genes are recombined by crossover events occurring on each homologous pair during prophase I; in addition, the random assortment of tetrads at metaphase produces a unique combination of maternal and paternal chromosomes that will make their way into the gametes.

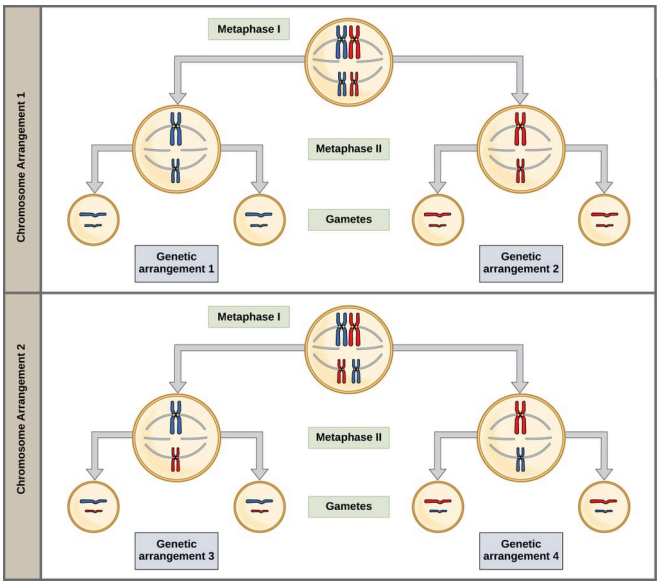


Figure 4.4.2**:** To demonstrate random, independent assortment at metaphase I, consider a cell with n = 2. In this case, there are two possible arrangements at the equatorial plane in metaphase I, as shown in the upper cell of each panel. These two possible orientations lead to the production of genetically different gametes. With more chromosomes, the number of possible arrangements increases dramatically.

In anaphase I, the spindle fibers pull the linked chromosomes apart. The sister chromatids remain tightly bound together at the centromere. It is the chiasma connections that are broken in anaphase I as the fibers attached to the fused kinetochores pull the homologous chromosomes apart (Figure 4.4.3).

In telophase I, the separated chromosomes arrive at opposite poles. The remainder of the typical telophase events may or may not occur depending on the species. In some organisms, the chromosomes decondense and nuclear envelopes form around the chromatids in telophase I.

Cytokinesis, the physical separation of the cytoplasmic components into two daughter cells, occurs without reformation of the nuclei in other organisms. In nearly all species, cytokinesis separates the cell contents by either a cleavage furrow (in animals and some fungi), or a cell plate that will ultimately lead to formation of cell walls that separate the two daughter cells (in plants). At each pole, there is just one member of each pair of the homologous chromosomes, so only one full set of the chromosomes is present. This is why the cells are considered haploid—there is only one chromosome set, even though there are duplicate copies of the set because each homolog still consists of two sister chromatids that are still attached to each other. However, although the sister chromatids were once duplicates of the same chromosome, they are no longer identical at this stage because of crossovers.

CONCEPT IN ACTION



Review the process of meiosis, observing how chromosomes align and migrate, at this site.

Meiosis II

In meiosis II, the connected sister chromatids remaining in the haploid cells from meiosis I will be split to form four haploid cells. In some species, cells enter a brief interphase, or interkinesis, that lacks an S phase, before entering meiosis II. Chromosomes are not duplicated during interkinesis. The two cells produced in meiosis I go through the events of meiosis II in synchrony. Overall, meiosis II resembles the mitotic division of a haploid cell.

In prophase II, if the chromosomes decondensed in telophase I, they condense again. If nuclear envelopes were formed, they fragment into vesicles. The centrosomes duplicated during interkinesis move away from each other toward opposite poles, and new spindles are formed. In prometaphase II, the nuclear envelopes are completely broken down, and the spindle is fully formed. Each sister chromatid forms an individual kinetochore that attaches to microtubules from opposite poles. In metaphase II, the sister chromatids are maximally condensed and aligned at the center of the cell. In anaphase II, the sister chromatids are pulled apart by the spindle fibers and move toward opposite poles.

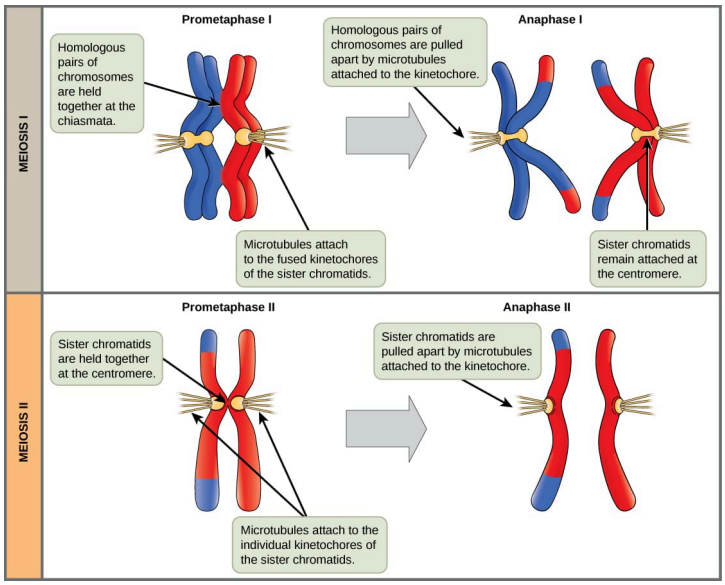


Figure 4.4.3**:** In prometaphase I, microtubules attach to the fused kinetochores of homologous chromosomes. In anaphase I, the homologous chromosomes are separated. In prometaphase II, microtubules attach to individual kinetochores of sister chromatids. In anaphase II, the sister chromatids are separated.

In telophase II, the chromosomes arrive at opposite poles and begin to decondense. Nuclear envelopes form around the chromosomes. Cytokinesis separates the two cells into four genetically unique haploid cells. At this point, the nuclei in the newly produced cells are both haploid and have only one copy of the single set of chromosomes. The cells produced are genetically unique because of the random assortment of paternal and maternal homologs and because of the recombination of maternal and paternal segments of chromosomes—with their sets of genes—that occurs during crossover.

Comparing Meiosis and Mitosis

Mitosis and meiosis, which are both forms of division of the nucleus in eukaryotic cells, share some similarities, but also exhibit distinct differences that lead to their very different outcomes. Mitosis is a single nuclear division that results in two nuclei, usually partitioned into two new cells. The nuclei resulting from a mitotic division are genetically identical to the original. They have the same number of sets of chromosomes: one in the case of haploid cells, and two in the case of diploid cells. On the other hand, meiosis is two nuclear divisions that result in four nuclei, usually partitioned into four new cells. The nuclei resulting from meiosis are never genetically identical, and they contain one chromosome set only—this is half the number of the original cell, which was diploid (Figure 4.4.4).

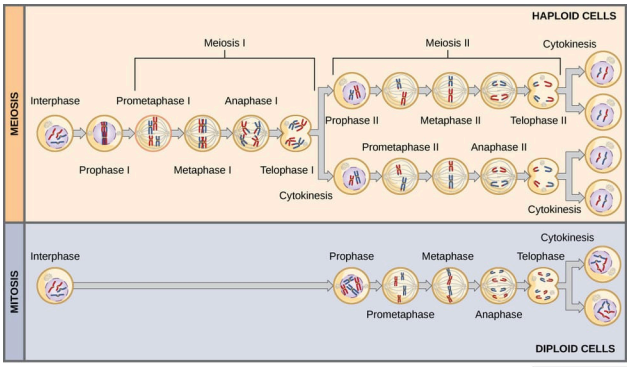
The differences in the outcomes of meiosis and mitosis occur because of differences in the behavior of the chromosomes during each process. Most of these differences in the processes occur in meiosis I, which is a very different nuclear division than mitosis. In meiosis I, the homologous chromosome pairs become associated with each other, are bound together, experience chiasmata and crossover between sister chromatids, and line up along the metaphase plate in tetrads with spindle fibers from opposite spindle poles attached to each kinetochore of a homolog in a tetrad. All of these events occur only in meiosis I, never in mitosis.

Homologous chromosomes move to opposite poles during meiosis I so the number of sets of chromosomes in each nucleus-to-be is reduced from two to one. For this reason, meiosis I is referred to as a reduction division. There is no such reduction in ploidy level in mitosis.

Meiosis II is much more analogous to a mitotic division. In this case, duplicated chromosomes (only one set of them) line up at the center of the cell with divided kinetochores attached to spindle fibers from opposite poles. During anaphase II, as in mitotic anaphase, the kinetochores divide and one sister chromatid is pulled to one pole and the other sister chromatid is pulled to the other pole. If it were not for the fact that there had been crossovers, the two products of each meiosis II division would be identical as in mitosis; instead, they are different because there has always been at least one crossover per chromosome. Meiosis II is not a reduction division because, although there are fewer copies of the genome in the resulting cells, there is still one set of chromosomes, as there was at the end of meiosis I.

Cells produced by mitosis will function in different parts of the body as a part of growth or replacing dead or damaged cells. They

may even be involved in asexual reproduction in some organisms. Cells produced by meiosis in a diploid-dominant organism such as an animal will only participate in sexual reproduction.



						OUTCOME
PROCESS	DNA synthesis	Synapsis of homologous chromosomes	Crossover	Homologous chromosomes line up at metaphase plate	Sister chromatids line up at metaphase plate	Number and genetic composition of daughter cells
MEIOSIS	Occurs in S phase of interphase	During prophase I	During prophase I	During metaphase I	During metaphase II	Four haploid cells at the end of meiosis II
MITOSIS	Occurs in S phase of interphase	Does not occur in mitosis	Does not occur in mitosis	Does not occur in mitosis	During metaphase	Two diploid cells at the end of mitosis

Figure 4.4.4**:** Meiosis and mitosis are both preceded by one round of DNA replication; however, meiosis includes two nuclear divisions. The four daughter cells resulting from meiosis are haploid and genetically distinct. The daughter cells resulting from mitosis are diploid and identical to the parent cell.

CONCEPT IN ACTION

For an animation comparing mitosis and meiosis, go to this website.

Section Summary

Sexual reproduction requires that diploid organisms produce haploid cells that can fuse during fertilization to form diploid offspring. The process that results in haploid cells is called meiosis. Meiosis is a series of events that arrange and separate chromosomes into daughter cells. During the interphase of meiosis, each chromosome is duplicated. In meiosis, there are two rounds of nuclear division resulting in four nuclei and usually four haploid daughter cells, each with half the number of

chromosomes as the parent cell. During meiosis, variation in the daughter nuclei is introduced because of crossover in prophase I and random alignment at metaphase I. The cells that are produced by meiosis are genetically unique.

Meiosis and mitosis share similarities, but have distinct outcomes. Mitotic divisions are single nuclear divisions that produce daughter nuclei that are genetically identical and have the same number of chromosome sets as the original cell. Meiotic divisions are two nuclear divisions that produce four daughter nuclei that are genetically different and have one chromosome set rather than the two sets the parent cell had. The main differences between the processes occur in the first division of meiosis. The homologous chromosomes separate into different nuclei during meiosis I causing a reduction of ploidy level. The second division of meiosis is much more similar to a mitotic division.

Glossary

chiasmata
: (singular = *chiasma*) the structure that forms at the crossover points after genetic material is exchanged

crossing over
: (also, recombination) the exchange of genetic material between homologous chromosomes resulting in chromosomes that incorporate genes from both parents of the organism forming reproductive cells

fertilization
: the union of two haploid cells typically from two individual organisms

interkinesis
: a period of rest that may occur between meiosis I and meiosis II; there is no replication of DNA during interkinesis

meiosis I
: the first round of meiotic cell division; referred to as reduction division because the resulting cells are haploid

meiosis II
: the second round of meiotic cell division following meiosis I; sister chromatids are separated from each other, and the result is four unique haploid cells

recombinant
: describing something composed of genetic material from two sources, such as a chromosome with both maternal and paternal segments of DNA

reduction division
: a nuclear division that produces daughter nuclei each having one-half as many chromosome sets as the parental nucleus; meiosis I is a reduction division

somatic cell
: all the cells of a multicellular organism except the gamete-forming cells

synapsis
: the formation of a close association between homologous chromosomes during prophase I

tetrad
: two duplicated homologous chromosomes (four chromatids) bound together by chiasmata during prophase I

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4.5: Mendelian Genetics

Johann Gregor Mendel (1822–1884) (Figure 4.5.1) was a lifelong learner, teacher, scientist, and man of faith. As a young adult, he joined the Augustinian Abbey of St. Thomas in Brno in what is now the Czech Republic. Supported by the monastery, he taught physics, botany, and natural science courses at the secondary and university levels. In 1856, he began a decade-long research pursuit involving inheritance patterns in honeybees and plants, ultimately settling on pea plants as his primary model system (a system with convenient characteristics that is used to study a specific biological phenomenon to gain understanding to be applied to other systems). In 1865, Mendel presented the results of his experiments with nearly 30,000 pea plants to the local natural history society. He demonstrated that traits are transmitted faithfully from parents to offspring in specific patterns. In 1866, he published his work, *Experiments in Plant Hybridization,*[1] in the proceedings of the Natural History Society of Brünn.



Figure 4.5.1: Johann Gregor Mendel set the framework for the study of genetics.

Mendel's work went virtually unnoticed by the scientific community, which incorrectly believed that the process of inheritance involved a blending of parental traits that produced an intermediate physical appearance in offspring. This hypothetical process appeared to be correct because of what we know now as continuous variation. Continuous variation is the range of small differences we see among individuals in a characteristic like human height. It does appear that offspring are a "blend" of their parents' traits when we look at characteristics that exhibit continuous variation. Mendel worked instead with traits that show discontinuous variation. Discontinuous variation is the variation seen among individuals when each individual shows one of two—or a very few—easily distinguishable traits, such as violet or white flowers. Mendel's choice of these kinds of traits allowed him to see experimentally that the traits were not blended in the offspring as would have been expected at the time, but that they were inherited as distinct traits. In 1868, Mendel became abbot of the monastery and exchanged his scientific pursuits for his pastoral duties. He was not recognized for his extraordinary scientific contributions during his lifetime; in fact, it was not until 1900 that his work was rediscovered, reproduced, and revitalized by scientists on the brink of discovering the chromosomal basis of heredity.

Mendel's Crosses

Mendel's seminal work was accomplished using the garden pea, *Pisum sativum*, to study inheritance. This species naturally self-fertilizes, meaning that pollen encounters ova within the same flower. The flower petals remain sealed tightly until pollination is completed to prevent the pollination of other plants. The result is highly inbred, or "true-breeding," pea plants. These are plants that always produce offspring that look like the parent. By experimenting with true-breeding pea plants, Mendel avoided the appearance of unexpected traits in offspring that might occur if the plants were not true breeding. The garden pea also grows to maturity within one season, meaning that several generations could be evaluated over a relatively short time. Finally, large quantities of garden peas could be cultivated simultaneously, allowing Mendel to conclude that his results did not come about

simply by chance.

Mendel performed hybridizations, which involve mating two true-breeding individuals that have different traits. In the pea, which is naturally self-pollinating, this is done by manually transferring pollen from the anther of a mature pea plant of one variety to the stigma of a separate mature pea plant of the second variety.

Plants used in first-generation crosses were called P, or parental generation, plants (Figure 4.5.2). Mendel collected the seeds produced by the P plants that resulted from each cross and grew them the following season. These offspring were called the F_1, or the first filial (filial = daughter or son), generation. Once Mendel examined the characteristics in the F_1 generation of plants, he allowed them to self-fertilize naturally. He then collected and grew the seeds from the F_1 plants to produce the F_2, or second filial, generation. Mendel's experiments extended beyond the F_2 generation to the F_3 generation, F_4 generation, and so on, but it was the ratio of characteristics in the P, F_1, and F_2 generations that were the most intriguing and became the basis of Mendel's postulates.

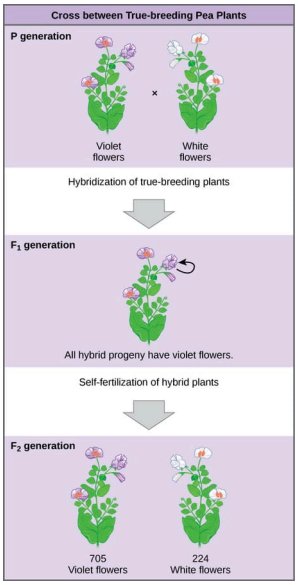


Figure 4.5.2: Mendel's process for performing crosses included examining flower color.

Garden Pea Characteristics Revealed the Basics of Heredity

In his 1865 publication, Mendel reported the results of his crosses involving seven different characteristics, each with two contrasting traits. A trait is defined as a variation in the physical appearance of a heritable characteristic. The characteristics included plant height, seed texture, seed color, flower color, pea-pod size, pea-pod color, and flower position. For the characteristic of flower color, for example, the two contrasting traits were white versus violet. To fully examine each characteristic, Mendel generated large numbers of F_1 and F_2 plants and reported results from thousands of F_2 plants.

What results did Mendel find in his crosses for flower color? First, Mendel confirmed that he was using plants that bred true for white or violet flower color. Irrespective of the number of generations that Mendel examined, all self-crossed offspring of parents with white flowers had white flowers, and all self-crossed offspring of parents with violet flowers had violet flowers. In addition, Mendel confirmed that, other than flower color, the pea plants were physically identical. This was an important check to make sure that the two varieties of pea plants only differed with respect to one trait, flower color.

Once these validations were complete, Mendel applied the pollen from a plant with violet flowers to the stigma of a plant with white flowers. After gathering and sowing the seeds that resulted from this cross, Mendel found that 100 percent of the F_1 hybrid generation had violet flowers. Conventional wisdom at that time would have predicted the hybrid flowers to be pale violet or for hybrid plants to have equal numbers of white and violet flowers. In other words, the contrasting parental traits were expected to blend in the offspring. Instead, Mendel's results demonstrated that the white flower trait had completely disappeared in the F_1 generation.

Importantly, Mendel did not stop his experimentation there. He allowed the F_1 plants to self-fertilize and found that 705 plants

in the F_2 generation had violet flowers and 224 had white flowers. This was a ratio of 3.15 violet flowers to one white flower, or approximately 3:1. When Mendel transferred pollen from a plant with violet flowers to the stigma of a plant with white flowers and vice versa, he obtained approximately the same ratio irrespective of which parent—male or female—contributed which trait. This is called a reciprocal cross—a paired cross in which the respective traits of the male and female in one cross become the respective traits of the female and male in the other cross. For the other six characteristics that Mendel examined, the F_1 and F_2 generations behaved in the same way that they behaved for flower color. One of the two traits would disappear completely from the F_1 generation, only to reappear in the F_2 generation at a ratio of roughly 3:1 (Figure 4.5.3).

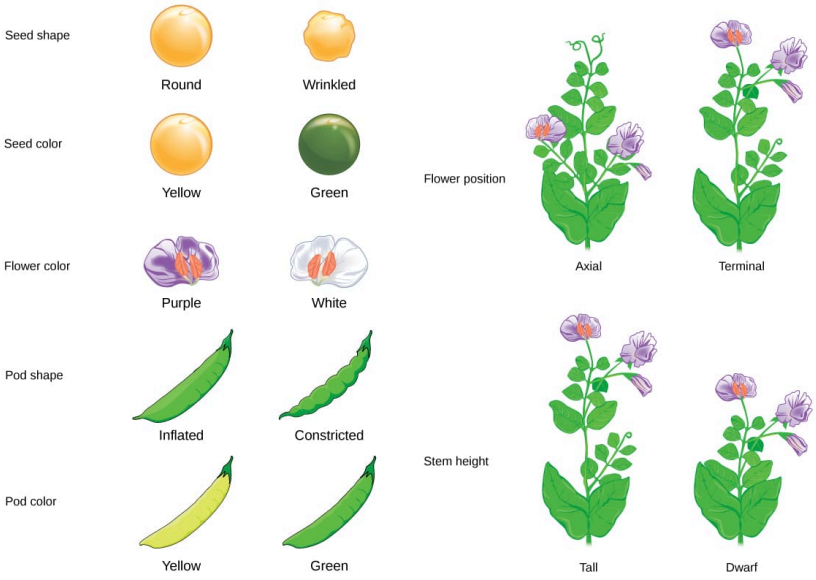


Figure 4.5.3: Mendel identified seven pea plant characteristics.

Upon compiling his results for many thousands of plants, Mendel concluded that the characteristics could be divided into expressed and latent traits. He called these dominant and recessive traits, respectively. Dominanttraits are those that are inherited unchanged in a hybridization. Recessive traits become latent, or disappear in the offspring of a hybridization. The recessive trait does, however, reappear in the progeny of the hybrid offspring. An example of a dominant trait is the violet-colored flower trait. For this same characteristic (flower color), white-colored flowers are a recessive trait. The fact that the recessive trait reappeared in the F_2 generation meant that the traits remained separate (and were not blended) in the plants of the F_1 generation. Mendel proposed that this was because the plants possessed two copies of the trait for the flower-color characteristic, and that each parent transmitted one of their two copies to their offspring, where they came together. Moreover, the physical observation of a dominant trait could mean that the genetic composition of the organism included two dominant versions of the characteristic, or that it included one dominant and one recessive version. Conversely, the observation of a recessive trait meant that the organism lacked any dominant versions of this characteristic.

Section Summary

Working with garden pea plants, Mendel found that crosses between parents that differed for one trait produced F_1 offspring that all expressed one parent's traits. The traits that were visible in the F_1 generation are referred to as dominant, and traits that disappear in the F_1 generation are described as recessive. When the F_1 plants in Mendel's experiment were self-crossed, the F_2 offspring exhibited the dominant trait or the recessive trait in a 3:1 ratio, confirming that the recessive trait had been transmitted faithfully from the original P parent. Reciprocal crosses generated identical F_1 and F_2 offspring ratios. By examining sample sizes, Mendel showed that traits were inherited as independent events.

Footnotes

1. 1 Johann Gregor Mendel, "Versuche über Pflanzenhybriden." *Verhandlungen des naturforschenden Vereines in Brünn*, Bd. IV für das Jahr, 1865 Abhandlungen (1866):3–47. [for English translation, see www.mendelweb.org/Mendel.plain.html]

Glossary

continuous variation
: a variation in a characteristic in which individuals show a range of traits with small differences between them

discontinuous variation
: a variation in a characteristic in which individuals show two, or a few, traits with large differences between them

dominant
: describes a trait that masks the expression of another trait when both versions of the gene are present in an individual

F_1
: the first filial generation in a cross; the offspring of the parental generation

F_2
: the second filial generation produced when F_1 individuals are self-crossed or fertilized with each other

hybridization
: the process of mating two individuals that differ, with the goal of achieving a certain characteristic in their offspring

model system
: a species or biological system used to study a specific biological phenomenon to gain understanding that will be applied to other species

P
: the parental generation in a cross

recessive
: describes a trait whose expression is masked by another trait when the alleles for both traits are present in an individual

reciprocal cross
: a paired cross in which the respective traits of the male and female in one cross become the respective traits of the female and male in the other cross

trait
: a variation in an inherited characteristic

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4.6: Patterns of Inheritance

The seven characteristics that Mendel evaluated in his pea plants were each expressed as one of two versions, or traits. Mendel deduced from his results that each individual had two discrete copies of the characteristic that are passed individually to offspring. We now call those two copies genes, which are carried on chromosomes. The reason we have two copies of each gene is that we inherit one from each parent. In fact, it is the chromosomes we inherit and the two copies of each gene are located on paired chromosomes. Recall that in meiosis these chromosomes are separated out into haploid gametes. This separation, or segregation, of the homologous chromosomes means also that only one of the copies of the gene gets moved into a gamete. The offspring are formed when that gamete unites with one from another parent and the two copies of each gene (and chromosome) are restored.

For cases in which a single gene controls a single characteristic, a diploid organism has two genetic copies that may or may not encode the same version of that characteristic. For example, one individual may carry a gene that determines white flower color and a gene that determines violet flower color. Gene variants that arise by mutation and exist at the same relative locations on homologous chromosomes are called alleles. Mendel examined the inheritance of genes with just two allele forms, but it is common to encounter more than two alleles for any given gene in a natural population.

Phenotypes and Genotypes

Two alleles for a given gene in a diploid organism are expressed and interact to produce physical characteristics. The observable traits expressed by an organism are referred to as its phenotype. An organism's underlying genetic makeup, consisting of both the physically visible and the non-expressed alleles, is called its genotype. Mendel's hybridization experiments demonstrate the difference between phenotype and genotype. For example, the phenotypes that Mendel observed in his crosses between pea plants with differing traits are connected to the diploid genotypes of the plants in the P, F_1, and F_2 generations. We will use a second trait that Mendel investigated, seed color, as an example. Seed color is governed by a single gene with two alleles. The yellow-seed allele is dominant and the green-seed allele is recessive. When true-breeding plants were cross-fertilized, in which one parent had yellow seeds and one had green seeds, all of the F_1hybrid offspring had yellow seeds. That is, the hybrid offspring were phenotypically identical to the true-breeding parent with yellow seeds. However, we know that the allele donated by the parent with green seeds was not simply lost because it reappeared in some of the F_2 offspring (Figure $4.6.1$). Therefore, the F_1 plants must have been genotypically different from the parent with yellow seeds.

The P plants that Mendel used in his experiments were each homozygous for the trait he was studying. Diploid organisms that are homozygous for a gene have two identical alleles, one on each of their homologous chromosomes. The genotype is often written as *YY* or *yy*, for which each letter represents one of the two alleles in the genotype. The dominant allele is capitalized and the recessive allele is lower case. The letter used for the gene (seed color in this case) is usually related to the dominant trait (yellow allele, in this case, or "*Y*"). Mendel's parental pea plants always bred true because both produced gametes carried the same allele. When P plants with contrasting traits were cross-fertilized, all of the offspring were heterozygous for the contrasting trait, meaning their genotype had different alleles for the gene being examined. For example, the F_1 yellow plants that received a *Y* allele from their yellow parent and a *y* allele from their green parent had the genotype *Yy*.

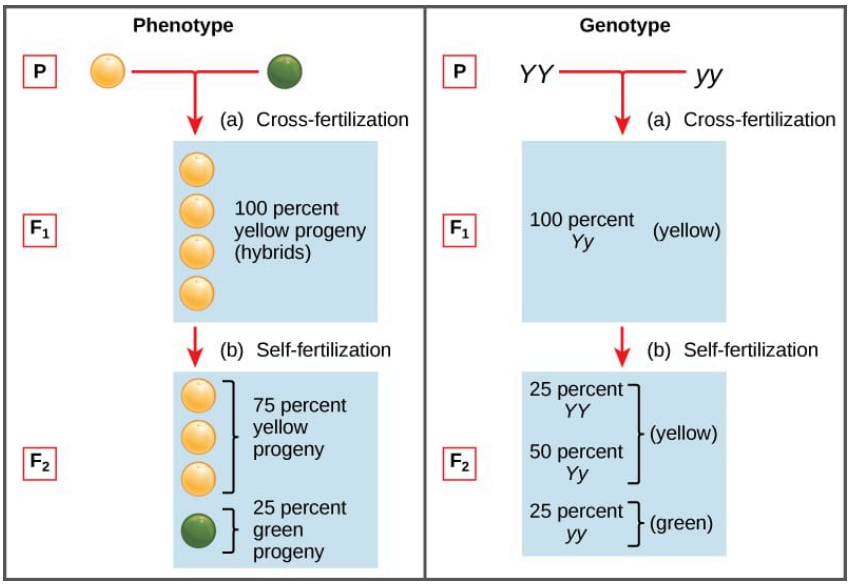


Figure 4.6.1**:** Phenotypes are physical expressions of traits that are transmitted by alleles. Capital letters represent dominant alleles and lowercase letters represent recessive alleles. The phenotypic ratios are the ratios of visible characteristics. The genotypic ratios are the ratios of gene combinations in the offspring, and these are not always distinguishable in the phenotypes.

Law of Dominance

Our discussion of homozygous and heterozygous organisms brings us to why the F_1 heterozygous offspring were identical to one of the parents, rather than expressing both alleles. In all seven pea-plant characteristics, one of the two contrasting alleles was dominant, and the other was recessive. Mendel called the dominant allele the expressed unit factor; the recessive allele was referred to as the latent unit factor. We now know that these so-called unit factors are actually genes on homologous chromosomes. For a gene that is expressed in a dominant and recessive pattern, homozygous dominant and heterozygous organisms will look identical (that is, they will have different genotypes but the same phenotype), and the recessive allele will only be observed in homozygous recessive individuals (Table 4.6.1).

Table 4.6.1**: Correspondence between Genotype and Phenotype for a Dominant-Recessive Characteristic.**

	Homozygous	Heterozygous	Homozygous
Genotype	*YY*	*Yy*	*yy*
Phenotype	yellow	yellow	green

Mendel's law of dominance states that in a heterozygote, one trait will conceal the presence of another trait for the same characteristic. For example, when crossing true-breeding violet-flowered plants with true-breeding white-flowered plants, all of the offspring were violet-flowered, even though they all had one allele for violet and one allele for white. Rather than both alleles contributing to a phenotype, the dominant allele will be expressed exclusively. The recessive allele will remain latent, but will be transmitted to offspring in the same manner as that by which the dominant allele is transmitted. The recessive trait will only be expressed by offspring that have two copies of this allele (Figure 4.6.2), and these offspring will breed true when self-crossed.

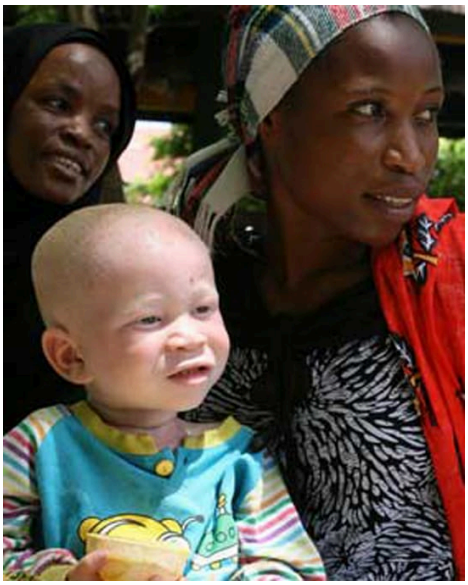


Figure 4.6.2**:** The allele for albinism, expressed here in humans, is recessive. Both of this child's parents carried the recessive allele.

Monohybrid Cross and the Punnett Square

When fertilization occurs between two true-breeding parents that differ by only the characteristic being studied, the process is called a monohybrid cross, and the resulting offspring are called monohybrids. Mendel performed seven types of monohybrid crosses, each involving contrasting traits for different characteristics. Out of these crosses, all of the F_1 offspring had the phenotype of one parent, and the F_2 offspring had a 3:1 phenotypic ratio. On the basis of these results, Mendel postulated that each parent in the monohybrid cross contributed one of two paired unit factors to each offspring, and every possible combination of unit factors was equally likely.

The results of Mendel's research can be explained in terms of probabilities, which are mathematical measures of likelihood. The probability of an event is calculated by the number of times the event occurs divided by the total number of opportunities for the event to occur. A probability of one (100 percent) for some event indicates that it is guaranteed to occur, whereas a probability of zero (0 percent) indicates that it is guaranteed to not occur, and a probability of 0.5 (50 percent) means it has an equal chance of occurring or not occurring.

To demonstrate this with a monohybrid cross, consider the case of true-breeding pea plants with yellow versus green seeds. The dominant seed color is yellow; therefore, the parental genotypes were *YY* for the plants with yellow seeds and *yy* for the plants with green seeds. A Punnett square, devised by the British geneticist Reginald Punnett, is useful for determining probabilities because it is drawn to predict all possible outcomes of all possible random fertilization events and their expected frequencies. Figure 4.6.5 shows a Punnett square for a cross between a plant with yellow peas and one with green peas. To prepare a Punnett square, all possible combinations of the parental alleles (the genotypes of the gametes) are listed along the top (for one parent) and side (for the other parent) of a grid. The combinations of egg and sperm gametes are then made in the boxes in the table on the basis of which alleles are combining. Each box then represents the diploid genotype of a zygote, or fertilized egg. Because each possibility is equally likely, genotypic ratios can be determined from a Punnett square. If the pattern of inheritance (dominant and recessive) is known, the phenotypic ratios can be inferred as well. For a monohybrid cross of two true-breeding parents, each parent contributes one type of allele. In this case, only one genotype is possible in the F_1 offspring. All offspring are *Yy* and have yellow seeds.

When the F_1 offspring are crossed with each other, each has an equal probability of contributing either a *Y* or a *y* to the F_2 offspring. The result is a 1 in 4 (25 percent) probability of both parents contributing a *Y*, resulting in an offspring with a yellow phenotype; a 25 percent probability of parent A contributing a *Y* and parent B a *y*, resulting in offspring with a yellow phenotype; a 25 percent probability of parent A contributing a *y* and parent B a *Y*, also resulting in a yellow phenotype; and a (25 percent) probability of both parents contributing a *y*, resulting in a green phenotype. When counting all four possible outcomes, there is a 3 in 4 probability of offspring having the yellow phenotype and a 1 in 4 probability of offspring having the green phenotype. This explains why the results of Mendel's F_2 generation occurred in a 3:1 phenotypic ratio. Using large numbers of crosses, Mendel was able to calculate probabilities, found that they fit the model of inheritance, and use these to predict the outcomes of other

crosses.

Law of Segregation

Observing that true-breeding pea plants with contrasting traits gave rise to F_1 generations that all expressed the dominant trait and F_2 generations that expressed the dominant and recessive traits in a 3:1 ratio, Mendel proposed the law of segregation. This law states that paired unit factors (genes) must segregate equally into gametes such that offspring have an equal likelihood of inheriting either factor. For the F_2 generation of a monohybrid cross, the following three possible combinations of genotypes result: homozygous dominant, heterozygous, or homozygous recessive. Because heterozygotes could arise from two different pathways (receiving one dominant and one recessive allele from either parent), and because heterozygotes and homozygous dominant individuals are phenotypically identical, the law supports Mendel's observed 3:1 phenotypic ratio. The equal segregation of alleles is the reason we can apply the Punnett square to accurately predict the offspring of parents with known genotypes. The physical basis of Mendel's law of segregation is the first division of meiosis in which the homologous chromosomes with their different versions of each gene are segregated into daughter nuclei. This process was not understood by the scientific community during Mendel's lifetime (Figure 4.6.3).

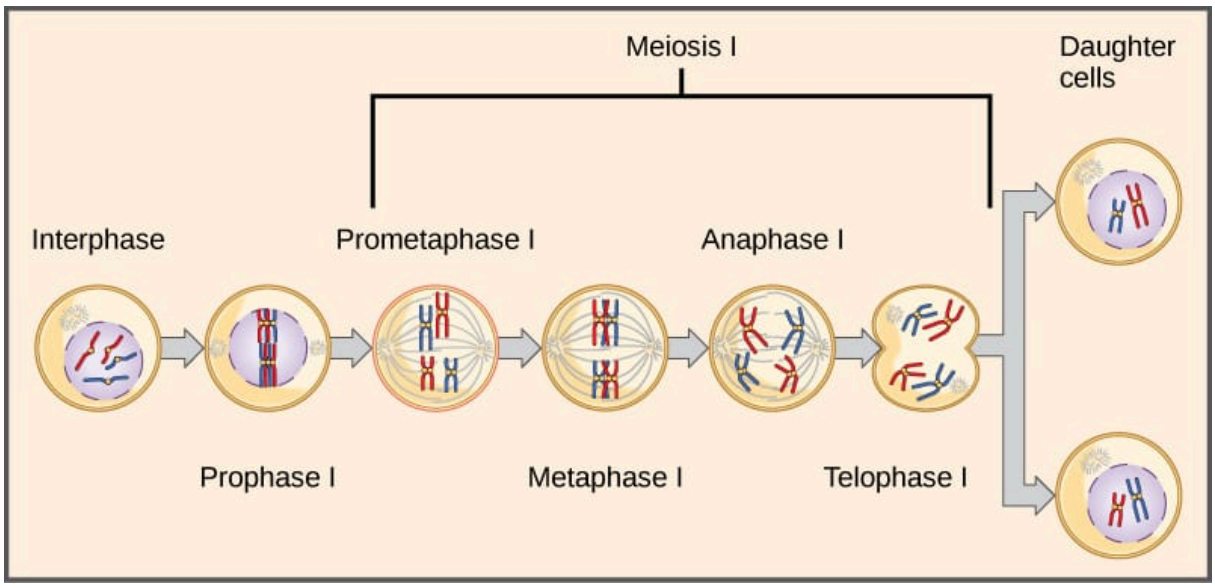


Figure 4.6.3: The first division in meiosis is shown.

Test Cross

Beyond predicting the offspring of a cross between known homozygous or heterozygous parents, Mendel also developed a way to determine whether an organism that expressed a dominant trait was a heterozygote or a homozygote. Called the test cross, this technique is still used by plant and animal breeders. In a test cross, the dominant-expressing organism is crossed with an organism that is homozygous recessive for the same characteristic. If the dominant-expressing organism is a homozygote, then all F_1 offspring will be heterozygotes expressing the dominant trait (Figure 4.6.4). Alternatively, if the dominant-expressing organism is a heterozygote, the F_1 offspring will exhibit a 1:1 ratio of heterozygotes and recessive homozygotes (Figure 4.6.4). The test cross further validates Mendel's postulate that pairs of unit factors segregate equally.

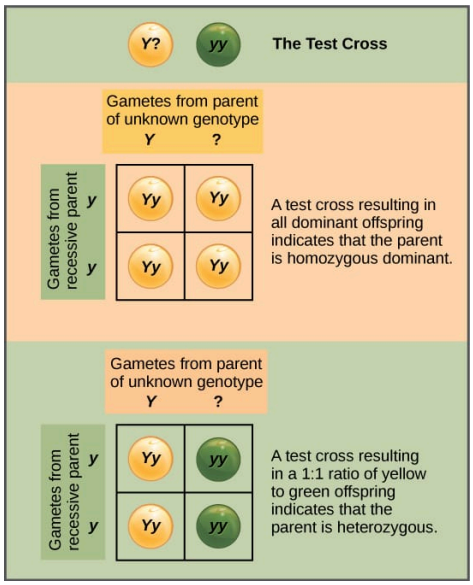


Figure 4.6.4**:** A test cross can be performed to determine whether an organism expressing a dominant trait is a homozygote or a heterozygote.

ART CONNECTION

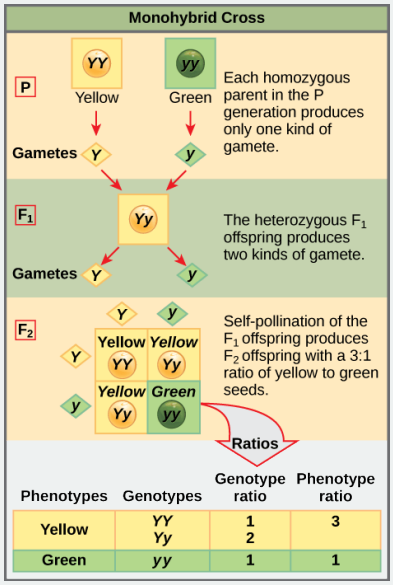


Figure 4.6.5**:** This Punnett square shows the cross between plants with yellow seeds and green seeds. The cross between the true-breeding P plants produces F_1 heterozygotes that can be self-fertilized. The self-cross of the F_1 generation can be analyzed with a Punnett square to predict the genotypes of the F_2 generation. Given an inheritance pattern of dominant–recessive, the genotypic and phenotypic ratios can then be determined.

In pea plants, round peas (*R*) are dominant to wrinkled peas (*r*). You do a test cross between a pea plant with wrinkled peas (genotype *rr*) and a plant of unknown genotype that has round peas. You end up with three plants, all which have round peas. From this data, can you tell if the parent plant is homozygous dominant or heterozygous?

Law of Independent Assortment

Mendel's law of independent assortment states that genes do not influence each other with regard to the sorting of alleles into gametes, and every possible combination of alleles for every gene is equally likely to occur. Independent assortment of genes can be illustrated by the dihybrid cross, a cross between two true-breeding parents that express different traits for two characteristics. Consider the characteristics of seed color and seed texture for two pea plants, one that has wrinkled, green seeds (*rryy*) and

another that has round, yellow seeds (*RRYY*). Because each parent is homozygous, the law of segregation indicates that the gametes for the wrinkled–green plant all are *ry*, and the gametes for the round–yellow plant are all *RY*. Therefore, the F_1 generation of offspring all are *RrYy* (Figure 4.6.6).

ART CONNECTION

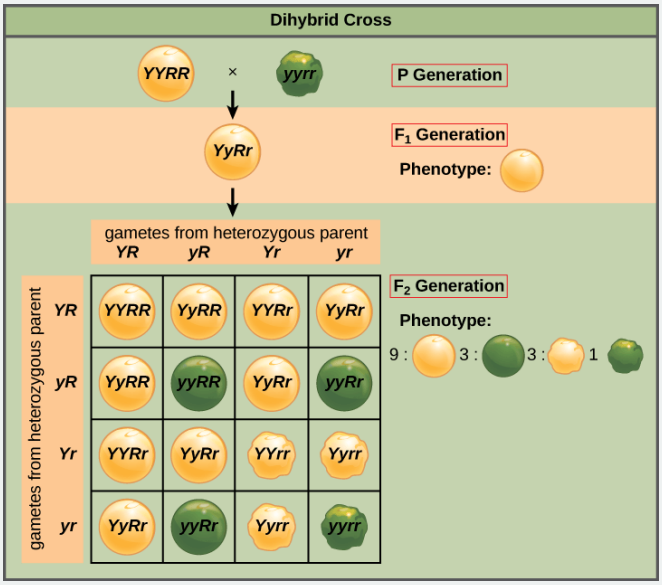


Figure 4.6.6: A dihybrid cross in pea plants involves the genes for seed color and texture. The P cross produces F_1 offspring that are all heterozygous for both characteristics. The resulting 9:3:3:1 F_2 phenotypic ratio is obtained using a Punnett square.

In pea plants, purple flowers (*P*) are dominant to white (*p*), and yellow peas (*Y*) are dominant to green (*y*). What are the possible genotypes and phenotypes for a cross between *PpYY* and *ppYy* pea plants? How many squares would you need to complete a Punnett square analysis of this cross?

The gametes produced by the F_1 individuals must have one allele from each of the two genes. For example, a gamete could get an *R* allele for the seed shape gene and either a *Y* or a *y* allele for the seed color gene. It cannot get both an *R* and an *r* allele; each gamete can have only one allele per gene. The law of independent assortment states that a gamete into which an *r* allele is sorted would be equally likely to contain either a *Y* or a *y* allele. Thus, there are four equally likely gametes that can be formed when the *RrYy* heterozygote is self-crossed, as follows: *RY*, *rY*, *Ry*, and *ry*. Arranging these gametes along the top and left of a 4 × 4 Punnett square (Figure 4.6.6) gives us 16 equally likely genotypic combinations. From these genotypes, we find a phenotypic ratio of 9 round–yellow:3 round–green:3 wrinkled–yellow:1 wrinkled–green (Figure 4.6.6). These are the offspring ratios we would expect, assuming we performed the crosses with a large enough sample size.

The physical basis for the law of independent assortment also lies in meiosis I, in which the different homologous pairs line up in random orientations. Each gamete can contain any combination of paternal and maternal chromosomes (and therefore the genes on them) because the orientation of tetrads on the metaphase plane is random (Figure 4.6.7).

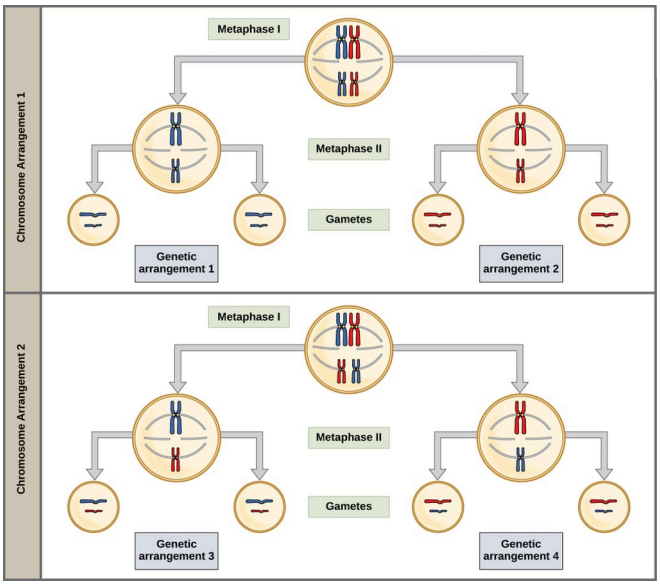


Figure 4.6.7**:** The random segregation into daughter nuclei that happens during the first division in meiosis can lead to a variety of possible genetic arrangements.

Section Summary

When true-breeding, or homozygous, individuals that differ for a certain trait are crossed, all of the offspring will be heterozygous for that trait. If the traits are inherited as dominant and recessive, the F_1 offspring will all exhibit the same phenotype as the parent homozygous for the dominant trait. If these heterozygous offspring are self-crossed, the resulting F_2 offspring will be equally likely to inherit gametes carrying the dominant or recessive trait, giving rise to offspring of which one quarter are homozygous dominant, half are heterozygous, and one quarter are homozygous recessive. Because homozygous dominant and heterozygous individuals are phenotypically identical, the observed traits in the F_2 offspring will exhibit a ratio of three dominant to one recessive.

Mendel postulated that genes (characteristics) are inherited as pairs of alleles (traits) that behave in a dominant and recessive pattern. Alleles segregate into gametes such that each gamete is equally likely to receive either one of the two alleles present in a diploid individual. In addition, genes are assorted into gametes independently of one another. That is, in general, alleles are not more likely to segregate into a gamete with a particular allele of another gene.

Art Connections

Figure 4.6.5: In pea plants, round peas (*R*) are dominant to wrinkled peas (*r*). You do a test cross between a pea plant with wrinkled peas (genotype *rr*) and a plant of unknown genotype that has round peas. You end up with three plants, all which have round peas. From this data, can you tell if the parent plant is homozygous dominant or heterozygous?

Answer

You cannot be sure if the plant is homozygous or heterozygous as the data set is too small: by random chance, all three plants might have acquired only the dominant gene even if the recessive one is present.

Figure 4.6.6: In pea plants, purple flowers (*P*) are dominant to white (*p*), and yellow peas (*Y*) are dominant to green (*y*). What are the possible genotypes and phenotypes for a cross between *PpYY* and *ppYy* pea plants? How many squares would you need to complete a Punnett square analysis of this cross?

Answer

The possible genotypes are *PpYY*, *PpYy*, *ppYY*, and *ppYy*. The former two genotypes would result in plants with purple flowers and yellow peas, while the latter two genotypes would result in plants with white flowers with yellow peas, for a 1:1 ratio of each phenotype. You only need a 2 × 2 Punnett square (four squares total) to do this analysis

because two of the alleles are homozygous.

Glossary

allele
one of two or more variants of a gene that determines a particular trait for a characteristic

dihybrid
the result of a cross between two true-breeding parents that express different traits for two characteristics

genotype
the underlying genetic makeup, consisting of both physically visible and non-expressed alleles, of an organism

heterozygous
having two different alleles for a given gene on the homologous chromosomes

homozygous
having two identical alleles for a given gene on the homologous chromosomes

law of dominance
in a heterozygote, one trait will conceal the presence of another trait for the same characteristic

law of independent assortment
genes do not influence each other with regard to sorting of alleles into gametes; every possible combination of alleles is equally likely to occur

law of segregation
paired unit factors (i.e., genes) segregate equally into gametes such that offspring have an equal likelihood of inheriting any combination of factors

monohybrid
the result of a cross between two true-breeding parents that express different traits for only one characteristic

phenotype
the observable traits expressed by an organism

Punnett square
a visual representation of a cross between two individuals in which the gametes of each individual are denoted along the top and side of a grid, respectively, and the possible zygotic genotypes are recombined at each box in the grid

test cross
a cross between a dominant expressing individual with an unknown genotype and a homozygous recessive individual; the offspring phenotypes indicate whether the unknown parent is heterozygous or homozygous for the dominant trait

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5: ANIMAL BODY PLANS, REPRODUCTION & DEVELOPMENT

5.1: Animal Body Plans and Tissues
5.2: Animal Reproduction
5.3: Animal Development and Organogenesis

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5.1: Animal Body Plans and Tissues

Even though members of the animal kingdom are incredibly diverse, animals share common features that distinguish them from organisms in other kingdoms. All animals are eukaryotic, multicellular organisms, and almost all animals have specialized tissues. Most animals are motile, at least during certain life stages. Animals require a source of food to grow and develop. All animals are heterotrophic, ingesting living or dead organic matter. This form of obtaining energy distinguishes them from autotrophic organisms, such as most plants, which make their own nutrients through photosynthesis and from fungi that digest their food externally. Animals may be carnivores, herbivores, omnivores, or parasites (Figure 5.1.1). Most animals reproduce sexually: The offspring pass through a series of developmental stages that establish a determined body plan, unlike plants, for example, in which the exact shape of the body is indeterminate. The body plan refers to the shape of an animal.



Figure 5.1.1: All animals that derive energy from food are heterotrophs. The (a) black bear is an omnivore, eating both plants and animals. The (b) heartworm Dirofilaria immitis is a parasite that derives energy from its hosts. It spends its larval stage in mosquitos and its adult stage infesting the hearts of dogs and other mammals, as shown here. (credit a: modification of work by USDA Forest Service; credit b: modification of work by Clyde Robinson)

Complex Tissue Structure

A hallmark trait of animals is specialized structures that are differentiated to perform unique functions. As multicellular organisms, most animals develop specialized cells that group together into tissues with specialized functions. A tissue is a collection of similar cells that had a common embryonic origin. There are four main types of animal tissues: nervous, muscle, connective, and epithelial. Nervous tissue contains neurons, or nerve cells, which transmit nerve impulses. Muscle tissue contracts to cause all types of body movement from locomotion of the organism to movements within the body itself. Animals also have specialized connective tissues that provide many functions, including transport and structural support. Examples of connective tissues include blood and bone. Connective tissue is comprised of cells separated by extracellular material made of organic and inorganic materials, such as the protein and mineral deposits of bone. Epithelial tissue covers the internal and external surfaces of organs inside the animal body and the external surface of the body of the organism.

CONCEPT IN ACTION



View this video to watch a presentation by biologist E.O. Wilson on the importance of animal diversity.

Animal Reproduction and Development

Most animals have diploid body (somatic) cells and a small number of haploid reproductive (gamete) cells produced through meiosis. Some exceptions exist: For example, in bees, wasps, and ants, the male is haploid because it develops from an unfertilized egg. Most animals undergo sexual reproduction, while many also have mechanisms of asexual reproduction.

Sexual Reproduction and Embryonic Development

Almost all animal species are capable of reproducing sexually; for many, this is the only mode of reproduction possible. This distinguishes animals from fungi, protists, and bacteria, where asexual reproduction is common or exclusive. During sexual reproduction, the male and female gametes of a species combine in a process called fertilization. Typically, the small, motile male sperm travels to the much larger, sessile female egg. Sperm form is diverse and includes cells with flagella or amoeboid cells to facilitate motility. Fertilization and fusion of the gamete nuclei produce a zygote. Fertilization may be internal, especially in land animals, or external, as is common in many aquatic species.

After fertilization, a developmental sequence ensues as cells divide and differentiate. Many of the events in development are shared in groups of related animal species, and these events are one of the main ways scientists classify high-level groups of animals. During development, animal cells specialize and form tissues, determining their future morphology and physiology. In many animals, such as mammals, the young resemble the adult. Other animals, such as some insects and amphibians, undergo complete metamorphosis in which individuals enter one or more larval stages. For these animals, the young and the adult have different diets and sometimes habitats. In other species, a process of incomplete metamorphosis occurs in which the young somewhat resemble the adults and go through a series of stages separated by molts (shedding of the skin) until they reach the final adult form.

Asexual Reproduction

Asexual reproduction, unlike sexual reproduction, produces offspring genetically identical to each other and to the parent. A number of animal species—especially those without backbones, but even some fish, amphibians, and reptiles—are capable of asexual reproduction. Asexual reproduction, except for occasional identical twinning, is absent in birds and mammals. The most common forms of asexual reproduction for stationary aquatic animals include budding and fragmentation, in which part of a parent individual can separate and grow into a new individual. In contrast, a form of asexual reproduction found in certain

invertebrates and rare vertebrates is called parthenogenesis (or “virgin beginning”), in which unfertilized eggs develop into new offspring.

Classification Features of Animals

Animals are classified according to morphological and developmental characteristics, such as a body plan. With the exception of sponges, the animal body plan is symmetrical. This means that their distribution of body parts is balanced along an axis. Additional characteristics that contribute to animal classification include the number of tissue layers formed during development, the presence or absence of an internal body cavity, and other features of embryological development.

ART CONNECTION

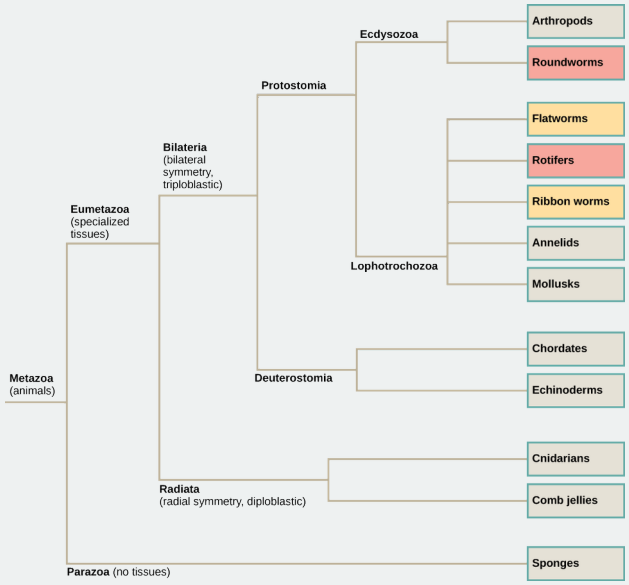


Figure 5.1.2**:** The phylogenetic tree of animals is based on morphological, fossil, and genetic evidence.

Which of the following statements is false?

a. Eumetazoa have specialized tissues and Parazoa do not.
b. Both acoelomates and pseudocoelomates have a body cavity.
c. Chordates are more closely related to echinoderms than to rotifers according to the figure.
d. Some animals have radial symmetry, and some animals have bilateral symmetry.

Body Symmetry

Animals may be asymmetrical, radial, or bilateral in form (Figure 5.1.3). Asymmetrical animals are animals with no pattern or symmetry; an example of an asymmetrical animal is a sponge (Figure 5.1.3**a**). An organism with radial symmetry (Figure 5.1.3**b**) has a longitudinal (up-and-down) orientation: Any plane cut along this up–down axis produces roughly mirror-image halves. An example of an organism with radial symmetry is a sea anemone.

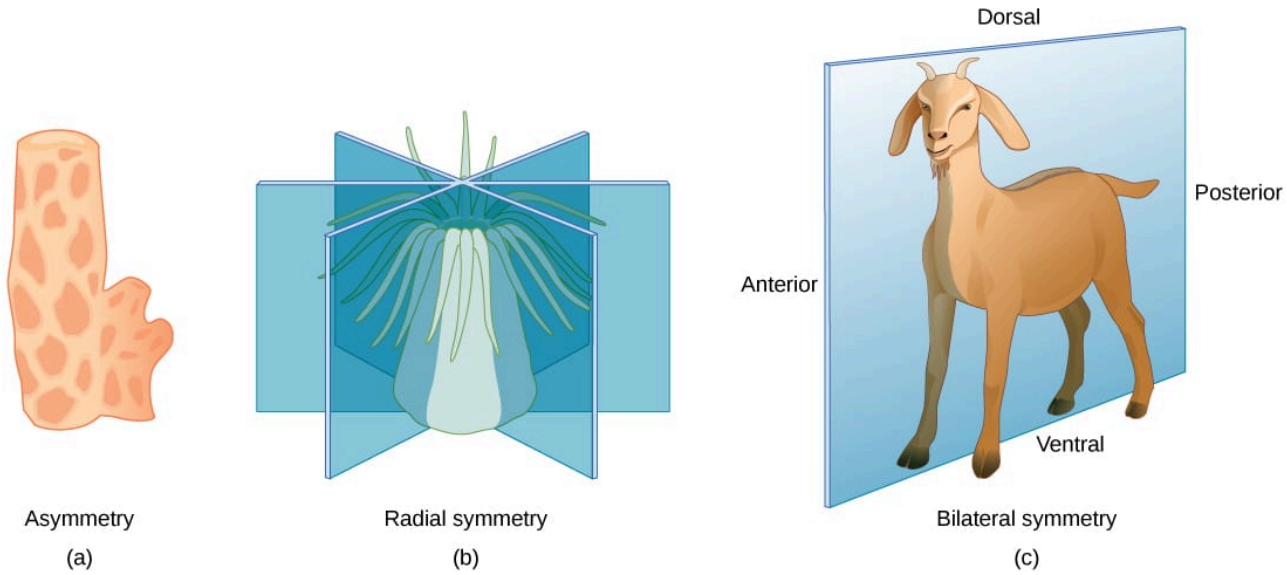


Figure 5.1.3**:** Animals exhibit different types of body symmetry. The (a) sponge is asymmetrical and has no planes of symmetry, the (b) sea anemone has radial symmetry with multiple planes of symmetry, and the (c) goat has bilateral symmetry with one plane of symmetry.

Bilateral symmetry is illustrated in Figure 5.1.3**c** using a goat. The goat also has upper and lower sides to it, but they are not symmetrical. A vertical plane cut from front to back separates the animal into roughly mirror-image right and left sides. Animals with bilateral symmetry also have a "head" and "tail" (anterior versus posterior) and a back and underside (dorsal versus ventral).

CONCEPT IN ACTION

This interactive element is not available in this format. Visit the link or scan the QR code to access it online.

View this YouTube Video online

Watch this video to see a quick sketch of the different types of body symmetry.

Layers of Tissues

Most animal species undergo a layering of early tissues during embryonic development. These layers are called germ layers. Each layer develops into a specific set of tissues and organs. Animals develop either two or three embryonic germs layers (Figure 5.1.4). The animals that display radial symmetry develop two germ layers, an inner layer (endoderm) and an outer layer (ectoderm). These animals are called diploblasts. Animals with bilateral symmetry develop three germ layers: an inner layer (endoderm), an outer layer (ectoderm), and a middle layer (mesoderm). Animals with three germ layers are called triploblasts.

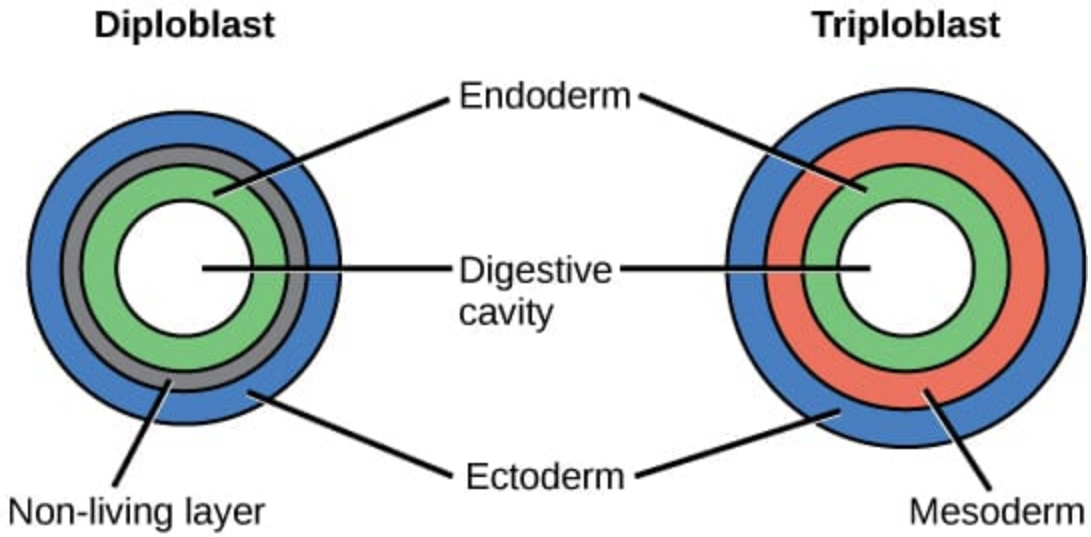


Figure 5.1.4**:** During embryogenesis, diploblasts develop two embryonic germ layers: an ectoderm and an endoderm. Triploblasts develop a third layer—the mesoderm—between the endoderm and ectoderm.

Presence or Absence of a Coelom

Triploblasts may develop an internal body cavity derived from mesoderm, called a coelom (pr. see-LŌM). This epithelial-lined cavity is a space, usually filled with fluid, which lies between the digestive system and the body wall. It houses organs such as the kidneys and spleen, and contains the circulatory system. Triploblasts that do not develop a coelom are called acoelomates, and their mesoderm region is completely filled with tissue, although they have a gut cavity. Examples of acoelomates include the flatworms. Animals with a true coelom are called eucoelomates (or coelomates) (Figure 5.1.5). A true coelom arises entirely within the mesoderm germ layer. Animals such as earthworms, snails, insects, starfish, and vertebrates are all eucoelomates. A third group of triploblasts has a body cavity that is derived partly from mesoderm and partly from endoderm tissue. These animals are called pseudocoelomates. Roundworms are examples of pseudocoelomates. New data on the relationships of pseudocoelomates suggest that these phyla are not closely related and so the evolution of the pseudocoelom must have occurred more than once (Figure 5.1.2). True coelomates can be further characterized based on features of their early embryological development.

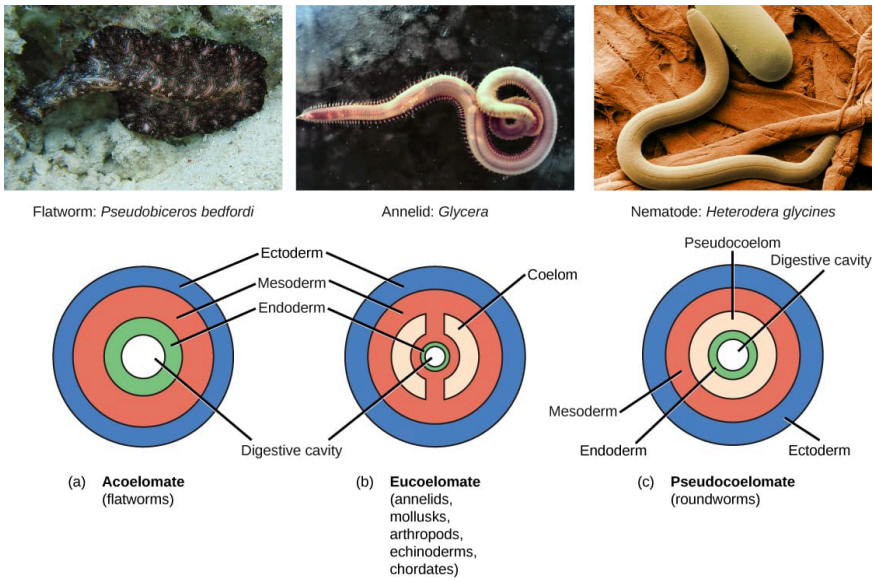


Figure 5.1.5**:** Triploblasts may be acoelomates, eucoelomates, or pseudocoelomates. Eucoelomates have a body cavity within the mesoderm, called a coelom, which is lined with mesoderm tissue. Pseudocoelomates have a similar body cavity, but it is lined with mesoderm and endoderm tissue. (credit a: modification of work by Jan Derk; credit b: modification of work by NOAA; credit c: modification of work by USDA, ARS)

Protostomes and Deuterostomes

Bilaterally symmetrical, triploblastic eucoelomates can be divided into two groups based on differences in their early embryonic development. Protostomes include phyla such as arthropods, mollusks, and annelids. Deuterostomes include the chordates and echinoderms. These two groups are named from which opening of the digestive cavity develops first: mouth or anus. The word *protostome* comes from Greek words meaning “mouth first,” and *deuterostome* originates from words meaning “mouth second” (in this case, the anus develops first). This difference reflects the fate of a structure called the blastopore (Figure 5.1.6), which becomes the mouth in protostomes and the anus in deuterostomes. Other developmental characteristics differ between protostomes and deuterostomes, including the mode of formation of the coelom and the early cell division of the embryo.

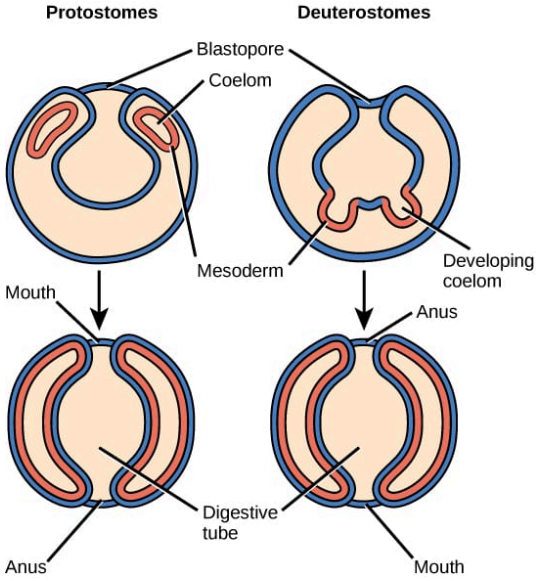


Figure 5.1.6**:** Eucoelomates can be divided into two groups, protostomes and deuterostomes, based on their early embryonic development. Two of these differences include the origin of the mouth opening and the way in which the coelom is formed.

Section Summary

Animals constitute a diverse kingdom of organisms. Although animals range in complexity from simple sea sponges to human beings, most members share certain features. Animals are eukaryotic, multicellular, heterotrophic organisms that ingest their food and usually develop into motile creatures with a fixed body plan. Most members of the animal kingdom have differentiated tissues of four main classes—nervous, muscular, connective, and epithelial—that are specialized to perform different functions. Most animals reproduce sexually, leading to a developmental sequence that is relatively similar across the animal kingdom.

Organisms in the animal kingdom are classified based on their body morphology and development. True animals are divided into those with radial versus bilateral symmetry. Animals with three germ layers, called triploblasts, are further characterized by the presence or absence of an internal body cavity called a coelom. Animals with a body cavity may be either coelomates or pseudocoelomates, depending on which tissue gives rise to the coelom. Coelomates are further divided into two groups called protostomes and deuterostomes, based on a number of developmental characteristics.

Art Connection

Figure 5.1.2: Which of the following statements is false?

A. Eumetazoa have specialized tissues and Parazoa do not.
B. Both acoelomates and pseudocoelomates have a body cavity.
C. Chordates are more closely related to echinoderms than to rotifers according to the figure.
D. Some animals have radial symmetry, and some animals have bilateral symmetry.

Answer

B

Glossary

acoelomate
without a body cavity

asymmetrical
having no plane of symmetry

bilateral symmetry
a type of symmetry in which there is only one plane of symmetry that creates two mirror-image sides

body plan
the shape and symmetry of an organism

coelom
a lined body cavity derived from mesodermal embryonic tissue

deuterostome
describing an animal in which the blastopore develops into the anus, with the second opening developing into the mouth

diploblast
an animal that develops from two embryonic germ layers

eucoelomate
describing animals with a body cavity completely lined with mesodermal tissue

germ layer
a collection of cells formed during embryogenesis that will give rise to future body tissues

protostome
describing an animal in which the mouth develops first during embryogenesis and a second opening developing into the anus

pseudocoelomate
an animal with a coelom that is not completely lined with tissues derived from the mesoderm as in eucoelomate animals

radial symmetry
a type of symmetry with multiple planes of symmetry all cross at an axis through the center of the organism

triploblast
an animal that develops from three germ layers

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5.2: Animal Reproduction

Some animals produce offspring through asexual reproduction while other animals produce offspring through sexual reproduction. Both methods have advantages and disadvantages. Asexual reproduction produces offspring that are genetically identical to the parent because the offspring are all clones of the original parent. A single individual can produce offspring asexually and large numbers of offspring can be produced quickly; these are two advantages that asexually reproducing organisms have over sexually reproducing organisms. In a stable or predictable environment, asexual reproduction is an effective means of reproduction because all the offspring will be adapted to that environment. In an unstable or unpredictable environment, species that reproduce asexually may be at a disadvantage because all the offspring are genetically identical and may not be adapted to different conditions.

During sexual reproduction, the genetic material of two individuals is combined to produce genetically diverse offspring that differ from their parents. The genetic diversity of sexually produced offspring is thought to give sexually reproducing individuals greater fitness because more of their offspring may survive and reproduce in an unpredictable or changing environment. Species that reproduce sexually (and have separate sexes) must maintain two different types of individuals, males and females. Only half the population (females) can produce the offspring, so fewer offspring will be produced when compared to asexual reproduction. This is a disadvantage of sexual reproduction compared to asexual reproduction.

Asexual Reproduction

Asexual reproduction occurs in prokaryotic microorganisms (bacteria and archaea) and in many eukaryotic, single-celled and multi-celled organisms. There are several ways that animals reproduce asexually, the details of which vary among individual species.

Fission

Fission, also called binary fission, occurs in some invertebrate, multi-celled organisms. It is in some ways analogous to the process of binary fission of single-celled prokaryotic organisms. The term fission is applied to instances in which an organism appears to split itself into two parts and, if necessary, regenerate the missing parts of each new organism. For example, species of turbellarian flatworms commonly called the planarians, such as *Dugesia dorotocephala*, are able to separate their bodies into head and tail regions and then regenerate the missing half in each of the two new organisms. Sea anemones (Cnidaria), such as species of the genus *Anthopleura* (Figure 5.2.1), will divide along the oral-aboral axis, and sea cucumbers (Echinodermata) of the genus *Holothuria,* will divide into two halves across the oral-aboral axis and regenerate the other half in each of the resulting individuals.



Figure 5.2.1**:** The *Anthopleura artemisia* sea anemone can reproduce through fission.

Budding

Budding is a form of asexual reproduction that results from the outgrowth of a part of the body leading to a separation of the "bud" from the original organism and the formation of two individuals, one smaller than the other. Budding occurs commonly in some invertebrate animals such as hydras and corals. In hydras, a bud forms that develops into an adult and breaks away from the main body (Figure 5.2.2).



(a) (b)

Figure 5.2.2**:** (a) Hydra reproduce asexually through budding: a bud forms on the tubular body of an adult hydra, develops a mouth and tentacles, and then detaches from its parent. The new hydra is fully developed and will find its own location for attachment. (b) Some coral, such as the *Lophelia pertusa* shown here, can reproduce through budding. (credit b: modification of work by Ed Bowlby, NOAA/Olympic Coast NMS; NOAA/OAR/Office of Ocean Exploration)

CONCEPT IN ACTION

This interactive element is not available in this format. Visit the link or scan the QR code to access it online.

View this YouTube Video online

View this video to see a hydra budding.

Fragmentation

Fragmentation is the breaking of an individual into parts followed by regeneration. If the animal is capable of fragmentation, and the parts are big enough, a separate individual will regrow from each part. Fragmentation may occur through accidental damage, damage from predators, or as a natural form of reproduction. Reproduction through fragmentation is observed in sponges, some cnidarians, turbellarians, echinoderms, and annelids. In some sea stars, a new individual can be regenerated from a broken arm and a piece of the central disc. This sea star (Figure 5.2.3) is in the process of growing a complete sea star from an arm that has been cut off. Fisheries workers have been known to try to kill the sea stars eating their clam or oyster beds by cutting them in half and throwing them back into the ocean. Unfortunately for the workers, the two parts can each regenerate a new half, resulting in twice as many sea stars to prey upon the oysters and clams.



Figure 5.2.3: (a) *Linckia multifora* is a species of sea star that can reproduce asexually via fragmentation. In this process, (b) an arm that has been shed grows into a new sea star. (credit a: modifiction of work by Dwayne Meadows, NOAA/NMFS/OPR)

Parthenogenesis

Parthenogenesis is a form of asexual reproduction in which an egg develops into an individual without being fertilized. The resulting offspring can be either haploid or diploid, depending on the process in the species. Parthenogenesis occurs in invertebrates such as water fleas, rotifers, aphids, stick insects, and ants, wasps, and bees. Ants, bees, and wasps use parthenogenesis to produce haploid males (drones). The diploid females (workers and queens) are the result of a fertilized egg.

Some vertebrate animals—such as certain reptiles, amphibians, and fish—also reproduce through parthenogenesis. Parthenogenesis has been observed in species in which the sexes were separated in terrestrial or marine zoos. Two female Komodo dragons, a hammerhead shark, and a blacktop shark have produced parthenogenic young when the females have been isolated from males. It is possible that the asexual reproduction observed occurred in response to unusual circumstances and

would normally not occur.

Sexual Reproduction

Sexual reproduction is the combination of reproductive cells from two individuals to form genetically unique offspring. The nature of the individuals that produce the two kinds of gametes can vary, having for example separate sexes or both sexes in each individual. Sex determination, the mechanism that determines which sex an individual develops into, also can vary.

Hermaphroditism

Hermaphroditism occurs in animals in which one individual has both male and female reproductive systems. Invertebrates such as earthworms, slugs, tapeworms, and snails (Figure 5.2.4) are often hermaphroditic. Hermaphrodites may self-fertilize, but typically they will mate with another of their species, fertilizing each other and both producing offspring. Self-fertilization is more common in animals that have limited mobility or are not motile, such as barnacles and clams. Many species have specific mechanisms in place to prevent self-fertilization, because it is an extreme form of inbreeding and usually produces less fit offspring.



(a) (b)

Figure 5.2.4: Many (a) snails are hermaphrodites. When two individuals (b) mate, they can produce up to 100 eggs each. (credit a: modification of work by Assaf Shtilman; credit b: modification of work by "Schristia"/Flickr)

Sex Determination

Mammalian sex is determined genetically by the combination of X and Y chromosomes. Individuals homozygous for X (XX) are female and heterozygous individuals (XY) are male. In mammals, the presence of a Y chromosome causes the development of male characteristics and its absence results in female characteristics. The XY system is also found in some insects and plants.

Bird sex determination is dependent on the combination of Z and W chromosomes. Homozygous for Z (ZZ) results in a male and heterozygous (ZW) results in a female. Notice that this system is the opposite of the mammalian system because in birds the female is the sex with the different sex chromosomes. The W appears to be essential in determining the sex of the individual, similar to the Y chromosome in mammals. Some fish, crustaceans, insects (such as butterflies and moths), and reptiles use the ZW system.

More complicated chromosomal sex determining systems also exist. For example, some swordtail fish have three sex chromosomes in a population.

The sex of some other species is not determined by chromosomes, but by some aspect of the environment. Sex determination in alligators, some turtles, and tuataras, for example, is dependent on the temperature during the middle third of egg development. This is referred to as environmental sex determination, or more specifically, as temperature-dependent sex determination. In

many turtles, cooler temperatures during egg incubation produce males and warm temperatures produce females, while in many other species of turtles, the reverse is true. In some crocodiles and some turtles, moderate temperatures produce males and both warm and cool temperatures produce females.

Individuals of some species change their sex during their lives, switching from one to the other. If the individual is female first, it is termed protogyny or “first female,” if it is male first, it is termed protandry or “first male.” Oysters are born male, grow in size, and become female and lay eggs. The wrasses, a family of reef fishes, are all sequential hermaphrodites. Some of these species live in closely coordinated schools with a dominant male and a large number of smaller females. If the male dies, a female increases in size, changes sex, and becomes the new dominant male.

Fertilization

The fusion of a sperm and an egg is a process called fertilization. This can occur either inside (internal fertilization) or outside (external fertilization) the body of the female. Humans provide an example of the former, whereas frog reproduction is an example of the latter.

External Fertilization

External fertilization usually occurs in aquatic environments where both eggs and sperm are released into the water. After the sperm reaches the egg, fertilization takes place. Most external fertilization happens during the process of spawning where one or several females release their eggs and the male(s) release sperm in the same area, at the same time. The spawning may be triggered by environmental signals, such as water temperature or the length of daylight. Nearly all fish spawn, as do crustaceans (such as crabs and shrimp), mollusks (such as oysters), squid, and echinoderms (such as sea urchins and sea cucumbers). Frogs, corals, molluscs, and sea cucumbers also spawn (Figure 5.2.5).



**Figure 5.2.5: ** During sexual reproduction in toads, the male grasps the female from behind and externally fertilizes the eggs as they are deposited. (credit: Bernie Kohl)

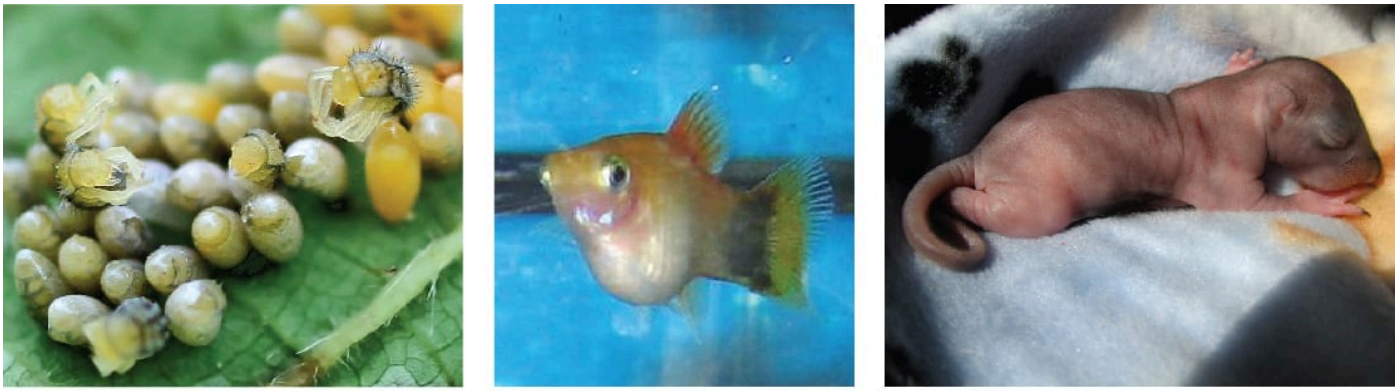
Internal Fertilization

Internal fertilization occurs most often in terrestrial animals, although some aquatic animals also use this method. Internal fertilization may occur by the male directly depositing sperm in the female during mating. It may also occur by the male depositing sperm in the environment, usually in a protective structure, which a female picks up to deposit the sperm in her reproductive tract. There are three ways that offspring are produced following internal fertilization. In oviparity, fertilized eggs are laid outside the female’s body and develop there, receiving nourishment from the yolk that is a part of the egg (Figure 5.2.6**a**). This occurs in some bony fish, some reptiles, a few cartilaginous fish, some amphibians, a few mammals, and all birds. Most non-avian reptiles and insects produce leathery eggs, while birds and some turtles produce eggs with high concentrations of calcium

carbonate in the shell, making them hard. Chicken eggs are an example of a hard shell. The eggs of the egg-laying mammals such as the platypus and echidna are leathery.

In ovoviparity, fertilized eggs are retained in the female, and the embryo obtains its nourishment from the egg's yolk. The eggs are retained in the female's body until they hatch inside of her, or she lays the eggs right before they hatch. This process helps protect the eggs until hatching. This occurs in some bony fish (like the platyfish *Xiphophorus maculatus,* Figure 5.2.6**b**), some sharks, lizards, some snakes (garter snake *Thamnophis sirtalis*), some vipers, and some invertebrate animals (Madagascar hissing cockroach *Gromphadorhina portentosa*).

In viviparity the young are born alive. They obtain their nourishment from the female and are born in varying states of maturity. This occurs in most mammals (Figure 5.2.6**c**), some cartilaginous fish, and a few reptiles.



(a) (b) (c)

Figure 5.2.6: In (a) oviparity, young develop in eggs outside the female body, as with these *Harmonia axydridis* beetles hatching. Some aquatic animals, like this (b) pregnant *Xiphophorus maculatus* are ovoviparous, with the egg developing inside the female and nutrition supplied primarily from the yolk. In mammals, nutrition is supported by the placenta, as was the case with this (c) newborn squirrel. (credit b: modification of work by Gourami Watcher; credit c: modification of work by "audreyjm529"/Flickr)

Section Summary

Reproduction may be asexual when one individual produces genetically identical offspring, or sexual when the genetic material from two individuals is combined to produce genetically diverse offspring. Asexual reproduction in animals occurs through fission, budding, fragmentation, and parthenogenesis. Sexual reproduction may involve fertilization inside the body or in the external environment. A species may have separate sexes or combined sexes; when the sexes are combined they may be expressed at different times in the life cycle. The sex of an individual may be determined by various chromosomal systems or environmental factors such as temperature.

Sexual reproduction starts with the combination of a sperm and an egg in a process called fertilization. This can occur either outside the bodies or inside the female. The method of fertilization varies among animals. Some species release the egg and sperm into the environment, some species retain the egg and receive the sperm into the female body and then expel the developing embryo covered with shell, while still other species retain the developing offspring throughout the gestation period.

Glossary

asexual reproduction
: a mechanism that produces offspring that are genetically identical to the parent

budding
: a form of asexual reproduction that results from the outgrowth of a part of an organism leading to a separation from the original animal into two individuals

external fertilization
: the fertilization of eggs by sperm outside an animal's body, often during spawning

fission
(also, binary fission) a form of asexual reproduction in which an organism splits into two separate organisms or two parts that regenerate the missing portions of the body

fragmentation
the breaking of an organism into parts and the growth of a separate individual from each part

hermaphroditism
the state of having both male and female reproductive structures within the same individual

internal fertilization
the fertilization of eggs by sperm inside the body of the female

oviparity
a process by which fertilized eggs are laid outside the female's body and develop there, receiving nourishment from the yolk that is a part of the egg

ovoviparity
a process by which fertilized eggs are retained within the female; the embryo obtains its nourishment from the egg's yolk, and the young are fully developed when they are hatched

parthenogenesis
a form of asexual reproduction in which an egg develops into a complete individual without being fertilized

sex determination
the mechanism by which the sex of individuals in sexually reproducing organisms is initially established

sexual reproduction
a form of reproduction in which cells containing genetic material from two individuals combines to produce genetically unique offspring

viviparity
a process in which the young develop within the female and are born in a nonembryonic state

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5.3: Animal Development and Organogenesis

The process by which an organism develops from a single-celled zygote to a multi-cellular organism is complex and well regulated. The regulation occurs through signaling between cells and tissues and responses in the form of differential gene expression.

Early Embryonic Development

Fertilization is the process in which gametes (an egg and sperm) fuse to form a zygote (Figure 5.3.1). To ensure that the offspring has only one complete diploid set of chromosomes, only one sperm must fuse with one egg. In mammals, a layer called the zona pellucida protects the egg. At the tip of the head of a sperm cell is a structure like a lysosome called the acrosome, which contains enzymes. When a sperm binds to the zona pellucida, a series of events, called the acrosomal reactions, take place. These reactions, involving enzymes from the acrosome, allow the sperm plasma membrane to fuse with the egg plasma membrane and permit the sperm nucleus to transfer into the ovum. The nuclear membranes of the egg and sperm break down and the two haploid nuclei fuse to form a diploid nucleus or genome.

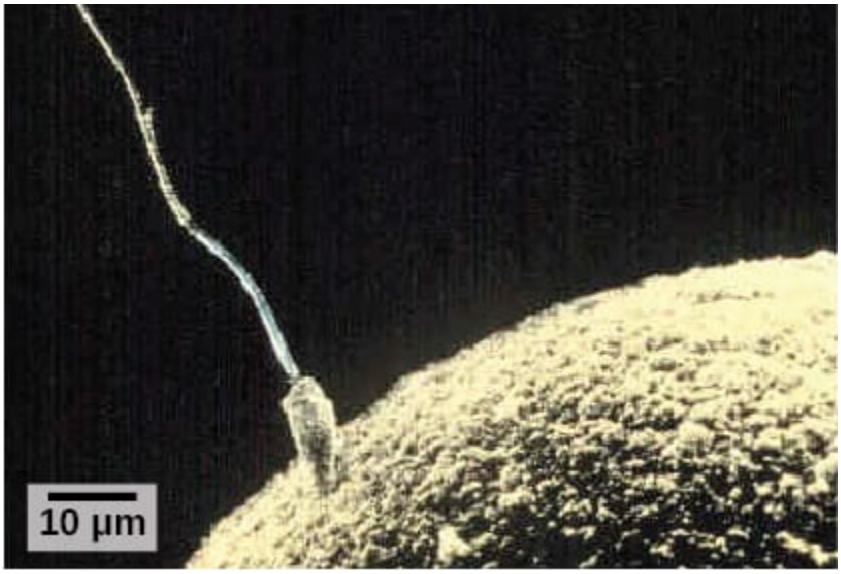
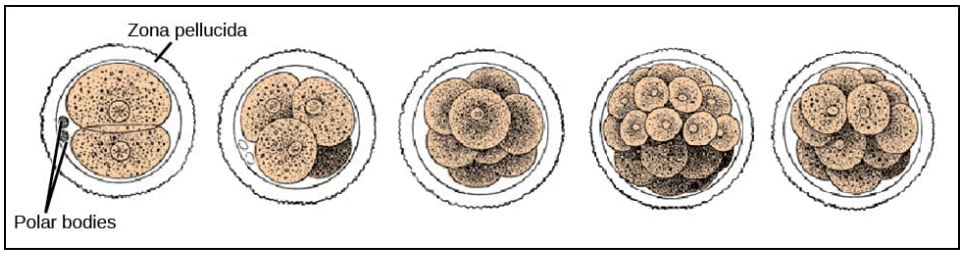


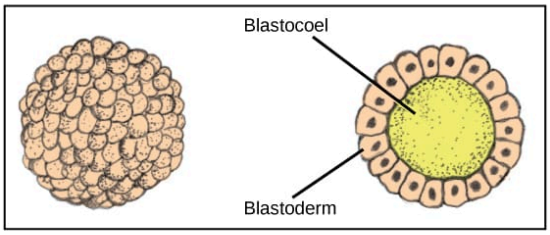
Figure 5.3.1**:** Fertilization is the process in which sperm and egg fuse to form a zygote. (credit: scale-bar data from Matt Russell)

To ensure that no more than one sperm fertilizes the egg, once the acrosomal reactions take place at one location of the egg membrane, the egg releases proteins in other locations to prevent other sperm from fusing with the egg.

The development of multi-cellular organisms begins from this single-celled zygote, which undergoes rapid cell division, called cleavage (Figure 5.3.2**a**), to form a hollow ball of cells called a blastula (Figure 5.3.2**b**).



(a)



(b)

Figure 5.3.2**:** (a) During cleavage, the zygote rapidly divides into multiple cells. (b) The cells rearrange themselves to form a hollow ball called the blastula. (credit a: modification of work by Gray's Anatomy; credit b: modification of work by Pearson Scott Foresman; donated to the Wikimedia Foundation)

In mammals, the blastula forms the blastocyst in the next stage of development. Here the cells in the blastula arrange themselves in two layers: the inner cell mass, and an outer layer called the trophoblast. The inner cell mass will go on to form the embryo. The trophoblast secretes enzymes that allow implantation of the blastocyst into the endometrium of the uterus. The trophoblast will contribute to the placenta and nourish the embryo.

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The cells in the blastula then rearrange themselves spatially to form three layers of cells. This process is called gastrulation. During gastrulation, the blastula folds in on itself and cells migrate to form the three layers of cells (Figure 5.3.3) in a structure, the gastrula, with a hollow space that will become the digestive tract. Each of the layers of cells is called a germ layer and will differentiate into different organ systems.

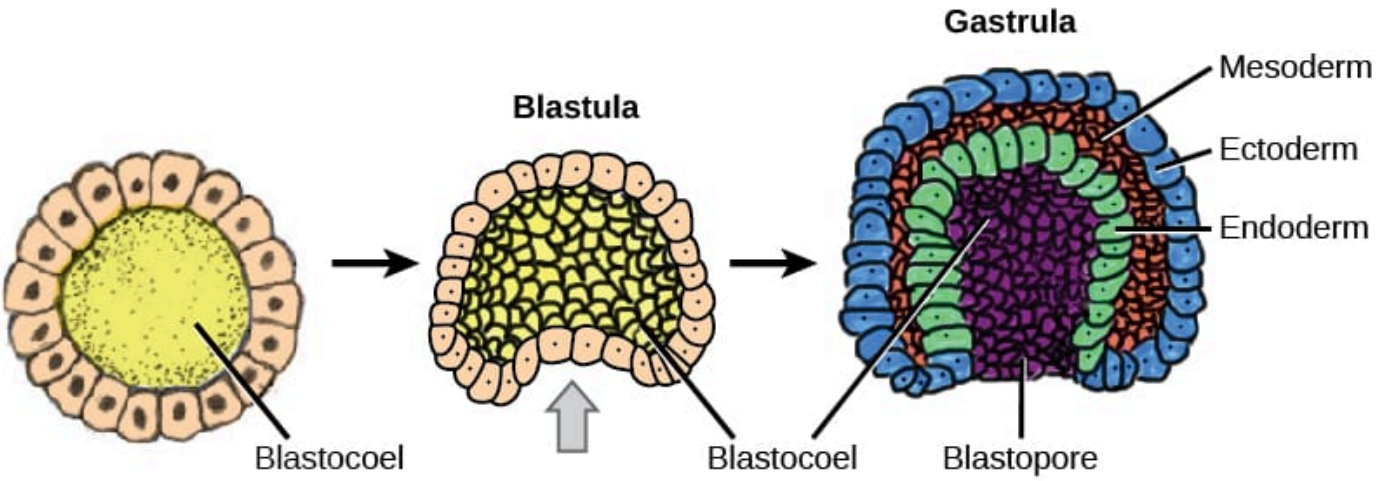


Figure 5.3.3**:** Gastrulation is the process wherein the cells in the blastula rearrange themselves to form the germ layers. (credit: modification of work by Abigail Pyne)

The three germ layers are the endoderm, the ectoderm, and the mesoderm. Cells in each germ layer differentiate into tissues and embryonic organs. The ectoderm gives rise to the nervous system and the epidermis, among other tissues. The mesoderm gives rise to the muscle cells and connective tissue in the body. The endoderm gives rise to the gut and many internal organs.

Organogenesis

Gastrulation leads to the formation of the three germ layers that give rise during further development to the different organs in the animal body. This process is called organogenesis.

Organs develop from the germ layers through the process of differentiation. During differentiation, the embryonic stem cells express specific sets of genes that will determine their ultimate cell type. For example, some cells in the ectoderm will express the genes specific to skin cells. As a result, these cells will take on the shape and characteristics of epidermal cells. The process of differentiation is regulated by location-specific chemical signals from the cell's embryonic environment that sets in play a cascade of events that regulates gene expression.

Summary

The early stages of embryonic development begin with fertilization. The process of fertilization is tightly controlled to ensure that only one sperm fuses with one egg. After fertilization, the zygote undergoes cleavage to form the blastula. The blastula, which in some species is a hollow ball of cells, undergoes a process called gastrulation, during which the three germ layers form. The ectoderm gives rise to the nervous system and the epidermal skin cells, the mesoderm gives rise to the muscle cells and connective tissue in the body, and the endoderm gives rise to the digestive system and other internal organs. Organogenesis is the formation of organs from the germ layers. Each germ layer gives rise to specific tissue types.

Glossary

blastocyst
: the structure formed when cells in the mammalian blastula separate into an inner and outer layer

gastrulation
: the process in which the blastula folds over itself to form the three germ layers

inner cell mass
: the inner layer of cells in the blastocyst, which becomes the embryo

organogenesis
: the process of organ formation during development

trophoblast
: the outer layer of cells in the blastocyst, which gives rise to the embryo's contribution to the placenta

zona pellucida
: the protective layer around the mammalian egg

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6: ANIMAL HOMEOSTASIS

6.1: Homeostasis & Osmoregulation

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6.1: Homeostasis & Osmoregulation

Homeostasis refers to the relatively stable state inside the body of an animal. Animal organs and organ systems constantly adjust to internal and external changes in order to maintain this steady state. Examples of internal conditions maintained homeostatically are the level of blood glucose, body temperature, blood calcium level. These conditions remain stable because of physiologic processes that result in negative feedback relationships. If the blood glucose or calcium rises, this sends a signal to organs responsible for lowering blood glucose or calcium. The signals that restore the normal levels are examples of negative feedback. When homeostatic mechanisms fail, the results can be unfavorable for the animal. Homeostatic mechanisms keep the body in dynamic equilibrium by constantly adjusting to the changes that the body's systems encounter. Even an animal that is apparently inactive is maintaining this homeostatic equilibrium. Two examples of factors that are regulated homeostatically are temperature and water content. The processes that maintain homeostasis of these two factors are called thermoregulation and osmoregulation.

Homeostasis

The goal of homeostasis is the maintenance of equilibrium around a specific value of some aspect of the body or its cells called a set point. While there are normal fluctuations from the set point, the body's systems will usually attempt to go back to this point. A change in the internal or external environment is called a stimulus and is detected by a receptor; the response of the system is to adjust the activities of the system so the value moves back toward the set point. For instance, if the body becomes too warm, adjustments are made to cool the animal. If glucose levels in the blood rise after a meal, adjustments are made to lower them and to get the nutrient into tissues that need it or to store it for later use.

When a change occurs in an animal's environment, an adjustment must be made so that the internal environment of the body and cells remains stable. The receptor that senses the change in the environment is part of a feedback mechanism. The stimulus—temperature, glucose, or calcium levels—is detected by the receptor. The receptor sends information to a control center, often the brain, which relays appropriate signals to an effector organ that is able to cause an appropriate change, either up or down, depending on the information the sensor was sending.

Thermoregulation

Animals can be divided into two groups: those that maintain a constant body temperature in the face of differing environmental temperatures, and those that have a body temperature that is the same as their environment and thus varies with the environmental temperature. Animals that do not have internal control of their body temperature are called ectotherms. The body temperature of these organisms is generally similar to the temperature of the environment, although the individual organisms may do things that keep their bodies slightly below or above the environmental temperature. This can include burrowing underground on a hot day or resting in the sunlight on a cold day. The ectotherms have been called cold-blooded, a term that may not apply to an animal in the desert with a very warm body temperature.

An animal that maintains a constant body temperature in the face of environmental changes is called an endotherm. These animals are able to maintain a level of activity that an ectothermic animal cannot because they generate internal heat that keeps their cellular processes operating optimally even when the environment is cold.

CONCEPT IN ACTION

This interactive element is not available in this format. Visit the link or scan the QR code to access it online.

View this YouTube Video online

Watch this Discovery Channel video on thermoregulation to see illustrations of the process in a variety of animals.

Animals conserve or dissipate heat in a variety of ways. Endothermic animals have some form of insulation. They have fur, fat, or feathers. Animals with thick fur or feathers create an insulating layer of air between their skin and internal organs. Polar bears and seals live and swim in a subfreezing environment and yet maintain a constant, warm, body temperature. The arctic fox, for example, uses its fluffy tail as extra insulation when it curls up to sleep in cold weather. Mammals can increase body heat production by shivering, which is an involuntary increase in muscle activity. In addition, arrectorpili muscles can contract causing individual hairs to stand up when the individual is cold. This increases the insulating effect of the hair. Humans retain this reaction, which does not have the intended effect on our relatively hairless bodies; it causes “goose bumps” instead. Mammals use layers of fat as insulation also. Loss of significant amounts of body fat will compromise an individual’s ability to conserve heat.

Ectotherms and endotherms use their circulatory systems to help maintain body temperature. Vasodilation, the opening up of arteries to the skin by relaxation of their smooth muscles, brings more blood and heat to the body surface, facilitating radiation and evaporative heat loss, cooling the body. Vasoconstriction, the narrowing of blood vessels to the skin by contraction of their smooth muscles, reduces blood flow in peripheral blood vessels, forcing blood toward the core and vital organs, conserving heat. Some animals have adaptions to their circulatory system that enable them to transfer heat from arteries to veins that are flowing next to each other, warming blood returning to the heart. This is called a countercurrent heat exchange; it prevents the cold venous blood from cooling the heart and other internal organs. The countercurrent adaptation is found in dolphins, sharks, bony fish, bees, and hummingbirds.

Some ectothermic animals use changes in their behavior to help regulate body temperature. They simply seek cooler areas during the hottest part of the day in the desert to keep from getting too warm. The same animals may climb onto rocks in the evening to capture heat on a cold desert night before entering their burrows.

Thermoregulation is coordinated by the nervous system (Figure 6.1.1). The processes of temperature control are centered in the hypothalamus of the advanced animal brain. The hypothalamus maintains the set point for body temperature through reflexes that cause vasodilation or vasoconstriction and shivering or sweating. The sympathetic nervous system under control of the hypothalamus directs the responses that effect the changes in temperature loss or gain that return the body to the set point. The set point may be adjusted in some instances. During an infection, compounds called pyrogens are produced and circulate to the hypothalamus resetting the thermostat to a higher value. This allows the body’s temperature to increase to a new homeostatic equilibrium point in what is commonly called a fever. The increase in body heat makes the body less optimal for bacterial growth and increases the activities of cells so they are better able to fight the infection.

ART CONNECTION

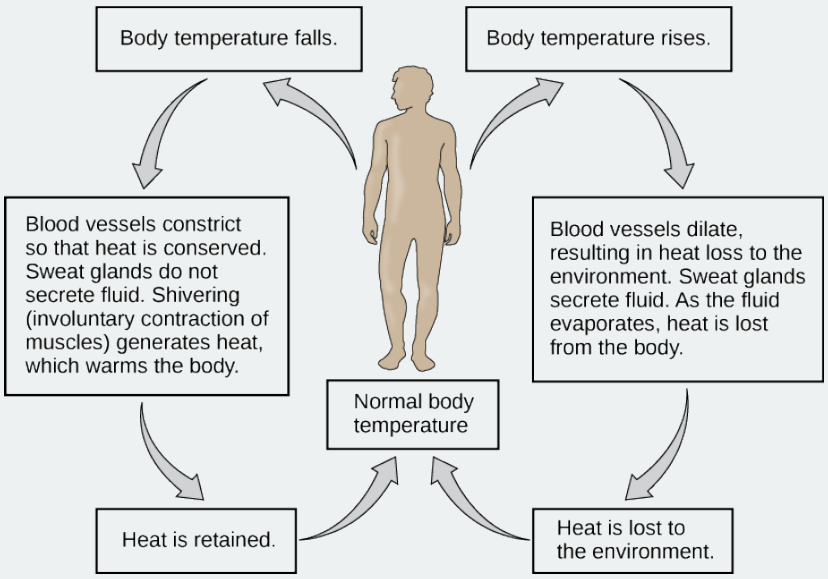


Figure 6.1.1: The body is able to regulate temperature in response to signals from the nervous system.

When bacteria are destroyed by leukocytes, pyrogens are released into the blood. Pyrogens reset the body’s thermostat to a higher temperature, resulting in fever. How might pyrogens cause the body temperature to rise?

Osmoregulation

Osmoregulation is the process of maintaining salt and water balance (osmotic balance) across membranes within the body. The fluids inside and surrounding cells are composed of water, electrolytes, and nonelectrolytes. An electrolyte is a compound that dissociates into ions when dissolved in water. A nonelectrolyte, in contrast, does not dissociate into ions in water. The body's fluids include blood plasma, fluid that exists within cells, and the interstitial fluid that exists in the spaces between cells and tissues of the body. The membranes of the body (both the membranes around cells and the "membranes" made of cells lining body cavities) are semipermeable membranes. Semipermeable membranes are permeable to certain types of solutes and to water, but typically cell membranes are impermeable to solutes.

The body does not exist in isolation. There is a constant input of water and electrolytes into the system. Excess water, electrolytes, and wastes are transported to the kidneys and excreted, helping to maintain osmotic balance. Insufficient fluid intake results in fluid conservation by the kidneys. Biological systems constantly interact and exchange water and nutrients with the environment by way of consumption of food and water and through excretion in the form of sweat, urine, and feces. Without a mechanism to regulate osmotic pressure, or when a disease damages this mechanism, there is a tendency to accumulate toxic waste and water, which can have dire consequences.

Mammalian systems have evolved to regulate not only the overall osmotic pressure across membranes, but also specific concentrations of important electrolytes in the three major fluid compartments: blood plasma, interstitial fluid, and intracellular fluid. Since osmotic pressure is regulated by the movement of water across membranes, the volume of the fluid compartments can also change temporarily. Since blood plasma is one of the fluid components, osmotic pressures have a direct bearing on blood pressure.

Excretory System

The human excretory system functions to remove waste from the body through the skin as sweat, the lungs in the form of exhaled carbon dioxide, and through the urinary system in the form of urine. All three of these systems participate in osmoregulation and waste removal. Here we focus on the urinary system, which is comprised of the paired kidneys, the ureter, urinary bladder and urethra (Figure 6.1.2). The kidneys are a pair of bean-shaped structures that are located just below the liver in the body cavity. Each of the kidneys contains more than a million tiny units called nephrons that filter blood containing the metabolic wastes from cells. All the blood in the human body is filtered about 60 times a day by the kidneys. The nephrons remove wastes, concentrate them, and form urine that is collected in the bladder.

Internally, the kidney has three regions—an outer cortex, a medulla in the middle, and the renal pelvis, which is the expanded end of the ureter. The renal cortex contains the nephrons—the functional unit of the kidney. The renal pelvis collects the urine and leads to the ureteron the outside of the kidney. The ureters are urine-bearing tubes that exit the kidney and empty into the urinary bladder.

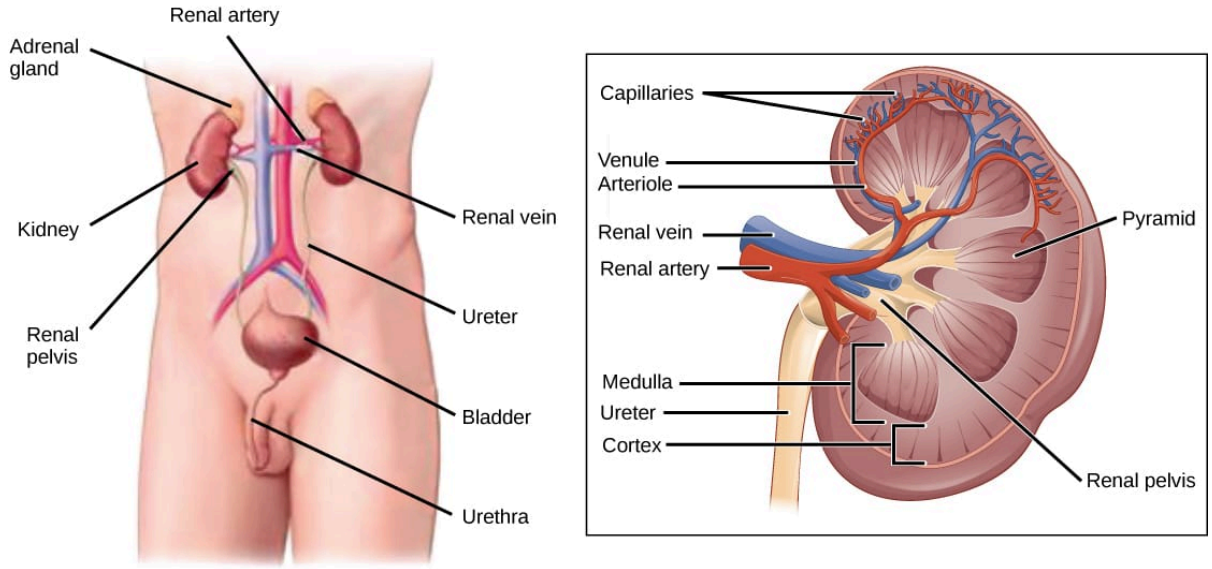


Figure 6.1.2**:** The human excretory system is made up of the kidneys, ureter, urinary bladder, and urethra. The kidneys filter blood and form urine, which is stored in the bladder until it is eliminated through the urethra. On the right, the internal structure of the kidney is shown. (credit: modification of work by NCI, NIH)

Blood enters each kidney from the aorta, the main artery supplying the body below the heart, through a renal artery. It is distributed in smaller vessels until it reaches each nephron in capillaries. Within the nephron the blood comes in intimate contact with the waste-collecting tubules in a structure called the glomerulus. Water and many solutes present in the blood, including ions of sodium, calcium, magnesium, and others; as well as wastes and valuable substances such as amino acids, glucose and vitamins, leave the blood and enter the tubule system of the nephron. As materials pass through the tubule much of the water, required ions, and useful compounds are reabsorbed back into the capillaries that surround the tubules leaving the wastes behind. Some of this reabsorption requires active transport and consumes ATP. Some wastes, including ions and some drugs remaining in the blood, diffuse out of the capillaries into the interstitial fluid and are taken up by the tubule cells. These wastes are then actively secreted into the tubules. The blood then collects in larger and larger vessels and leaves the kidney in the renal vein. The renal vein joins the inferior vena cava, the main vein that returns blood to the heart from the lower body. The amounts of water and ions reabsorbed into the circulatory system are carefully regulated and this is an important way the body regulates its water content and ion levels. The waste is collected in larger tubules and then leaves the kidney in the ureter, which leads to the bladder where urine, the combination of waste materials and water, is stored.

The bladder contains sensory nerves, stretch receptors that signal when it needs to be emptied. These signals create the urge to urinate, which can be voluntarily suppressed up to a limit. The conscious decision to urinate sets in play signals that open the sphincters, rings of smooth muscle that close off the opening, to the urethra that allows urine to flow out of the bladder and the body.

CAREER IN ACTION: Dialysis Technician

Dialysis is a medical process of removing wastes and excess water from the blood by diffusion and ultrafiltration. When kidney function fails, dialysis must be done to artificially rid the body of wastes and fluids. This is a vital process to keep patients alive. In some cases, the patients undergo artificial dialysis until they are eligible for a kidney transplant. In others who are not candidates for kidney transplants, dialysis is a lifelong necessity.

Dialysis technicians typically work in hospitals and clinics. While some roles in this field include equipment development and maintenance, most dialysis technicians work in direct patient care. Their on-the-job duties, which typically occur under the direct supervision of a registered nurse, focus on providing dialysis treatments. This can include reviewing patient history and current condition, assessing and responding to patient needs before and during treatment, and monitoring the dialysis process. Treatment may include taking and reporting a patient's vital signs, preparing solutions and equipment to ensure accurate and sterile procedures.

Section Summary

Homeostasis is a dynamic equilibrium that is maintained in body tissues and organs. It is dynamic because it is constantly adjusting to the changes that the systems encounter. It is an equilibrium because body functions are kept within a normal range, with some fluctuations around a set point. The kidneys are the main osmoregulatory organs in mammalian systems; they function to filter blood and maintain the dissolved ion concentrations of body fluids. They are made up internally of three distinct regions—the cortex, medulla, and pelvis. The blood vessels that transport blood into and out of the kidneys arise from and merge with the aorta and inferior vena cava, respectively. The nephron is the functional unit of the kidney, which actively filters blood and generates urine. The urine leaves the kidney through the ureter and is stored in the urinary bladder. Urine is voided from the body through the urethra.

Art Connections

Figure 6.1.1: When bacteria are destroyed by leukocytes, pyrogens are released into the blood. Pyrogens reset the body's thermostat to a higher temperature, resulting in fever. How might pyrogens cause the body temperature to rise?

Answer

Pyrogens increase body temperature by causing the blood vessels to constrict, inducing shivering, and stopping sweat glands from secreting fluid.

Glossary

ectotherm
an organism that relies primarily on environmental heat sources to maintain its body temperature

endotherm
an organism that relies primarily on internal heat sources to maintain its body temperature

interstitial fluid
the fluid found between cells in the body, similar in constitution to the fluid component of blood, but without the high concentrations of proteins

kidney
the organ that performs excretory and osmoregulatory functions

nephron
the functional unit of the kidney

osmoregulation
the mechanism by which water and solute concentrations are maintained at desired levels

osmotic balance
the appropriate values of water and solute concentrations for a healthy organism

renal artery
the artery that delivers blood to the kidney

renal vein
the vein that drains blood from the kidney

set point
the target value of a physiological state in homeostasis

ureter
the urine-bearing tubes coming out of the kidney

urethra
the tube that conducts urine from the urinary bladder to the external environment

urinary bladder
: the structure that the ureters empty the urine into

Contributors and Attributions

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7: EVOLUTION & NATURAL SELECTION

7.1: Discovering How Populations Change
7.2: Mechanisms of Evolution
7.3: Evidence of Evolution
7.4: Speciation
7.5: Common Misconceptions about Evolution

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7.1: Discovering How Populations Change

The theory of evolution by natural selection describes a mechanism for species change over time. That species change had been suggested and debated well before Darwin. The view that species were static and unchanging was grounded in the writings of Plato, yet there were also ancient Greeks that expressed evolutionary ideas.

In the eighteenth century, ideas about the evolution of animals were reintroduced by the naturalist Georges-Louis Leclerc, Comte de Buffon and even by Charles Darwin's grandfather, Erasmus Darwin. During this time, it was also accepted that there were extinct species. At the same time, James Hutton, the Scottish naturalist, proposed that geological change occurred gradually by the accumulation of small changes from processes (over long periods of time) just like those happening today. This contrasted with the predominant view that the geology of the planet was a consequence of catastrophic events occurring during a relatively brief past. Hutton's view was later popularized by the geologist Charles Lyell in the nineteenth century. Lyell became a friend to Darwin and his ideas were very influential on Darwin's thinking. Lyell argued that the greater age of Earth gave more time for gradual change in species, and the process provided an analogy for gradual change in species.

In the early nineteenth century, Jean-Baptiste Lamarck published a book that detailed a mechanism for evolutionary change that is now referred to as inheritance of acquired characteristics. In Lamarck's theory, modifications in an individual caused by its environment, or the use or disuse of a structure during its lifetime, could be inherited by its offspring and, thus, bring about change in a species. While this mechanism for evolutionary change as described by Lamarck was discredited, Lamarck's ideas were an important influence on evolutionary thought. The inscription on the statue of Lamarck that stands at the gates of the Jardin des Plantes in Paris describes him as the "founder of the doctrine of evolution."

Charles Darwin and Natural Selection

The actual mechanism for evolution was independently conceived of and described by two naturalists, Charles Darwin and Alfred Russell Wallace, in the mid-nineteenth century. Importantly, each spent time exploring the natural world on expeditions to the tropics. From 1831 to 1836, Darwin traveled around the world on *H.M.S. Beagle*, visiting South America, Australia, and the southern tip of Africa. Wallace traveled to Brazil to collect insects in the Amazon rainforest from 1848 to 1852 and to the Malay Archipelago from 1854 to 1862. Darwin's journey, like Wallace's later journeys in the Malay Archipelago, included stops at several island chains, the last being the Galápagos Islands (west of Ecuador). On these islands, Darwin observed species of organisms on different islands that were clearly similar, yet had distinct differences. For example, the ground finches inhabiting the Galápagos Islands comprised several species that each had a unique beak shape (Figure 7.1.1). He observed both that these finches closely resembled another finch species on the mainland of South America and that the group of species in the Galápagos formed a graded series of beak sizes and shapes, with very small differences between the most similar. Darwin imagined that the island species might be all species modified from one original mainland species. In 1860, he wrote, "Seeing this gradation and diversity of structure in one small, intimately related group of birds, one might really fancy that from an original paucity of birds in this archipelago, one species had been taken and modified for different ends."[1]

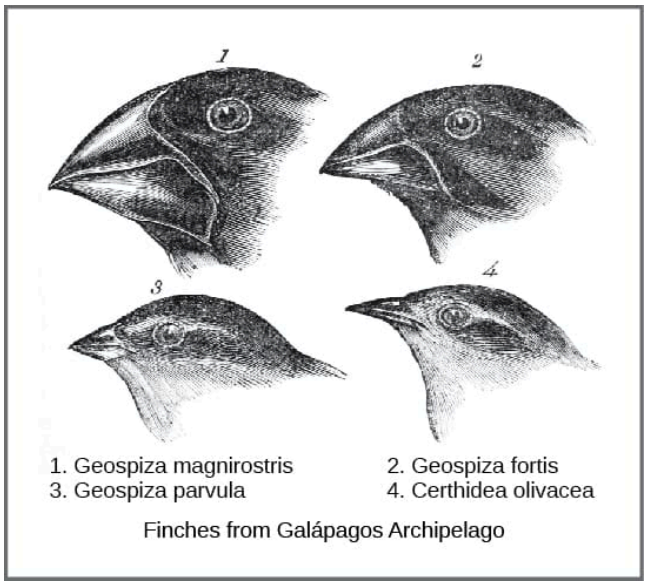


Figure 7.1.1**:** Darwin observed that beak shape varies among finch species. He postulated that the beak of an ancestral species had adapted over time to equip the finches to acquire different food sources. This illustration shows the beak shapes for four species of ground finch: 1. Geospiza magnirostris (the large ground finch), 2. G. fortis (the medium ground finch), 3. G. parvula (the small tree finch), and 4. Certhidea olivacea (the green-warbler finch).

Wallace and Darwin both observed similar patterns in other organisms and independently conceived a mechanism to explain how and why such changes could take place. Darwin called this mechanism natural selection. Natural selection, Darwin argued, was an inevitable outcome of three principles that operated in nature. First, the characteristics of organisms are inherited, or passed from parent to offspring. Second, more offspring are produced than are able to survive; in other words, resources for survival and reproduction are limited. The capacity for reproduction in all organisms outstrips the availability of resources to support their numbers. Thus, there is a competition for those resources in each generation. Both Darwin and Wallace's understanding of this principle came from reading an essay by the economist Thomas Malthus, who discussed this principle in relation to human populations. Third, offspring vary among each other in regard to their characteristics and those variations are inherited. Out of these three principles, Darwin and Wallace reasoned that offspring with inherited characteristics that allow them to best compete for limited resources will survive and have more offspring than those individuals with variations that are less able to compete. Because characteristics are inherited, these traits will be better represented in the next generation. This will lead to change in populations over generations in a process that Darwin called "descent with modification."

Papers by Darwin and Wallace (Figure 7.1.2) presenting the idea of natural selection were read together in 1858 before the Linnaean Society in London. The following year Darwin's book, *On the Origin of Species,* was published, which outlined in considerable detail his arguments for evolution by natural selection.



(a) (b)

Figure 7.1.2**:** (a) Charles Darwin and (b) Alfred Wallace wrote scientific papers on natural selection that were presented together before the Linnean Society in 1858.

Demonstrations of evolution by natural selection can be time consuming. One of the best demonstrations has been in the very birds that helped to inspire the theory, the Galápagos finches. Peter and Rosemary Grant and their colleagues have studied Galápagos finch populations every year since 1976 and have provided important demonstrations of the operation of natural selection. The Grants found changes from one generation to the next in the beak shapes of the medium ground finches on the Galápagos island of Daphne Major. The medium ground finch feeds on seeds. The birds have inherited variation in the bill shape with some individuals having wide, deep bills and others having thinner bills. Large-billed birds feed more efficiently on large, hard seeds, whereas smaller billed birds feed more efficiently on small, soft seeds. During 1977, a drought period altered vegetation on the island. After this period, the number of seeds declined dramatically: the decline in small, soft seeds was greater than the decline in large, hard seeds. The large-billed birds were able to survive better than the small-billed birds the following year. The year following the drought when the Grants measured beak sizes in the much-reduced population, they found that the average bill size was larger (Figure 7.1.3). This was clear evidence for natural selection (differences in survival) of bill size caused by the availability of seeds. The Grants had studied the inheritance of bill sizes and knew that the surviving large-billed birds would tend to produce offspring with larger bills, so the selection would lead to evolution of bill size. Subsequent studies by the Grants have demonstrated selection on and evolution of bill size in this species in response to changing conditions on the island. The evolution has occurred both to larger bills, as in this case, and to smaller bills when large seeds became rare.

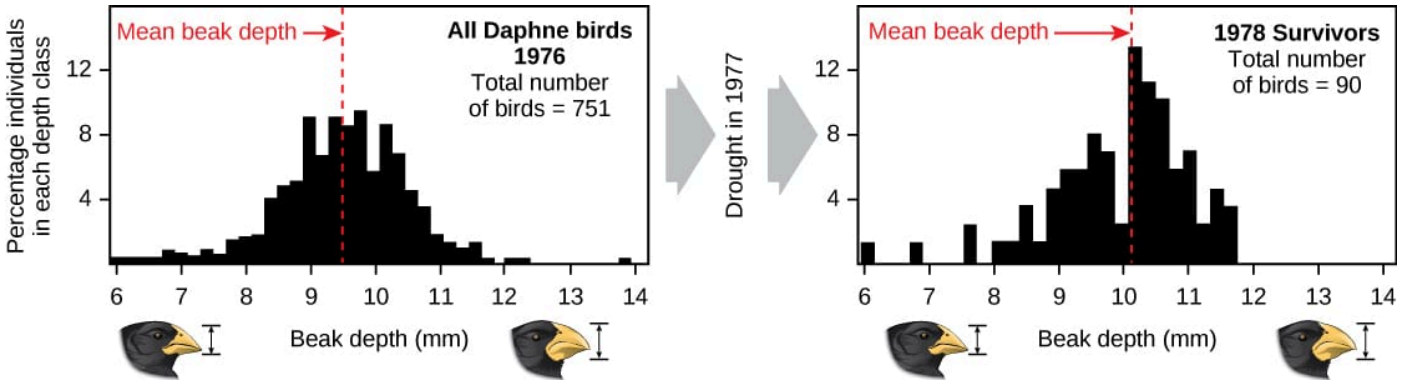


Figure 7.1.3**:** A drought on the Galápagos island of Daphne Major in 1977 reduced the number of small seeds available to finches, causing many of the small-beaked finches to die. This caused an increase in the finches' average beak size between 1976 and 1978.

Variation and Adaptation

Natural selection can only take place if there is variation, or differences, among individuals in a population. Importantly, these differences must have some genetic basis; otherwise, selection will not lead to change in the next generation. This is critical because variation among individuals can be caused by non-genetic reasons, such as an individual being taller because of better

nutrition rather than different genes.

Genetic diversity in a population comes from two main sources: mutation and sexual reproduction. Mutation, a change in DNA, is the ultimate source of new alleles or new genetic variation in any population. An individual that has a mutated gene might have a different trait than other individuals in the population. However, this is not always the case. A mutation can have one of three outcomes on the organisms' appearance (or phenotype):

- A mutation may affect the phenotype of the organism in a way that gives it reduced fitness—lower likelihood of survival, resulting in fewer offspring.
- A mutation may produce a phenotype with a beneficial effect on fitness.
- Many mutations, called neutral mutations, will have no effect on fitness.

Mutations may also have a whole range of effect sizes on the fitness of the organism that expresses them in their phenotype, from a small effect to a great effect. Sexual reproduction and crossing over in meiosis also lead to genetic diversity: when two parents reproduce, unique combinations of alleles assemble to produce unique genotypes and, thus, phenotypes in each of the offspring.

A heritable trait that aids the survival and reproduction of an organism in its present environment is called an adaptation. An adaptation is a "match" of the organism to the environment. Adaptation to an environment comes about when a change in the range of genetic variation occurs over time that increases or maintains the match of the population with its environment. The variations in finch beaks shifted from generation to generation providing adaptation to food availability.

Whether or not a trait is favorable depends on the environment at the time. The same traits do not always have the same relative benefit or disadvantage because environmental conditions can change. For example, finches with large bills were benefited in one climate, while small bills were a disadvantage; in a different climate, the relationship reversed.

Patterns of Evolution

The evolution of species has resulted in enormous variation in form and function. When two species evolve in different directions from a common point, it is called divergent evolution. Such divergent evolution can be seen in the forms of the reproductive organs of flowering plants, which share the same basic anatomies; however, they can look very different as a result of selection in different physical environments, and adaptation to different kinds of pollinators (Figure 7.1.4).

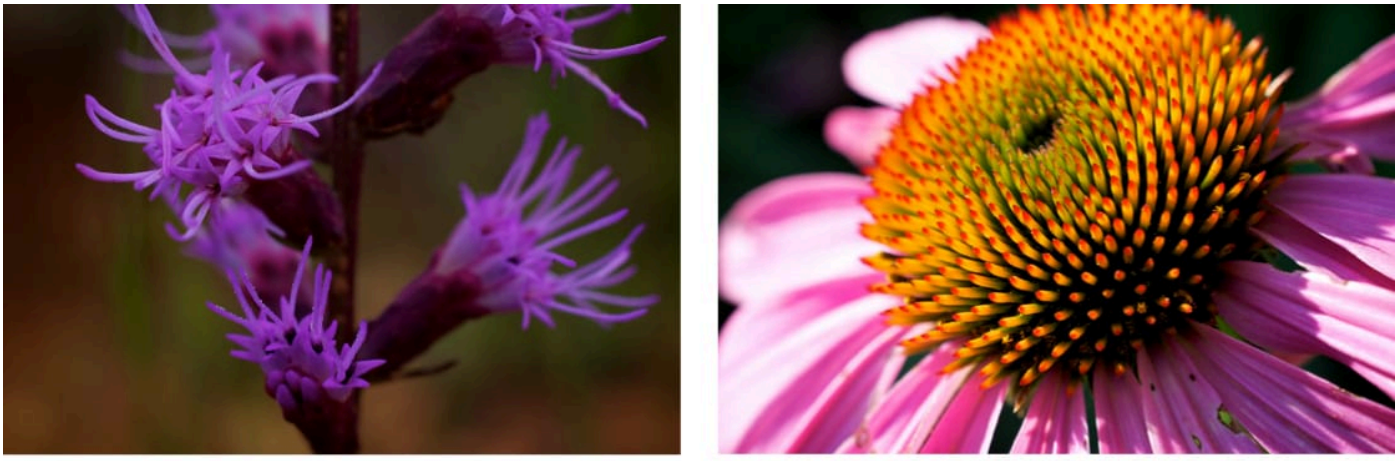


Figure 7.1.4: Flowering plants evolved from a common ancestor. Notice that the (a) dense blazing star and (b) purple coneflower vary in appearance, yet both share a similar basic morphology. (credit a, b: modification of work by Cory Zanker)

In other cases, similar phenotypes evolve independently in distantly related species. For example, flight has evolved in both bats and insects, and they both have structures we refer to as wings, which are adaptations to flight. The wings of bats and insects, however, evolved from very different original structures. When similar structures arise through evolution independently in different species it is called convergent evolution. The wings of bats and insects are called analogous structures; they are similar in function and appearance, but do not share an origin in a common ancestor. Instead they evolved independently in the two lineages. The wings of a hummingbird and an ostrich are homologous structures, meaning they share similarities (despite their

differences resulting from evolutionary divergence). The wings of hummingbirds and ostriches did not evolve independently in the hummingbird lineage and the ostrich lineage—they descended from a common ancestor with wings.

The Modern Synthesis

The mechanisms of inheritance, genetics, were not understood at the time Darwin and Wallace were developing their idea of natural selection. This lack of understanding was a stumbling block to comprehending many aspects of evolution. In fact, blending inheritance was the predominant (and incorrect) genetic theory of the time, which made it difficult to understand how natural selection might operate. Darwin and Wallace were unaware of the genetics work by Austrian monk Gregor Mendel, which was published in 1866, not long after publication of *On the Origin of Species*. Mendel's work was rediscovered in the early twentieth century at which time geneticists were rapidly coming to an understanding of the basics of inheritance. Initially, the newly discovered particulate nature of genes made it difficult for biologists to understand how gradual evolution could occur. But over the next few decades genetics and evolution were integrated in what became known as the modern synthesis—the coherent understanding of the relationship between natural selection and genetics that took shape by the 1940s and is generally accepted today. In sum, the modern synthesis describes how evolutionary pressures, such as natural selection, can affect a population's genetic makeup, and, in turn, how this can result in the gradual evolution of populations and species. The theory also connects this gradual change of a population over time, called microevolution, with the processes that gave rise to new species and higher taxonomic groups with widely divergent characters, called macroevolution.

Population Genetics

Recall that a gene for a particular character may have several variants, or alleles, that code for different traits associated with that character. For example, in the ABO blood type system in humans, three alleles determine the particular blood-type protein on the surface of red blood cells. Each individual in a population of diploid organisms can only carry two alleles for a particular gene, but more than two may be present in the individuals that make up the population. Mendel followed alleles as they were inherited from parent to offspring. In the early twentieth century, biologists began to study what happens to all the alleles in a population in a field of study known as population genetics.

Until now, we have defined evolution as a change in the characteristics of a population of organisms, but behind that phenotypic change is genetic change. In population genetic terms, evolution is defined as a change in the frequency of an allele in a population. Using the ABO system as an example, the frequency of one of the alleles, I^A, is the number of copies of that allele divided by all the copies of the ABO gene in the population. For example, a study in Jordan found a frequency of I^A to be 26.1 percent.[2] The I^B, i^0 alleles made up 13.4 percent and 60.5 percent of the alleles respectively, and all of the frequencies add up to 100 percent. A change in this frequency over time would constitute evolution in the population.

There are several ways the allele frequencies of a population can change. One of those ways is natural selection. If a given allele confers a phenotype that allows an individual to have more offspring that survive and reproduce, that allele, by virtue of being inherited by those offspring, will be in greater frequency in the next generation. Since allele frequencies always add up to 100 percent, an increase in the frequency of one allele always means a corresponding decrease in one or more of the other alleles. Highly beneficial alleles may, over a very few generations, become "fixed" in this way, meaning that every individual of the population will carry the allele. Similarly, detrimental alleles may be swiftly eliminated from the gene pool, the sum of all the alleles in a population. Part of the study of population genetics is tracking how selective forces change the allele frequencies in a population over time, which can give scientists clues regarding the selective forces that may be operating on a given population. The studies of changes in wing coloration in the peppered moth from mottled white to dark in response to soot-covered tree trunks and then back to mottled white when factories stopped producing so much soot is a classic example of studying evolution in natural populations (Figure 7.1.5).

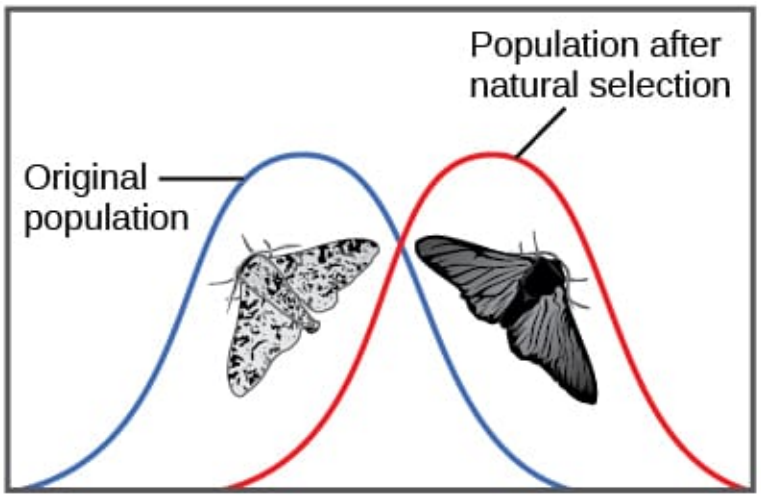


Figure 7.1.5**:** As the Industrial Revolution caused trees to darken from soot, darker colored peppered moths were better camouflaged than the lighter colored ones, which caused there to be more of the darker colored moths in the population.

In the early twentieth century, English mathematician Godfrey Hardy and German physician Wilhelm Weinberg independently provided an explanation for a somewhat counterintuitive concept. Hardy's original explanation was in response to a misunderstanding as to why a "dominant" allele, one that masks a recessive allele, should not increase in frequency in a population until it eliminated all the other alleles. The question resulted from a common confusion about what "dominant" means, but it forced Hardy, who was not even a biologist, to point out that if there are no factors that affect an allele frequency those frequencies will remain constant from one generation to the next. This principle is now known as the Hardy-Weinberg equilibrium. The theory states that a population's allele and genotype frequencies are inherently stable—unless some kind of evolutionary force is acting on the population, the population would carry the same alleles in the same proportions generation after generation. Individuals would, as a whole, look essentially the same and this would be unrelated to whether the alleles were dominant or recessive. The four most important evolutionary forces, which will disrupt the equilibrium, are natural selection, mutation, genetic drift, and migration into or out of a population. A fifth factor, nonrandom mating, will also disrupt the Hardy-Weinberg equilibrium but only by shifting genotype frequencies, not allele frequencies. In nonrandom mating, individuals are more likely to mate with like individuals (or unlike individuals) rather than at random. Since nonrandom mating does not change allele frequencies, it does not cause evolution directly. Natural selection has been described. Mutation creates one allele out of another one and changes an allele's frequency by a small, but continuous amount each generation. Each allele is generated by a low, constant mutation rate that will slowly increase the allele's frequency in a population if no other forces act on the allele. If natural selection acts against the allele, it will be removed from the population at a low rate leading to a frequency that results from a balance between selection and mutation. This is one reason that genetic diseases remain in the human population at very low frequencies. If the allele is favored by selection, it will increase in frequency. Genetic drift causes random changes in allele frequencies when populations are small. Genetic drift can often be important in evolution, as discussed in the next section. Finally, if two populations of a species have different allele frequencies, migration of individuals between them will cause frequency changes in both populations. As it happens, there is no population in which one or more of these processes are not operating, so populations are always evolving, and the Hardy-Weinberg equilibrium will never be exactly observed. However, the Hardy-Weinberg principle gives scientists a baseline expectation for allele frequencies in a non-evolving population to which they can compare evolving populations and thereby infer what evolutionary forces might be at play. The population is evolving if the frequencies of alleles or genotypes deviate from the value expected from the Hardy-Weinberg principle.

Darwin identified a special case of natural selection that he called sexual selection. Sexual selection affects an individual's ability to mate and thus produce offspring, and it leads to the evolution of dramatic traits that often appear maladaptive in terms of survival but persist because they give their owners greater reproductive success. Sexual selection occurs in two ways: through male–male competition for mates and through female selection of mates. Male–male competition takes the form of conflicts between males, which are often ritualized, but may also pose significant threats to a male's survival. Sometimes the competition is for territory, with females more likely to mate with males with higher quality territories. Female choice occurs when females choose a male based on a particular trait, such as feather colors, the performance of a mating dance, or the building of an elaborate structure. In some cases male–male competition and female choice combine in the mating process. In each of these cases, the traits selected for, such as fighting ability or feather color and length, become enhanced in the males. In general, it is thought that sexual selection can proceed to a point at which natural selection against a character's further enhancement prevents its further evolution because it negatively impacts the male's ability to survive. For example, colorful feathers or an elaborate display make the male more obvious to predators.

Summary

Evolution by natural selection arises from three conditions: individuals within a species vary, some of those variations are heritable, and organisms have more offspring than resources can support. The consequence is that individuals with relatively advantageous variations will be more likely to survive and have higher reproductive rates than those individuals with different traits. The advantageous traits will be passed on to offspring in greater proportion. Thus, the trait will have higher representation in the next and subsequent generations leading to genetic change in the population.

The modern synthesis of evolutionary theory grew out of the reconciliation of Darwin's, Wallace's, and Mendel's thoughts on evolution and heredity. Population genetics is a theoretical framework for describing evolutionary change in populations through the change in allele frequencies. Population genetics defines evolution as a change in allele frequency over generations. In the absence of evolutionary forces allele frequencies will not change in a population; this is known as Hardy-Weinberg equilibrium principle. However, in all populations, mutation, natural selection, genetic drift, and migration act to change allele frequencies.

Footnotes

1. 1 Charles Darwin, *Journal of Researches into the Natural History and Geology of the Countries Visited during the Voyage of H.M.S. Beagle Round the World, under the Command of Capt. Fitz Roy, R.N*, 2nd. ed. (London: John Murray, 1860), http://www.archive.org/details/journalofresea00darw.
2. 2 Sahar S. Hanania, Dhia S. Hassawi, and Nidal M. Irshaid, "Allele Frequency and Molecular Genotypes of ABO Blood Group System in a Jordanian Population," *Journal of Medical Sciences* 7 (2007): 51-58, doi:10.3923/jms.2007.51.58

Glossary

adaptation
: a heritable trait or behavior in an organism that aids in its survival in its present environment

analogous structure
: a structure that is similar because of evolution in response to similar selection pressures resulting in convergent evolution, not similar because of descent from a common ancestor

convergent evolution
: an evolution that results in similar forms on different species

divergent evolution
: an evolution that results in different forms in two species with a common ancestor

gene pool
: all of the alleles carried by all of the individuals in the population

genetic drift
: the effect of chance on a population's gene pool

homologous structure
: a structure that is similar because of descent from a common ancestor

inheritance of acquired characteristics
: a phrase that describes the mechanism of evolution proposed by Lamarck in which traits acquired by individuals through use or disuse could be passed on to their offspring thus leading to evolutionary change in the population

macroevolution
: a broader scale of evolutionary changes seen over paleontological time

microevolution
: the changes in a population's genetic structure (i.e., allele frequency)

migration
: the movement of individuals of a population to a new location; in population genetics it refers to the movement of individuals and their alleles from one population to another, potentially changing allele frequencies in both the old

and the new population

modern synthesis
the overarching evolutionary paradigm that took shape by the 1940s and is generally accepted today

natural selection
the greater relative survival and reproduction of individuals in a population that have favorable heritable traits, leading to evolutionary change

population genetics
the study of how selective forces change the allele frequencies in a population over time

variation
the variety of alleles in a population

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7.2: Mechanisms of Evolution

The Hardy-Weinberg equilibrium principle says that allele frequencies in a population will remain constant in the absence of the four factors that could change them. Those factors are natural selection, mutation, genetic drift, and migration (gene flow). In fact, we know they are probably always affecting populations.

Natural Selection

Natural selection has already been discussed. Alleles are expressed in a phenotype. Depending on the environmental conditions, the phenotype confers an advantage or disadvantage to the individual with the phenotype relative to the other phenotypes in the population. If it is an advantage, then that individual will likely have more offspring than individuals with the other phenotypes, and this will mean that the allele behind the phenotype will have greater representation in the next generation. If conditions remain the same, those offspring, which are carrying the same allele, will also benefit. Over time, the allele will increase in frequency in the population.

Mutation

Mutation is a source of new alleles in a population. Mutation is a change in the DNA sequence of the gene. A mutation can change one allele into another, but the net effect is a change in frequency. The change in frequency resulting from mutation is small, so its effect on evolution is small unless it interacts with one of the other factors, such as selection. A mutation may produce an allele that is selected against, selected for, or selectively neutral. Harmful mutations are removed from the population by selection and will generally only be found in very low frequencies equal to the mutation rate. Beneficial mutations will spread through the population through selection, although that initial spread is slow. Whether or not a mutation is beneficial or harmful is determined by whether it helps an organism survive to sexual maturity and reproduce. It should be noted that mutation is the ultimate source of genetic variation in all populations—new alleles, and, therefore, new genetic variations arise through mutation.

Genetic Drift

Another way a population's allele frequencies can change is genetic drift (Figure 7.2.1), which is simply the effect of chance. Genetic drift is most important in small populations. Drift would be completely absent in a population with infinite individuals, but, of course, no population is this large. Genetic drift occurs because the alleles in an offspring generation are a random sample of the alleles in the parent generation. Alleles may or may not make it into the next generation due to chance events including mortality of an individual, events affecting finding a mate, and even the events affecting which gametes end up in fertilizations. If one individual in a population of ten individuals happens to die before it leaves any offspring to the next generation, all of its genes—a tenth of the population's gene pool—will be suddenly lost. In a population of 100, that 1 individual represents only 1 percent of the overall gene pool; therefore, it has much less impact on the population's genetic structure and is unlikely to remove all copies of even a relatively rare allele.

Imagine a population of ten individuals, half with allele *A* and half with allele *a* (the individuals are haploid). In a stable population, the next generation will also have ten individuals. Choose that generation randomly by flipping a coin ten times and let heads be *A* and tails be *a*. It is unlikely that the next generation will have exactly half of each allele. There might be six of one and four of the other, or some different set of frequencies. Thus, the allele frequencies have changed and evolution has occurred. A coin will no longer work to choose the next generation (because the odds are no longer one half for each allele). The frequency in each generation will drift up and down on what is known as a random walk until at one point either all *A* or all *a* are chosen and that allele is fixed from that point on. This could take a very long time for a large population. This simplification is not very biological, but it can be shown that real populations behave this way. The effect of drift on frequencies is greater the smaller a population is. Its effect is also greater on an allele with a frequency far from one half. Drift will influence every allele, even those that are being naturally selected.

ART CONNECTION

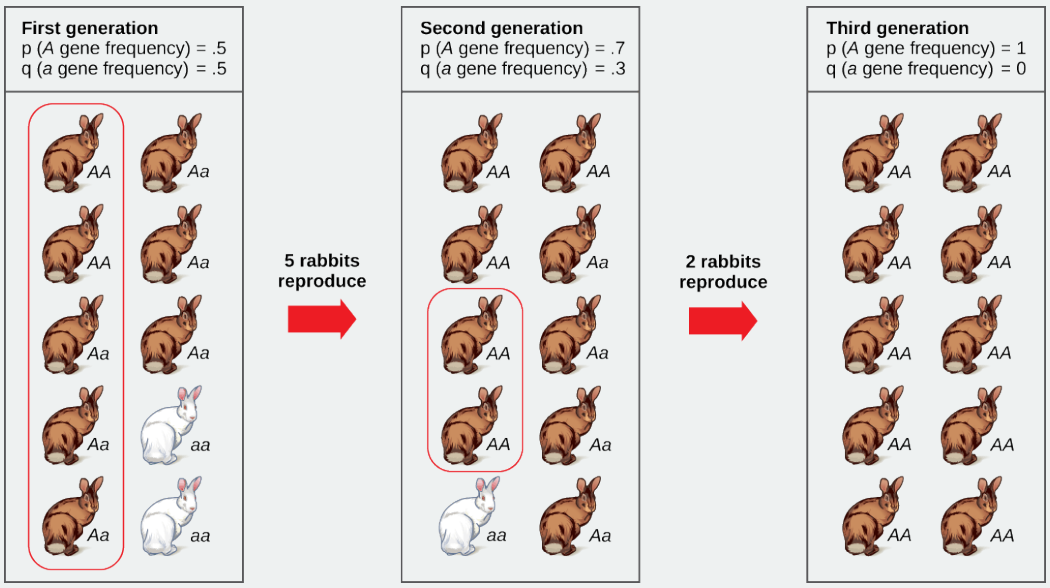


Figure 7.2.1**:** Genetic drift in a population can lead to the elimination of an allele from a population by chance. In each generation, a random set of individuals reproduces to produce the next generation. The frequency of alleles in the next generation is equal to the frequency of alleles among the individuals reproducing.

Do you think genetic drift would happen more quickly on an island or on the mainland?

Genetic drift can also be magnified by natural or human-caused events, such as a disaster that randomly kills a large portion of the population, which is known as the bottleneck effectthat results in a large portion of the genome suddenly being wiped out (Figure 7.2.2). In one fell swoop, the genetic structure of the survivors becomes the genetic structure of the entire population, which may be very different from the pre-disaster population. The disaster must be one that kills for reasons unrelated to the organism's traits, such as a hurricane or lava flow. A mass killing caused by unusually cold temperatures at night, is likely to affect individuals differently depending on the alleles they possess that confer cold hardiness.

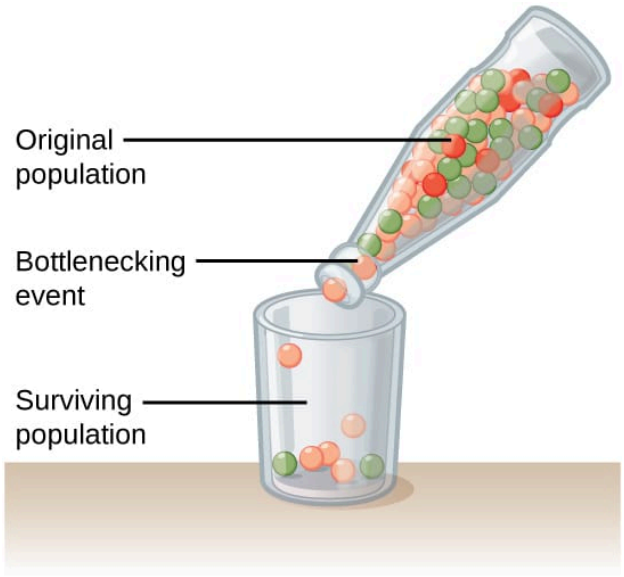


Figure 7.2.2**:** A chance event or catastrophe can reduce the genetic variability within a population.

Another scenario in which populations might experience a strong influence of genetic drift is if some portion of the population leaves to start a new population in a new location, or if a population gets divided by a physical barrier of some kind. In this situation, those individuals are unlikely to be representative of the entire population which results in the founder effect. The

founder effect occurs when the genetic structure matches that of the new population's founding fathers and mothers. The founder effect is believed to have been a key factor in the genetic history of the Afrikaner population of Dutch settlers in South Africa, as evidenced by mutations that are common in Afrikaners but rare in most other populations. This is likely due to a higher-than-normal proportion of the founding colonists, which were a small sample of the original population, carried these mutations. As a result, the population expresses unusually high incidences of Huntington's disease (HD) and Fanconi anemia (FA), a genetic disorder known to cause bone marrow and congenital abnormalities, and even cancer.[1]

CONCEPT IN ACTION

Visit this site to learn more about genetic drift and to run simulations of allele changes caused by drift.

Gene Flow

Another important evolutionary force is gene flow, or the flow of alleles in and out of a population resulting from the migration of individuals or gametes (Figure 7.2.3). While some populations are fairly stable, others experience more flux. Many plants, for example, send their seeds far and wide, by wind or in the guts of animals; these seeds may introduce alleles common in the source population to a new population in which they are rare.

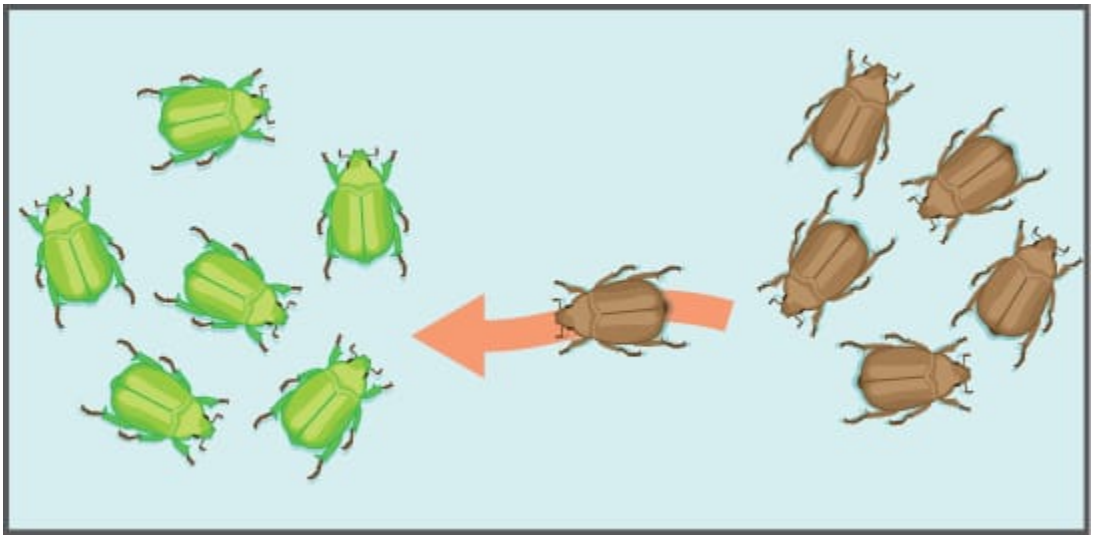


Figure 7.2.3: Gene flow can occur when an individual travels from one geographic location to another and joins a different population of the species. In the example shown here, the brown allele is introduced into the green population.

Summary

There are four factors that can change the allele frequencies of a population. Natural selection works by selecting for alleles that confer beneficial traits or behaviors, while selecting against those for deleterious qualities. Mutations introduce new alleles into a population. Genetic drift stems from the chance occurrence that some individuals have more offspring than others and results in changes in allele frequencies that are random in direction. When individuals leave or join the population, allele frequencies can change as a result of gene flow.

Art Connections

Figure 7.2.1: Do you think genetic drift would happen more quickly on an island or on the mainland?

Answer

Genetic drift is likely to occur more rapidly on an island, where smaller populations are expected to occur.

Footnotes

1. 1 A. J. Tipping et al., “Molecular and Genealogical Evidence for a Founder Effect in Fanconi Anemia Families of the Afrikaner Population of South Africa,” *PNAS* 98, no. 10 (2001): 5734-5739, doi: 10.1073/pnas.091402398.

Glossary

bottleneck effect
: the magnification of genetic drift as a result of natural events or catastrophes

founder effect
: a magnification of genetic drift in a small population that migrates away from a large parent population carrying with it an unrepresentative set of alleles

gene flow
: the flow of alleles in and out of a population due to the migration of individuals or gametes

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7.3: Evidence of Evolution

The evidence for evolution is compelling and extensive. Looking at every level of organization in living systems, biologists see the signature of past and present evolution. Darwin dedicated a large portion of his book, *On the Origin of Species*, identifying patterns in nature that were consistent with evolution and since Darwin our understanding has become clearer and broader.

Fossils

Fossils provide solid evidence that organisms from the past are not the same as those found today; fossils show a progression of evolution. Scientists determine the age of fossils and categorize them all over the world to determine when the organisms lived relative to each other. The resulting fossil record tells the story of the past, and shows the evolution of form over millions of years (Figure 7.3.1). For example, highly detailed fossil records have been recovered for sequences of species in the evolution of whales and modern horses. The fossil record of horses in North America is especially rich and many contain transition fossils: those showing intermediate anatomy between earlier and later forms. The fossil record extends back to a dog-like ancestor some 55 million years ago that gave rise to the first horse-like species 55 to 42 million years ago in the genus *Eohippus*. The series of fossils tracks the change in anatomy resulting from a gradual drying trend that changed the landscape from a forested one to a prairie. Successive fossils show the evolution of teeth shapes and foot and leg anatomy to a grazing habit, with adaptations for escaping predators, for example in species of *Mesohippus* found from 40 to 30 million years ago. Later species showed gains in size, such as those of *Hipparion*, which existed from about 23 to 2 million years ago. The fossil record shows several adaptive radiations in the horse lineage, which is now much reduced to only one genus, *Equus*, with several species.

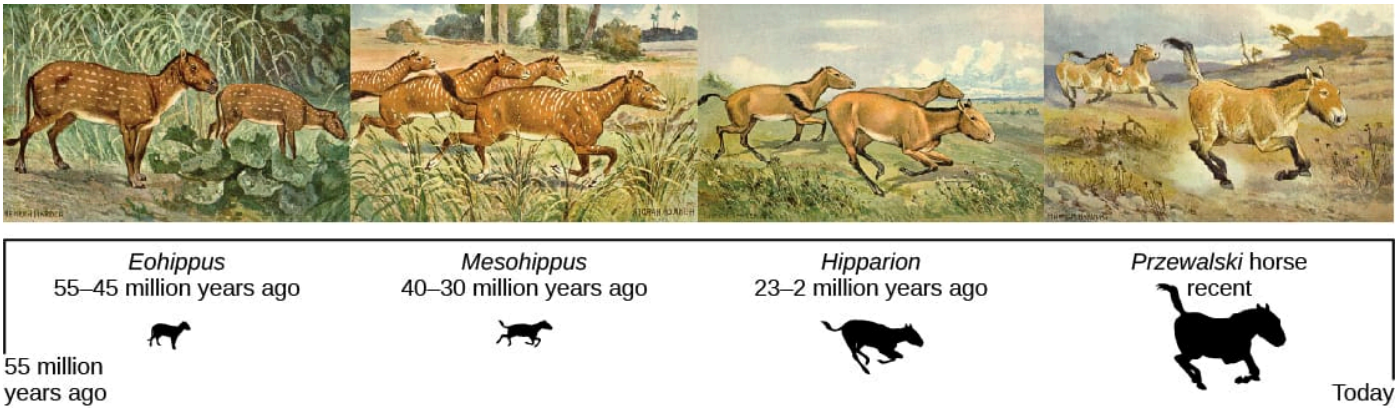


Figure 7.3.1**:** This illustration shows an artist's renderings of these species derived from fossils of the evolutionary history of the horse and its ancestors. The species depicted are only four from a very diverse lineage that contains many branches, dead ends, and adaptive radiations. One of the trends, depicted here is the evolutionary tracking of a drying climate and increase in prairie versus forest habitat reflected in forms that are more adapted to grazing and predator escape through running. Przewalski's horse is one of a few living species of horse.

Anatomy and Embryology

Another type of evidence for evolution is the presence of structures in organisms that share the same basic form. For example, the bones in the appendages of a human, dog, bird, and whale all share the same overall construction (Figure 7.3.2). That similarity results from their origin in the appendages of a common ancestor. Over time, evolution led to changes in the shapes and sizes of these bones in different species, but they have maintained the same overall layout, evidence of descent from a common ancestor. Scientists call these synonymous parts homologous structures. Some structures exist in organisms that have no apparent function at all, and appear to be residual parts from a past ancestor. For example, some snakes have pelvic bones despite having no legs because they descended from reptiles that did have legs. These unused structures without function are called vestigial structures. Other examples of vestigial structures are wings on flightless birds (which may have other functions), leaves on some cacti, traces of pelvic bones in whales, and the sightless eyes of cave animals.

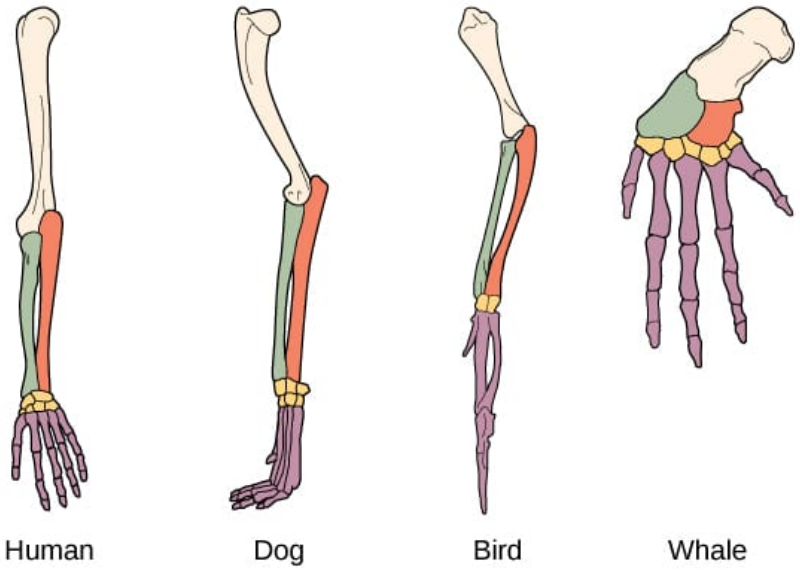


Figure 7.3.2**:** The similar construction of these appendages indicates that these organisms share a common ancestor.

Another evidence of evolution is the convergence of form in organisms that share similar environments. For example, species of unrelated animals, such as the arctic fox and ptarmigan (a bird), living in the arctic region have temporary white coverings during winter to blend with the snow and ice (Figure 7.3.3). The similarity occurs not because of common ancestry, indeed one covering is of fur and the other of feathers, but because of similar selection pressures—the benefits of not being seen by predators.



Figure 7.3.3**:** The white winter coat of (a) the arctic fox and (b) the ptarmigan's plumage are adaptations to their environments. (credit a: modification of work by Keith Morehouse)

Embryology, the study of the development of the anatomy of an organism to its adult form also provides evidence of relatedness between now widely divergent groups of organisms. Structures that are absent in some groups often appear in their embryonic forms and disappear by the time the adult or juvenile form is reached. For example, all vertebrate embryos, including humans, exhibit gill slits at some point in their early development. These disappear in the adults of terrestrial groups, but are maintained in adult forms of aquatic groups such as fish and some amphibians. Great ape embryos, including humans, have a tail structure during their development that is lost by the time of birth. The reason embryos of unrelated species are often similar is that mutational changes that affect the organism during embryonic development can cause amplified differences in the adult, even while the embryonic similarities are preserved.

Biogeography

The geographic distribution of organisms on the planet follows patterns that are best explained by evolution in conjunction with the movement of tectonic plates over geological time. Broad groups that evolved before the breakup of the supercontinent Pangaea (about 200 million years ago) are distributed worldwide. Groups that evolved since the breakup appear uniquely in regions of the planet, for example the unique flora and fauna of northern continents that formed from the supercontinent Laurasia and of the southern continents that formed from the supercontinent Gondwana. The presence of Proteaceae in Australia, southern Africa, and South America is best explained by the plant family's presence there prior to the southern supercontinent Gondwana breaking up (Figure 7.3.4).

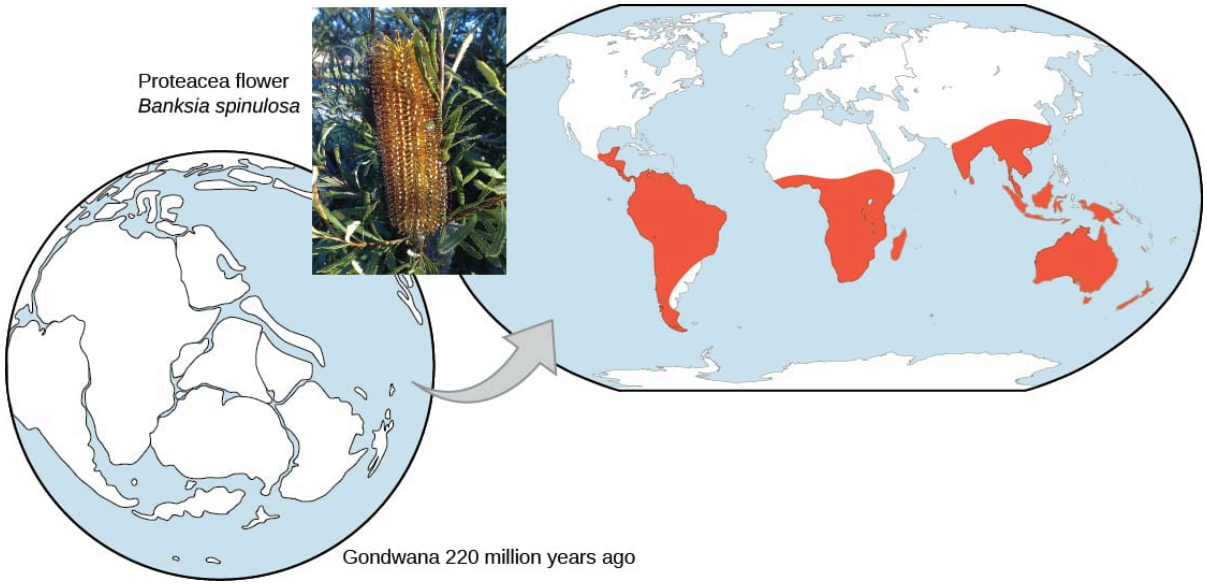


Figure 7.3.4: The Proteacea family of plants evolved before the supercontinent Gondwana broke up. Today, members of this plant family are found throughout the southern hemisphere (shown in red). (credit "Proteacea flower": modification of work by "dorofofoto"/Flickr)

The great diversification of the marsupials in Australia and the absence of other mammals reflects that island continent's long isolation. Australia has an abundance of endemic species—species found nowhere else—which is typical of islands whose isolation by expanses of water prevents migration of species to other regions. Over time, these species diverge evolutionarily into new species that look very different from their ancestors that may exist on the mainland. The marsupials of Australia, the finches on the Galápagos, and many species on the Hawaiian Islands are all found nowhere else but on their island, yet display distant relationships to ancestral species on mainlands.

Molecular Biology

Like anatomical structures, the structures of the molecules of life reflect descent with modification. Evidence of a common ancestor for all of life is reflected in the universality of DNA as the genetic material and of the near universality of the genetic code and the machinery of DNA replication and expression. Fundamental divisions in life between the three domains are reflected in major structural differences in otherwise conservative structures such as the components of ribosomes and the structures of membranes. In general, the relatedness of groups of organisms is reflected in the similarity of their DNA sequences—exactly the pattern that would be expected from descent and diversification from a common ancestor.

DNA sequences have also shed light on some of the mechanisms of evolution. For example, it is clear that the evolution of new functions for proteins commonly occurs after gene duplication events. These duplications are a kind of mutation in which an entire gene is added as an extra copy (or many copies) in the genome. These duplications allow the free modification of one copy by mutation, selection, and drift, while the second copy continues to produce a functional protein. This allows the original function for the protein to be kept, while evolutionary forces tweak the copy until it functions in a new way.

Section Summary

The evidence for evolution is found at all levels of organization in living things and in the extinct species we know about through fossils. Fossils provide evidence for the evolutionary change through now extinct forms that led to modern species. For example, there is a rich fossil record that shows the evolutionary transitions from horse ancestors to modern horses that document intermediate forms and a gradual adaptation to changing ecosystems. The anatomy of species and the embryological development of that anatomy reveal common structures in divergent lineages that have been modified over time by evolution. The geographical distribution of living species reflects the origins of species in particular geographic locations and the history of continental movements. The structures of molecules, like anatomical structures, reflect the relationships of living species and match patterns of similarity expected from descent with modification.

Glossary

vestigial structure
: a physical structure present in an organism but that has no apparent function and appears to be from a functional structure in a distant ancestor

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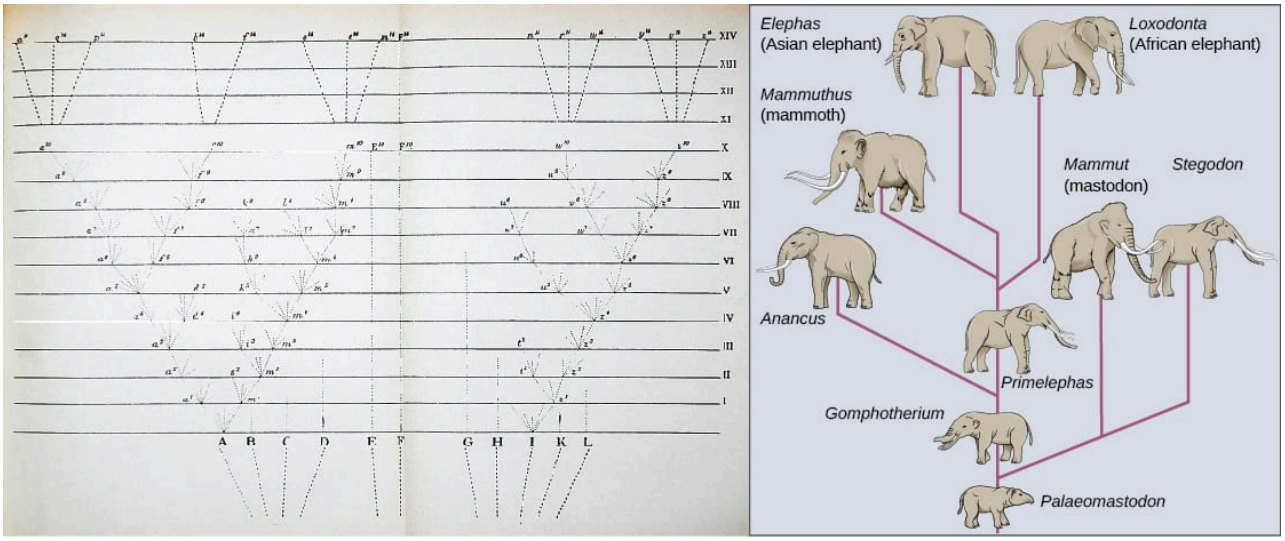
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7.4: Speciation

The biological definition of species, which works for sexually reproducing organisms, is a group of actually or potentially interbreeding individuals. According to this definition, one species is distinguished from another by the possibility of matings between individuals from each species to produce fertile offspring. There are exceptions to this rule. Many species are similar enough that hybrid offspring are possible and may often occur in nature, but for the majority of species this rule generally holds. In fact, the presence of hybrids between similar species suggests that they may have descended from a single interbreeding species and that the speciation process may not yet be completed.

Given the extraordinary diversity of life on the planet there must be mechanisms for speciation: the formation of two species from one original species. Darwin envisioned this process as a branching event and diagrammed the process in the only illustration found in *On the Origin of Species* (Figure 7.4.1**a**). For speciation to occur, two new populations must be formed from one original population, and they must evolve in such a way that it becomes impossible for individuals from the two new populations to interbreed. Biologists have proposed mechanisms by which this could occur that fall into two broad categories. Allopatric speciation, meaning speciation in "other homelands," involves a geographic separation of populations from a parent species and subsequent evolution. Sympatric speciation, meaning speciation in the "same homeland," involves speciation occurring within a parent species while remaining in one location.

Biologists think of speciation events as the splitting of one ancestral species into two descendant species. There is no reason why there might not be more than two species formed at one time except that it is less likely and such multiple events can also be conceptualized as single splits occurring close in time.



(a) (b)

Figure 7.4.1**:** The only illustration in Darwin's On the Origin of Species is (a) a diagram showing speciation events leading to biological diversity. The diagram shows similarities to phylogenetic charts that are drawn today to illustrate the relationships of species. (b) Modern elephants evolved from the Palaeomastodon, a species that lived in Egypt 35–50 million years ago.

Speciation through Geographic Separation

A geographically continuous population has a gene pool that is relatively homogeneous. Gene flow, the movement of alleles across the range of the species, is relatively free because individuals can move and then mate with individuals in their new location. Thus, the frequency of an allele at one end of a distribution will be similar to the frequency of the allele at the other end. When populations become geographically discontinuous that free-flow of alleles is prevented. When that separation lasts for a period of time, the two populations are able to evolve along different trajectories. Thus, their allele frequencies at numerous genetic loci gradually become more and more different as new alleles independently arise by mutation in each population. Typically, environmental conditions, such as climate, resources, predators, and competitors, for the two populations will differ causing natural selection to favor divergent adaptations in each group. Different histories of genetic drift, enhanced because the

populations are smaller than the parent population, will also lead to divergence.

Given enough time, the genetic and phenotypic divergence between populations will likely affect characters that influence reproduction enough that were individuals of the two populations brought together, mating would be less likely, or if a mating occurred, offspring would be non-viable or infertile. Many types of diverging characters may affect the reproductive isolation (inability to interbreed) of the two populations. These mechanisms of reproductive isolation can be divided into prezygotic mechanisms (those that operate before fertilization) and postzygotic mechanisms (those that operate after fertilization). Prezygotic mechanisms include traits that allow the individuals to find each other, such as the timing of mating, sensitivity to pheromones, or choice of mating sites. If individuals are able to encounter each other, character divergence may prevent courtship rituals from leading to a mating either because female preferences have changed or male behaviors have changed. Physiological changes may interfere with successful fertilization if mating is able to occur. Postzygotic mechanisms include genetic incompatibilities that prevent proper development of the offspring, or if the offspring live, they may be unable to produce viable gametes themselves as in the example of the mule, the infertile offspring of a female horse and a male donkey.

If the two isolated populations are brought back together and the hybrid offspring that formed from matings between individuals of the two populations have lower survivorship or reduced fertility, then selection will favor individuals that are able to discriminate between potential mates of their own population and the other population. This selection will enhance the reproductive isolation.

Isolation of populations leading to allopatric speciation can occur in a variety of ways: from a river forming a new branch, erosion forming a new valley, or a group of organisms traveling to a new location without the ability to return, such as seeds floating over the ocean to an island. The nature of the geographic separation necessary to isolate populations depends entirely on the biology of the organism and its potential for dispersal. If two flying insect populations took up residence in separate nearby valleys, chances are that individuals from each population would fly back and forth, continuing gene flow. However, if two rodent populations became divided by the formation of a new lake, continued gene flow would be unlikely; therefore, speciation would be more likely.

Biologists group allopatric processes into two categories. If a few members of a species move to a new geographical area, this is called dispersal. If a natural situation arises to physically divide organisms, this is called vicariance.

Scientists have documented numerous cases of allopatric speciation taking place. For example, along the west coast of the United States, two separate subspecies of spotted owls exist. The northern spotted owl has genetic and phenotypic differences from its close relative, the Mexican spotted owl, which lives in the south (Figure 7.4.2). The cause of their initial separation is not clear, but it may have been caused by the glaciers of the ice age dividing an initial population into two.[1]

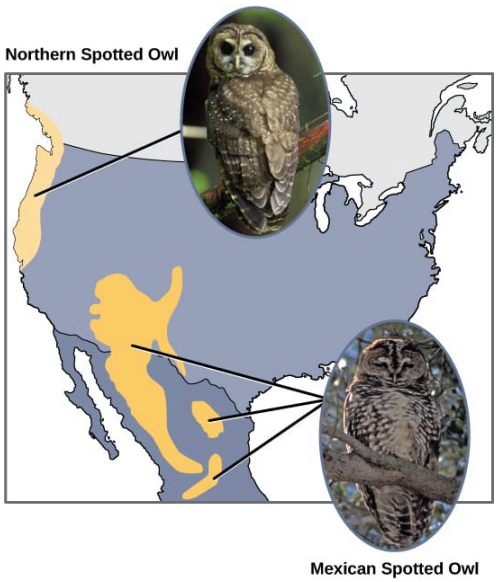


Figure 7.4.2**:** The northern spotted owl and the Mexican spotted owl inhabit geographically separate locations with different climates and ecosystems. The owl is an example of incipient speciation. (credit “northern spotted owl”: modification of work by John and Karen Hollingsworth, USFWS; credit “Mexican spotted owl”: modification of work by Bill Radke, USFWS)

Additionally, scientists have found that the further the distance between two groups that once were the same species, the more likely for speciation to take place. This seems logical because as the distance increases, the various environmental factors would

likely have less in common than locations in close proximity. Consider the two owls; in the north, the climate is cooler than in the south; the other types of organisms in each ecosystem differ, as do their behaviors and habits; also, the hunting habits and prey choices of the owls in the south vary from the northern ones. These variances can lead to evolved differences in the owls, and over time speciation will likely occur unless gene flow between the populations is restored.

In some cases, a population of one species disperses throughout an area, and each finds a distinct niche or isolated habitat. Over time, the varied demands of their new lifestyles lead to multiple speciation events originating from a single species, which is called adaptive radiation. From one point of origin, many adaptations evolve causing the species to radiate into several new ones. Island archipelagos like the Hawaiian Islands provide an ideal context for adaptive radiation events because water surrounds each island, which leads to geographical isolation for many organisms (Figure 7.4.3). The Hawaiian honeycreeper illustrates one example of adaptive radiation. From a single species, called the founder species, numerous species have evolved, including the eight shown in Figure 7.4.3.

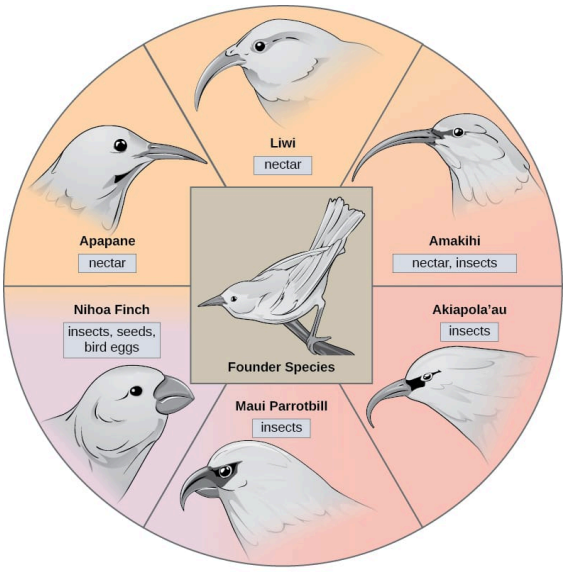


Figure 7.4.3**:** The honeycreeper birds illustrate adaptive radiation. From one original species of bird, multiple others evolved, each with its own distinctive characteristics.

Notice the differences in the species' beaks in Figure 7.4.3. Change in the genetic variation for beaks in response to natural selection based on specific food sources in each new habitat led to evolution of a different beak suited to the specific food source. The fruit and seed-eating birds have thicker, stronger beaks which are suited to break hard nuts. The nectar-eating birds have long beaks to dip into flowers to reach their nectar. The insect-eating birds have beaks like swords, appropriate for stabbing and impaling insects. Darwin's finches are another well-studied example of adaptive radiation in an archipelago.

Speciation without Geographic Separation

Can divergence occur if no physical barriers are in place to separate individuals who continue to live and reproduce in the same habitat? A number of mechanisms for sympatric speciation have been proposed and studied.

One form of sympatric speciation can begin with a chromosomal error during meiosis or the formation of a hybrid individual with too many chromosomes. Polyploidy is a condition in which a cell, or organism, has an extra set, or sets, of chromosomes. Scientists have identified two main types of polyploidy that can lead to reproductive isolation of an individual in the polyploid state. In some cases a polyploid individual will have two or more complete sets of chromosomes from its own species in a condition called autopolyploidy (Figure 7.4.4). The prefix "auto" means self, so the term means multiple chromosomes from one's own species. Polyploidy results from an error in meiosis in which all of the chromosomes move into one cell instead of separating.

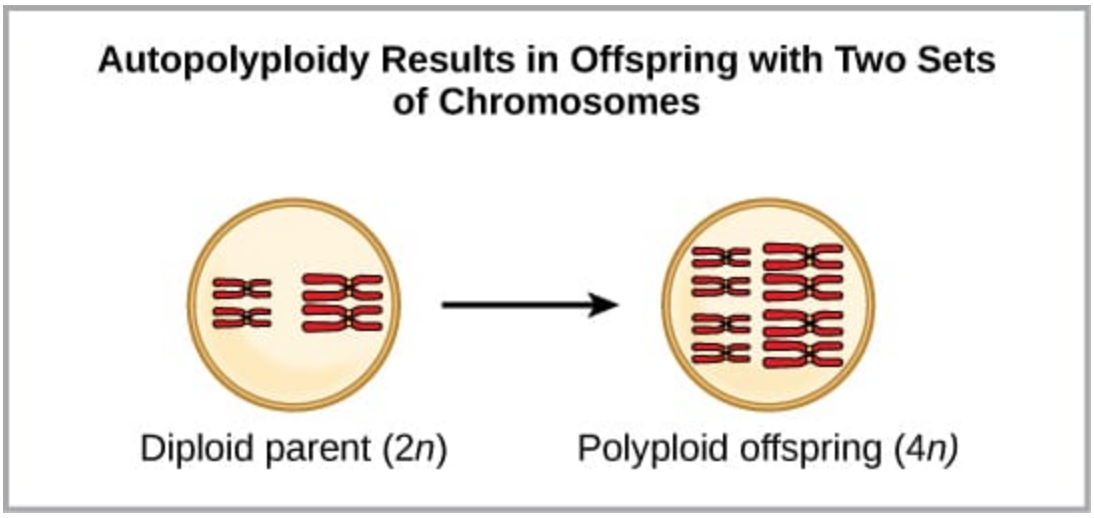


Figure 7.4.4**:** Autopolyploidy results when mitosis is not followed by cytokinesis.

For example, if a plant species with $2n = 6$ produces autopolyploid gametes that are also diploid ($2n = 6$, when they should be $n = 3$), the gametes now have twice as many chromosomes as they should have. These new gametes will be incompatible with the normal gametes produced by this plant species. But they could either self-pollinate or reproduce with other autopolyploid plants with gametes having the same diploid number. In this way, sympatric speciation can occur quickly by forming offspring with $4n$ called a tetraploid. These individuals would immediately be able to reproduce only with those of this new kind and not those of the ancestral species. The other form of polyploidy occurs when individuals of two different species reproduce to form a viable offspring called an allopolyploid. The prefix "allo" means "other" (recall from allopatric); therefore, an allopolyploid occurs when gametes from two different species combine. Figure 7.4.5 illustrates one possible way an allopolyploidy can form. Notice how it takes two generations, or two reproductive acts, before the viable fertile hybrid results.

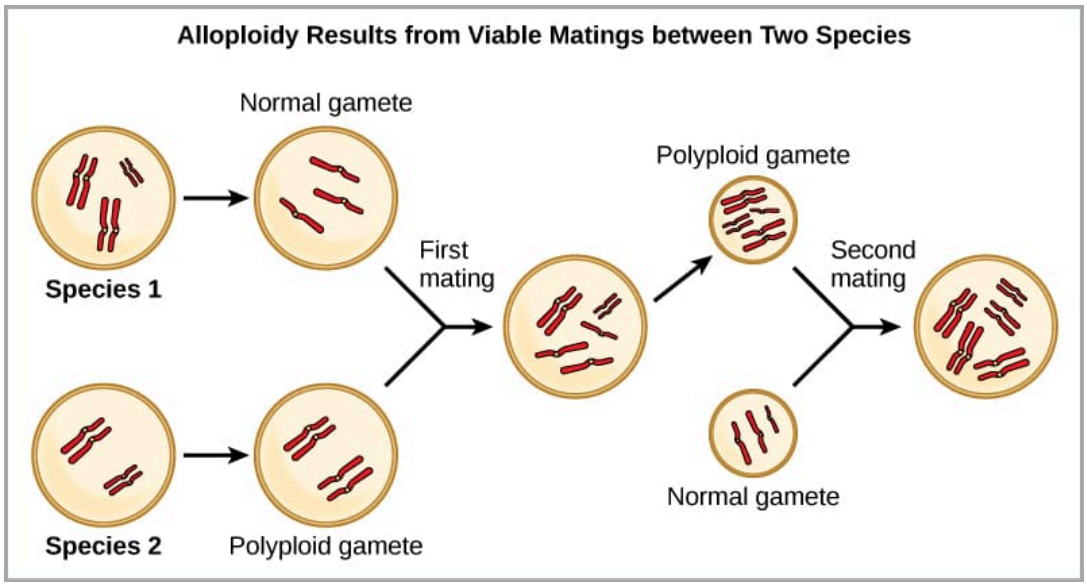


Figure 7.4.5**:** Alloploidy results when two species mate to produce viable offspring. In the example shown, a normal gamete from one species fuses with a polyploid gamete from another. Two matings are necessary to produce viable offspring.

The cultivated forms of wheat, cotton, and tobacco plants are all allopolyploids. Although polyploidy occurs occasionally in animals, most chromosomal abnormalities in animals are lethal; it takes place most commonly in plants. Scientists have discovered more than 1/2 of all plant species studied relate back to a species evolved through polyploidy.

Sympatric speciation may also take place in ways other than polyploidy. For example, imagine a species of fish that lived in a lake. As the population grew, competition for food also grew. Under pressure to find food, suppose that a group of these fish had the genetic flexibility to discover and feed off another resource that was unused by the other fish. What if this new food source was found at a different depth of the lake? Over time, those feeding on the second food source would interact more with

each other than the other fish; therefore they would breed together as well. Offspring of these fish would likely behave as their parents and feed and live in the same area, keeping them separate from the original population. If this group of fish continued to remain separate from the first population, eventually sympatric speciation might occur as more genetic differences accumulated between them.

This scenario does play out in nature, as do others that lead to reproductive isolation. One such place is Lake Victoria in Africa, famous for its sympatric speciation of cichlid fish. Researchers have found hundreds of sympatric speciation events in these fish, which have not only happened in great number, but also over a short period of time. Figure 7.4.6 shows this type of speciation among a cichlid fish population in Nicaragua. In this locale, two types of cichlids live in the same geographic location; however, they have come to have different morphologies that allow them to eat various food sources.

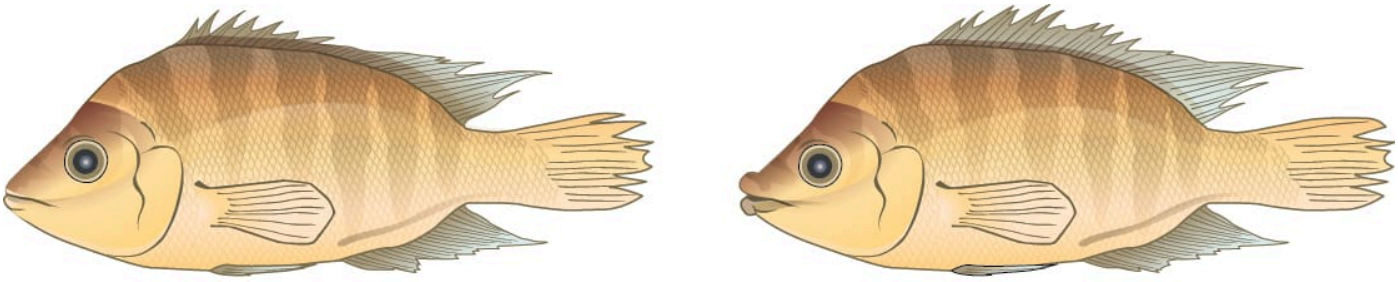


Figure 7.4.6**:** Cichlid fish from Lake Apoyeque, Nicaragua, show evidence of sympatric speciation. Lake Apoyeque, a crater lake, is 1800 years old, but genetic evidence indicates that the lake was populated only 100 years ago by a single population of cichlid fish. Nevertheless, two populations with distinct morphologies and diets now exist in the lake, and scientists believe these populations may be in an early stage of speciation.

Finally, a well-documented example of ongoing sympatric speciation occurred in the apple maggot fly, *Rhagoletis pomonella,* which arose as an isolated population sometime after the introduction of the apple into North America. The native population of flies fed on hawthorn species and is host-specific: it only infests hawthorn trees. Importantly, it also uses the trees as a location to meet for mating. It is hypothesized that either through mutation or a behavioral mistake, flies jumped hosts and met and mated in apple trees, subsequently laying their eggs in apple fruit. The offspring matured and kept their preference for the apple trees effectively dividing the original population into two new populations separated by host species, not by geography. The host jump took place in the nineteenth century, but there are now measureable differences between the two populations of fly. It seems likely that host specificity of parasites in general is a common cause of sympatric speciation.

Section Summary

Speciation occurs along two main pathways: geographic separation (allopatric speciation) and through mechanisms that occur within a shared habitat (sympatric speciation). Both pathways force reproductive isolation between populations. Sympatric speciation can occur through errors in meiosis that form gametes with extra chromosomes, called polyploidy. Autopolyploidy occurs within a single species, whereas allopolyploidy occurs because of a mating between closely related species. Once the populations are isolated, evolutionary divergence can take place leading to the evolution of reproductive isolating traits that prevent interbreeding should the two populations come together again. The reduced viability of hybrid offspring after a period of isolation is expected to select for stronger inherent isolating mechanisms.

Footnotes

1. 1 Courtney, S.P., et al, “Scientific Evaluation of the Status of the Northern Spotted Owl,” Sustainable Ecosystems Institute (2004), Portland, OR.

Glossary

adaptive radiation
: a speciation when one species radiates out to form several other species

allopatric speciation
: a speciation that occurs via a geographic separation

dispersal
: an allopatric speciation that occurs when a few members of a species move to a new geographical area

speciation
: a formation of a new species

sympatric speciation
: a speciation that occurs in the same geographic space

vicariance
: an allopatric speciation that occurs when something in the environment separates organisms of the same species into separate groups

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7.5: Common Misconceptions about Evolution

Although the theory of evolution initially generated some controversy, by 20 years after the publication of *On the Origin of Species* it was almost universally accepted by biologists, particularly younger biologists. Nevertheless, the theory of evolution is a difficult concept and misconceptions about how it works abound. In addition, there are those that reject it as an explanation for the diversity of life.

CONCEPT IN ACTION

This website addresses some of the main misconceptions associated with the theory of evolution.

Evolution Is Just a Theory

Critics of the theory of evolution dismiss its importance by purposefully confounding the everyday usage of the word "theory" with the way scientists use the word. In science, a "theory" is understood to be a concept that has been extensively tested and supported over time. We have a theory of the atom, a theory of gravity, and the theory of relativity, each of which describes what scientists understand to be facts about the world. In the same way, the theory of evolution describes facts about the living world. As such, a theory in science has survived significant efforts to discredit it by scientists, who are naturally skeptical. While theories can sometimes be overturned or revised, this does not lessen their weight but simply reflects the constantly evolving state of scientific knowledge. In contrast, a "theory" in common vernacular means a guess or suggested explanation for something. This meaning is more akin to the concept of a "hypothesis" used by scientists, which is a tentative explanation for something that is proposed to either be supported or disproved. When critics of evolution say evolution is "just a theory," they are implying that there is little evidence supporting it and that it is still in the process of being rigorously tested. This is a mischaracterization. If this were the case, geneticist Theodosius Dobzhansky would not have said that "nothing in biology makes sense, except in the light of evolution."[1]

Individuals Evolve

An individual is born with the genes it has—these do not change as the individual ages. Therefore, an individual cannot evolve or adapt through natural selection. Evolution is the change in genetic composition of a population over time, specifically over generations, resulting from differential reproduction of individuals with certain alleles. Individuals do change over their lifetime, but this is called development; it involves changes programmed by the set of genes the individual acquired at birth in coordination with the individual's environment. When thinking about the evolution of a characteristic, it is probably best to think about the change of the average value of the characteristic in the population over time. For example, when natural selection leads to bill-size change in medium ground finches in the Galápagos, this does not mean that individual bills on the finches are changing. If one measures the average bill size among all individuals in the population at one time, and then measures the average bill size in the population several years later after there has been a strong selective pressure, this average value may be different as a result of evolution. Although some individuals may survive from the first time to the second, those individuals will still have the same bill size. However, there may be enough new individuals with different bill sizes to change the average bill size.

Evolution Explains the Origin of Life

It is a common misunderstanding that evolution includes an explanation of life's origins. Conversely, some of the theory's critics complain that it cannot explain the origin of life. The theory does not try to explain the origin of life. The theory of evolution explains how populations change over time and how life diversifies—the origin of species. It does not shed light on the beginnings of life including the origins of the first cells, which is how life is defined. The mechanisms of the origin of life on Earth are a particularly difficult problem because it occurred a very long time ago, over a very long time, and presumably just occurred once. Importantly, biologists believe that the presence of life on Earth precludes the possibility that the events that led to life on Earth can be repeated because the intermediate stages would immediately become food for existing living things. The early stages of life included the formation of organic molecules such as carbohydrates, amino acids, or nucleotides. If these were formed from inorganic precursors today, they would simply be broken down by living things. The early stages of life also probably included

more complex aggregations of molecules into enclosed structures with an internal environment, a boundary layer of some form, and the external environment. Such structures, if they were formed now, would be quickly consumed or broken down by living organisms.

However, once a mechanism of inheritance was in place in the form of a molecule like DNA or RNA, either within a cell or within a pre-cell, these entities would be subject to the principle of natural selection. More effective reproducers would increase in frequency at the expense of inefficient reproducers. So while evolution does not explain the origin of life, it may have something to say about some of the processes operating once pre-living entities acquired certain properties.

Organisms Evolve on Purpose

Statements such as “organisms evolve in response to a change in an environment,” are quite common. There are two easy misunderstandings possible with such a statement. First of all, the statement must not be understood to mean that individual organisms evolve, as was discussed above. The statement is shorthand for “a population evolves in response to a changing environment.” However, a second misunderstanding may arise by interpreting the statement to mean that the evolution is somehow intentional. A changed environment results in some individuals in the population, those with particular phenotypes, benefiting and, therefore, producing proportionately more offspring than other phenotypes. This results in change in the population if the characters are genetically determined.

It is also important to understand that the variation that natural selection works on is already in a population and does not arise in response to an environmental change. For example, applying antibiotics to a population of bacteria will, over time, select for a population of bacteria that are resistant to antibiotics. The resistance, which is caused by a gene, did not arise by mutation because of the application of the antibiotic. The gene for resistance was already present in the gene pool of the bacteria, likely at a low frequency. The antibiotic, which kills the bacterial cells without the resistance gene, strongly selects for individuals that are resistant, since these would be the only ones that survived and divided. Experiments have demonstrated that mutations for antibiotic resistance do not arise as a result of antibiotic application.

In a larger sense, evolution is also not goal directed. Species do not become “better” over time; they simply track their changing environment with adaptations that maximize their reproduction in a particular environment at a particular time. Evolution has no goal of making faster, bigger, more complex, or even smarter species. This kind of language is common in popular literature. Certain organisms, ourselves included, are described as the “pinnacle” of evolution, or “perfected” by evolution. What characteristics evolve in a species are a function of the variation present and the environment, both of which are constantly changing in a non-directional way. What trait is fit in one environment at one time may well be fatal at some point in the future. This holds equally well for a species of insect as it does the human species.

Evolution Is Controversial among Scientists

The theory of evolution was controversial when it was first proposed in 1859, yet within 20 years virtually every working biologist had accepted evolution as the explanation for the diversity of life. The rate of acceptance was extraordinarily rapid, partly because Darwin had amassed an impressive body of evidence. The early controversies involved both scientific arguments against the theory and the arguments of religious leaders. It was the arguments of the biologists that were resolved after a short time, while the arguments of religious leaders have persisted to this day.

The theory of evolution replaced the predominant theory at the time that species had all been specially created within relatively recent history. Despite the prevalence of this theory, it was becoming increasingly clear to naturalists during the nineteenth century that it could no longer explain many observations of geology and the living world. The persuasiveness of the theory of evolution to these naturalists lay in its ability to explain these phenomena, and it continues to hold extraordinary explanatory power to this day. Its continued rejection by some religious leaders results from its replacement of special creation, a tenet of their religious belief. These leaders cannot accept the replacement of special creation by a mechanistic process that excludes the actions of a deity as an explanation for the diversity of life including the origins of the human species. It should be noted, however, that most of the major denominations in the United States have statements supporting the acceptance of evidence for evolution as compatible with their theologies.

The nature of the arguments against evolution by religious leaders has evolved over time. One current argument is that the theory is still controversial among biologists. This claim is simply not true. The number of working scientists who reject the theory of evolution, or question its validity and say so, is small. A Pew Research poll in 2009 found that 97 percent of the 2500 scientists polled believe species evolve.[2] The support for the theory is reflected in signed statements from many scientific societies such as

the American Association for the Advancement of Science, which includes working scientists as members. Many of the scientists that reject or question the theory of evolution are non-biologists, such as engineers, physicians, and chemists. There are no experimental results or research programs that contradict the theory. There are no papers published in peer-reviewed scientific journals that appear to refute the theory. The latter observation might be considered a consequence of suppression of dissent, but it must be remembered that scientists are skeptics and that there is a long history of published reports that challenged scientific orthodoxy in unpopular ways. Examples include the endosymbiotic theory of eukaryotic origins, the theory of group selection, the microbial cause of stomach ulcers, the asteroid-impact theory of the Cretaceous extinction, and the theory of plate tectonics. Research with evidence and ideas with scientific merit are considered by the scientific community. Research that does not meet these standards is rejected.

Other Theories Should Be Taught

A common argument from some religious leaders is that alternative theories to evolution should be taught in public schools. Critics of evolution use this strategy to create uncertainty about the validity of the theory without offering actual evidence. In fact, there are no viable alternative scientific theories to evolution. The last such theory, proposed by Lamarck in the nineteenth century, was replaced by the theory of natural selection. A single exception was a research program in the Soviet Union based on Lamarck's theory during the early twentieth century that set that country's agricultural research back decades. Special creation is not a viable alternative scientific theory because it is not a scientific theory, since it relies on an untestable explanation. Intelligent design, despite the claims of its proponents, is also not a scientific explanation. This is because intelligent design posits the existence of an unknown designer of living organisms and their systems. Whether the designer is unknown or supernatural, it is a cause that cannot be measured; therefore, it is not a scientific explanation. There are two reasons not to teach nonscientific theories. First, these explanations for the diversity of life lack scientific usefulness because they do not, and cannot, give rise to research programs that promote our understanding of the natural world. Experiments cannot test non-material explanations for natural phenomena. For this reason, teaching these explanations as science in public schools is not in the public interest. Second, in the United States, it is illegal to teach them as science because the U.S. Supreme Court and lower courts have ruled that the teaching of religious belief, such as special creation or intelligent design, violates the establishment clause of the First Amendment of the U.S. Constitution, which prohibits government sponsorship of a particular religion.

The theory of evolution and science in general is, by definition, silent on the existence or non-existence of the spiritual world. Science is only able to study and know the material world. Individual biologists have sometimes been vocal atheists, but it is equally true that there are many deeply religious biologists. Nothing in biology precludes the existence of a god, indeed biology as a science has nothing to say about it. The individual biologist is free to reconcile her or his personal and scientific knowledge as they see fit. The Voices for Evolution project (http://ncse.com/voices), developed through the National Center for Science Education, works to gather the diversity of perspectives on evolution to advocate it being taught in public schools.

Section Summary

The theory of evolution is a difficult concept and misconceptions abound. The factual nature of evolution is often challenged by wrongly associating the scientific meaning of a theory with the vernacular meaning. Evolution is sometimes mistakenly interpreted to mean that individuals evolve, when in fact only populations can evolve as their gene frequencies change over time. Evolution is often assumed to explain the origin of life, which it does not speak to. It is often spoken in goal-directed terms by which organisms change through intention, and selection operates on mutations present in a population that have not arisen in response to a particular environmental stress. Evolution is often characterized as being controversial among scientists; however, it is accepted by the vast majority of working scientists. Critics of evolution often argue that alternative theories to evolution should be taught in public schools; however, there are no viable alternative scientific theories to evolution. The alternative religious beliefs should not be taught as science because it cannot be proven, and in the United States it is unconstitutional. Science is silent on the question of the existence of a god while scientists are able to reconcile religious belief and scientific knowledge.

Footnotes

1. 1 Theodosius Dobzhansky. "Biology, Molecular and Organismic." *American Zoologist* 4, no. 4 (1964): 449.
2. 2 Pew Research Center for the People & the Press, *Public Praises Science; Scientists Fault Public, Media* (Washington, DC, 2009), 37.Contributors

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8: TAXONOMY, SYSTEMATICS & PHYLOGENY

8.1: Taxonomy & Classification
8.2: Determining Evolutionary Relationships
8.3: Features Used to Classify Animals
8.4: Animal Phylogeny

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8.1: Taxonomy & Classification

All life on Earth evolved from a common ancestor. Biologists map how organisms are related by constructing phylogenetic trees. In other words, a “tree of life” can be constructed to illustrate when different organisms evolved and to show the relationships among different organisms, as shown in Figure 8.1.1. Notice that from a single point, the three domains of Archaea, Bacteria, and Eukarya diverge and then branch repeatedly. The small branch that plants and animals (including humans) occupy in this diagram shows how recently these groups had their origin compared with other groups.

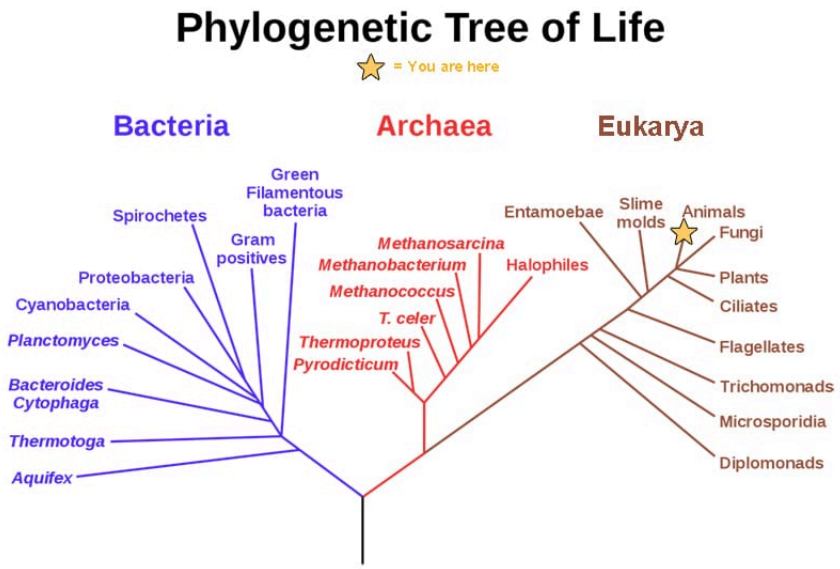


Figure 8.1.1**:** In the evolution of life on Earth, the three domains of life—Archaea, Bacteria, and Eukarya—branch from a single point. (credit: modification of work by Eric Gaba)

The phylogenetic tree in Figure 8.1.1 illustrates the pathway of evolutionary history. The pathway can be traced from the origin of life to any individual species by navigating through the evolutionary branches between the two points. Also, by starting with a single species and tracing backward to any branch point, the organisms related to it by various degrees of closeness can be identified.

A phylogeny is the evolutionary history and the relationships among a species or group of species. The study of organisms with the purpose of deriving their relationships is called systematics.

Many disciplines within the study of biology contribute to understanding how past and present life evolved over time, and together they contribute to building, updating, and maintaining the “tree of life.” Information gathered may include data collected from fossils, from studying morphology, from the structure of body parts, or from molecular structure, such as the sequence of amino acids in proteins or DNA nucleotides. By considering the trees generated by different sets of data scientists can put together the phylogeny of a species.

Scientists continue to discover new species of life on Earth as well as new character information, thus trees change as new data arrive.

The Levels of Classification

Taxonomy (which literally means “arrangement law”) is the science of naming and grouping species to construct an internationally shared classification system. The taxonomic classification system (also called the Linnaean system after its inventor, Carl Linnaeus, a Swedish naturalist) uses a hierarchical model. A hierarchical system has levels and each group at one of the levels includes groups at the next lowest level, so that at the lowest level each member belongs to a series of nested groups. An analogy is the nested series of directories on the main disk drive of a computer. For example, in the most inclusive grouping, scientists divide organisms into three domains: Bacteria, Archaea, and Eukarya. Within each domain is a second level called a kingdom.

Each domain contains several kingdoms. Within kingdoms, the subsequent categories of increasing specificity are: phylum, class, order, family, genus, and species.

As an example, the classification levels for the domestic dog are shown in Figure 8.1.2. The group at each level is called a taxon (plural: taxa). In other words, for the dog, Carnivora is the taxon at the order level, Canidae is the taxon at the family level, and so forth. Organisms also have a common name that people typically use, such as domestic dog, or wolf. Each taxon name is capitalized except for species, and the genus and species names are italicized. Scientists refer to an organism by its genus and species names together, commonly called a scientific name, or Latin name. This two-name system is called binomial nomenclature. The scientific name of the wolf is therefore *Canis lupus*. Recent study of the DNA of domestic dogs and wolves suggest that the domestic dog is a subspecies of the wolf, not its own species, thus it is given an extra name to indicate its subspecies status, *Canis lupus familiaris*.

Figure 8.1.2 also shows how taxonomic levels move toward specificity. Notice how within the domain we find the dog grouped with the widest diversity of organisms. These include plants and other organisms not pictured, such as fungi and protists. At each sublevel, the organisms become more similar because they are more closely related. Before Darwin's theory of evolution was developed, naturalists sometimes classified organisms using arbitrary similarities, but since the theory of evolution was proposed in the 19th century, biologists work to make the classification system reflect evolutionary relationships. This means that all of the members of a taxon should have a common ancestor and be more closely related to each other than to members of other taxa.

Recent genetic analysis and other advancements have found that some earlier taxonomic classifications do not reflect actual evolutionary relationships, and therefore, changes and updates must be made as new discoveries take place. One dramatic and recent example was the breaking apart of prokaryotic species, which until the 1970s were all classified as bacteria. Their division into Archaea and Bacteria came about after the recognition that their large genetic differences warranted their separation into two of three fundamental branches of life.

ART CONNECTION

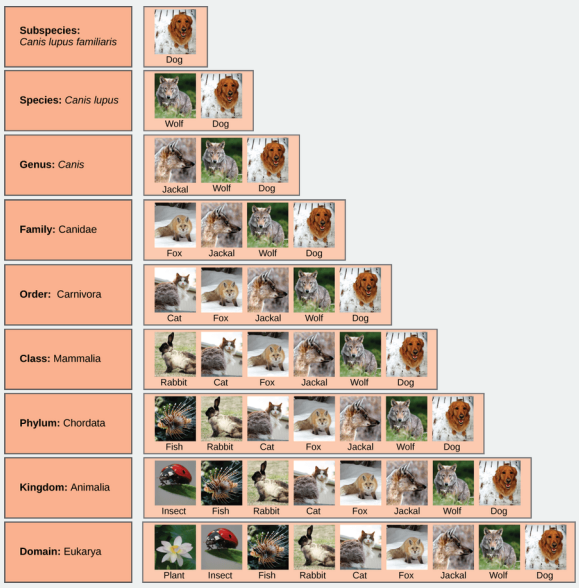


Figure 8.1.2: At each sublevel in the taxonomic classification system, organisms become more similar. Dogs and wolves are the same species because they can breed and produce viable offspring, but they are different enough to be classified as different subspecies. (credit "plant": modification of work by "berduchwal"/Flickr; credit "insect": modification of work by Jon Sullivan; credit "fish": modification of work by Christian Mehlführer; credit "rabbit": modification of work by Aidan Wojtas; credit "cat": modification of work by Jonathan Lidbeck; credit "fox": modification of work by Kevin Bacher, NPS; credit "jackal": modification of work by Thomas A. Hermann, NBII, USGS; credit "wolf" modification of work by Robert Dewar; credit "dog": modification of work by "digital_image_fan"/Flickr)

In what levels are cats and dogs considered to be part of the same group?

CONCEPT IN ACTION

Visit this site to learn more about taxonomy.

Classification and Phylogeny

Scientists use a tool called a phylogenetic tree to show the evolutionary pathways and relationships between organisms. A phylogenetic tree is a diagram used to reflect evolutionary relationships among organisms or groups of organisms. The hierarchical classification of groups nested within more inclusive groups is reflected in diagrams. Scientists consider phylogenetic trees to be a hypothesis of the evolutionary past because one cannot go back through time to confirm the proposed relationships.

Unlike with a taxonomic classification, a phylogenetic tree can be read like a map of evolutionary history, as shown in Figure 8.1.3. Shared characteristics are used to construct phylogenetic trees. The point where a split occurs in a tree, called a branch point, represents where a single lineage evolved into distinct new ones. Many phylogenetic trees have a single branch point at the base representing a common ancestor of all the branches in the tree. Scientists call such trees rooted, which means there is a single ancestral taxon at the base of a phylogenetic tree to which all organisms represented in the diagram descend from. When two lineages stem from the same branch point, they are called sister taxa, for example the two species of orangutans. A branch point with more than two groups illustrates a situation for which scientists have not definitively determined relationships. An example is illustrated by the three branches leading to the gorilla subspecies; their exact relationships are not yet understood. It is important to note that sister taxa share an ancestor, which does not mean that one taxon evolved from the other. The branch point, or split, represents a common ancestor that existed in the past, but that no longer exists. Humans did not evolve from chimpanzees (nor did chimpanzees evolve from humans) although they are our closest living relatives. Both humans and chimpanzees evolved from a common ancestor that lived, scientists believe, six million years ago and looked different from both modern chimpanzees and modern humans.

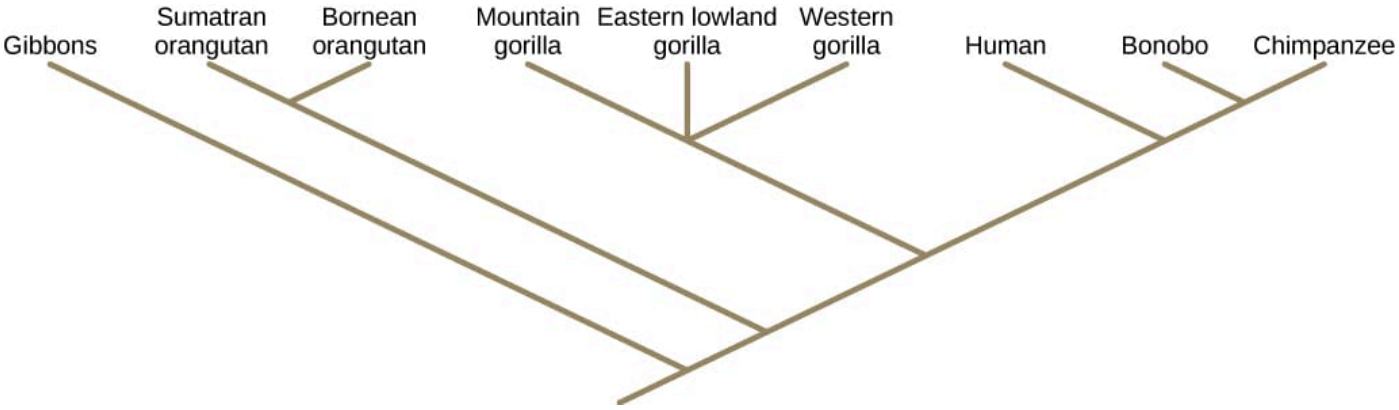


Figure 8.1.3**:** A phylogenetic tree is rooted and shows how different organisms, in this case the species and subspecies of living apes, evolved from a common ancestor.

The branch points and the branches in phylogenetic tree structure also imply evolutionary change. Sometimes the significant character changes are identified on a branch or branch point. For example, in Figure 8.1.4, the branch point that gives rise to the mammal and reptile lineage from the frog lineage shows the origin of the amniotic egg character. Also the branch point that gives rise to organisms with legs is indicated at the common ancestor of mammals, reptiles, amphibians, and jawed fishes.

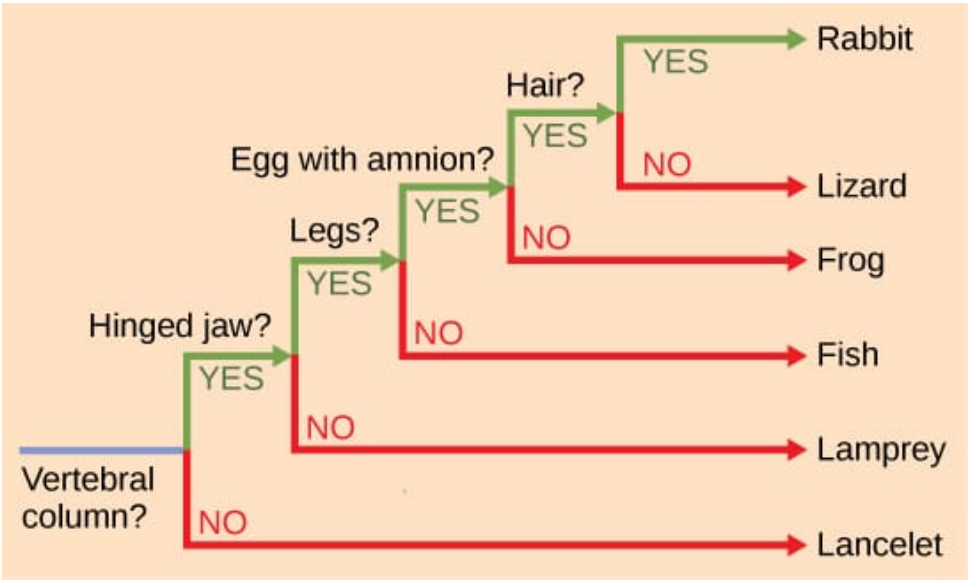


Figure 8.1.4**:** This phylogenetic tree is rooted by an organism that lacked a vertebral column. At each branch point, organisms with different characters are placed in different groups.

Limitations of Phylogenetic Trees

It is easy to assume that more closely related organisms look more alike, and while this is often the case, it is not always true. If two closely related lineages evolved under significantly different surroundings or after the evolution of a major new adaptation, they may look quite different from each other, even more so than other groups that are not as closely related. For example, the phylogenetic tree in Figure 8.1.4 shows that lizards and rabbits both have amniotic eggs, whereas salamanders (within the frog lineage) do not; yet on the surface, lizards and salamanders appear more similar than the lizards and rabbits.

Another aspect of phylogenetic trees is that, unless otherwise indicated, the branches do not show length of time, they show only the order in time of evolutionary events. In other words, a long branch does not necessarily mean more time passed, nor does a short branch mean less time passed— unless specified on the diagram. For example, in Figure 8.1.4, the tree does not indicate how much time passed between the evolution of amniotic eggs and hair. What the tree does show is the order in which things took place. Again using Figure 8.1.4, the tree shows that the oldest trait is the vertebral column, followed by hinged jaws, and so forth. Remember that any phylogenetic tree is a part of the greater whole, and similar to a real tree, it does not grow in only one direction after a new branch develops. So, for the organisms in Figure 8.1.4, just because a vertebral column evolved does not

mean that invertebrate evolution ceased, it only means that a new branch formed. Also, groups that are not closely related, but evolve under similar conditions, may appear more similar to each other than to a close relative.

Section Summary

Scientists continually obtain new information that helps to understand the evolutionary history of life on Earth. Each group of organisms went through its own evolutionary journey, called its phylogeny. Each organism shares relatedness with others, and based on morphologic and genetic evidence scientists attempt to map the evolutionary pathways of all life on Earth. Historically, organisms were organized into a taxonomic classification system. However, today many scientists build phylogenetic trees to illustrate evolutionary relationships and the taxonomic classification system is expected to reflect evolutionary relationships.

Art Connections

Figure 8.1.2: In what levels are cats and dogs considered to be part of the same group?

Answer

Cats and dogs are part of the same group at five levels: both are in the domain Eukarya, the kingdom Animalia, the phylum Chordata, the class Mammalia, and the order Carnivora.

Glossary

binomial nomenclature
a system of two-part scientific names for an organism, which includes genus and species names

branch point
a point on a phylogenetic tree where a single lineage splits to distinct new ones

class
the category in the taxonomic classification system that falls within phylum and includes orders

domain
the highest level category in the classification system and that includes all taxonomic classifications below it; it is the most inclusive taxon

family
the category in the taxonomic classification system that falls within order and includes genera

genus
the category in the taxonomic classification system that falls within family and includes species; the first part of the scientific name

kingdom
the category in the taxonomic classification system that falls within domain and includes phyla

order
the category in the taxonomic classification system that falls within class and includes families

phylogenetic tree
diagram used to reflect the evolutionary relationships between organisms or groups of organisms

phylogeny
evolutionary history and relationship of an organism or group of organisms

phylum
the category in the taxonomic classification system that falls within kingdom and includes classes

rooted
describing a phylogenetic tree with a single ancestral lineage to which all organisms represented in the diagram

relate

sister taxa
two lineages that diverged from the same branch point

species
the most specific category of classification

systematics
the science of determining the evolutionary relationships of organisms

taxon
a single level in the taxonomic classification system

taxonomy
the science of classifying organisms

Contributors

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

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8.2: Determining Evolutionary Relationships

Scientists collect information that allows them to make evolutionary connections between organisms. Similar to detective work, scientists must use evidence to uncover the facts. In the case of phylogeny, evolutionary investigations focus on two types of evidence: morphologic (form and function) and genetic.

Two Measures of Similarity

Organisms that share similar physical features *and* genetic sequences tend to be more closely related than those that do not. Features that overlap both morphologically and genetically are referred to as homologous structures; the similarities stem from common evolutionary paths. For example, as shown in Figure 8.2.1, the bones in the wings of bats and birds, the arms of humans, and the foreleg of a horse are homologous structures. Notice the structure is not simply a single bone, but rather a grouping of several bones arranged in a similar way in each organism even though the elements of the structure may have changed shape and size.



Figure 8.2.1**:** Bat and bird wings, the foreleg of a horse, the flipper of a whale, and the arm of a human are homologous structures, indicating that bats, birds, horses, whales, and humans share a common evolutionary past. (credit a photo: modification of work by Steve Hillebrand, USFWS; credit b photo: modification of work by U.S. BLM; credit c photo: modification of work by Virendra Kankariya; credit d photo: modification of work by Russian Gov./Wikimedia Commons)

Misleading Appearances

Some organisms may be very closely related, even though a minor genetic change caused a major morphological difference to make them look quite different. For example, chimpanzees and humans, the skulls of which are shown in Figure 8.2.2 are very similar genetically, sharing 99 percent[1] of their genes. However, chimpanzees and humans show considerable anatomical differences, including the degree to which the jaw protrudes in the adult and the relative lengths of our arms and legs.



(a) (b)

Figure 8.2.2**:** (a) The chimpanzee jaw protrudes to a much greater degree than (b) the human jaw. (credit a: modification of work by "Pastorius"/Wikimedia Commons)

However, unrelated organisms may be distantly related yet appear very much alike, usually because common adaptations to similar environmental conditions evolved in both. An example is the streamlined body shapes, the shapes of fins and appendages, and the shape of the tails in fishes and whales, which are mammals. These structures bear superficial similarity because they are adaptations to moving and maneuvering in the same environment—water. When a characteristic that is similar occurs by adaptive convergence (convergent evolution), and not because of a close evolutionary relationship, it is called an analogous structure. In another example, insects use wings to fly like bats and birds. We call them both wings because they perform the same function and have a superficially similar form, but the embryonic origin of the two wings is completely different. The difference in the development, or embryogenesis, of the wings in each case is a signal that insects and bats or birds do not share a common ancestor that had a wing. The wing structures, shown in Figure 8.2.3 evolved independently in the two lineages.

Similar traits can be either homologous or analogous. Homologous traits share an evolutionary path that led to the development of that trait, and analogous traits do not. Scientists must determine which type of similarity a feature exhibits to decipher the phylogeny of the organisms being studied.



(a) Bat wing (b) Bird wing



(c) Insect wing

Figure 8.2.3**:** The wing of a honey bee is similar in shape to a bird wing and a bat wing and serves the same function (flight). The bird and bat wings are homologous structures. However, the honey bee wing has a different structure (it is made of a chitinous exoskeleton, not a boney endoskeleton) and embryonic origin. The bee and bird or bat wing types illustrate an analogy—similar structures that do not share an evolutionary history. (credit a photo: modification of work by U.S. BLM; credit b: modification of work by Steve Hillebrand, USFWS; credit c: modification of work by Jon Sullivan)

Molecular Comparisons

With the advancement of DNA technology, the area of molecular systematics, which describes the use of information on the molecular level including DNA sequencing, has blossomed. New analysis of molecular characters not only confirms many earlier classifications, but also uncovers previously made errors. Molecular characters can include differences in the amino-acid sequence of a protein, differences in the individual nucleotide sequence of a gene, or differences in the arrangements of genes. Phylogenies based on molecular characters assume that the more similar the sequences are in two organisms, the more closely related they are. Different genes change evolutionarily at different rates and this affects the level at which they are useful at identifying relationships. Rapidly evolving sequences are useful for determining the relationships among closely related species. More slowly evolving sequences are useful for determining the relationships between distantly related species. To determine the relationships between very different species such as Eukarya and Archaea, the genes used must be very ancient, slowly evolving genes that are present in both groups, such as the genes for ribosomal RNA. Comparing phylogenetic trees using different sequences and finding them similar helps to build confidence in the inferred relationships.

Sometimes two segments of DNA in distantly related organisms randomly share a high percentage of bases in the same locations, causing these organisms to appear closely related when they are not. For example, the fruit fly shares 60 percent of its DNA with humans.[2] In this situation, computer-based statistical algorithms have been developed to help identify the actual relationships, and ultimately, the coupled use of both morphologic and molecular information is more effective in determining phylogeny.

EVOLUTION IN ACTION: Why Does Phylogeny Matter?

In addition to enhancing our understanding of the evolutionary history of species, our own included, phylogenetic analysis has numerous practical applications. Two of those applications include understanding the evolution and transmission of disease and making decisions about conservation efforts. A 2010 study[3] of MRSA (methicillin-resistant *Staphylococcus aureus*), an antibiotic resistant pathogenic bacterium, traced the origin and spread of the strain throughout the past 40 years. The study uncovered the timing and patterns in which the resistant strain moved from its point of origin in Europe to centers of infection and evolution in South America, Asia, North America, and Australasia. The study suggested that introductions of the bacteria to new populations occurred very few times, perhaps only once, and then spread from that limited number of individuals. This is in contrast to the possibility that many individuals had carried the bacteria from one place to another. This result suggests that public health officials should concentrate on quickly identifying the contacts of individuals infected with a new strain of bacteria to control its spread.

A second area of usefulness for phylogenetic analysis is in conservation. Biologists have argued that it is important to protect species throughout a phylogenetic tree rather than just those from one branch of the tree. Doing this will preserve more of the variation produced by evolution. For example, conservation efforts should focus on a single species without sister species rather than another species that has a cluster of close sister species that recently evolved. If the single evolutionarily distinct species goes extinct a disproportionate amount of variation from the tree will be lost compared to one species in the cluster of closely related species. A study published in 2007[4] made recommendations for conservation of mammal species worldwide based on how evolutionarily distinct and at risk of extinction they are. The study found that their recommendations differed from priorities based on simply the level of extinction threat to the species. The study recommended protecting some threatened and valued large mammals such as the orangutans, the giant and lesser pandas, and the African and Asian elephants. But they also found that some much lesser known species should be protected based on how evolutionary distinct they are. These include a number of rodents, bats, shrews and hedgehogs. In addition there are some critically endangered species that did not rate as very important in evolutionary distinctiveness including species of deer mice and gerbils. While many criteria affect conservation decisions, preserving phylogenetic diversity provides an objective way to protect the full range of diversity generated by evolution.

Building Phylogenetic Trees

How do scientists construct phylogenetic trees? Presently, the most accepted method for constructing phylogenetic trees is a method called cladistics. This method sorts organisms into clades, groups of organisms that are most closely related to each other and the ancestor from which they descended. For example, in Figure 8.2.4, all of the organisms in the shaded region evolved from a single ancestor that had amniotic eggs. Consequently, all of these organisms also have amniotic eggs and make a single clade, also called a monophyletic group. Clades must include the ancestral species and all of the descendants from a branch point.

ART CONNECTION

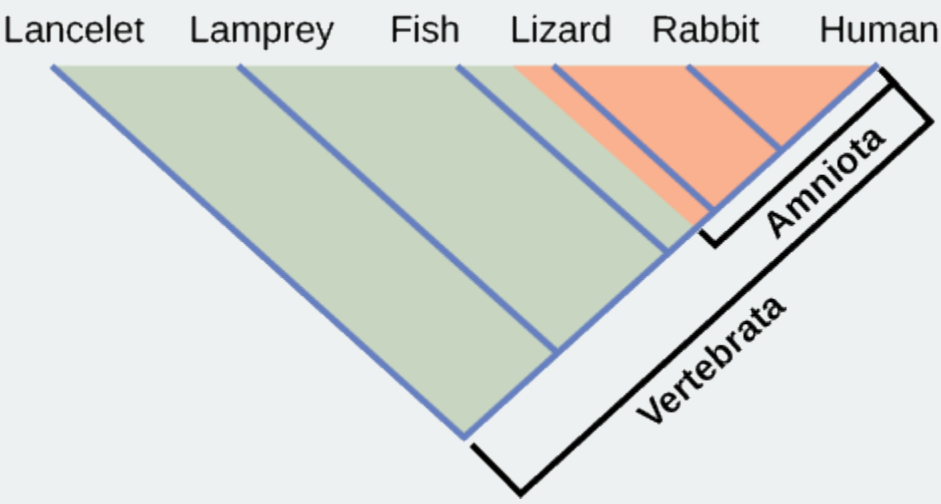


Figure 8.2.4: Lizards, rabbits, and humans all descend from a common ancestor in which the amniotic egg evolved. Thus, lizards, rabbits, and humans all belong to the clade Amniota. Vertebrata is a larger clade that also includes fish and lamprey.

Which animals in this figure belong to a clade that includes animals with hair? Which evolved first: hair or the amniotic egg?

Clades can vary in size depending on which branch point is being referenced. The important factor is that all of the organisms in the clade or monophyletic group stem from a single point on the tree. This can be remembered because monophyletic breaks down into “mono,” meaning one, and “phyletic,” meaning evolutionary relationship.

Shared Characteristics

Cladistics rests on three assumptions. The first is that living things are related by descent from a common ancestor, which is a general assumption of evolution. The second is that speciation occurs by splits of one species into two, never more than

two at a time, and essentially at one point in time. This is somewhat controversial, but is acceptable to most biologists as a simplification. The third assumption is that traits change enough over time to be considered to be in a different state .It is also assumed that one can identify the actual direction of change for a state. In other words, we assume that an amniotic egg is a later character state than non-amniotic eggs. This is called the polarity of the character change. We know this by reference to a group outside the clade: for example, insects have non-amniotic eggs; therefore, this is the older or ancestral character state. Cladistics compares ingroups and outgroups. An ingroup (lizard, rabbit and human in our example) is the group of taxa being analyzed. An outgroup (lancelet, lamprey and fish in our example) is a species or group of species that diverged before the lineage containing the group(s) of interest. By comparing ingroup members to each other and to the outgroup members, we can determine which characteristics are evolutionary modifications determining the branch points of the ingroup's phylogeny.

If a characteristic is found in all of the members of a group, it is a shared ancestral characterbecause there has been no change in the trait during the descent of each of the members of the clade. Although these traits appear interesting because they unify the clade, in cladistics they are considered not helpful when we are trying to determine the relationships of the members of the clade because every member is the same. In contrast, consider the amniotic egg characteristic of Figure 8.2.4. Only some of the organisms have this trait, and to those that do, it is called a shared derived character because this trait changed at some point during descent. This character does tell us about the relationships among the members of the clade; it tells us that lizards, rabbits, and humans group more closely together than any of these organisms do with fish, lampreys, and lancelets.

A sometimes confusing aspect of "ancestral" and "derived" characters is that these terms are relative. The same trait could be either ancestral or derived depending on the diagram being used and the organisms being compared. Scientists find these terms useful when distinguishing between clades during the building of phylogenetic trees, but it is important to remember that their meaning depends on context.

Choosing the Right Relationships

Constructing a phylogenetic tree, or cladogram, from the character data is a monumental task that is usually left up to a computer. The computer draws a tree such that all of the clades share the same list of derived characters. But there are other decisions to be made, for example, what if a species presence in a clade is supported by all of the shared derived characters for that clade except one? One conclusion is that the trait evolved in the ancestor, but then changed back in that one species. Also a character state that appears in two clades must be assumed to have evolved independently in those clades. These inconsistencies are common in trees drawn from character data and complicate the decision-making process about which tree most closely represents the real relationships among the taxa.

To aid in the tremendous task of choosing the best tree, scientists often use a concept called maximum parsimony, which means that events occurred in the simplest, most obvious way. This means that the "best" tree is the one with the fewest number of character reversals, the fewest number of independent character changes, and the fewest number of character changes throughout the tree. Computer programs search through all of the possible trees to find the small number of trees with the simplest evolutionary pathways. Starting with all of the homologous traits in a group of organisms, scientists can determine the order of evolutionary events of which those traits occurred that is the most obvious and simple.

CONCEPT IN ACTION



Practice Parsimony: Go to this website to learn how maximum parsimony is used to create phylogenetic trees (be sure to continue to the second page).

These tools and concepts are only a few of the strategies scientists use to tackle the task of revealing the evolutionary history of life on Earth. Recently, newer technologies have uncovered surprising discoveries with unexpected relationships, such as the fact that people seem to be more closely related to fungi than fungi are to plants. Sound unbelievable? As the information about DNA sequences grows, scientists will become closer to mapping the evolutionary history of all life on Earth.

Section Summary

To build phylogenetic trees, scientists must collect character information that allows them to make evolutionary connections between organisms. Using morphologic and molecular data, scientists work to identify homologous characteristics and genes. Similarities between organisms can stem either from shared evolutionary history (homologies) or from separate evolutionary paths (analogies). After homologous information is identified, scientists use cladistics to organize these events as a means to determine an evolutionary timeline. Scientists apply the concept of maximum parsimony, which states that the likeliest order of events is probably the simplest shortest path. For evolutionary events, this would be the path with the least number of major divergences that correlate with the evidence.

Art Connections

Figure 8.2.3: Which animals in this figure belong to a clade that includes animals with hair? Which evolved first: hair or the amniotic egg?

Answer

Rabbits and humans belong in the clade that includes animals with hair. The amniotic egg evolved before hair, because the Amniota clade branches off earlier than the clade that encompasses animals with hair.

Footnotes

1. 1 Gibbons, A. (2012, June 13). *Science Now*. Retrieved from news.sciencemag.org/scienceno...sequenced.html
2. 2 *Background on comparative genomic analysis*. (2002, December). Retrieved from http://www.genome.gov/10005835
3. 3 Harris, S.R. et al. 2010. Evolution of MRSA during hospital transmission and intercontinental spread. *Science* 327:469–474.

4. 4 Isaac NJ, Turvey ST, Collen B, Waterman C, Baillie JE (2007) Mammals on the EDGE: Conservation Priorities Based on Threat and Phylogeny. PLoS ONE 2(3): e296. doi:10.1371/journal.pone.0000296

Glossary

analogous structure
: a character found in two taxa that looks similar because of convergent evolution, not because of descent from a common ancestor

clade
: a group of taxa with the same set of shared derived characters, including an ancestral species and all its descendants

cladistics
: a method used to organize homologous traits to describe phylogenies using common descendent as the primary criterion used to classify organisms

maximum parsimony
: applying the simplest, most obvious way with the least number of steps

molecular systematics
: the methods of using molecular evidence to identify phylogenetic relationships

monophyletic group
: (also, clade) organisms that share a single ancestor

shared ancestral character
: a character on a phylogenetic branch that is shared by a particular clade

shared derived character
: a character on a phylogenetic tree that is shared only by a certain clade of organisms

Contributors and Attributions

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8.3: Features Used to Classify Animals

Learning Objectives

By the end of this section, you will be able to do the following:

- Explain the differences in animal body plans that support basic animal classification
- Compare and contrast the embryonic development of protostomes and deuterostomes

Scientists have developed a classification scheme that categorizes all members of the animal kingdom, although there are exceptions to most "rules" governing animal classification (Figure 27.6). Animals have been traditionally classified according to two characteristics: body plan and developmental pathway. The major feature of the body plan is its symmetry: how the body parts are distributed along the major body axis. Symmetrical animals can be divided into roughly equivalent halves along at least one axis. Developmental characteristics include the number of germ tissue layers formed during development, the origin of the mouth and anus, the presence or absence of an internal body cavity, and other features of embryological development, such as larval types or whether or not periods of growth are interspersed with molting.

Visual Connection

Visual Connection

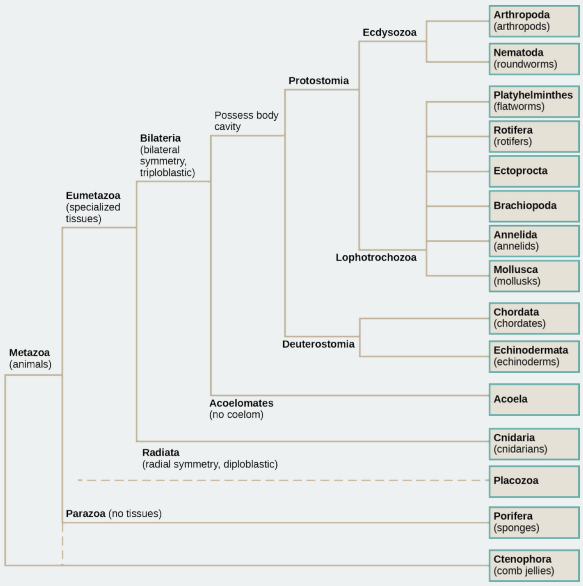


Figure 27.6 Animal phylogeny. The phylogenetic tree of animals is based on morphological, fossil, and genetic evidence. The Ctenophora and Porifera are both considered to be basal because of the absence of Hox genes in this group, but how they are related to the "Parahoxozoa" (Placozoa + Eumetazoa) or to each other, continues to be a matter of debate.

Which of the following statements is false?

a. Eumetazoans have specialized tissues and parazoans don't.
b. Lophotrochozoa and Ecdysozoa are both Bilataria.
c. Acoela and Cnidaria both possess radial symmetry.
d. Arthropods are more closely related to nematodes than they are to annelids.

Animal Characterization Based on Body Symmetry

At a very basic level of classification, true animals can be largely divided into three groups based on the type of symmetry of their

body plan: radially symmetrical, bilaterally symmetrical, and asymmetrical. Asymmetry is seen in two modern clades, the Parazoa (Figure 27.7a) and Placozoa. (Although we should note that the ancestral fossils of the Parazoa apparently exhibited bilateral symmetry.) One clade, the Cnidaria (Figure 27.7b,c), exhibits radial or biradial symmetry: Ctenophores have rotational symmetry (Figure 27.7e). Bilateral symmetry is seen in the largest of the clades, the Bilateria (Figure 27.7d); however the Echinodermata are bilateral as larvae and metamorphose secondarily into radial adults. All types of symmetry are well suited to meet the unique demands of a particular animal's lifestyle.

Radial symmetry is the arrangement of body parts around a central axis, as is seen in a bicycle wheel or pie. It results in animals having top and bottom surfaces but no left and right sides, nor front or back. If a radially symmetrical animal is divided in any direction along the oral/aboral axis (the side with a mouth is "oral side," and the side without a mouth is the "aboral side"), the two halves will be mirror images. This form of symmetry marks the body plans of many animals in the phyla Cnidaria, including jellyfish and adult sea anemones (Figure 27.7b, c). Radial symmetry equips these sea creatures (which may be sedentary or only capable of slow movement or floating) to experience the environment equally from all directions. Bilaterally symmetrical animals, like butterflies (Figure 27.7d) have only a single plane along which the body can be divided into equivalent halves. The Ctenophora (Figure 27.7e), although they look similar to jellyfish, are considered to have rotational symmetry rather than radial or biradial symmetry because division of the body into two halves along the oral/aboral axis divides them into two copies of the same half, with one copy rotated 180°, rather than two mirror images.

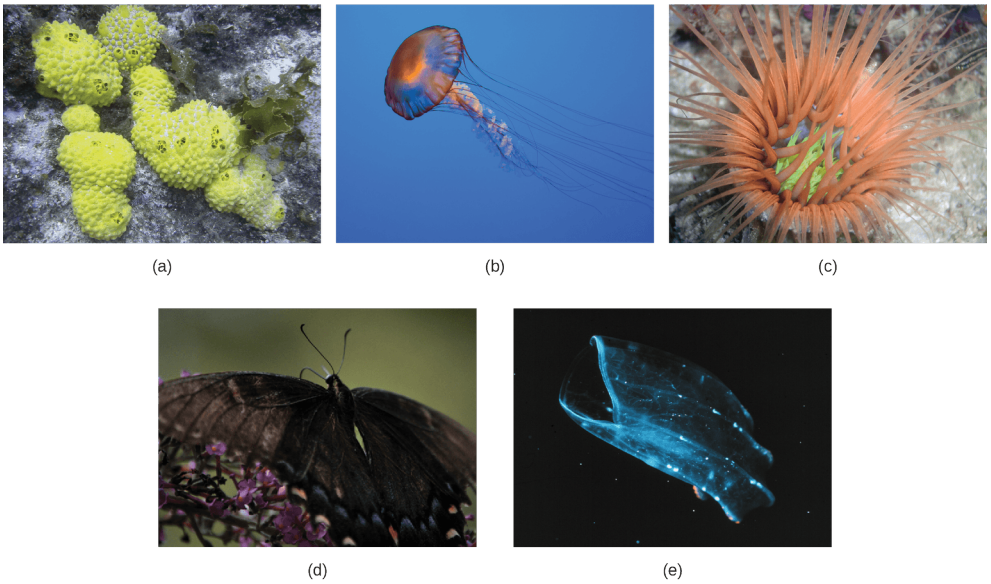


Figure 27.7 Symmetry in animals. The (a) sponge is asymmetrical. The (b) jellyfish and (c) anemone are radially symmetrical, the (d) butterfly is bilaterally symmetrical. Rotational symmetry (e) is seen in the ctenophore *Beroe,* shown swimming open-mouthed. (credit a: modification of work by Andrew Turner; credit b: modification of work by Robert Freiburger; credit c: modification of work by Samuel Chow; credit d: modification of work by Cory Zanker; credit e: modification of work by NOAA)

Bilateral symmetry involves the division of the animal through a midsagittal plane, resulting in two superficially mirror images, right and left halves, such as those of a butterfly (Figure 27.7d), crab, or human body. Animals with bilateral symmetry have a "head" and "tail" (anterior vs. posterior), front and back (dorsal vs. ventral), and right and left sides (Figure 27.8). All Eumetazoa except those with secondary radial symmetry are bilaterally symmetrical. The evolution of bilateral symmetry that allowed for the formation of anterior and posterior (head and tail) ends promoted a phenomenon called cephalization, which refers to the collection of an organized nervous system at the animal's anterior end. In contrast to radial symmetry, which is best suited for stationary or limited-motion lifestyles, bilateral symmetry allows for streamlined and directional motion. In evolutionary terms, this simple form of symmetry promoted active and controlled directional mobility and increased sophistication of resource-seeking and predator-prey relationships.

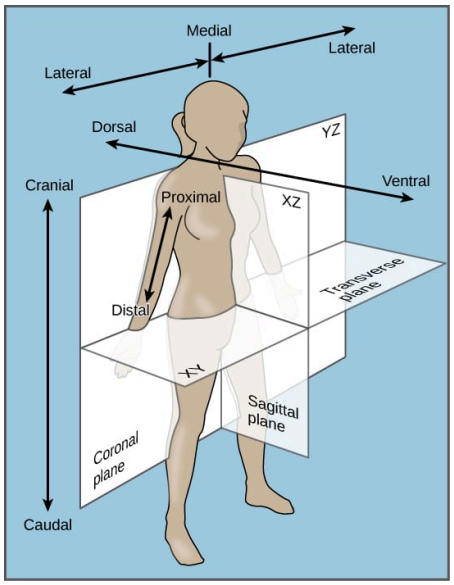


Figure 27.8 Bilateral symmetry. The bilaterally symmetrical human body can be divided by several planes.

Animals in the phylum Echinodermata (such as sea stars, sand dollars, and sea urchins) display modified radial symmetry as adults, but as we have noted, their larval stages (such as the bipinnaria) initially exhibit bilateral symmetry until they metamorphose in animals with radial symmetry (this is termed secondary radial symmetry). Echinoderms evolved from bilaterally symmetrical animals; thus, they are classified as bilaterally symmetrical.

Link to Learning

Link to Learning

Watch this video to see a quick sketch of the different types of body symmetry.

Click to view content

Interactive Content

This interactive element is not available in this format. Visit the link or scan the QR code to access it online.

View this Interactive Content online

Animal Characterization Based on Features of Embryological Development

Most animal species undergo a separation of tissues into germ layers during embryonic development. Recall that these germ layers are formed during *gastrulation*, and that each germ layer typically gives rise to specific types of embryonic tissues and organs. Animals develop either two or three embryonic germ layers (Figure 27.9). The animals that display radial, biradial, or rotational symmetry develop two germ layers, an inner layer (*endoderm* or *mesendoderm*) and an outer layer (*ectoderm*). These animals are called diploblasts, and have a nonliving middle layer between the endoderm and ectoderm (although individual cells may be distributed through this middle layer, there is no *coherent* third layer of tissue). The four clades considered to be diploblastic have different levels of complexity and different developmental pathways, although there is little information about development in Placozoa. More complex animals (usually those with bilateral symmetry) develop three tissue layers: an inner layer (endoderm), an outer layer (ectoderm), and a middle layer (mesoderm). Animals with three tissue layers are called triploblasts.

Visual Connection

Visual Connection

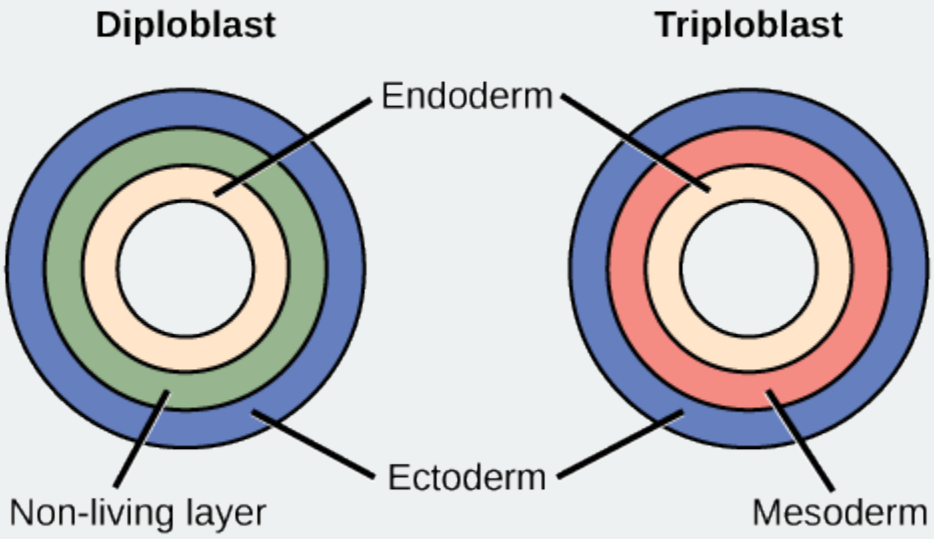


Figure 27.9 Diploblastic and triploblastic embryos. During embryogenesis, diploblasts develop two embryonic germ layers: an ectoderm and an endoderm or mesendoderm. Triploblasts develop a third layer—the mesoderm—which arises from mesendoderm and resides between the endoderm and ectoderm.

Which of the following statements about diploblasts and triploblasts is false?

a. Animals that display only radial symmetry during their lifespans are diploblasts.
b. Animals that display bilateral symmetry are triploblasts.
c. The endoderm gives rise to the lining of the digestive tract and the respiratory tract.
d. The mesoderm gives rise to the central nervous system.

Each of the three germ layers is programmed to give rise to specific body tissues and organs, although there are variations on these themes. Generally speaking, the endoderm gives rise to the lining of the digestive tract (including the stomach, intestines, liver, and pancreas), as well as to the lining of the trachea, bronchi, and lungs of the respiratory tract, along with a few other structures. The ectoderm develops into the outer epithelial covering of the body surface, the central nervous system, and a few other structures. The mesoderm is the third germ layer; it forms between the endoderm and ectoderm in triploblasts. This germ layer gives rise to all specialized muscle tissues (including the cardiac tissues and muscles of the intestines), connective tissues such as the skeleton and blood cells, and most other visceral organs such as the kidneys and the spleen. Diploblastic animals may have cell types that serve multiple functions, such as epitheliomuscular cells, which serve as a covering as well as contractile cells.

Presence or Absence of a Coelom

Further subdivision of animals with three germ layers (triploblasts) results in the separation of animals that may develop an internal *body cavity* derived from mesoderm, called a coelom, and those that do not. This epithelial cell-lined *coelomic cavity*, usually filled with fluid, lies between the visceral organs and the body wall. It houses many organs such as the digestive, urinary, and reproductive systems, the heart and lungs, and also contains the major arteries and veins of the circulatory system. In mammals, the body cavity is divided into the thoracic cavity, which houses the heart and lungs, and the abdominal cavity, which houses the digestive organs. In the thoracic cavity further subdivision produces the pleural cavity, which provides space for the lungs to expand during breathing, and the pericardial cavity, which provides room for movements of the heart. The evolution of the coelom is associated with many functional advantages. For example, the coelom provides cushioning and shock absorption for the major organ systems that it encloses. In addition, organs housed within the coelom can grow and move freely, which promotes optimal organ development and placement. The coelom also provides space for the diffusion of gases and nutrients, as well as body flexibility, promoting improved animal motility.

Triploblasts that do not develop a coelom are called acoelomates, and their mesoderm region is completely filled with tissue,

although they do still have a gut cavity. Examples of acoelomates include animals in the phylum Platyhelminthes, also known as flatworms. Animals with a true coelom are called eucoelomates (or coelomates) (Figure 27.10). In such cases, a true coelom arises entirely within the mesoderm germ layer and is lined by an epithelial membrane. This membrane also lines the organs within the coelom, connecting and holding them in position while allowing them some freedom of movement. Annelids, mollusks, arthropods, echinoderms, and chordates are all eucoelomates. A third group of triploblasts has a slightly different coelom lined partly by mesoderm and partly by endoderm. Although still functionally a coelom, these are considered “false” coeloms, and so we call these animals pseudocoelomates. The phylum Nematoda (roundworms) is an example of a pseudocoelomate. True coelomates can be further characterized based on other features of their early embryological development.

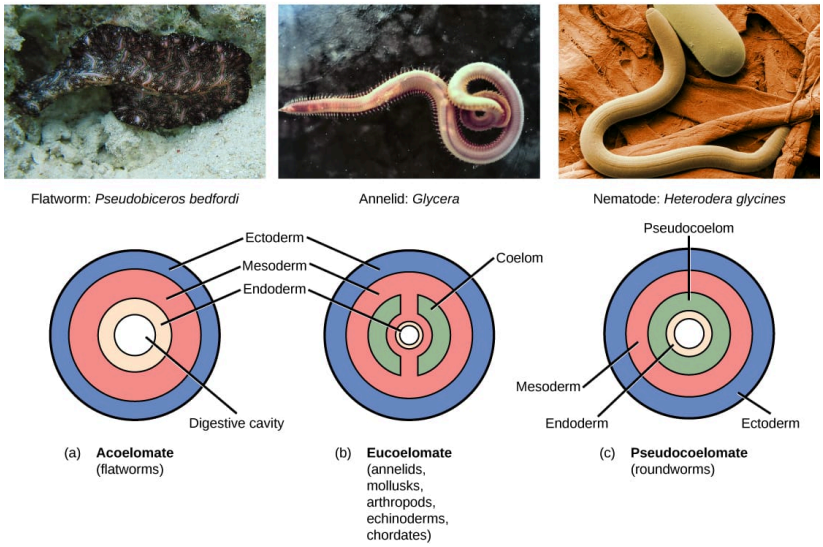


Figure 27.10 Body cavities. Triploblasts may be (a) acoelomates, (b) eucoelomates, or (c) pseudocoelomates. Acoelomates have no body cavity. Eucoelomates have a body cavity within the mesoderm, called a coelom, in which both the gut and the body wall are lined with mesoderm. Pseudocoelomates also have a body cavity, but only the body wall is lined with mesoderm. (credit a: modification of work by Jan Derk; credit b: modification of work by NOAA; credit c: modification of work by USDA, ARS)

Embryonic Development of the Mouth

Bilaterally symmetrical, tribloblastic eucoelomates can be further divided into two groups based on differences in the origin of the mouth. When the primitive gut forms, the opening that first connects the gut cavity to the outside of the embryo is called the blastopore. Most animals have openings at both ends of the gut: mouth at one end and anus at the other. One of these openings will develop at or near the site of the blastopore. In Protostomes ("mouth first"), the mouth develops at the blastopore (Figure 27.11). In Deuterostomes ("mouth second"), the mouth develops at the other end of the gut (Figure 27.11) and the anus develops at the site of the blastopore. Protostomes include arthropods, mollusks, and annelids. Deuterostomes include more complex animals such as chordates but also some “simple” animals such as echinoderms. Recent evidence has challenged this simple view of the relationship between the location of the blastopore and the formation of the mouth, however, and the theory remains under debate. Nevertheless, these details of mouth and anus formation reflect *general* differences in the organization of protostome and deuterostome embryos, which are also expressed in other developmental features.

One of these differences between protostomes and deuterostomes is the method of coelom formation, beginning from the gastrula stage. Since body cavity formation tends to accompany the formation of the mesoderm, the mesoderm of protostomes and deuterostomes forms differently. The coelom of most protostomes is formed through a process called schizocoely. The mesoderm in these organisms is usually the product of specific *blastomere*s, which migrate into the interior of the embryo and form two clumps of mesodermal tissue. Within each clump, cavities develop and merge to form the hollow opening of the coelom. Deuterostomes differ in that their coelom forms through a process called enterocoely. Here, the mesoderm develops as pouches that are pinched off from the endoderm tissue. These pouches eventually fuse and expand to fill the space between the gut and the body wall, giving rise to the coelom.

Another difference in organization of protostome and deuterostome embryos is expressed during cleavage. Protostomes undergo spiral cleavage, meaning that the cells of one pole of the embryo are rotated, and thus misaligned, with respect to the cells of the opposite pole. This is due to the oblique angle of cleavage relative to the two poles of the embryo. Deuterostomes undergo radial

cleavage, where the cleavage axes are either parallel or perpendicular to the polar axis, resulting in the parallel (up-and-down) alignment of the cells between the two poles.

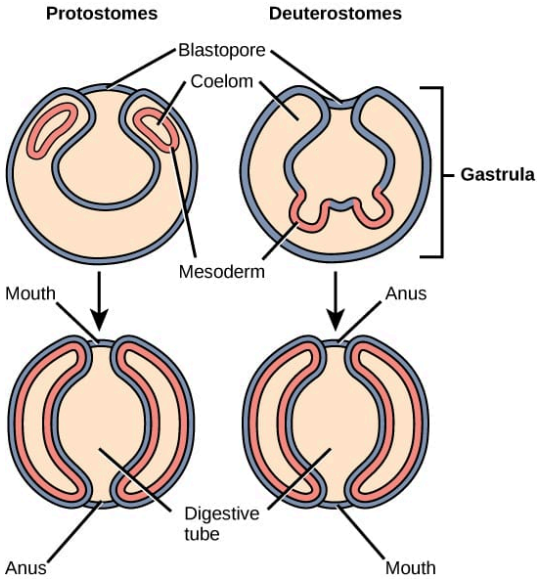


Figure 27.11 Protostomes and deuterostomes. Eucoelomates can be divided into two groups based on their early embryonic development. In protostomes, the mouth forms at or near the site of the blastopore and the body cavity forms by splitting the mesodermal mass during the process of schizocoely. In deuterostomes, the mouth forms at a site opposite the blastopore end of the embryo and the mesoderm pinches off to form the coelom during the process of enterocoely.

A second distinction between the types of cleavage in protostomes and deuterostomes relates to the fate of the resultant *blastomeres* (cells produced by cleavage). In addition to spiral cleavage, protostomes also undergo determinate cleavage. This means that even at this early stage, the developmental fate of each embryonic cell is already determined. A given cell does not have the ability to develop into any cell type other than its original destination. Removal of a blastomere from an embryo with determinate cleavage can result in missing structures, and embryos that fail to develop. In contrast, deuterostomes undergo indeterminate cleavage, in which cells are not yet fully committed at this early stage to develop into specific cell types. Removal of individual blastomeres from these embryos does not result in the loss of embryonic structures. In fact, twins (clones) can be produced as a result from blastomeres that have been separated from the original mass of blastomere cells. Unlike protostomes, however, if some blastomeres are damaged during embryogenesis, adjacent cells are able to compensate for the missing cells, and the embryo is not damaged. These cells are referred to as undetermined cells. This characteristic of deuterostomes is reflected in the existence of familiar *embryonic stem cells*, which have the ability to develop into any cell type until their fate is programmed at a later developmental stage.

Evolution Connection

Evolution Connection

The Evolution of the CoelomOne of the first steps in the classification of animals is to examine the animal's body. One structure that is used in classification of animals is the body cavity or coelom. The body cavity develops *within* the mesoderm, so only triploblastic animals can have body cavities. Therefore body cavities are found only within the Bilateria. In other animal clades, the gut is either close to the body wall or separated from it by a jelly-like material. The body cavity is important for two reasons. Fluid within the body cavity protects the organs from shock and compression. In addition, since in triploblastic embryos, most muscle, connective tissue, and blood vessels develop from mesoderm, these tissues developing within the lining of the body cavity can reinforce the gut and body wall, aid in motility, and efficiently circulate nutrients.

To recap what we have discussed above, animals that do not have a coelom are called *acoelomates*. The major acoelomate group in the Bilateria is the flatworms, including both free-living and parasitic forms such as tapeworms. In these animals, mesenchyme fills the space between the gut and the body wall. Although two layers of muscle are found just under the epidermis, there is no muscle or other mesodermal tissue around the gut. Flatworms rely on passive diffusion for nutrient transport across their body.

In *pseudocoelomates*, there is a body cavity between the gut and the body wall, but only the body wall has mesodermal tissue. In these animals, the mesoderm forms, but does not develop cavities within it. Major pseudocoelomate phyla are the rotifers and nematodes. Animals that have a true coelom are called *eucoelomates*; all vertebrates, as well as molluscs, annelids, arthropods, and echinoderms, are eucoelomates. The coelom develops within the mesoderm during embryogenesis. Of the major bilaterian phyla, the molluscs, annelids, and arthropods are *schizocoels*, in which the mesoderm splits to form the body cavity, while the echinoderms and chordates are *enterocoels*, in which the mesoderm forms as two or more buds off of the gut. These buds separate from the gut and coalesce to form the body cavity. In the vertebrates, mammals have a subdivided body cavity, with the thoracic cavity separated from the abdominal cavity. The pseudocoelomates may have had eucoelomate ancestors and may have lost their ability to form a complete coelom through genetic mutations. Thus, this step in early embryogenesis—the formation of the coelom—has had a large evolutionary impact on the various species of the animal kingdom.

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8.4: Animal Phylogeny

Learning Objectives

By the end of this section, you will be able to do the following:

- Interpret the metazoan phylogenetic tree
- Describe the types of data that scientists use to construct and revise animal phylogeny
- List some of the relationships within the modern phylogenetic tree that have been discovered as a result of modern molecular data

Biologists strive to understand the evolutionary history and relationships of members of the animal kingdom, and all of life, for that matter. The study of *phylogeny* (the branching sequence of evolution) aims to determine the evolutionary relationships between phyla. Currently, most biologists divide the animal kingdom into 35 to 40 phyla. Scientists develop phylogenetic trees, which serve as *hypotheses* about which species have evolved from which ancestors.

Recall that until recently, only morphological characteristics and the fossil record were used to determine phylogenetic relationships among animals. Scientific understanding of the distinctions and hierarchies between anatomical characteristics provided much of this knowledge. Used alone, however, this information can be misleading. Morphological characteristics (such as skin color, body shape, etc.) may evolve multiple times, and independently, through evolutionary history. Analogous characteristics may appear similar between animals, but their underlying evolution may be very different. With the advancement of *molecular technologies*, modern phylogenetics is now informed by genetic and molecular analyses, in addition to traditional morphological and fossil data. With a growing understanding of genetics, the animal evolutionary tree has changed substantially and continues to change as new DNA and RNA analyses are performed on additional animal species.

Constructing an Animal Phylogenetic Tree

The current understanding of evolutionary relationships among animal, or Metazoa, phyla begins with the distinction between animals with *true differentiated tissues*, called Eumetazoa, and animal phyla that do not have true differentiated tissues, such as the sponges (Porifera) and the Placozoa. Similarities between the feeding cells of sponges (choanocytes) and choanoflagellate protists (Figure 27.12) have been used to suggest that Metazoa evolved from a common ancestral organism that resembled the modern colonial choanoflagellates.

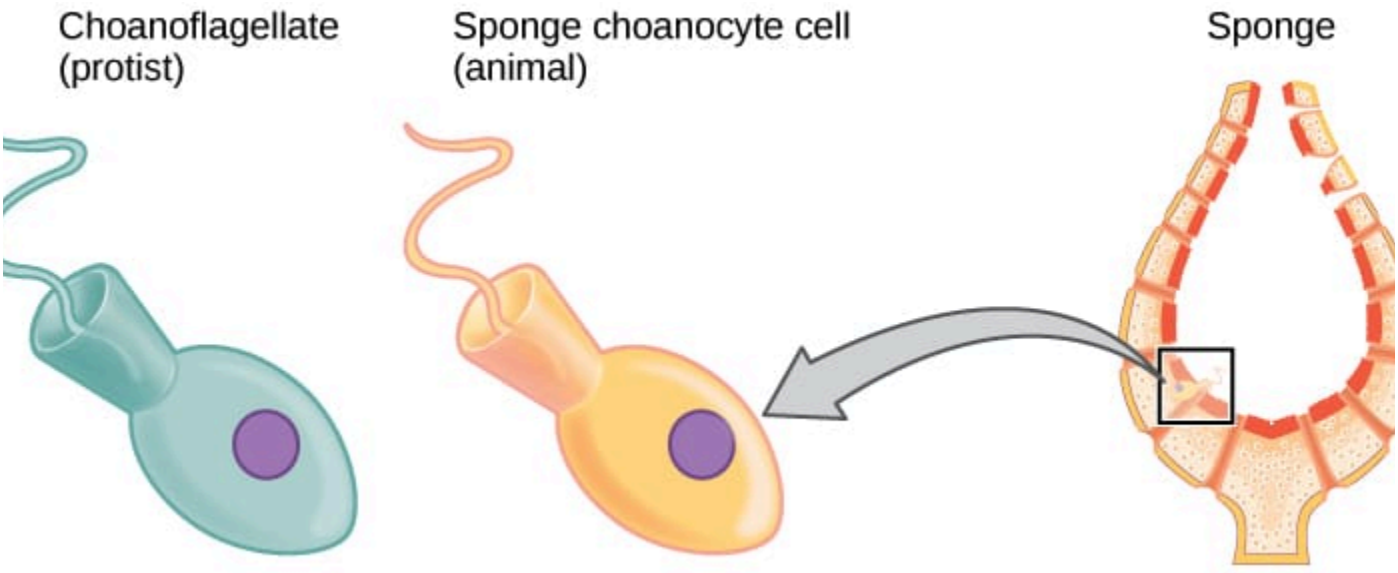


Figure 27.12 Choanoflagellates and choanocytes. Cells of the protist choanoflagellate clade closely resemble sponge choanocyte cells. Beating of choanocyte flagella draws water through the sponge so that nutrients can be extracted and waste removed.

Eumetazoa are subdivided into radially symmetrical animals and bilaterally symmetrical animals, and are thus classified into the clades Bilateria and Radiata, respectively. As mentioned earlier, the cnidarians and ctenophores are animal phyla with true radial, biradial, or rotational symmetry. All other Eumetazoa are members of the Bilateria clade. The bilaterally symmetrical animals are further divided into deuterostomes (including chordates and echinoderms) and two distinct clades of protostomes (including ecdysozoans and lophotrochozoans) (Figure 27.13a,b). Ecdysozoa includes nematodes and arthropods; they are so named for a commonly found characteristic among the group: the physiological process of exoskeletal *molting* followed by the "stripping" of the outer cuticular layer, called *ecdysis*. Lophotrochozoa is named for two structural features, each common to certain phyla within the clade. Some lophotrochozoan phyla are characterized by a larval stage called *trochophore larvae*, and other phyla are characterized by the presence of a feeding structure called a *lophophore* (thus, the shorter term, "lopho-trocho-zoa").



(a) (b)

Figure 27.13 Ecdysozoa. Animals that molt their exoskeletons, such as these (a) Madagascar hissing cockroaches, are in the clade Ecdysozoa. (b) Phoronids are in the clade Lophotrochozoa. The tentacles are part of a feeding structure called a lophophore. (credit a: modification of work by Whitney Cranshaw, Colorado State University, Bugwood.org; credit b: modification of work by NOAA)

Link to Learning

Link to Learning

Explore an interactive tree of life here. Zoom in and out and click to learn more about the organisms and their evolutionary relationships.

Modern Advances in Phylogenetic Understanding Come from Molecular Analyses

The phylogenetic groupings are continually being debated and refined by evolutionary biologists. Each year, new evidence emerges that further alters the relationships described by a phylogenetic tree diagram.

Link to Learning

Link to Learning

Watch the following video to learn how biologists use genetic data to determine relationships among organisms.

Nucleic acid and protein analyses have greatly modified and refined the modern phylogenetic animal tree. These data come

from a variety of molecular sources, such as mitochondrial DNA, nuclear DNA, ribosomal RNA (rRNA), and certain cellular proteins. Many evolutionary relationships in the modern tree have only recently been determined from the molecular evidence. For example, a previously classified group of animals called lophophorates, which included brachiopods and bryozoans, were long-thought to be primitive deuterostomes. Extensive molecular analysis using rRNA data found these animals are actually protostomes, more closely related to annelids and mollusks. This discovery allowed for the distinction of the protostome clade Lophotrochozoa. Molecular data have also shed light on some differences within the lophotrochozoan group, and the placement of the Platyhelminthes is particularly problematic. Some scientists believe that the phyla Platyhelminthes and Rotifera should actually belong to their own clade of protostomes termed Platyzoa.

Molecular research similar to the discoveries that brought about the distinction of the lophotrochozoan clade has also revealed a dramatic rearrangement of the relationships between mollusks, annelids, arthropods, and nematodes, and as a result, a new ecdysozoan clade was formed. Due to morphological similarities in their segmented body types, annelids and arthropods were once thought to be closely related. However, molecular evidence has revealed that arthropods are actually more closely related to nematodes, now comprising the ecdysozoan clade, and annelids are more closely related to mollusks, brachiopods, and other phyla in the lophotrochozoan clade. These two clades now make up the protostomes.

Another change to former phylogenetic groupings because of modern molecular analyses includes the emergence of an entirely new phylum of worm called Acoelomorpha. These acoel flatworms were long thought to belong to the phylum Platyhelminthes because of their similar “flatworm” morphology. However, molecular analyses revealed this to be a false relationship and originally suggested that acoels represented living species of some of the earliest divergent bilaterians. More recent research into the acoelomorphs has called this hypothesis into question and suggested that the acoels are more closely related to deuterostomes. The placement of this new phylum remains disputed, but scientists agree that with sufficient molecular data, their true phylogeny will be determined.

Another example of phylogenetic reorganization involves the identification of the Ctenophora as the basal clade of the animal kingdom. Ctenophora, or comb jellies, were once considered to be a sister group of the Cnidaria, and the sponges (Porifera) were placed as the basal animal group, sister to other animals. The presence of nerve and muscle cells in both the Ctenophores and the Cnidaria and their absence in the Porifera strengthened this view of the relationships among simple animal forms. However, recent molecular analysis has shown that many of the genes that support neural development in other animals are absent from the Ctenophore genome. The muscle cells are restricted to the mouth and tentacles and are derived from cells in the mesoglea. The mitochondrial genome of the Ctenophores is small and lacks many genes found in other animal mitochondrial genomes. These features plus the absence of *Hox* genes from the Ctenophores have been used to argue that the Ctenophores should be considered basal or as a sister group of the Porifera, and that the evolution of specialized nerve and muscle tissue may have occurred more than once in the history of animal life. Although Ctenophores have been shown as basal to other animals in the phylogeny presented in Chapter 27.2, debate on this issue is likely to continue as Ctenophores are more closely studied.

Changes to the phylogenetic tree can be difficult to track and understand, and are evidence of the process of science. Data and analytical methods play a significant role in the development of phylogenies. For this reason – because molecular analysis and reanalysis are not complete -- we cannot necessarily dismiss a former phylogenetic tree as inaccurate. A recent reanalysis of molecular evidence by an international group of evolutionary biologists refuted the proposition that comb jellies are the phylogenetically oldest extant metazoan group. The study, which relied on more sophisticated methods of analyzing the original genetic data, reaffirms the traditional view that the sponges were indeed the first phylum to diverge from the common ancestor of metazoans. The ongoing discussion concerning the location of sponges and comb jellies on the animal “family tree” is an example of what drives science forward.

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9: SPONGES

9.1: Sponge Structure and Diversity

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9.1: Sponge Structure and Diversity

Learning Objectives

By the end of this section, you will be able to do the following:

- Describe the organizational features of the simplest multicellular organisms
- Explain the various body forms and bodily functions of sponges

As we have seen, the vast majority of invertebrate animals do *not* possess a defined bony vertebral endoskeleton, or a bony cranium. However, one of the most ancestral groups of deuterostome invertebrates, the Echinodermata, do produce tiny skeletal "bones" called *ossicle*s that make up a true endoskeleton, or internal skeleton, covered by an epidermis.

We will start our investigation with the simplest of all the invertebrates—animals sometimes classified within the clade Parazoa ("beside the animals"). This clade currently includes only the phylum Placozoa (containing a single species, *Trichoplax adhaerens*), and the phylum Porifera, containing the more familiar sponges (Figure 28.2). The split between the Parazoa and the Eumetazoa (all animal clades above Parazoa) likely took place over a billion years ago.

We should reiterate here that the Porifera do not possess "true" tissues that are embryologically homologous to those of all other derived animal groups such as the insects and mammals. This is because they do not create a true gastrula during embryogenesis, and as a result do not produce a true endoderm or ectoderm. But even though they are not considered to have true tissues, they do have specialized cells that perform specific functions *like tissue*s (for example, the external "pinacoderm" of a sponge acts like our epidermis). Thus, *functionally*, the poriferans can be said to have tissues; however, these tissues are likely not *embryologically* homologous to our own.

Sponge larvae (e.g., parenchymula and amphiblastula) are flagellated and able to swim; however, adults are non-motile and spend their life attached to a substratum. Since water is vital to sponges for feeding, excretion, and gas exchange, their body structure facilitates the movement of water through the sponge. Various canals, chambers, and cavities enable water to move through the sponge to allow the exchange of food and waste as well as the exchange of gases to nearly all body cells.



Figure 28.2 Sponges. Sponges are members of the phylum Porifera, which contains the simplest invertebrates. (credit: Andrew Turner)

Morphology of Sponges

There are at least 5,000 named species of sponges, likely with thousands more yet to be classified. The morphology of the simplest sponges takes the shape of an irregular cylinder with a large central cavity, the spongocoel, occupying the inside of the cylinder (Figure 28.3). Water enters into the spongocoel through numerous pores, or *ostia*, that create openings in the body wall. Water entering the spongocoel is expelled via a large common opening called the osculum. However, we should note that sponges exhibit a range of diversity in body forms, including variations in the size and shape of the spongocoel, as well as the number and arrangement of feeding chambers within the body wall. In some sponges, multiple feeding chambers open off of a central spongocoel and in others, several feeding chambers connecting to one another may lie between the entry pores and the spongocoel.

While sponges do not exhibit true tissue-layer organization, they do have a number of functional "tissues" composed of different cell types specialized for distinct functions. For example, epithelial-like cells called *pinacocytes* form the outermost body, called a *pinacoderm*, that serves a protective function similar that of our epidermis. Scattered among the pinacoderm are the ostia that allow entry of water into the body of the sponge. These pores have given the sponges their phylum name Porifera—pore-bearers. In some sponges, ostia are formed by *porocytes*, single tube-shaped cells that act as valves to regulate the flow of water into the spongocoel. In other sponges, ostia are formed by folds in the body wall of the sponge. Between the outer layer and the feeding chambers of the sponge is a jelly-like substance called the mesohyl, which contains collagenous fibers. Various cell types reside within the mesohyl, including amoebocytes, the "stem cells" of sponges, and *sclerocytes*, which produce skeletal materials. The gel-like consistency of mesohyl acts like an endoskeleton and maintains the tubular morphology of sponges.

The feeding chambers inside the sponge are lined by choanocytes ("collar cells"). The structure of a choanocyte is critical to its function, which is to generate a *directed* water current through the sponge and to trap and ingest microscopic food particles by phagocytosis. These feeding cells are similar in appearance to unicellular *choanoflagellates* (Protista). This similarity suggests that sponges and choanoflagellates are closely related and likely share common ancestry. The body of the choanocyte is embedded in mesohyl and contains all the organelles required for normal cell function. Protruding into the "open space" inside the feeding chamber is a mesh-like collar composed of microvilli with a single flagellum in the center of the column. The beating of the flagella from all choanocytes draws water into the sponge through the numerous ostia, into the spaces lined by choanocytes, and eventually out through the osculum (or osculi, if the sponge consists of a colony of attached sponges). Food particles, including waterborne bacteria and unicellular organisms such as algae and various animal-like protists, are trapped by the sieve-like collar of the choanocytes, slide down toward the body of the cell, and are ingested by phagocytosis. Choanocytes also serve another surprising function: They can differentiate into sperm for sexual reproduction, at which time they become dislodged from the mesohyl and leave the sponge with expelled water through the osculum.

Link to Learning

Link to Learning

Watch this video to see the movement of water through the sponge body.

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Interactive Content

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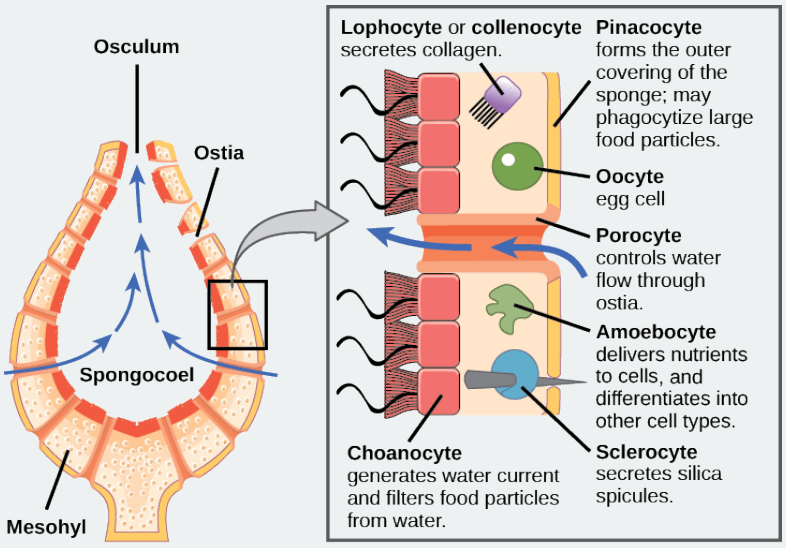
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The amoebocytes (derived from stem-cell-like archaeocytes), are so named because they move throughout the mesohyl in an amoeba-like fashion. They have a variety of functions: In addition to delivering nutrients from choanocytes to other cells within the sponge, they also give rise to eggs for sexual reproduction. (The eggs remain in the mesohyl, whereas the sperm cells are released into the water.) The amoebocytes can differentiate into other cell types of the sponge, such as collenocytes and lophocytes, which produce the collagen-like protein that support the mesohyl. Amoebocytes can also give rise to sclerocytes, which produce *spicules* (skeletal spikes of silica or calcium carbonate) in some sponges, and spongocytes, which produce the protein spongin in

the majority of sponges. These different cell types in sponges are shown in Figure 28.3.

Visual Connection

Visual Connection



(a) Basic sponge body plan (b) Some sponge cell types

Figure 28.3 Simple sponge body plan and cell types. The sponge's (a) basic body plan and (b) some of the specialized cell types found in sponges are shown.

Which of the following statements is false?

a. Choanocytes have flagella that propel water through the body.
b. Pinacocytes can transform into any cell type.
c. Lophocytes secrete collagen.
d. Porocytes control the flow of water through pores in the sponge body.

Link to Learning

Link to Learning

Take an up-close tour through the sponge and its cells.

As we've seen, most sponges are supported by small bone-like *spicules* (usually tiny pointed structures made of calcium carbonate or silica) in the mesohyl. Spicules provide support for the body of the sponge, and may also deter predation. The presence and composition of spicules form the basis for differentiating three of the four classes of sponges (Figure 28.4). Sponges in class Calcarea produce calcium carbonate spicules and no spongin; those in class Hexactinellida produce six-rayed siliceous (glassy) spicules and no spongin; and those in class Demospongia contain spongin and may or may not have spicules; if present, those spicules are siliceous. Sponges in this last class have been used as bath sponges. Spicules are most conspicuously present in the glass sponges, class Hexactinellida. Some of the spicules may attain gigantic proportions. For example, relative to typical glass sponge spicules, whose size generally ranges from 3 to 10 mm, some of the *basal spicules* of the hexactinellid *Monorhaphis chuni* are enormous and grow up to 3 meters long! The glass sponges are also unusual in that most of their body cells are fused together to form a *multinucleate syncytium*. Because their cells are interconnected in this way, the hexactinellid sponges have no mesohyl. A fourth class of sponges, the Sclerospongiae, was described from species discovered in underwater tunnels. These are also called coralline sponges after their multilayered calcium carbonate skeletons. Dating based on the rate of deposition of the skeletal layers suggests that some of these sponges are hundreds of years old.



Figure 28.4 Several classes of sponges. (a) *Clathrina clathrus* belongs to class Calcarea, (b) *Staurocalyptus* spp. (common name: yellow Picasso sponge) belongs to class Hexactinellida, and (c) *Acarnus erithacus* belongs to class Demospongia. (credit a: modification of work by Parent Géry; credit b: modification of work by Monterey Bay Aquarium Research Institute, NOAA; credit c: modification of work by Sanctuary Integrated Monitoring Network, Monterey Bay National Marine Sanctuary, NOAA)

Link to Learning

Link to Learning

Use the Interactive Sponge Guide to identify species of sponges based on their external form, mineral skeleton, fiber, and skeletal architecture.

Physiological Processes in Sponges

Sponges, despite being simple organisms, regulate their different physiological processes through a variety of mechanisms. These processes regulate their metabolism, reproduction, and locomotion.

Digestion

Sponges lack complex digestive, respiratory, circulatory, and nervous systems. Their food is trapped as water passes through the ostia and out through the osculum. Bacteria smaller than 0.5 microns in size are trapped by choanocytes, which are the principal cells engaged in feeding, and are ingested by phagocytosis. However, particles that are larger than the ostia may be phagocytized at the sponge's surface by pinacocytes. In some sponges, amoebocytes transport food from cells that have ingested food particles to those that do not. In sponges, in spite of what looks like a large digestive cavity, all digestion is *intracellular*. The limit of this type of digestion is that food particles must be smaller than individual sponge cells.

All other major body functions in the sponge (gas exchange, circulation, excretion) are performed by diffusion between the cells that line the openings within the sponge and the water that is passing through those openings. All cell types within the sponge obtain oxygen from water through diffusion. Likewise, carbon dioxide is released into seawater by diffusion. In addition, nitrogenous waste produced as a byproduct of protein metabolism is excreted via diffusion by individual cells into the water as it passes through the sponge.

Some sponges host green algae or cyanobacteria as endosymbionts within archeocytes and other cells. It may be a surprise to learn that there are nearly 150 species of carnivorous sponges, which feed primarily on tiny crustaceans, snaring them through sticky threads or hooked spicules!

Although there is no specialized nervous system in sponges, there is intercellular communication that can regulate events like

contraction of the sponge's body or the activity of the choanocytes.

Reproduction

Sponges reproduce by sexual as well as asexual methods. The typical means of asexual reproduction is either fragmentation (during this process, a piece of the sponge breaks off, settles on a new substrate, and develops into a new individual), or budding (a genetically identical outgrowth grows from the parent and eventually detaches or remains attached to form a colony). An atypical type of asexual reproduction is found only in freshwater sponges and occurs through the formation of *gemmules*. Gemmules are environmentally resistant structures produced by adult sponges (e.g., in the freshwater sponge *Spongilla*). In gemmules, an inner layer of archeocytes (amoebocytes) is surrounded by a pneumatic cellular layer that may be reinforced with spicules. In freshwater sponges, gemmules may survive hostile environmental conditions like changes in temperature, and then serve to recolonize the habitat once environmental conditions improve and stabilize. Gemmules are capable of attaching to a substratum and generating a new sponge. Since gemmules can withstand harsh environments, are resistant to desiccation, and remain dormant for long periods, they are an excellent means of colonization for a sessile organism.

Sexual reproduction in sponges occurs when gametes are generated. Oocytes arise by the differentiation of amoebocytes and are retained within the spongocoel, whereas spermatozoa result from the differentiation of choanocytes and are ejected via the osculum. Sponges are monoecious (hermaphroditic), which means that one individual can produce both gametes (eggs and sperm) simultaneously. In some sponges, production of gametes may occur throughout the year, whereas other sponges may show sexual cycles depending upon water temperature. Sponges may also become *sequentially hermaphroditic*, producing oocytes first and spermatozoa later. This temporal separation of gametes produced by the same sponge helps to encourage cross-fertilization and genetic diversity. Spermatozoa carried along by water currents can fertilize the oocytes borne in the mesohyl of other sponges. Early larval development occurs within the sponge, and free-swimming larvae (such as flagellated *parenchymula*) are then released via the osculum.

Locomotion

Sponges are generally sessile as adults and spend their lives attached to a fixed substratum. They do not show movement over large distances like other free-swimming marine invertebrates. However, sponge cells are capable of creeping along substrata via *organizational plasticity*, i.e., rearranging their cells. Under experimental conditions, researchers have shown that sponge cells spread on a physical support demonstrate a leading edge for directed movement. It has been speculated that this localized creeping movement may help sponges adjust to microenvironments near the point of attachment. It must be noted, however, that this pattern of movement has been documented in laboratories, it remains to be observed in natural sponge habitats.

Link to Learning

Link to Learning

Watch this BBC video showing the array of sponges seen along the Cayman Wall during a submersible dive.

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10: CNIDARIANS

10.1: Cnidarian Structure and Diversity

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10.1: Cnidarian Structure and Diversity

Learning Objectives

By the end of this section, you will be able to do the following:

- Compare structural and organization characteristics of Porifera and Cnidaria
- Describe the progressive development of tissues and their relevance to animal complexity
- Identify the two general body forms found in the Cnidaria
- Describe the identifying features of the major cnidarian classes

Phylum Cnidaria includes animals that exhibit radial or biradial symmetry and are diploblastic, meaning that they develop from two embryonic layers, ectoderm and endoderm. Nearly all (about 99 percent) cnidarians are marine species.

Whereas the defining cell type for the sponges is the choanocyte, the defining cell type for the cnidarians is the cnidocyte, or stinging cell. These cells are located around the mouth and on the tentacles, and serve to capture prey or repel predators. Cnidocytes have large stinging organelles called nematocysts, which usually contain barbs at the base of a long coiled thread. The outer wall of the cell has a hairlike projection called a *cnidocil*, which is sensitive to tactile stimulation. If the cnidocils are touched, the hollow threads evert with enormous acceleration, approaching 40,000 times that of gravity. The microscopic threads then either entangle the prey or instantly penetrate the flesh of the prey or predator, releasing toxins (including neurotoxins and pore-forming toxins that can lead to cell lysis) into the target, thereby immobilizing it or paralyzing it (see Figure 28.5).

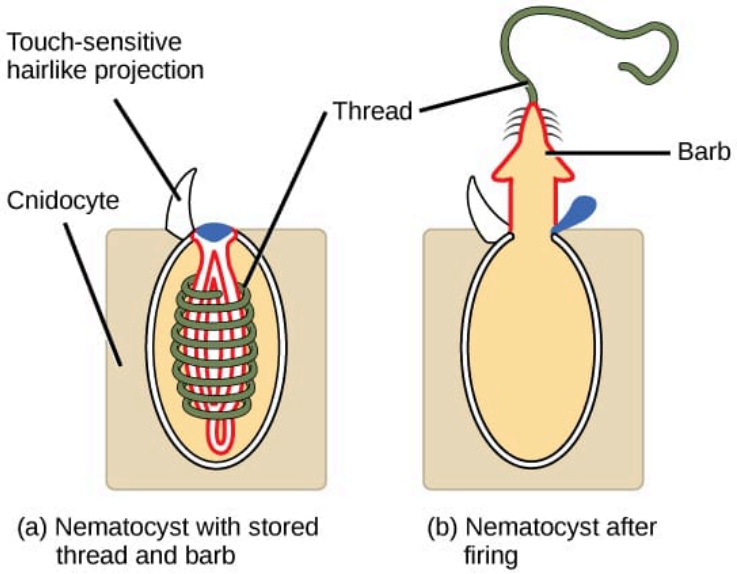


Figure 28.5 Cnidocytes. Animals from the phylum Cnidaria have stinging cells called cnidocytes. Cnidocytes contain large organelles called (a) nematocysts that store a coiled thread and barb, the nematocyst. When the hairlike cnidocil on the cell surface is touched, even lightly, (b) the thread, barb, and a toxin are fired from the organelle.

Link to Learning

Link to Learning

View this video animation showing two anemones engaged in a battle.

Two distinct body plans are found in Cnidarians: the polyp or tuliplike "stalk" form and the medusa or "bell" form. (Figure 28.6). An example of the polyp form is found in the genus *Hydra*, whereas the most typical form of medusa is found in the group called

the “sea jellies” (jellyfish). Polyp forms are sessile as adults, with a single opening (the mouth/anus) to the digestive cavity facing up with tentacles surrounding it. Medusa forms are motile, with the mouth and tentacles hanging down from an umbrella-shaped bell.

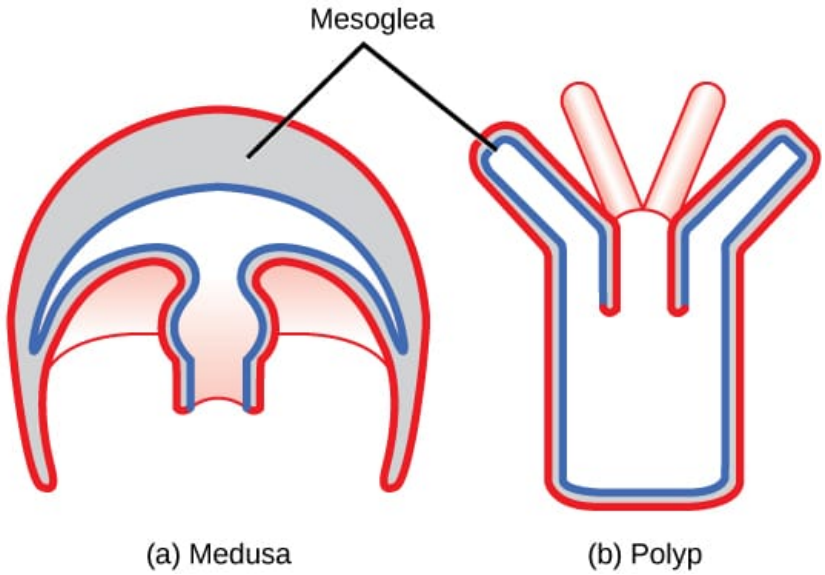


Figure 28.6 Cnidarian body forms. Cnidarians have two distinct body plans, the medusa (a) and the polyp (b). All cnidarians have two membrane layers, with a jelly-like mesoglea between them.

Some cnidarians are dimorphic, that is, they exhibit both body plans during their life cycle. In these species, the polyp serves as the asexual phase, while the medusa serves as the sexual stage and produces gametes. However, both body forms are diploid.

An example of cnidarian dimorphism can be seen in the colonial hydroid *Obelia*. The sessile asexual colony has two types of polyps, shown in Figure 28.7. The first is the *gastrozooid*, which is adapted for capturing prey and feeding. In *Obelia*, all polyps are connected through a common digestive cavity called a *coenosarc*. The other type of polyp is the *gonozooid*, adapted for the asexual budding and the production of sexual medusae. The reproductive buds from the gonozooid break off and mature into free-swimming medusae, which are either male or female (dioecious). Each medusa has either several testes or several ovaries in which meiosis occurs to produce sperm or egg cells. Interestingly, the gamete-producing cells do not arise within the gonad itself, but migrate into it from the tissues in the gonozooid. This separate origin of gonad and gametes is common throughout the eumetazoa. The gametes are released into the surrounding water, and after fertilization, the zygote develops into a blastula, which soon develops into a ciliated, bilaterally symmetrical planula larva. The planula swims freely for a while, but eventually attaches to a substrate and becomes a single polyp, from which a new colony of polyps is formed by budding.

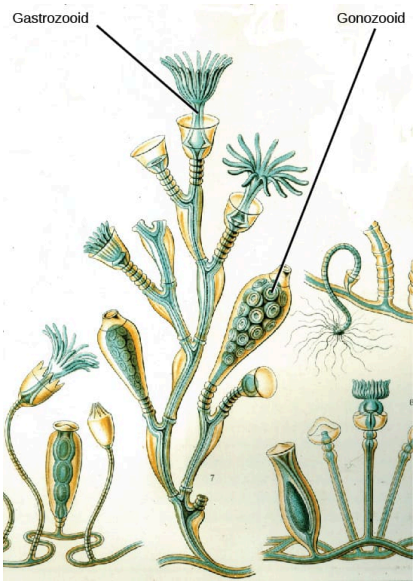


Figure 28.7 *Obelia*. The colonial sessile form of *Obelia geniculata* has two types of polyps: gastrozooids, which are adapted for capturing prey, and gonozooids, which asexually bud to produce medusae.

Link to Learning

Link to Learning

Click here to follow an *Obelia* life cycle animation.

All cnidarians are diploblastic and thus have two “epithelial” layers in the body that are derived from the endoderm and ectoderm of the embryo. The outer layer (from ectoderm) is called the *epidermis* and lines the outside of the animal, whereas the inner layer (from endoderm) is called the *gastrodermis* and lines the digestive cavity. In the planula larva, a layer of ectoderm surrounds a solid mass of endoderm, but as the polyp develops, the digestive or gastrovascular cavity opens within the endoderm. A non-living, jelly-like mesoglea lies between these two epithelial layers. In terms of cellular complexity, cnidarians show the presence of differentiated cell types in each tissue layer, such as nerve cells, contractile epithelial cells, enzyme-secreting cells, and nutrient-absorbing cells, as well as the presence of intercellular connections. However, with a few notable exceptions such as *statocysts* and *rhopalia* (see below), the development of organs or organ systems is not advanced in this phylum.

The nervous system is rudimentary, with nerve cells organized in a network scattered across the body. This nerve net may show the presence of groups of cells that form nerve plexi (singular: plexus) or nerve cords. Organization of the nervous system in the motile medusa is more complex than that of the sessile polyp, with a nerve ring around the edge of the medusa bell that controls the action of the tentacles. Cnidarian nerve cells show mixed characteristics of motor and sensory neurons. The predominant signaling molecules in these primitive nervous systems are peptides, which perform both excitatory and inhibitory functions. Despite the simplicity of the nervous system, it is remarkable that it coordinates the complicated movement of the tentacles, the drawing of captured prey to the mouth, the digestion of food, and the expulsion of waste.

The gastrovascular cavity has only one opening that serves as both a mouth and an anus; this arrangement is called an incomplete digestive system. In the gastrovascular cavity, extracellular digestion occurs as food is taken into the gastrovascular cavity, enzymes are secreted into the cavity, and the cells lining the cavity absorb nutrients. However, some intracellular digestion also occurs. The gastrovascular cavity distributes nutrients throughout the body of the animal, with nutrients passing from the digestive cavity across the mesoglea to the epidermal cells. Thus, this cavity serves both digestive and circulatory functions.

Cnidarian cells exchange oxygen and carbon dioxide by diffusion between cells in the epidermis and water in the environment, and between cells in the gastrodermis and water in the gastrovascular cavity. The lack of a circulatory system to move dissolved gases limits the thickness of the body wall and necessitates a non-living mesoglea between the layers. In the cnidarians with a thicker mesoglea, a number of canals help to distribute both nutrients and gases. There is neither an excretory system nor organs, and nitrogenous wastes simply diffuse from the cells into the water outside the animal or into the gastrovascular cavity.

The phylum Cnidaria contains about 10,000 described species divided into two monophyletic clades: the Anthozoa and the Medusozoa. The Anthozoa include the corals, sea fans, sea whips, and the sea anemones. The Medusozoa include several classes of Cnidaria in two clades: The Hydrozoa include sessile forms, some medusoid forms, and swimming colonial forms like the Portuguese man-of-war. The other clade contains various types of jellies including both Scyphozoa and Cubozoa. The Anthozoa contain only sessile polyp forms, while the Medusozoa include species with both polyp and medusa forms in their life cycle.

Class Anthozoa

The class Anthozoa ("flower animals") includes sea anemones (Figure 28.8), sea pens, and corals, with an estimated number of 6,100 described species. Sea anemones are usually brightly colored and can attain a size of 1.8 to 10 cm in diameter. Individual animals are cylindrical in shape and are attached directly to a substrate.

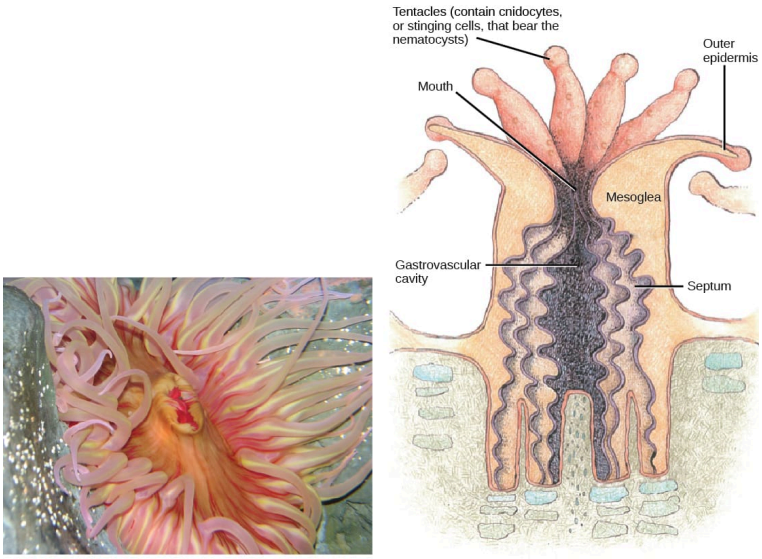


Figure 28.8 Sea anemone. The sea anemone is shown (a) photographed and (b) in a diagram illustrating its morphology. (credit a: modification of work by "Dancing With Ghosts"/Flickr; credit b: modification of work by NOAA)

The mouth of a sea anemone is surrounded by tentacles that bear cnidocytes. The slit-like mouth opening and flattened pharynx are lined with ectoderm. This structure of the pharynx makes anemones bilaterally symmetrical. A ciliated groove called a siphonoglyph is found on two opposite sides of the pharynx and directs water into it. The pharynx is the muscular part of the digestive system that serves to ingest as well as egest food, and may extend for up to two-thirds the length of the body before opening into the gastrovascular cavity. This cavity is divided into several chambers by longitudinal septa called *mesenteries*. Each mesentery consists of a fold of gastrodermal tissue with a layer of mesoglea between the sheets of gastrodermis. Mesenteries do not divide the gastrovascular cavity completely, and the smaller cavities coalesce at the pharyngeal opening. The adaptive benefit of the mesenteries appears to be an increase in surface area for absorption of nutrients and gas exchange, as well as additional mechanical support for the body of the anemone.

Sea anemones feed on small fish and shrimp, usually by immobilizing their prey with nematocysts. Some sea anemones establish a mutualistic relationship with hermit crabs when the crab seizes and attaches them to their shell. In this relationship, the anemone gets food particles from prey caught by the crab, and the crab is protected from the predators by the stinging cells of the anemone. Some species of anemone fish, or clownfish, are also able to live with sea anemones because they build up an acquired immunity to the toxins contained within the nematocysts and also secrete a protective mucus that prevents them from being stung.

The structure of coral polyps is similar to that of anemones, although the individual polyps are usually smaller and part of a colony, some of which are massive and the size of small buildings. Coral polyps feed on smaller planktonic organisms, including algae, bacteria, and invertebrate larvae. Some anthozoans have symbiotic associations with dinoflagellate algae called zooxanthellae. The mutually beneficial relationship between zooxanthellae and modern corals—which provides the algae with shelter—gives coral reefs their colors and supplies both organisms with nutrients. This complex mutualistic association began more than 210 million years ago, according to a new study by an international team of scientists. That this symbiotic relationship arose during a time of massive worldwide coral-reef expansion suggests that the interconnection of algae and coral is crucial for the health of coral reefs, which provide habitat for roughly one-fourth of all marine life. Reefs are threatened by a trend in ocean warming that has caused corals to expel their zooxanthellae algae and turn white, a process called coral bleaching.

Anthozoans remain *polypoid* (note that this term is easily confused with "polyploid") throughout their lives and can reproduce asexually by budding or fragmentation, or sexually by producing gametes. Male or female gametes produced by a polyp fuse to give rise to a free-swimming planula larva. The larva settles on a suitable substratum and develops into a sessile polyp.

Class Scyphozoa

Class Scyphozoa ("cup animals") includes all (and only) the marine jellies, with about 200 known species. The medusa is the prominent stage in the life cycle, although there is a polyp stage in the life cycle of most species. Most jellies range from 2 to 40 cm in length but the largest scyphozoan species, *Cyanea capillata*, can reach a size of two meters in diameter. Scyphozoans

display a characteristic bell-like morphology (Figure 28.9).

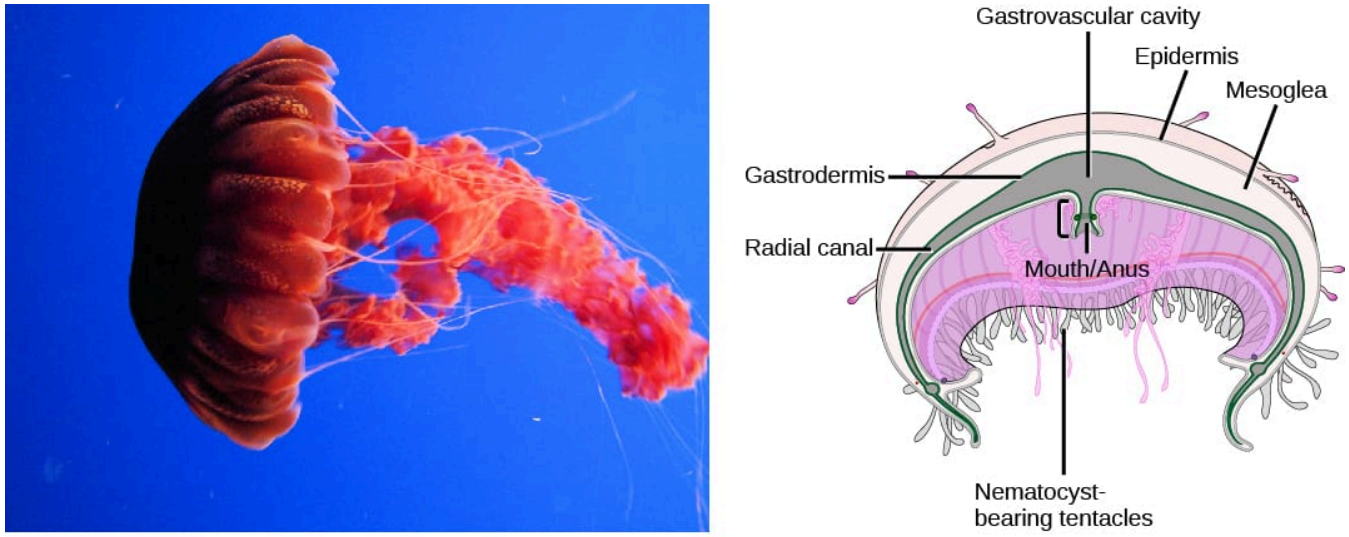


Figure 28.9 A sea jelly. A jelly is shown (a) photographed and (b) in a diagram illustrating its morphology. (credit a: modification of work by "Jimg944"/Flickr; credit b: modification of work by Mariana Ruiz Villareal)

In the sea jelly, a mouth opening is present on the underside of the animal, surrounded by hollow tentacles bearing nematocysts. Scyphozoans live most of their life cycle as free-swimming, solitary carnivores. The mouth leads to the gastrovascular cavity, which may be sectioned into four interconnected sacs, called *diverticuli*. In some species, the digestive system may branch further into *radial canals*. Like the septa in anthozoans, the branched gastrovascular cells serve two functions: to increase the surface area for nutrient absorption and diffusion, and to support the body of the animal.

In scyphozoans, nerve cells are organized in a nerve net that extends over the entire body, with a nerve ring around the edge of the bell. Clusters of sensory organs called rhopalia may be present in pockets in the edge of the bell. Jellies have a ring of muscles lining the dome of the body, which provides the contractile force required to swim through water, as well as to draw in food from the water as they swim. Scyphozoans have separate sexes. The gonads are formed from the gastrodermis and gametes are expelled through the mouth. Planula larvae are formed by external fertilization; they settle on a substratum in a polypoid form. These polyps may bud to form additional polyps or begin immediately to produce medusa buds. In a few species, the planula larva may develop directly into the medusa. The life cycle (Figure 28.10) of most scyphozoans includes both sexual medusoid and asexual polypoid body forms.

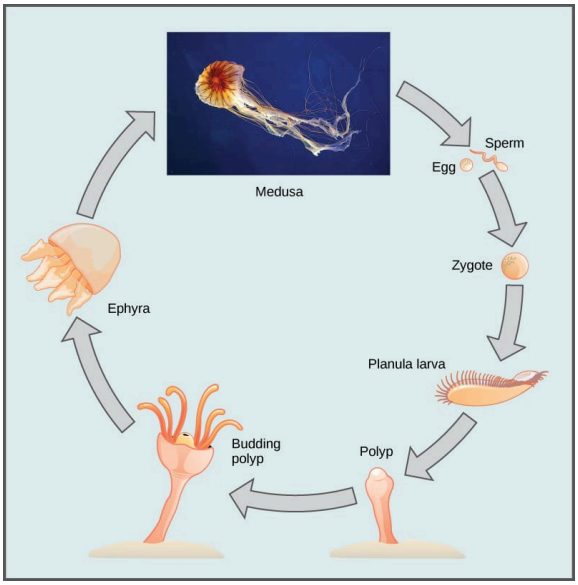


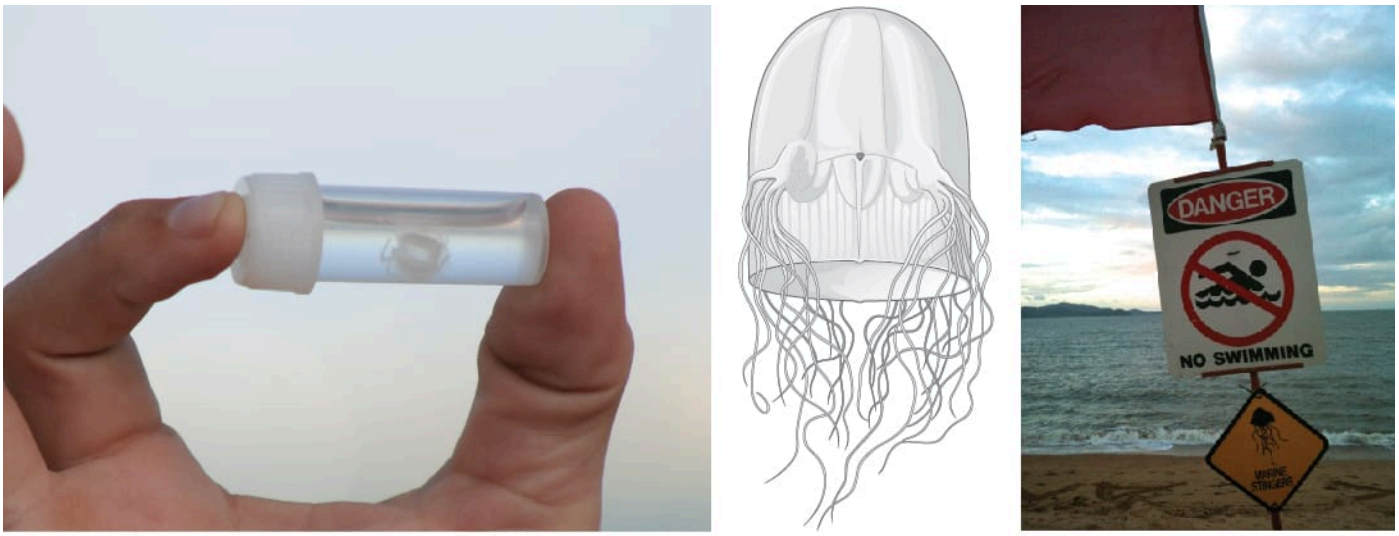
Figure 28.10 Scyphozoan life cycle. The lifecycle of most jellyfish includes two stages: the medusa stage and the polyp stage. The polyp reproduces asexually by budding, and the medusa reproduces sexually. (credit "medusa": modification of work by Francesco Crippa)

Class Cubozoa

This class includes jellies that have a box-shaped medusa, or a bell that is square in cross-section, and are colloquially known as “box jellyfish.” These species may achieve sizes of 15 to 25 cm, but typically members of the Cubozoa are not as large as those of the Scyphozoa. However, cubozoans display overall morphological and anatomical characteristics that are similar to those of the scyphozoans. A prominent difference between the two classes is the arrangement of tentacles. The cubozoans contain muscular pads called pedalia at the corners of the square bell canopy, with one or more tentacles attached to each pedalium. In some cases, the digestive system may extend into the pedalia. Nematocysts may be arranged in a spiral configuration along the tentacles; this arrangement helps to effectively subdue and capture prey. Cubozoans include the most venomous of all the cnidarians (Figure 28.11).

These animals are unusual in having image-forming eyes, including a cornea, lens, and retina. Because these structures are made from a number of interactive tissues, they can be called *true organs*. Eyes are located in four clusters between each pair of pedalia. Each cluster consists of four simple eye spots plus two image-forming eyes oriented in different directions. How images formed by these very complex eyes are processed remains a mystery, since cubozoans have extensive nerve nets but no distinct brain. Nonetheless, the presence of eyes helps the cubozoans to be active and effective hunters of small marine animals like worms, arthropods, and fish.

Cubozoans have separate sexes and fertilization occurs inside the female. Planula larvae may develop inside the female or be released, depending on species. Each planula develops into a polyp. These polyps may bud to form more polyps to create a colony; each polyp then transforms into a single medusa.



(a) (b) (c)

Figure 28.11 A cubozoan. The (a) tiny cubozoan jelly *Malo kingi* is thimble-shaped and, like all cubozoan jellies, (b) has four muscular pedalia to which the tentacles attach. *M. kingi* is one of two species of jellies known to cause Irukandji syndrome, a condition characterized by excruciating muscle pain, vomiting, increased heart rate, and psychological symptoms. Two people in Australia, where Irukandji jellies are most commonly found, are believed to have died from Irukandji stings. (c) A sign on a beach in northern Australia warns swimmers of the danger. (credit c: modification of work by Peter Shanks)

Class Hydrozoa

Hydrozoa is a diverse group that includes nearly 3,200 species; most are marine, although some freshwater species are known (Figure 28.12). Most species exhibit both polypoid and medusoid forms in their lifecycles, although the familiar *Hydra* has only the polyp form. The medusoid form has a muscular veil or velum below the margin of the bell and for this reason is called a *hydromedusa*. In contrast, the medusoid form of Scyphozoa lacks a velum and is termed a *scyphomedusa*.

The polyp form in these animals often shows a cylindrical morphology with a central gastrovascular cavity lined by the gastrodermis. The gastrodermis and epidermis have a simple layer of mesoglea sandwiched between them. A mouth opening, surrounded by tentacles, is present at the oral end of the animal. Many hydrozoans form sessile, branched colonies of specialized polyps that share a common, branching gastrovascular cavity (coenosarc), such as is found in the colonial hydroid *Obelia*.

Free-floating colonial species called siphonophores contain both medusoid and polypoid individuals that are specialized for feeding, defense, or reproduction. The distinctive rainbow-hued float of the Portuguese man o' war (*Physalia physalis*) creates a pneumatophore with which it regulates buoyancy by filling and expelling carbon monoxide gas. At first glance, these complex superorganisms appear to be a single organism; but the reality is that even the tentacles are actually composed of zooids laden with nematocysts. Thus, although it superficially resembles a typical medusozoan jellyfish, *P. physalis* is a free-floating hydrozoan *colony*; each specimen is made up of many hundreds of organisms, each specialized for a certain function, including motility and buoyancy, feeding, reproduction and defense. Although they are carnivorous and feed on many soft bodied marine animals, *P. physalis* lack stomachs and instead have specialized polyps called gastrozooids that they use to digest their prey in the open water.

Physalia has male and female colonies, which release their gametes into the water. The zygote develops into a single individual, which then buds asexually to form a new colony. Siphonophores include the largest known floating cnidarian colonies such as *Praya dubia*, whose chain of zooids can get up to 50 meters (165 feet) long. Other hydrozoan species are solitary polyps (*Hydra*) or solitary hydromedusae (*Gonionemus*). One defining characteristic shared by the hydrozoans is that their gonads are derived from epidermal tissue, whereas in all other cnidarians they are derived from gastrodermal tissue.

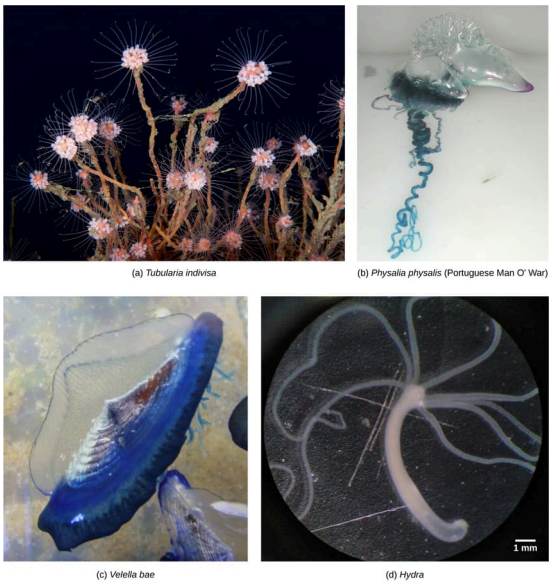


Figure 28.12 Hydrozoans. The *Tubularia indivisa* (a), siphonophore colonies *Physalia* (b) *physalis*, known as the Portuguese man o' war and *Velella bae* (c), and the solitary polyp *Hydra* (d) have different body shapes but all belong to the family Hydrozoa. (credit a: modification of work by Bernard Picton/Wikimedia Commons; credit b: modification of work by NOAA; scale-bar data from Matt Russell)

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11: FLATWORMS, ROTIFERS & NEMATODES

11.1: Flatworm and Rotifer Structure and Diversity
11.2: Nematode Structure and Diversity

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11.1: Flatworm and Rotifer Structure and Diversity

Learning Objectives

By the end of this section, you will be able to do the following:

- Describe the unique anatomical and morphological features of flatworms, rotifers, and Nemertea
- Identify an important extracoelomic cavity found in Nemertea
- Explain the key features of Platyhelminthes and their importance as parasites

Animals belonging to superphylum Lophotrochozoa are triploblastic (have three germ layers) and unlike the cnidarians, they possess an embryonic mesoderm sandwiched between the ectoderm and endoderm. These phyla are also bilaterally symmetrical, meaning that a longitudinal section will divide them into right and left sides that are superficially symmetrical. In these phyla, we also see the beginning of cephalization, the evolution of a concentration of nervous tissues and sensory organs in the head of the organism—exactly where a mobile bilaterally symmetrical organism first encounters its environment.

Lophotrochozoa are also protostomes, in which the blastopore, or the point of invagination of the ectoderm (outer germ layer), becomes the mouth opening into the alimentary canal. This developmental pattern is called protostomy or “first mouth.” Protostomes include acoelomate, pseudocoelomate, and eucoelomate phyla. The coelom is a cavity that separates the ectoderm from the endoderm. In acoelomates, a *solid mass* of mesoderm is sandwiched between the ectoderm and endoderm and does not form a cavity or “coelom,” leaving little room for organ development; in pseudocoelomates, there is a cavity or *pseudocoelom* that replaces the blastocoel (the cavity within the blastula), but it is only lined by mesoderm on the outside of the cavity, leaving the gut tube and organs unlined; in eucoelomates, the cavity that obliterates the blastocoel as the coelom develops is lined both on the outside of the cavity (parietal layer) *and* also on the inside of the cavity, around the gut tube and the internal organs (visceral layer).

Eucoelmate protostomes are schizocoels, in which mesoderm-producing cells typically migrate into the blastocoel during gastrulation and multiply to form a solid mass of cells. Cavities then develop within the cell mass to form the coelom. Since the forming body cavity splits the mesoderm, this protostomic coelom is termed a schizocoelom. As we will see later in this chapter, chordates, the phylum to which we belong, generally develop a coelom by enterocoely: pouches of mesoderm pinch off the invaginating primitive gut, or *archenteron*, and then fuse to form a complete coelom. We should note here that a eucoelomate can form its “true coelom” by either schizocoely or enterocoely. The process that produces the coelom is different and of taxonomic importance, but the result is the same: a complete, mesodermally lined coelom.

Most organisms placed in the superphylum Lophotrochozoa possess either a *lophophore* feeding apparatus or a *trochophore* larvae (thus the contracted name, “lopho-trocho-zoa”). The lophophore is a feeding structure composed of a set of ciliated tentacles surrounding the mouth. A trochophore is a free-swimming larva characterized by two bands of cilia surrounding a top-like body. Some of the phyla classified as Lophotrochozoa may be missing one or both of these defining structures. Nevertheless their placement with the Lophotrochozoa is upheld when ribosomal RNA and other gene sequences are compared. The systematics of this complex group is still unclear and much more work remains to resolve the cladistic relationships among them.

Phylum Platyhelminthes

The flatworms are acoelomate organisms that include many free-living and parasitic forms. The flatworms possess neither a lophophore nor trochophore larvae, although the larvae of one group of flatworms, the Polycladida (named after its many-branched digestive tract), are considered to be homologous to trochophore larvae. Spiral cleavage is also seen in the polycladids and other basal flatworm groups. The developmental pattern of some of the free-living forms is obscured by a phenomenon called "*blastomere anarchy*," in which a sort of temporary feeding larva forms, followed by a regrouping of cells within the embryo that gives rise to a second-stage embryo. However, both the monophyly of the flatworms and their placement in the Lophotrochozoa has been supported by molecular analyses.

The Platyhelminthes consist of two monophyletic lineages: the Catenulida and the Rhabditophora. The Catenulida, or "chain worms," is a small clade of just over 100 species. These worms typically reproduce asexually by budding. However, the offspring

do not fully detach from the parents and the formation resembles a chain in appearance. All of the flatworms discussed here are part of the Rhabditophora ("rhabdite bearers"). Rhabdites are rodlike structures discharged in the mucus produced by some free-living flatworms; Eucoelmate protostomes are schizocoels, in which mesoderm-producing cells typically migrate into the blastocoel during gastrulation likely serve in both defense and to provide traction for ciliary gliding along the substrate. Unlike free-living flatworms, many species of trematodes and cestodes are parasitic, including important parasites of humans.





Figure 28.13 Flatworms exhibit significant diversity. (a) A blue Pseudoceros flatworm *(Pseudoceros bifurcus)*; (b) gold speckled flatworm *(Thysanozoon nigropapillosum)*. (credit a: modification of work by Stephen Childs; b: modification of work by Pril Fish.)

Flatworms have three embryonic tissue layers that give rise to epidermal tissues (from ectoderm), the lining of the digestive system (from endoderm), and other internal tissues (from mesoderm). The epidermal tissue is a single layer of cells or a layer of fused cells (syncytium) that covers two layers of muscle, one circular and the other longitudinal. The mesodermal tissues include mesenchymal cells that contain collagen and support secretory cells that produce mucus and other materials at the surface. Because flatworms are acoelomates, the mesodermal layer forms a solid mass between the outer epidermal surface and the cavity of the digestive system.

Physiological Processes of Flatworms

The free-living species of flatworms are predators or scavengers. Parasitic forms feed by absorbing nutrients provided by their hosts. Most flatworms, such as the planarian shown in Figure 28.14, have a branching gastrovascular cavity rather than a complete digestive system. In such animals, the “mouth” is also used to expel waste materials from the digestive system, and thus also serves as an anus. (A few species may have a second anal pore or opening.) The gut may be a simple sac or highly branched. Digestion is primarily extracellular, with digested materials taken into the cells of the gut lining by phagocytosis. One parasitic group, the tapeworms (cestodes), lacks a digestive system altogether, and absorb digested food from the host.

Flatworms have an excretory system with a network of tubules attached to flame cells, whose cilia beat to direct waste fluids concentrated in the tubules out of the body through excretory pores. The system is responsible for the regulation of dissolved salts and the excretion of nitrogenous wastes. The nervous system consists of a pair of lateral nerve cords running the length of the body with transverse connections between them. Two large cerebral ganglia—concentrations of nerve cell bodies at the anterior end of the worm—are associated with photosensory and chemosensory cells. There is neither a circulatory nor a respiratory system, with gas and nutrient exchange dependent on diffusion and cell-to-cell junctions. This necessarily limits the thickness of the body in these organisms, constraining them to be “flat” worms. Most flatworm species are *monoecious* (both male and female reproductive organs are found in the same individual), and fertilization is typically internal. Asexual reproduction by fission is common in some groups.

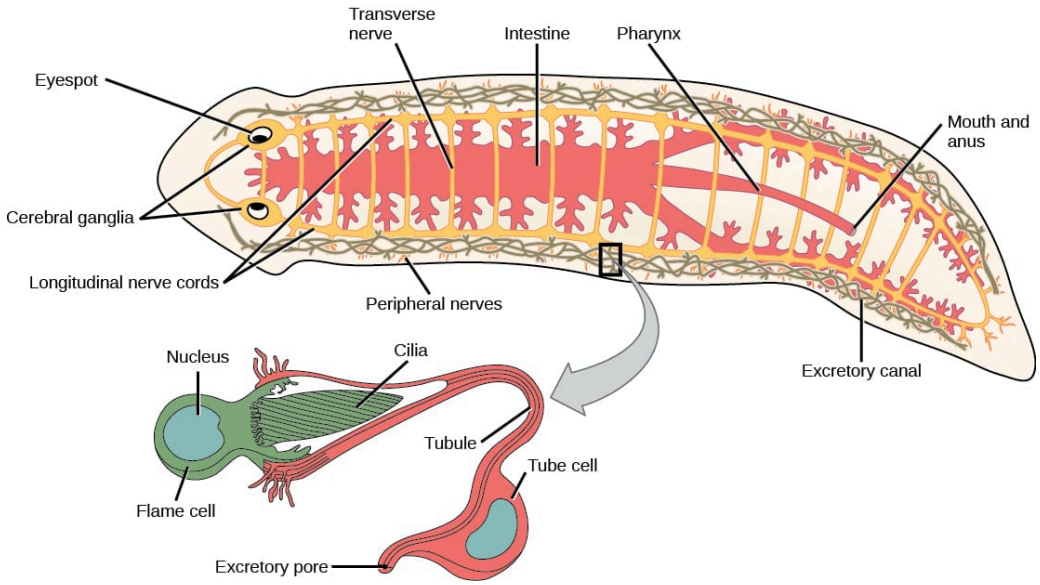


Figure 28.14 *Planaria*, a free-living flatworm. The planarian is a flatworm that has a gastrovascular cavity with one opening that serves as both mouth and anus. The excretory system is made up of flame cells and tubules connected to excretory pores on both sides of the body. The nervous system is composed of two interconnected nerve cords running the length of the body, with cerebral ganglia and eyespots at the anterior end.

Diversity of Flatworms

The flatworms have been traditionally divided into four classes: Turbellaria, Monogenea, Trematoda, and Cestoda (Figure 28.15). However, the relationships among members of these classes has recently been reassessed, with the turbellarians in particular now viewed as paraphyletic, since its descendants may also include members of the other three classes. Members of the clade or class Rhabditophora are now dispersed among multiple orders of Platyhelminthes, the most familiar of these being the Polycladida, which contains the large marine flatworms; the Tricladida (which includes *Dugesia* [“planaria”] and *Planaria* and its relatives); and the major parasitic orders: Monogenea (fish ectoparasites), Trematoda (flukes), and Cestoda (tapeworms), which together form a monophyletic clade.

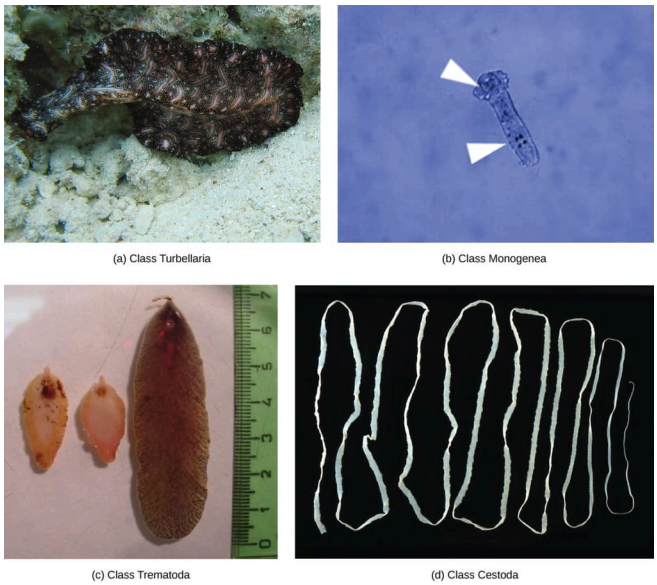


Figure 28.15 Traditional flatworm classes. Phylum Platyhelminthes was previously divided into four classes. (a) Class Turbellaria includes the free-living polycladid Bedford’s flatworm (*Pseudobiceros bedfordi*), which is about 8 to 10 cm in length. (b) The parasitic class Monogenea includes *Dactylogyrus* spp, commonly called gill flukes, which are about 0.2 mm in length and have two anchors, indicated by arrows used to attach the parasite on to the gills of host fish. (c) The class Trematoda includes *Fascioloides magna* (right) and *Fasciola hepatica* (two specimens on left, also known as the common liver fluke). (d) Class Cestoda includes

tapeworms such as this *Taenia saginata*, infects both cattle and humans, and can reach 4 to 10 meters in length; the specimen shown here is about four meters long. (credit a: modification of work by Jan Derk; credit d: modification of work by CDC)

Most free-living flatworms are marine polycladids, although tricladid species live in freshwater or moist terrestrial environments, and there are a number of members from other orders in both environments. The ventral epidermis of free-living flatworms is ciliated, which facilitates their locomotion. Some free-living flatworms are capable of remarkable feats of regeneration in which an individual may regrow its head or tail after being severed, or even several heads if the planaria is cut lengthwise.

The monogeneans are *ectoparasites*, mostly of fish, with simple life cycles that consist of a free-swimming larva that attaches to a fish, prior to its transformation to the ectoparasitic adult form. The parasite has only one host and that host is usually very specific. The worms may produce enzymes that digest the host tissues, or they may simply graze on surface mucus and skin particles. Most monogeneans are hermaphroditic, but the male gametes develop first and so cross-fertilization is quite common.

The trematodes, or flukes, are internal parasites of mollusks and many other groups, including humans. Trematodes have complex life cycles that involve a primary host in which sexual reproduction occurs, and one or more secondary hosts in which asexual reproduction occurs. The primary host is usually a vertebrate and the secondary host is almost always a mollusk, in which multiple larvae are produced asexually. Trematodes, which attached internally to the host via an oral and medial sucker, are responsible for serious human diseases including schistosomiasis, caused by several species of the blood fluke, *Schistosoma* spp. Various forms of schistosomiasis infect an estimated 200 million people in the tropics, leading to organ damage, secondary infection by bacteria, and chronic symptoms like fatigue. Infection occurs when the human enters the water and metacercaria larvae, released from the snail host, locate and penetrate the skin. The parasite infects various organs in the body and feeds on red blood cells before reproducing.

Many of the eggs are released in feces and find their way into a waterway, where they are able to reinfect the snail host. The eggs, which have a barb on them, can damage the vascular system of the human host, causing ulceration, abscesses, and bloody diarrhea, wherever they reside, thereby allowing other pathogens to cause secondary infections. In fact, it is the parasite's eggs that produce most of the main ill effects of schistosomiasis. Many eggs do not make the transit through the veins of the host for elimination, and are swept by blood flow back to the liver and other locations, where they can cause severe inflammation. In the liver, the errant eggs may impede circulation and cause cirrhosis. Control is difficult in impoverished areas in unsanitary, crowded conditions, and prognosis is poor in people with heavy infections of *Schistosoma japonicum*, without early treatment.

The cestodes, or tapeworms, are also internal parasites, mainly of vertebrates (Figure 28.16). Tapeworms, such as those of *Taenia* spp, live in the intestinal tract of the primary host and remain fixed using a sucker or hooks on the anterior end, or scolex, of the tapeworm body, which is essentially a colony of similar subunits called proglottids. Each proglottid may contain an excretory system with flame cells, along with reproductive structures, both male and female. Because they are so long and flat, tapeworms do not need a digestive system; instead, they absorb nutrients from the food matter surrounding them in the host's intestine by diffusion.

Proglottids are produced at the scolex and gradually migrate to the end of the tapeworm; at this point, they are "mature" and all structures except fertilized eggs have degenerated. Most reproduction occurs by cross-fertilization between different worms in the same host, but may also occur between proglottids. The mature proglottids detach from the body of the worm and are released into the feces of the organism. The eggs are eaten by an intermediate host, typically another vertebrate. The juvenile worm infects the intermediate host and takes up residence, usually in muscle tissue. When the muscle tissue is consumed by the primary host, the cycle is completed. There are several tapeworm parasites of humans that are transmitted by eating uncooked or poorly cooked pork, beef, or fish.

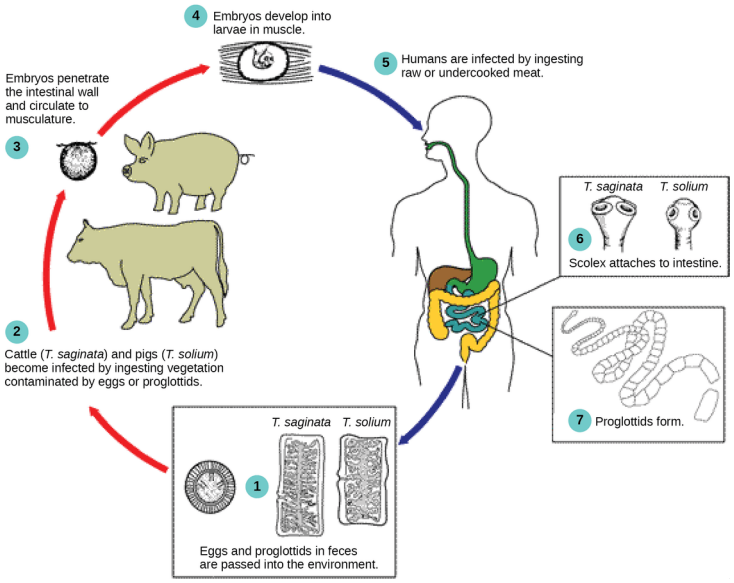
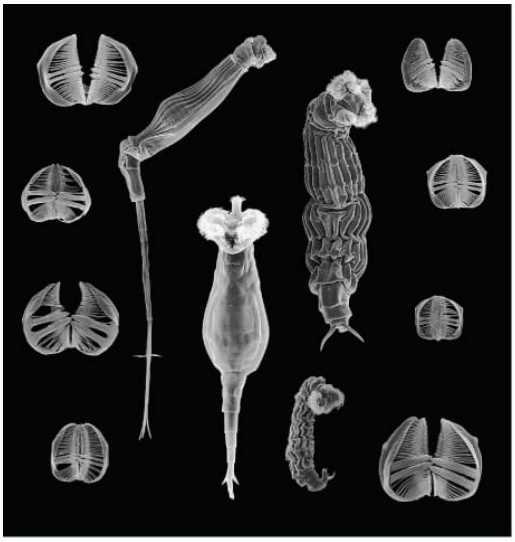


Figure 28.16 Tapeworm life cycle. Tapeworm (*Taenia* spp.) infections occur when humans consume raw or undercooked infected meat. (credit: modification of work by CDC)

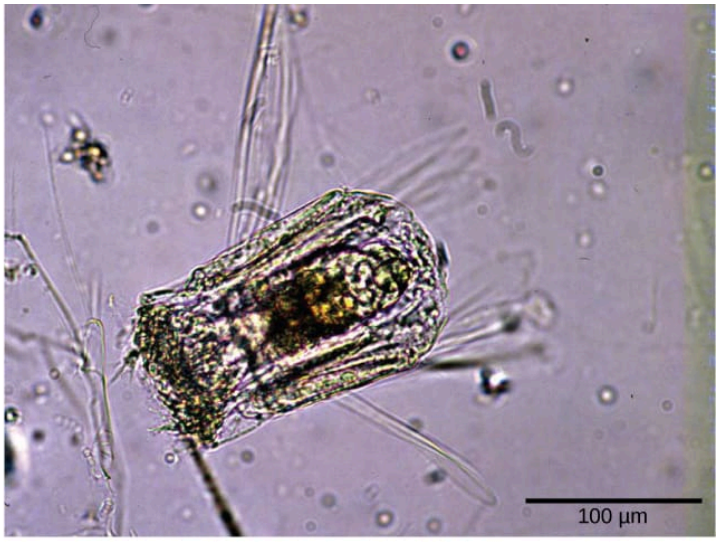
Phylum Rotifera

The rotifers ("wheel-bearer") belong to a group of microscopic (about 100 µm to 2 mm) mostly aquatic animals that get their name from the corona—a pair of ciliated feeding structures that appear to rotate when viewed under the light microscope (Figure 28.17). Although their taxonomic status is currently in flux, one treatment places the rotifers in three classes: Bdelloidea, Monogononta, and Seisonidea. In addition, the parasitic “spiny headed worms” currently in phylum Acanthocephala, appear to be modified rotifers and will probably be placed into the group in the near future. Undoubtedly the rotifers will continue to be revised as more phylogenetic evidence becomes available.

The pseudocoelomate body of a rotifer is remarkably complex for such a small animal (roughly the size of a *Paramecium*) and is divided into three sections: a *head* (which contains the corona), a *trunk* (which contains most of the internal organs), and the *foot*. A cuticle, rigid in some species and flexible in others, covers the body surface. They have both skeletal muscle associated with locomotion and visceral muscles associated with the gut, both composed of single cells. Rotifers are typically free-swimming or planktonic (drifting) organisms, but the toes or extensions of the foot can secrete a sticky material to help them adhere to surfaces. The head contains a number of eyespots and a bilobed “brain,” with nerves extending into the body.



(a) Bdelloidea



(a) Monogonota

Figure 28.17 Rotifers. Shown are examples from two of the three classes of rotifer. (a) Species from the class Bdelloidea are characterized by a large corona. The whole animals in the center of this scanning electron micrograph are shown surrounded by several sets of jaws from the mastax of rotifers. (b) *Polyarthra*, from the largest rotifer class Monogononta, has a smaller corona than bdelloid rotifers, and a single gonad, which give the class its name. (credit a: modification of work by Diego Fontaneto; credit b: modification of work by U.S. EPA; scale-bar data from Cory Zanker)

Rotifers are commonly found in freshwater and some saltwater environments throughout the world. As filter feeders, they will eat dead material, algae, and other microscopic living organisms, and are therefore very important components of aquatic food webs. A rotifer's food is directed toward the mouth by the current created from the movement of the coronal cilia. The food particles enter the mouth and travel first to the mastax—a muscular pharynx with toothy jaw-like structures. Examples of the jaws of various rotifers are seen in Figure 28.17a. Masticated food passes near digestive and salivary glands, into the stomach, and then to the intestines. Digestive and excretory wastes are collected in a cloacal bladder before being released out the anus.

Link to Learning

Link to Learning

Watch this video to see rotifers feeding.

About 2,200 species of rotifers have been identified. Figure 28.18 shows the anatomy of a rotifer belonging to class Bdelloidea. Some rotifers are dioecious organisms and exhibit sexual dimorphism (males and females have different forms). In many dioecious species, males are short-lived and smaller with no digestive system and a single testis. Many rotifer species exhibit haplodiploidy, a method of sex determination in which a fertilized egg develops into a female and an unfertilized egg develops into a male. However, reproduction in the bdelloid rotifers is exclusively parthenogenetic and appears to have been so for millions of years: Thus, all bdelloid rotifers and their progeny are female! The bdelloids may compensate for this genetic insularity by borrowing genes from the DNA of other species. Up to 10% of a bdelloid genome comprises genes imported from related species. Some rotifer eggs are capable of extended dormancy for protection during harsh environmental conditions.

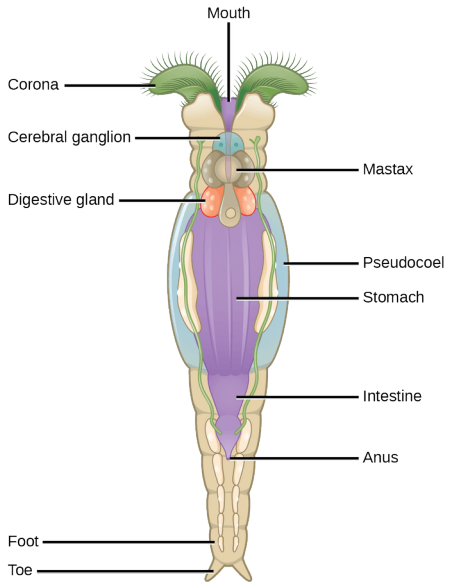


Figure 28.18 A bdelloid rotifer. This illustration shows the anatomy of a bdelloid rotifer.

Phylum Nemertea

The Nemertea are colloquially known as *ribbon worms* or proboscis worms. Most species of phylum Nemertea are marine and predominantly benthic (bottom dwellers), with an estimated 900 known species. However, nemerteans have been recorded in freshwater and very damp terrestrial habitats as well. Most nemerteans are carnivores, feeding on worms, clams, and crustaceans. Some species are scavengers, and some, like *Malacobdella grossa*, have also evolved commensal relationships with mollusks. Economically important species have at times devastated commercial fishing of clams and crabs. Nemerteans have almost no

predators and two species are sold as fish bait.

Morphology

Nemerteans vary in size from 1 cm to several meters. They show bilateral symmetry and remarkable contractile properties. Because of their contractility, they can change their morphological presentation in response to environmental cues. Animals in phylum Nemertea are soft and unsegmented animals, with a morphology like a flattened tube. (Figure 28.19).

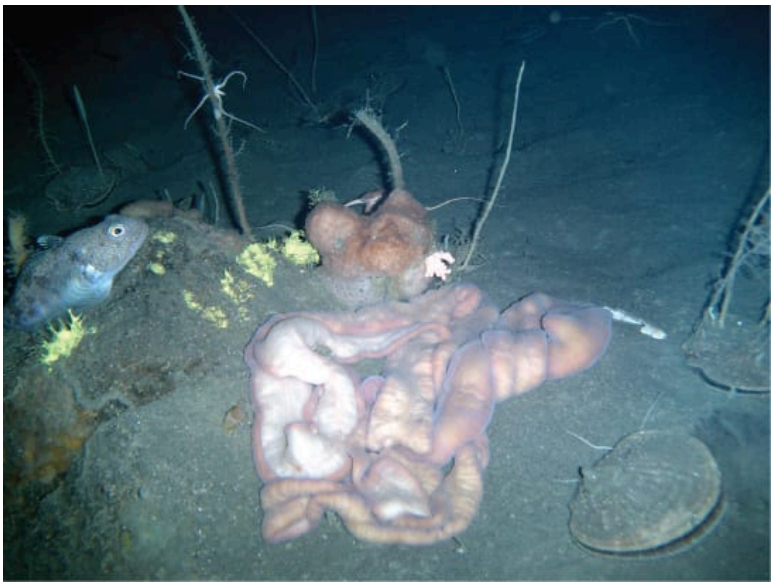


Figure 28.19 A proboscis worm. The proboscis worm (*Parborlasia corrugatus*) is a scavenger that combs the sea floor for food. The species is a member of the phylum Nemertea. The specimen shown here was photographed in the Ross Sea, Antarctica. (credit: Henry Kaiser, National Science Foundation)

A unique characteristic of this phylum is the presence of an eversible proboscis enclosed in a pocket called a rhynchocoel (not part of the animal's actual coelom). The proboscis is located dorsal to the gut and serves as a harpoon or tentacle for food capture. In some species it is ornamented with barbs. The rhynchocoel is a fluid-filled cavity that extends from the head to nearly two-thirds of the length of the gut in these animals (Figure 28.20). The proboscis may be extended by hydrostatic pressure generated by contraction of muscle of the rhynchocoel and retracted by a retractor muscle attached to the rear wall of the rhynchocoel.

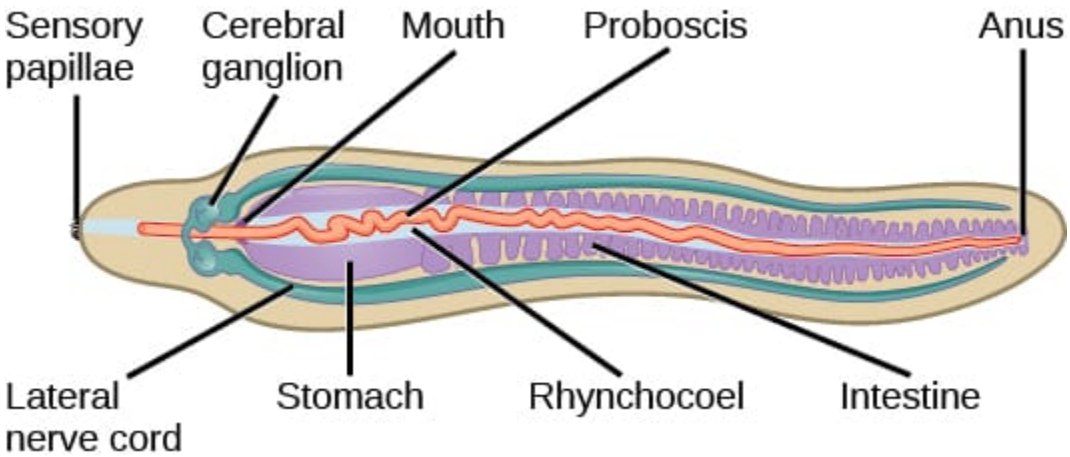


Figure 28.20 The anatomy of a Nemertean is shown.

Link to Learning

Link to Learning

Watch this video to see a nemertean attack a polychaete with its proboscis.

Digestive System

The nemerteans, which are primarily predators of annelids and crustaceans, have a well-developed digestive system. A mouth opening that is ventral to the rhynchocoel leads into the foregut, followed by the intestine. The intestine is present in the form of diverticular pouches and ends in a rectum that opens via an anus. Gonads are interspersed with the intestinal diverticular pouches and open outward via genital pores.

Nemerteans are sometimes classified as acoels, but because their closed circulatory system is derived from the coelomic cavity of the embryo, they may be regarded as coelomic. Their circulatory system consists of a closed loop formed by a connected pair of lateral blood vessels. Some species may also have a dorsal vessel or cross-connecting vessels in addition to lateral ones. Although the circulatory fluid contains cells, it is often colorless. However, the blood cells of some species bear hemoglobin as well as other yellow or green pigments. The blood vessels are contractile, although there is usually no regular circulatory pathway, and movement of blood is also facilitated by the contraction of muscles in the body wall. The circulation of fluids in the rhynchocoel is more or less independent of the blood circulation, although blind branches from the blood vessels into the rhynchocoel wall can mediate exchange of materials between them. A pair of protonephridia, or excretory tubules, is present in these animals to facilitate osmoregulation. Gaseous exchange occurs through the skin.

Nervous System

Nemerteans have a "brain" composed of four ganglia situated at the anterior end, around the rhynchocoel. Paired longitudinal nerve cords emerge from the brain ganglia and extend to the posterior end. Additional nerve cords are found in some species. Interestingly, the brain can contain hemoglobin, which acts as an oxygen reserve. *Ocelli* or eyespots are present in pairs, in multiples of two in the anterior portion of the body. It is speculated that the eyespots originate from neural tissue and not from the epidermis.

Reproduction

Nemerteans, like flatworms, have excellent powers of regeneration, and asexual reproduction by fragmentation is seen in some species. Most animals in phylum Nemertea are dioecious, although freshwater species may be hermaphroditic. Stem cells that become gametes aggregate within gonads placed along the digestive tract. Eggs and sperm are released into the water, and fertilization occurs externally. Like most lophotrochozoan protostomes, cleavage is spiral, and development is usually direct, although some species have a trochophore-like larva, in which a young worm is constructed from a series of imaginal discs that begin as invaginations from the body surface of the larva.

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11.2: Nematode Structure and Diversity

Learning Objectives

By the end of this section, you will be able to do the following:

- Describe the structural organization of nematodes
- Describe the importance of Caenorhabditis elegans in research
- Describe the features of Tardigrades

Superphylum Ecdysozoa

The superphylum Ecdysozoa contains an incredibly large number of species. This is because it contains two of the most diverse animal groups: phylum Nematoda (the roundworms) and phylum Arthropoda (the arthropods). The most prominent distinguishing feature of ecdysozoans is the cuticle—a tough, but flexible exoskeleton that protects these animals from water loss, predators, and other dangers of the external environment. One small phylum within the Ecdysozoa, with exceptional resistance to desiccation and other environmental hazards, is the Tardigrada. The nematodes, tardigrades, and arthropods all belong to the superphylum Ecdysozoa, which is believed to be monophyletic—a clade consisting of all evolutionary descendants from one common ancestor. All members of this superphylum periodically go through a molting process that culminates in ecdysis—the actual shedding of the old exoskeleton. (The term “ecdysis” translates roughly as “take off” or “strip.”) During the molting process, old cuticle is replaced by a new cuticle, which is secreted beneath it, and which will last until the next growth period.

Phylum Nematoda

The Nematoda, like other members of the superphylum Ecdysozoa, are triploblastic and possess an embryonic mesoderm that is sandwiched between the ectoderm and endoderm. They are also bilaterally symmetrical, meaning that a longitudinal section will divide them into right and left sides that are superficially symmetrical. In contrast with flatworms, nematodes are pseudocoelomates and show a tubular morphology and circular cross-section. Nematodes include both free-living and parasitic forms.

In 1914, N.A. Cobb said, “In short, if all the matter in the universe except the nematodes were swept away, our world would still be dimly recognizable, and if, as disembodied spirits, we could then investigate it, we should find its mountains, hills, vales, rivers, lakes and oceans represented by a thin film of nematodes…” To paraphrase Cobb, nematodes are so abundant that if all the non-nematode matter of the biosphere were removed, there would still remain a shadow of the former world outlined by nematodes![1] The phylum Nematoda includes more than 28,000 species with an estimated 16,000 being parasitic in nature. However, nematologists believe there may be over one million unclassified species.

The name Nematoda is derived from the Greek word “Nemos,” which means “thread,” and includes all true roundworms. Nematodes are present in all habitats, typically with each species occurring in great abundance. The free-living nematode, *Caenorhabditis elegans*, has been extensively used as a model system for many different avenues of biological inquiry in laboratories all over the world.

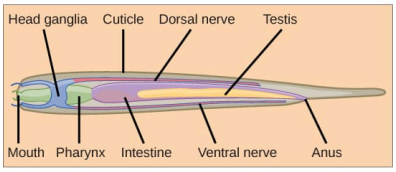
Morphology

The cylindrical body form of the nematodes is seen in Figure 28.32. These animals have a complete digestive system with a distinct mouth and anus, whereas only one opening is present in the digestive tract of flatworms. The mouth opens into a muscular pharynx and intestine, which leads to a rectum and anal opening at the posterior end. The epidermis can be either a single layer of cells or a syncytium—a multinucleated tissue that in this case is formed by the fusion of many single cells. The cuticle of nematodes is rich in collagen and a polymer called chitin, which forms a protective armor outside the epidermis. The cuticle extends into both ends of the digestive tract, the pharynx, and rectum. In the head, an anterior mouth opening is composed of three (or six) “lips” as well as teeth derived from the cuticle (in some species). Some nematodes may present other modifications of the cuticle such as rings, head shields, or warts. These external rings, however, do not reflect *true* internal body segmentation,

which as we have seen is a hallmark of phylum Annelida. The attachment of the muscles of nematodes differs from that of most animals: they have a longitudinal layer only, and their direct attachment to the dorsal and ventral nerve cords creates a strong muscular contraction that results in a whiplike, almost spastic, body movement.



(a)



(b)

Figure 28.32 Nematode morphology. Scanning electron micrograph shows (a) the soybean cyst nematode (*Heterodera glycines*) and a nematode egg. (b) A schematic representation shows the anatomy of a typical nematode. (credit a: modification of work by USDA ARS; scale-bar data from Matt Russell)

Excretory System

In nematodes, specialized excretory systems are not well developed. Nitrogenous wastes, largely in the form of *ammonia*, are released directly across the body wall. In some nematodes, osmoregulation and salt balance are performed by simple excretory cells or glands that may be connected to paired canals that release wastes through an anterior pore. In marine nematodes, the excretory cells are called renette cells, which are unique to nematodes.

Nervous system

Most nematodes have four longitudinal nerve cords that run along the length of the body in dorsal, ventral, and lateral positions. The ventral nerve cord is better developed than the dorsal and lateral cords. Nonetheless, all nerve cords fuse at the anterior end, to form a pharyngeal nerve ring around the pharynx, which acts as the head ganglion or the “brain” of the roundworm. A similar fusion forms a posterior ganglion at the tail. In *C. elegans*, the nervous system accounts for nearly one-third of the total number of cells in the animal!

Reproduction

Nematodes employ a variety of reproductive strategies ranging from monoecious to dioecious to parthenogenetic, depending upon the species. *C. elegans* is a mostly monoecious species with both self-fertilizing hermaphrodites and some males. In the hermaphrodites, ova and sperm develop at different times in the same gonad. Ova are contained in a uterus and amoeboid sperm are contained in a spermatheca ("sperm receptacle"). The uterus has an external opening known as the vulva. The female genital pore is near the middle of the body, whereas the male genital pore is nearer to the tip. In anatomical males, specialized structures called *copulatory spicules* at the tail of the male keep him in place and open the vulva of the female into which the amoeboid sperm travel into the spermatheca.

Fertilization is internal, and embryonic development starts very soon after fertilization. The embryo is released from the vulva during the gastrulation stage. The embryonic development stage lasts for 14 hours; development then continues through four successive larval stages with molting and ecdysis taking place between each stage—L1, L2, L3, and L4—ultimately leading to the development of a young adult worm. Adverse environmental conditions such as overcrowding or lack of food can result in the formation of an intermediate larval stage known as the *dauer larva*. An unusual feature of some nematodes is eutely: the body of

a given species contains a specific number of cells as the consequence of a rigid developmental pathway.

Everyday Connection

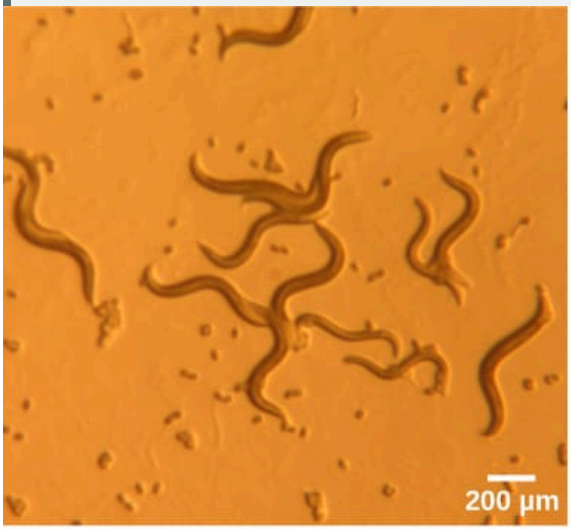
Everyday Connection

C. elegans: The Model System for Linking Developmental Studies with Genetics If biologists wanted to research how nicotine dependence develops in the body, how lipids are regulated, or observe the attractant or repellant properties of certain odors, they would clearly need to design three very different experiments. However, they might only need one subject of study: *Caenorhabditis elegans*. The nematode *C. elegans* was brought into the focus of mainstream biological research by Dr. Sydney Brenner. Since 1963, Dr. Brenner and scientists worldwide have used this animal as a model system to study many different physiological and developmental mechanisms.

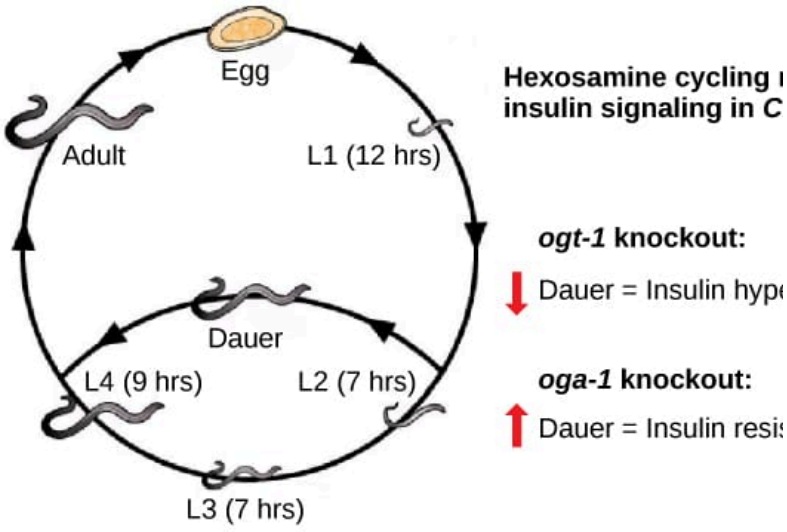
C. elegans is a free-living nematode found in soil. Only about a millimeter long, it can be cultured on agar plates (10,000 worms/plate!), feeding on the common intestinal bacterium *Escherichia coli* (another long-term resident of biological laboratories worldwide), and therefore can be readily grown and maintained in a laboratory. The biggest asset of this nematode is its transparency, which helps researchers to observe and monitor changes within the animal with ease. It is also a simple organism with about 1,000 cells and a genome of only 20,000 genes. Its chromosomes are organized into five pairs of autosomes plus a pair of sex chromosomes, making it an ideal candidate with which to study genetics. Since every cell can be visualized and identified, this organism is useful for studying cellular phenomena like cell-to-cell interactions, cell-fate determinations, cell division, apoptosis (cell death), and intracellular transport.

Another tremendous asset is the short life cycle of this worm (Figure 28.33). It takes only three days to achieve the "egg to adult to daughter egg"; therefore, the developmental consequences of genetic changes can be quickly identified. The total life span of *C. elegans* is two to three weeks; hence, age-related phenomena are also easy to observe. There are two sexes in this species: hermaphrodites (XX) and males (XO). However, anatomical males are relatively infrequently obtained from matings between hermaphrodites, since their XO chromosome composition requires meiotic nondisjunction when both parents are XX. Another feature that makes *C. elegans* an excellent experimental model is that the position and number of the 959 cells present in adult hermaphrodites of this organism is *constant*. This feature is extremely significant when studying cell differentiation, cell-to-cell communication, and apoptosis. Lastly, *C. elegans* is also amenable to genetic manipulations using molecular methods, rounding off its usefulness as a model system.

Biologists worldwide have created information banks and groups dedicated to research using *C. elegans*. Their findings have led, for example, to better understandings of cell communication during development, neuronal signaling, and insight into lipid regulation (which is important in addressing health issues like the development of obesity and diabetes). In recent years, studies of the cilia in *C. elegans* have enlightened the medical community with a better understanding of polycystic kidney disease. This simple organism has led biologists to complex and significant findings, growing the field of science in ways that touch the everyday world.



(a)



(b)

Figure 28.33 *Caenorhabditis elegans*. (a) This light micrograph shows the bodies of a group of roundworms. These hermaphrodites consist of exactly 959 cells. (b) The life cycle of *C. elegans* has four juvenile stages (L1 through L4) and an adult stage. Under ideal conditions, the nematode spends a set amount of time at each juvenile stage, but under stressful conditions, it may enter a *dauer sta*te that does not age significantly and is somewhat analogous to the diapausing state of some insects. (credit a: modification of work by "snickclunk"/Flickr: credit b: modification of work by NIDDK, NIH; scale-bar data from Matt Russell)

Parasitic Nematodes

A number of common parasitic nematodes serve as prime examples of parasitism (endoparasitism). These economically and medically important animals exhibit complex life cycles that often involve multiple hosts, and they can have significant medical and veterinary impacts. Here is a partial list of nasty nematodes: Humans may become infected by *Dracunculus medinensis*, known as guinea worms, when they drink unfiltered water containing copepods (Figure 28.34), an intermediate crustacean host. Hookworms, such as *Ancylostoma* and *Necator*, infest the intestines and feed on the blood of mammals, especially of dogs, cats, and humans. Trichina worms (*Trichinella*) are the causal organism of trichinosis in humans, often resulting from the consumption of undercooked pork; *Trichinella* can infect other mammalian hosts as well. *Ascaris*, a large intestinal roundworm, steals nutrition from its human host and may create physical blockage of the intestines. The filarial worms, such as *Dirofilaria* and *Wuchereria*, are commonly vectored by mosquitoes, which pass the infective agents among mammals through their blood-sucking activity. One species, *Wuchereria bancrofti*, infects the lymph nodes of over 120 million people worldwide, usually producing a non-lethal but deforming condition called *elephantiasis*. In this disease, parts of the body often swell to gigantic proportions due to obstruction of lymphatic drainage, inflammation of lymphatic tissues, and resulting edema. *Dirofilaria immitis*, a blood-infective parasite, is the notorious dog heartworm species.

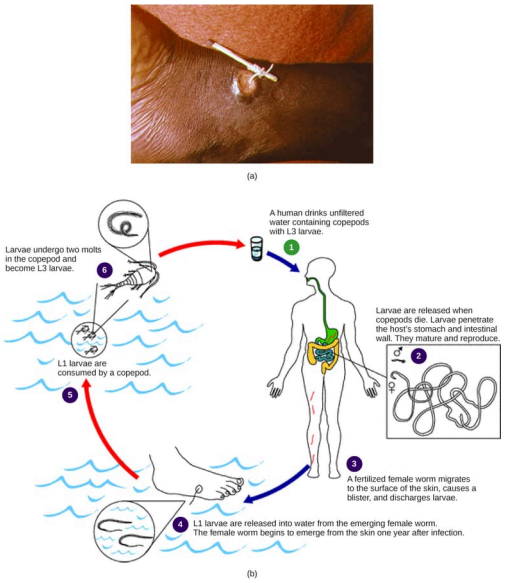


Figure 28.34 Life cycle of the guinea worm. The guinea worm *Dracunculus medinensis* infects about 3.5 million people annually, mostly in Africa. (a) Here, the worm is wrapped around a stick so it can be slowly extracted. (b) Infection occurs when people consume water contaminated by infected copepods, but this can easily be prevented by simple filtration systems. (credit: modification of work by CDC)

Phylum Tardigrada

The tardigrades ("slow-steppers") comprise a phylum of inconspicuous little animals living in marine, freshwater, or damp terrestrial environments throughout the world. They are commonly called "water bears" because of their plump bodies and the large claws on their stubby legs. There are over 1,000 species, most of which are less than 1 mm in length. A chitinous cuticle covers the body surface and may be divided into plates (Figure 28.35). Tardigrades are known for their ability to enter a state called cryptobiosis, which provides them with are resistance to multiple environmental challenges, including desiccation, very low temperatures, vacuum, high pressure, and radiation. They can suspend their metabolic activity for years, and survive the loss of up to 99% of their water content. Their remarkable resistance has recently been attributed to unique proteins that replace water in their cells and protect their internal cell structure and their DNA from damage.

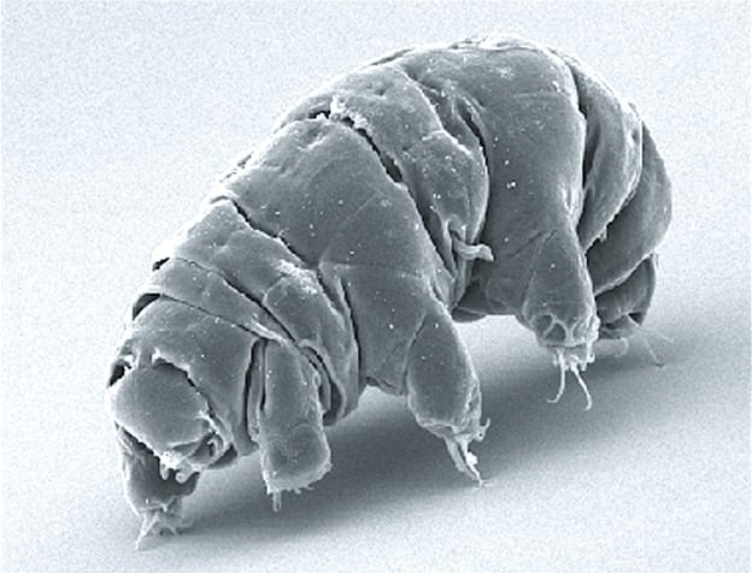


Figure 28.35 Scanning electronmicrograph of *Milnesium tardigradum*. (credit: Schokraie E, Warnken U, Hotz-Wagenblatt A, Grohme MA, Hengherr S, et al. (2012) -https://commons.wikimedia.org/w/index.php?curid=22716809)

Morphology and Physiology

Tardigrades have cylindrical bodies, with four pairs of legs terminating in a number of claws. The cuticle is periodically shed, including the cuticular covering of the claws. The first three pairs of legs are used for walking, and the posterior pair for clinging to the substrate. A circular mouth leads to a muscular pharynx and salivary glands. Tardigrades feed on plants, algae, or small animals. Plant cells are pierced with a chitinous stylet and the cellular contents are then sucked into the gut by the muscular pharynx. Bands of single muscle cells are attached to the various points of the epidermis and extend into the legs to provide ambulatory movement. The major body cavity is a *hemocoel*, but there are no specialized circulatory structures for moving the blood, nor are there specialized respiratory structures. Malpighian tubules in the hemocoel remove metabolic wastes and transport them to the gut. A dorsal brain is connected to a ventral nerve cord with segmental ganglia associated with the appendages. Sensory structures are greatly reduced, but there is a pair of simple eyespots on the head, and sensory cilia or bristles concentrated toward the head end of the animal.

Reproduction

Most tardigrades are dioecious, and males and females each have a single gonad. Mating usually occurs at the time of a molt and fertilization is external. Eggs may be deposited in a molted cuticle or attached to other objects. Development is direct, and the animal may molt a dozen times during its lifetime. In tardigrades, like nematodes, development produces a fixed number of cells, with the actual number of cells being dependent on the species. Further growth occurs by enlarging the cells, not by multiplying them.

Footnotes

- 1Stoll, N. R., “This wormy world. 1947,” *Journal of Parasitology* 85(3) (1999): 392-396.

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12: MOLLUSKS & ANNELIDS

12.1: Mollusk and Annelid Structure and Diversity

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12.1: Mollusk and Annelid Structure and Diversity

Learning Objectives

By the end of this section, you will be able to do the following:

- Describe the unique anatomical and morphological features of molluscs and annelids
- Describe the formation of the coelom
- Identify an important extracoelomic cavity in molluscs
- Describe the major body regions of Mollusca and how they vary in different molluscan classes
- Discuss the advantages of true body segmentation
- Describe the features of animals classified in phylum Annelida

The annelids and the mollusks are the most familiar of the lophotrochozoan protostomes. They are also more “typical” lophotrochozoans, since both groups include aquatic species with trochophore larvae, which unite both taxa in common ancestry. These phyla show how a flexible body plan can lead to biological success in terms of abundance and species diversity. The phylum Mollusca has the second greatest number of species of all animal phyla with nearly 100,000 described extant species, and about 80,000 described extinct species. In fact, it is estimated that about 25 percent of all known marine species are mollusks! The annelids and mollusca are both bilaterally symmetrical, cephalized, triploblastic, schizocoelous eucoelomates They include animals you are likely to see in your backyard or on your dinner plate!

Phylum Mollusca

The name “Mollusca” means “soft” body, since the earliest descriptions of molluscs came from observations of “squishy,” unshelled cuttlefish. Molluscs are predominantly a marine group of animals; however, they are also known to inhabit freshwater as well as terrestrial habitats. This enormous phylum includes chitons, tusk shells, snails, slugs, nudibranchs, sea butterflies, clams, mussels, oysters, squids, octopuses, and nautiluses. Molluscs display a wide range of morphologies in each class and subclass, but share a few key characteristics (Figure 28.21). The chief locomotor structure is usually a muscular foot. Most internal organs are contained in a region called the visceral mass. Overlying the visceral mass is a fold of tissue called the mantle; within the cavity formed by the mantle are respiratory structures called gills, that typically fold over the visceral mass. The mouths of most mollusks, except bivalves (e.g., clams) contain a specialized feeding organ called a radula, an abrasive tonguelike structure. Finally, the mantle secretes a calcium-carbonate-hardened shell in most molluscs, although this is greatly reduced in the class Cephalopoda, which contains the octopuses and squids.

Visual Connection

Visual Connection

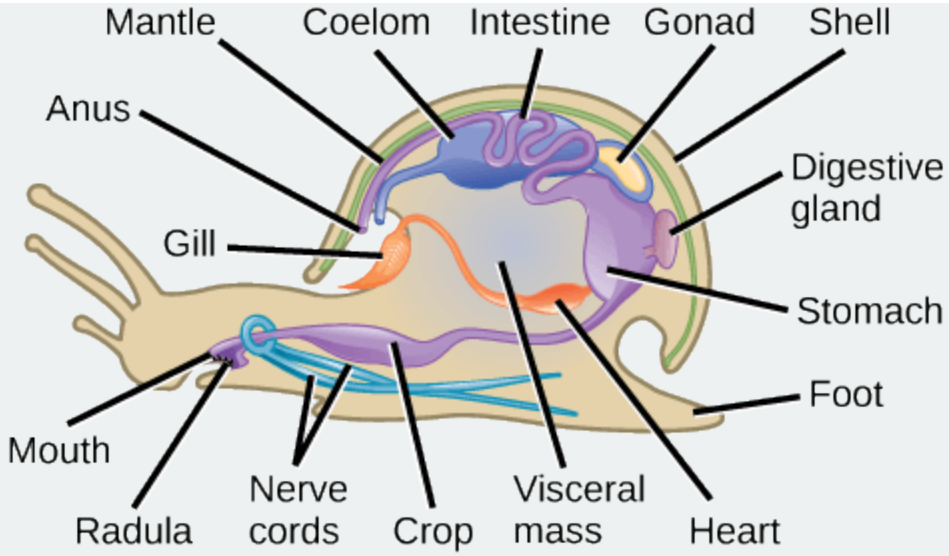


Figure 28.21 Molluscan body regions. There are many species and variations of molluscs; this illustration shows the anatomy of an aquatic gastropod. In a terrestrial gastropod, the mantle cavity itself would serve as a respiratory organ.

Which of the following statements about the anatomy of a mollusc is false?

1. Most molluscs have a radula for grinding food.
2. A digestive gland is connected to the stomach.
3. The tissue beneath the shell is called the mantle.
4. The digestive system includes a gizzard, a stomach, a digestive gland, and the intestine.

The muscular foot is the ventral-most organ, whereas the mantle is the limiting dorsal organ that folds over the visceral mass. The foot, which is used for locomotion and anchorage, varies in shape and function, depending on the type of mollusk under study. In shelled mollusks, the foot is usually the same size as the opening of the shell. The foot is both retractable and extendable. In the class Cephalopoda (“head-foot”), the foot takes the form of a funnel for expelling water at high velocity from the mantle cavity; and the anterior margin of the foot has been modified into a circle of *arms* and *tentacles*.

The visceral mass is present above the foot, in the visceral hump. This mass contains digestive, nervous, excretory, reproductive, and respiratory systems. Molluscan species that are exclusively aquatic have gills that extend into the mantle cavity, whereas some terrestrial species have "lungs" formed from the lining of the mantle cavity. Mollusks are schizocoelous eucoelomates, but the coelomic cavity in adult animals has been largely reduced to a cavity around the heart. However, a reduced coelom sometimes surrounds the gonads, part of the kidneys, and intestine as well. This overall coelomic reduction makes the mantle cavity the major internal body chamber.

Most mollusks have a special rasp-like organ, the radula, which bears chitinous filelike teeth. The radula is present in all groups except the bivalves, and serves to shred or scrape food before it enters the digestive tract. The mantle (also known as the *pallium*) is the dorsal epidermis in mollusks; all mollusks except some cephalopods are specialized to secrete a calcareous shell that protects the animal's soft body.

Most mollusks are dioecious animals and fertilization occurs externally, although this is not the case in terrestrial mollusks, such as snails and slugs, or in cephalopods. In most aquatic mollusks, the zygote hatches and produces a trochophore larva, with several bands of cilia around a toplike body, and an additional apical tuft of cilia. In some species, the trochophore may be followed by additional larval stages, such as a veliger larvae, before the final metamorphosis to the adult form. Most cephalopods develop directly into small versions of their adult form.

Classification of Phylum Mollusca

Phylum Mollusca comprises a very diverse group of organisms that exhibits a dramatic variety of forms, ranging from chitons to snails to squids, the latter of which typically show a high degree of intelligence. This variability is a consequence of modification of the basic body regions, especially the foot and mantle. The phylum is organized into eight classes: Caudofoveata, Solenogastres, Monoplacophora, Polyplacophora, Gastropoda, Cephalopoda, Bivalvia, and Scaphopoda. Although each molluscan class appears

to be monophyletic, their relationship to one another is unclear and still being reviewed.

Both the Caudofoveata and the Solenogastres include shell-less, worm-like animals primarily found in benthic marine habitats. Although these animals lack a calcareous shell, they get some protection from calcareous spicules embedded in a cuticle that covers their epidermis. The mantle cavity is reduced, and both groups lack eyes, tentacles, and nephridia (excretory organs). The Caudofoveata possess a radula, but the Solenogastres do not have a radula or gills. The foot is also reduced in the Solenogastres and absent from the Caudofoveata.

Long thought to be extinct, the first living specimens of Monoplacophora, *Neopilina galatheae*, were discovered in 1952 on the ocean bottom near the west coast of Costa Rica. Today there are over 25 described species. Members of class Monoplacophora ("bearing one plate") possess a single, cap-like shell that covers the dorsal body. The morphology of the shell and the underlying animal can vary from circular to ovate. They have a simple radula, a looped digestive system, multiple pairs of excretory organs, and a pair of gonads. Multiple gills are located between the foot and the edge of the mantle.

Animals in class Polyplacophora ("bearing many plates") are commonly known as "chitons" and bear eight limy plates that make up the dorsal shell (Figure 28.22). These animals have a broad, ventral foot that is adapted for suction onto rocks and other substrates, and a mantle that extends beyond the edge of the shell. Calcareous spines on the exposed mantle edge provide protection from predators. Respiration is facilitated by multiple pairs of gills in the mantle cavity. Blood from the gills is collected in a posterior heart, and then sent to the rest of the body in a hemocoel—an *open circulation system* in which the blood is contained in connected chambers surrounding various organs rather than within individual blood vessels. The radula, which has teeth composed of an ultra-hard magnetite, is used to scrape food organisms off rocky surfaces. Chiton teeth have been shown to exhibit the greatest hardness and stiffness of any biomineral material reported to date, being as much as three-times harder than human enamel and the calcium carbonate-based shells of mollusks.

The nervous system is rudimentary with only buccal or "cheek" ganglia present at the anterior end. Multiple tiny sensory structures, including photosensors, extend from the mantle into channels in the upper layer of the shell. These structures are called esthetes and are unique to the chitons. Another sensory structure under the radula is used to sample the feeding environment. A single pair of nephridia is used for the excretion of nitrogenous wastes.



Figure 28.22 A chiton. This chiton from the class Polyplacaphora has the eight-plated shell for which its class is named. (credit: Jerry Kirkhart)

Class Bivalvia ("two-valves") includes clams, oysters, mussels, scallops, geoducks, and shipworms. Some bivalves are almost microscopic, while others, in the genus *Tridacna,* may be one meter in length and weigh 225 kilograms. Members of this class are found in marine as well as freshwater habitats. As the name suggests, bivalves are enclosed in two-part valves or shells (Figure 28.23a) fused on the dorsal side by hinge ligaments as well as shell teeth on the ventral side that keep the two halves aligned. The two shells, which consist of an outer organic layer, a middle prismatic layer, and a very smooth nacreous layer, are joined at the oldest part of the shell called the umbo. Anterior and posterior adductor and abductor muscles close and open the shell respectively.

The overall body of the bivalve is laterally flattened; the foot is wedge-shaped; and the head region is poorly developed (with no obvious mouth). Bivalves are filter-feeders, and a radula is absent in this class of mollusks. The mantle cavity is fused along the edges except for openings for the foot and for the intake and expulsion of water, which is circulated through the mantle cavity by the actions of the incurrent and excurrent siphons. During water intake by the incurrent siphon, food particles are captured by the paired posterior gills (ctenidia) and then carried by the movement of cilia forward to the mouth. Excretion and osmoregulation are performed by a pair of nephridia. Eyespots and other sensory structures are located along the edge of the mantle in some species. The "eyes" are especially conspicuous in scallops (Figure 28.23b). Three pairs of connected ganglia regulate activity of different body structures.



Figure 28.23 Bivalves. These mussels (a), found in the intertidal zone in Cornwall, England, show the bivalve shell. The scallop *Argopecten irradians* (b) has a fluted shell and conspicuous eyespots. (credit (a): Mark A. Wilson. credit (b) Rachael Norris and Marina Freudzon. https://commons.wikimedia.org/w/index.php?curid=17251065)

One of the functions of the mantle is to secrete the shell. Some bivalves, like oysters and mussels, possess the unique ability to secrete and deposit a calcareous nacre or “mother of pearl” around foreign particles that may enter the mantle cavity. This property has been commercially exploited to produce pearls.

Link to Learning

Link to Learning

Watch the animations of bivalves feeding: View the process in clams and mussels at these sites.

More than half of molluscan species are in the class Gastropoda (“stomach foot”), which includes well-known mollusks like snails, slugs, conchs, cowries, limpets, and whelks. Aquatic gastropods include both marine and freshwater species, and all terrestrial mollusks are gastropods. Gastropoda includes shell-bearing species as well as species without shells. Gastropod bodies are asymmetrical and usually present a coiled shell (Figure 28.24a). Shells may be *planospiral* (like a garden hose wound up), commonly seen in garden snails, or *conispiral*, (like a spiral staircase), commonly seen in marine conches. Cowrie shells have a polished surface because the mantle extends up over the top of the shell as it is secreted.



(a) (b)

Figure 28.24 Gastropods. Snails(a) and slugs(b) are both gastropods, but slugs lack a shell. (credit a: modification of work by Murray Stevenson; credit b: modification of work by Rosendahl)

A key characteristic of some gastropods is the embryonic development of torsion. During this process, the mantle and visceral mass are rotated around the perpendicular axis over the center of the foot to bring the anal opening forward just behind the head (Figure 28.25), creating a very peculiar situation. The left gill, kidney, and heart atrium are now on the right side, whereas the original right gill, kidney, and heart atrium are on the left side. Even stranger, the nerve cords have been twisted and contorted into a figure-eight pattern. Because of the space made available by torsion in the mantle cavity, the animal's sensitive head end can now be withdrawn into the protection of the shell, and the tougher foot (and sometimes the protective covering or operculum) forms a barrier to the outside. The strange arrangement that results from torsion poses a serious sanitation problem by creating the possibility of wastes being washed back over the gills, causing fouling. There is actually no really perfect explanation for the embryonic development of torsion, and some groups that formerly exhibited torsion in their ancestral groups are now known to have reversed the process.

Gastropods also have a foot that is modified for crawling. Most gastropods have a well-defined head with tentacles and eyes. A complex radula is used to scrape up food particles. In aquatic gastropods, the mantle cavity encloses the gills (ctenidia), but in land gastropods, the mantle itself is the major respiratory structure, acting as a kind of lung. Nephridia ("kidneys") are also found in the mantle cavity.

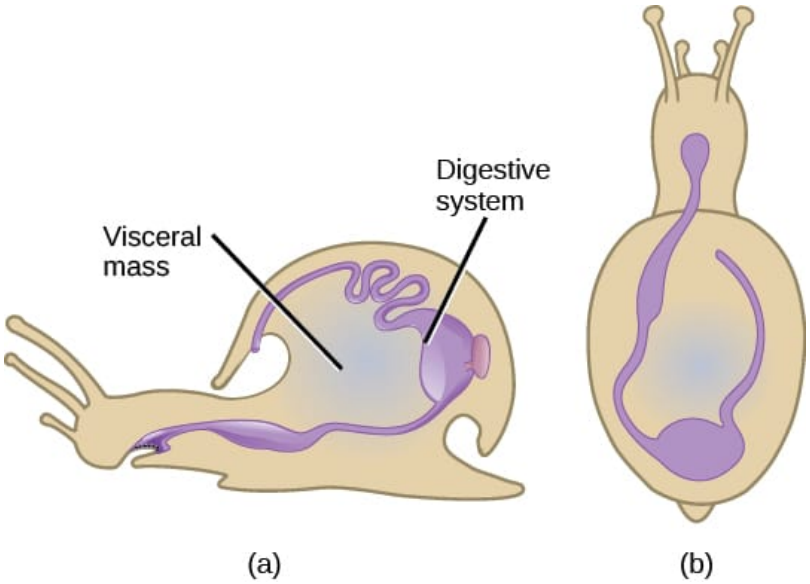


Figure 28.25 Torsion in gastropods. During embryonic development of some gastropods, the visceral mass undergoes torsion, or

counterclockwise rotation of the visceral anatomical features. As a result, the anus of the adult animal is located over the head. Although torsion is always counterclockwise, the shell may coil in either direction; thus coiling of a shell is *not* the same as torsion of the visceral mass.

Everyday Connection

Everyday Connection

Can Snail Venom Be Used as a Pharmacological Painkiller?Marine snails of the genus *Conus* (Figure 28.26) attack prey with a venomous stinger, modified from the radula. The toxin released, known as conotoxin, is a peptide with internal disulfide linkages. Conotoxins can bring about paralysis in humans, indicating that this toxin attacks neurological targets. Some conotoxins have been shown to block neuronal ion channels. These findings have led researchers to study conotoxins for possible medical applications.

Conotoxins are an exciting area of potential pharmacological development, since these peptides may be possibly modified and used in specific medical conditions to inhibit the activity of specific neurons. For example, conotoxins or modifications of them may be used to induce paralysis in muscles in specific health applications, similar to the use of botulinum toxin. Since the entire spectrum of conotoxins, as well as their mechanisms of action, is not completely known, the study of their potential applications is still in its infancy. Most research to date has focused on their use to treat neurological diseases. They have also shown some efficacy in relieving chronic pain, and the pain associated with conditions like sciatica and shingles. The study and use of biotoxins—toxins derived from living organisms—are an excellent example of the application of biological science to modern medicine.



Figure 28.26 *Conus*. Members of the genus *Conus* produce neurotoxins that may one day have medical uses. The tube above the eyes is a siphon used both to circulate water over the gills and to sample the water for chemical evidence of prey nearby. Note the eyes below the siphon. The proboscis, through which the venomous harpoon is projected, is located between the eyes. (credit: David Burdick, NOAA)

Class Cephalopoda (“head foot” animals), includes octopuses, squids, cuttlefish, and nautiluses. Cephalopods include both animals with shells as well as animals in which the shell is reduced or absent. In the shell-bearing *Nautilus,* the spiral shell is multi-chambered. These chambers are filled with gas or water to regulate buoyancy. A siphuncle runs through the chambers, and it is this tube that regulates the amount of water and gases (nitrogen, carbon dioxide, and oxygen mixture) present in the chambers. Ammonites and other nautiloid shells are commonly seen in the fossil record. The shell structure in squids and cuttlefish is reduced and is present internally in the form of a squid pen and cuttlefish bone, respectively. Cuttle bone is sold in pet stores to help smooth the beaks of birds and also to provide birds such as egg-laying chickens and quail with an inexpensive natural source of calcium carbonate. Examples of cephalopods are shown in Figure 28.27.

Cephalopods can display vivid and rapidly changing coloration, almost like flashing neon signs. Typically these flashing displays are seen in squids and octopuses, where they may be used for camouflage and possibly as signals for mating displays. We should

note, however, that researchers are not entirely sure if squid can actually see color, or see color in the same way as we do. We know that pigments in the skin are contained in special pigment cells (chromatophores), which can expand or contract to produce different color patterns. But chromatophores can only make yellow, red, brown, and black pigmentation; however, underneath them is a whole different set of elements called iridophores and leucophores that reflect light and can make blue, green, and white. It is possible that squid skin might actually be able to detect some light on its own, without even needing its eyes!

All animals in this class are carnivorous predators and have beak-like jaws in addition to the radula. Cephalopods include the most intelligent of the mollusks, and have a well-developed nervous system along with image-forming eyes. Unlike other mollusks, they have a closed circulatory system, in which the blood is entirely contained in vessels rather than in a hemocoel.

The foot is lobed and subdivided into arms and tentacles. Suckers with chitinized rings are present on the arms and tentacles of octopuses and squid. Siphons are well developed and the expulsion of water is used as their primary mode of locomotion, which resembles jet propulsion. Gills (ctenidia) are attached to the wall of the mantle cavity and are serviced by large blood vessels, each with its own heart. A pair of nephridia is present within the mantle cavity for water balance and excretion of nitrogenous wastes. Cephalopods such as squids and octopuses also produce sepia or a dark ink, which contains melanin. The ink gland is located between the gills and can be released into the excurrent water stream. Ink clouds can be used either as a "smoke screen" to hide the animal from predators during a quick attempt at escape, or to create a fake image to distract predators.

Cephalopods are dioecious. Members of a species mate, and the female then lays the eggs in a secluded and protected niche. Females of some species care for the eggs for an extended period of time and may end up dying during that time period. While most other aquatic mollusks produce trochophore larvae, cephalopod eggs develop directly into a juvenile without an intervening larval stage.

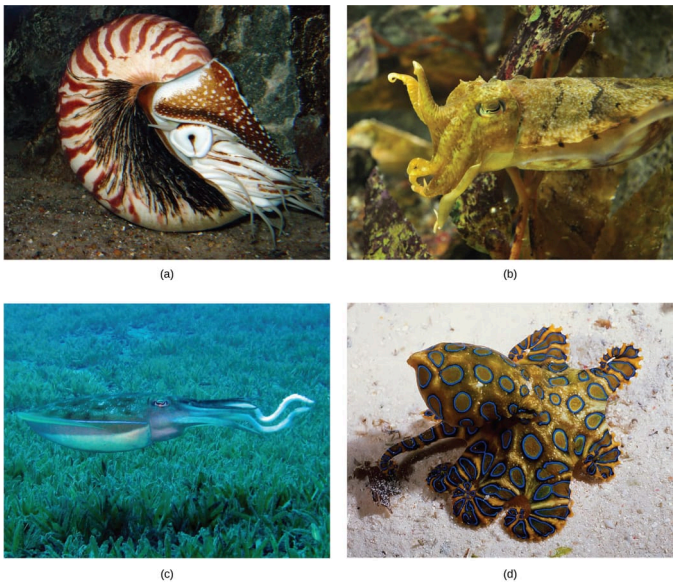


Figure 28.27 Cephalopods. The (a) nautilus, (b) giant cuttlefish, (c) reef squid, and (d) blue-ring octopus are all members of the class Cephalopoda. (credit a: modification of work by J. Baecker; credit b: modification of work by Adrian Mohedano; credit c: modification of work by Silke Baron; credit d: modification of work by Angell Williams)

Members of class Scaphopoda ("boat feet") are known colloquially as "tusk shells" or "tooth shells," as evident when examining *Dentalium*, one of the few remaining scaphopod genera (Figure 28.28). Scaphopods are usually buried in sand with the anterior opening exposed to water. These animals have a single conical shell, which is open on both ends. The head is not well developed, but the mouth, containing a radula, opens among a group of tentacles that terminate in ciliated bulbs used to catch and manipulate prey. Scaphopods also have a foot similar to that seen in bivalves. Ctenidia are absent in these animals; the mantle cavity forms a tube open at both ends and serves as the respiratory structure in these animals.

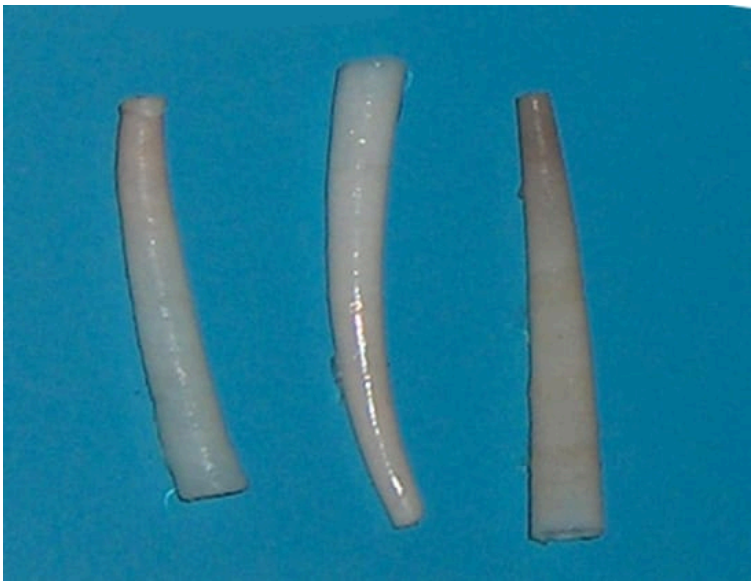


Figure 28.28 Tooth shells. *Antalis vulgaris* shows the classic Dentaliidae shape that gives these animals their common name of "tusk shell." (credit: Georges Jansoone)

Phylum Annelida

Phylum Annelida comprises the true, segmented worms. These animals are found in marine, terrestrial, and freshwater habitats, but the presence of water or humidity is a critical factor for their survival in terrestrial habitats. The annelids are often called “segmented worms” due to their key characteristic of metamerism, or true segmentation. Approximately 22,000 species have been described in phylum Annelida, which includes polychaete worms (marine annelids with multiple appendages), and oligochaetes (earthworms and leeches). Some animals in this phylum show parasitic and commensal symbioses with other species in their habitat.

Morphology

Annelids display bilateral symmetry and are worm-like in overall morphology. The name of the phylum is derived from the Latin word *annulus*, which means a small ring, an apt description of the ring-like segmentation of the body. Annelids have a body plan with metameric segmentation, in which several internal and external morphological features are repeated in each body segment. Metamerism allows animals to become bigger by adding “compartments,” while making their movement more efficient. The overall body can be divided into head, body, and pygidium (or tail). During development, the segments behind the head arise sequentially from a growth region anterior to the pygidium, a pattern called teloblastic growth. In the Oligochaetes, the clitellum is a reproductive structure that generates mucus to aid sperm transfer and also produces a “cocoon,” within which fertilization occurs; it appears as a permanent, fused band located on the anterior third of the animal (Figure 28.29).



Figure 28.29 The clitellum of an earthworm. The clitellum, seen here as a protruding segment with different coloration than the rest of the body, is a structure that aids in oligochaete reproduction. (credit: Rob Hille)

Anatomy

The epidermis is protected by a collagenous, external cuticle, which is much thinner than the cuticle found in the ecdysozoans and does not require periodic shedding for growth. Circular as well as longitudinal muscles are located interior to the epidermis. Chitinous bristles called setae (or chaetae) are anchored in the epidermis, each with its own muscle. In the polychaetes, the setae are borne on paired appendages called parapodia.

Most annelids have a well-developed and complete digestive system. Feeding mechanisms vary widely across the phylum. Some polychaetes are filter-feeders that use feather-like appendages to collect small organisms. Others have tentacles, jaws, or an eversible pharynx to capture prey. Earthworms collect small organisms from soil as they burrow through it, and most leeches are blood-feeders armed with teeth or a muscular proboscis. In earthworms, the digestive tract includes a mouth, muscular pharynx, esophagus, crop, and muscular gizzard. The gizzard leads to the intestine, which ends in an anal opening in the terminal segment. A cross-sectional view of a body segment of an earthworm is shown in Figure 28.30; each segment is limited by a membranous septum that divides the coelomic cavity into a series of compartments.

Most annelids possess a closed circulatory system of dorsal and ventral blood vessels that run parallel to the alimentary canal as well as capillaries that service individual tissues. In addition, the dorsal and ventral vessels are connected by transverse loops in every segment. Some polychaetes and leeches have an open system in which the major blood vessels open into a hemocoel. In many species, the blood contains hemoglobin, but not contained in cells. Annelids lack a well-developed respiratory system, and gas exchange occurs across the moist body surface. In the polychaetes, the parapodia are highly vascular and serve as respiratory structures. Excretion is facilitated by a pair of metanephridia (a type of primitive “kidney” that consists of a convoluted tubule and an open, ciliated funnel) that is present in every segment toward the ventral side. Annelids show well-developed nervous systems with a ring of fused ganglia present around the pharynx. The nerve cord is ventral in position and bears enlarged nodes or ganglia in each segment.

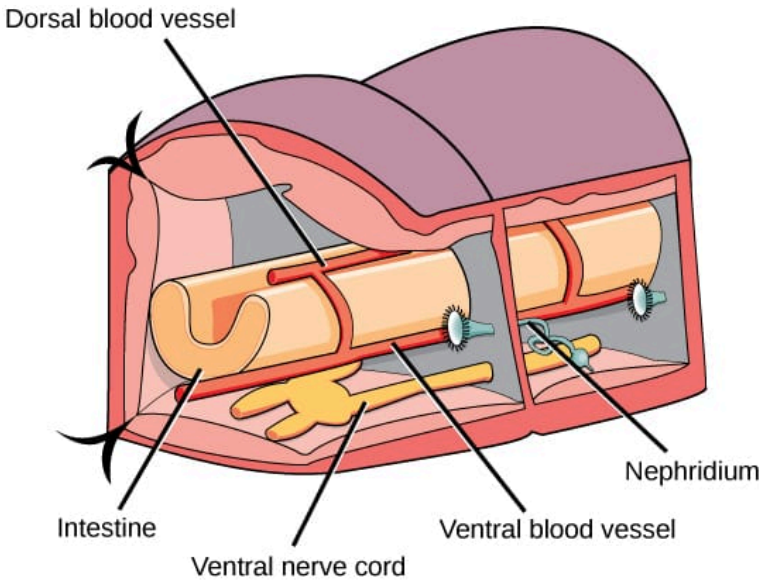


Figure 28.30 Segmental anatomy of an earthworm. This schematic drawing shows the basic anatomy of annelids in a cross-sectional view.

Annelids may be either monoecious with permanent gonads (as in earthworms and leeches) or dioecious with temporary or seasonal gonads (as in polychaetes). However, cross-fertilization is preferred even in hermaphroditic animals. Earthworms may show simultaneous mutual fertilization when they are aligned for copulation. Some leeches change their sex over their reproductive lifetimes. In most polychaetes, fertilization is external and development includes a trochophore larva, which then metamorphizes to the adult form. In oligochaetes, fertilization is typically internal and the fertilized eggs develop in a cocoon produced by the clitellum; development is direct. Polychaetes are excellent regenerators and some even reproduce asexually by budding or fragmentation.

Link to Learning

Link to Learning

This combination video and animation provides a close-up look at annelid anatomy.

Classification of Phylum Annelida

Phylum Annelida contains the class Polychaeta (the polychaetes) and the class Oligochaeta (the earthworms, leeches, and their relatives). The earthworms and the leeches form a monophyletic clade within the polychaetes, which are therefore paraphyletic as a group.

There are more than 22,000 different species of annelids, and more than half of these are marine polychaetes ("many bristles"). In the polychaetes, bristles are arranged in clusters on their parapodia—fleshy, flat, paired appendages that protrude from each segment. Many polychaetes use their parapodia to crawl along the sea floor, but others are adapted for swimming or floating. Some are sessile, living in tubes. Some polychaetes live near hydrothermal vents. These deepwater tubeworms have no digestive tract, but have a symbiotic relationship with bacteria living in their bodies.

Earthworms are the most abundant members of the class Oligochaeta ("few bristles"), distinguished by the presence of a permanent clitellum as well as the small number of reduced chaetae on each segment. (Recall that oligochaetes do not have parapodia.) The oligochaete subclass Hirudinea, includes leeches such as the medicinal leech, *Hirudo medicinalis*, which is effective at increasing blood circulation and breaking up blood clots, and thus can be used to treat some circulatory disorders and cardiovascular diseases. Their use goes back thousands of years. These animals produce a seasonal clitellum, unlike the permanent clitellum of other oligochaetes. A significant difference between leeches and other annelids is the lack of setae and the development of suckers at the anterior and posterior ends, which are used to attach to the host animal. Additionally, in leeches, the segmentation of the body wall may not correspond to the internal segmentation of the coelomic cavity. This adaptation

possibly helps the leeches to elongate when they ingest copious quantities of blood from host vertebrates, a condition in which they are said to be “engorged.” The subclass Brachiobdella includes tiny leechlike worms that attach themselves to the gills or body surface of crayfish.



(b)

Figure 28.31 Annelid groups. The (a) earthworm, (b) leech, and (c) featherduster are all annelids. The earthworm and leech are oligochaetes, while the featherduster worm is a tube-dwelling filter-feeding polychaete. (credit a: modification of work by S. Shepherd; credit b: modification of work by “Sarah G...”/Flickr; credit c: modification of work by Chris Gotschalk, NOAA)

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13: ARTHROPODS

13.1: Arthropod Structure and Diversity

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13.1: Arthropod Structure and Diversity

Learning Objectives

By the end of this section, you will be able to do the following:

- Compare the internal systems and appendage specializations of phylum Arthropoda
- Discuss the environmental importance of arthropods
- Discuss the reasons for arthropod success and abundance

The superphylum Ecdysozoa also includes the phylum Arthropoda, one of the most successful clades of animals on the planet. Arthropods are coelomate organisms characterized by a sturdy chitinous exoskeleton and jointed appendages. There are well over a million arthropod species described, and systematists believe that there are millions of species awaiting proper classification. Like other Ecdysozoa, all arthropods periodically go through the physiological process of molting, followed by ecdysis (the actual shedding of the exoskeleton), as they grow. Arthropods are eucoelomate, protostomic organisms, often with incredibly complicated life cycles.

Phylum Arthropoda

The name “arthropoda” means “jointed feet.” The name aptly describes the invertebrates included in this phylum. Arthropods have probably always dominated the animal kingdom in terms of number of species and likely will continue to do so: An estimated 85 percent of all known species are included in this phylum! In effect, life on Earth could conceivably be called the Age of Arthropods beginning nearly 500 million years ago.

The principal characteristics of all the animals in this phylum are the structural and functional segmentation of the body and the presence of jointed appendages. Arthropods have an exoskeleton made principally of chitin—a waterproof, tough polysaccharide composed of N-acetylglucosamine. Phylum Arthropoda is the most speciose clade in the animal world (Table 28.1), and insects form the single largest class within this phylum. For comparison, refer to the approximate numbers of species in the phyla listed below.

Phylum	**# species**
Ctenophora	100
Porifera	5,000
Cnidaria	11,000
Platyhelminthes	25,000
Rotifera	2,000
Nemertea	1,200
Annelida	22,000
Mollusca	112,000
Nematoda	28,000+
Tardigrades	>1,000
Arthropoda	1,134,000
Echinodermata	7,000
Chordata	100,000

Table 28.1

Phylum Arthropoda includes animals that have been successful in colonizing terrestrial, aquatic, and aerial habitats. This phylum is further classified into five subphyla: Trilobita (trilobites, all extinct), Chelicerata (horseshoe crabs, spiders, scorpions, ticks, mites, and daddy longlegs or harvestmen), Myriapoda (millipedes, centipedes, and their relatives), Crustacea (crabs, lobsters, crayfish, isopods, barnacles, and some zooplankton), and Hexapoda (insects and their six-legged relatives). Trilobites, an extinct group of arthropods found chiefly in the pre-Cambrian Era (about 500 million years ago), are probably most closely related to the Chelicerata. These are identified based on their fossils; they were quite diverse and radiated significantly into thousands of species before their complete extinction at the end of the Permian about 240 million years ago (Figure 28.36).



Figure 28.36 A trilobite. Trilobites, like the one in this fossil, are an extinct group of arthropods. Their name "trilobite" refers to the *three longitudinal lobes* making up the body: right pleural lobe, axial lobe, and left pleural lobe (credit: Kevin Walsh).

Morphology

Characteristic features of the arthropods include the presence of jointed appendages, body segmentation, and chitinized exoskeleton. Fusion of adjacent groups of segments gave rise to functional body regions called tagmata (singular = tagma). Tagmata may be in the form of a head, thorax, and abdomen, or a cephalothorax and abdomen, or a head and trunk, depending on the taxon. Commonly described tagmata may be composed of different numbers of segments; for example, the head of most insects results from the fusion of six ancestral segments, whereas the “head” of another arthropod may be made of fewer ancestral segments, due to independent evolutionary events. Jointed arthropod appendages, often in segmental pairs, have been specialized for various functions: sensing their environment (antennae), capturing and manipulating food (mandibles and maxillae), as well as for walking, jumping, digging, and swimming.

In the arthropod body, a central cavity, called the hemocoel (or blood cavity), is present, and the hemocoel fluids are moved by contraction of regions of the tubular dorsal blood vessel called "hearts." Groups of arthropods also differ in the organs used for nitrogenous waste excretion, with crustaceans possessing *green glands* and insects using *Malpighian tubules*, which work in conjunction with the hindgut to reabsorb water while ridding the body of nitrogenous waste. The nervous system tends to be distributed among the segments, with larger ganglia in segments with sensory structures or appendages. The ganglia are connected by a ventral nerve cord.

Respiratory systems vary depending on the group of arthropod. Insects and myriapods use a series of tubes (tracheae) that branch through the body, ending in minute tracheoles. These fine respiratory tubes perform gas exchange *directly* between the air and cells within the organism. The major tracheae open to the surface of the cuticle via apertures called spiracles. We should note that these tracheal systems of ventilation have evolved independently in hexapods, myriapods, and arachnids. Although the tracheal system works extremely well in terrestrial environments, it also works well in freshwater aquatic environments: In fact, numerous species of aquatic insects in both immature and adult stages possess tracheal systems. However, although there are insects that live on the surface of marine environments, none is strictly marine—meaning that they complete their entire metamorphosis *in* salt water.

In contrast, aquatic crustaceans utilize gills, terrestrial chelicerates employ book lungs, and aquatic chelicerates use book gills

(Figure 28.37). The book lungs of arachnids (scorpions, spiders, ticks, and mites) contain a vertical stack of hemocoel wall tissue that somewhat resembles the pages of a book. Between each of the "pages" of tissue is an air space. This allows both sides of the tissue to be in contact with the air at all times, greatly increasing the efficiency of gas exchange. The gills of crustaceans are filamentous structures that exchange gases with the surrounding water.

The cuticle is the hard “covering” of an arthropod. It is made up of two layers: the *epicuticle*, which is a thin, waxy, water-resistant outer layer containing no chitin, and the layer beneath it, the *chitinous procuticle*, which itself is composed of an *exocuticle* and a lower *endocuticle*, all supported ultimately by a *basement membrane*. The exoskeleton is very protective (it is sometimes difficult to squish a big beetle!), but does not sacrifice flexibility or mobility. Both the exocuticle (which is secreted *before* a molt), and an endocuticle, (which is secreted *after* a molt), are composed of chitin bound with a protein; chitin is insoluble in water, alkalis, and weak acids. The procuticle is not only flexible and lightweight, but also provides protection against dehydration and other biological and physical stresses. Some arthropods, such as the crustaceans, add calcium salts to their exoskeleton, which increases the strength of the cuticle, but does reduce its flexibility. In some cases, such as lobsters, the amount of calcium salt deposited within the chitin is extreme. In order to grow, the arthropod must “shed” the exoskeleton during the physiological process called molting, following by the actual stripping of the outer cuticle, called ecdysis (“to strip off”). At first, this seems to be a dangerous method of growth, because while the new exoskeleton is hardening, the animal is vulnerable to predation; however, molting and ecdysis also allow for growth and change in morphology, as well as for great diversification in size, simply because the numbers of molts can be modified through evolution.

The characteristic morphology of representative animals from each subphylum is described below.

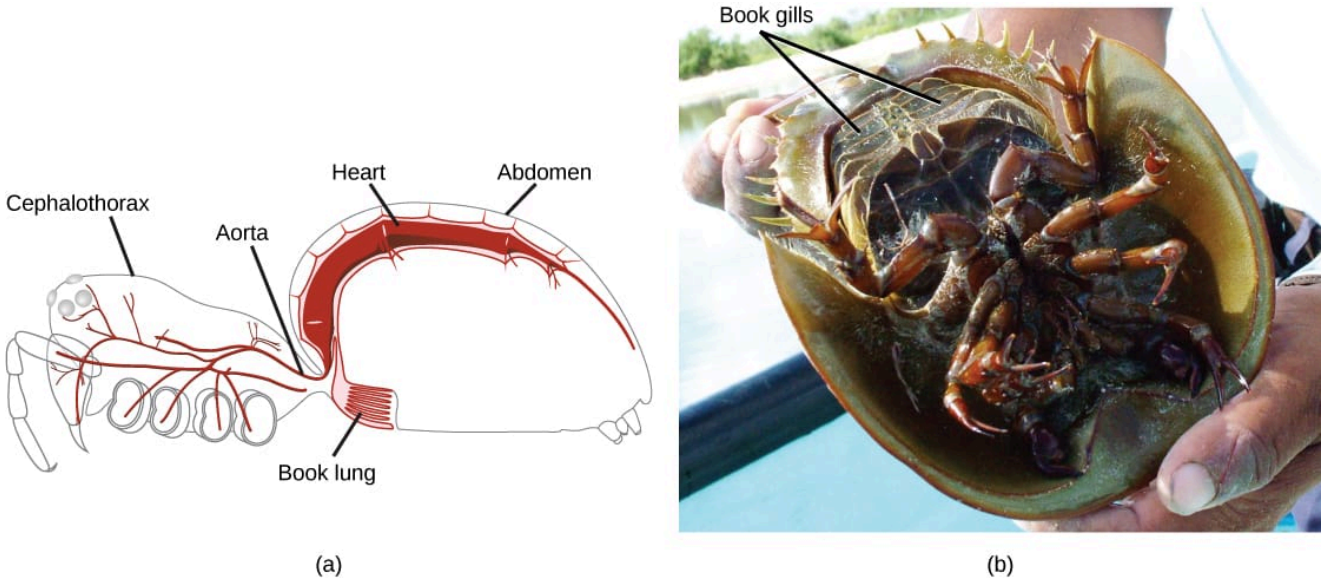


Figure 28.37 Arthropod respiratory structures. The book lungs of (a) arachnids are made up of alternating air pockets and hemocoel tissue shaped like a stack of books (hence the name, “book lung”). The book gills of (b) horseshoe crabs are similar to book lungs but are external so that gas exchange can occur with the surrounding water. (credit a: modification of work by Ryan Wilson based on original work by John Henry Comstock; credit b: modification of work by Angel Schatz)

Subphylum Chelicerata

This subphylum includes animals such as horseshoe crabs, sea spiders, spiders, mites, ticks, scorpions, whip scorpions, and harvestmen. Chelicerates are predominantly terrestrial, although some freshwater and marine species also exist. An estimated 77,000 species of chelicerates can be found in almost all terrestrial habitats.

The body of chelicerates is divided into two tagmata: prosoma and opisthosoma, which are basically the equivalents of a *cephalothorax* (usually smaller) and an *abdomen* (usually larger). A distinct “head” tagma is not usually discernible. The phylum derives its name from the first pair of appendages: the chelicerae (Figure 28.38), which serve as specialized clawlike or fanglike mouthparts. We should note here that chelicerae are actually *modified legs*, but they are not the exact serial equivalent of mandibles, which are the modified leglike chewing mouthparts of insects and crustaceans: The chelicerae are borne on the *first segment* making up the prosoma, whereas the mandibles are embryonically on the *fourth segment* of the mandibulate head. The chelicerates have secondarily lost their antennae and hence do not have them. Some of the functions of the antennae (such

as touch) are now performed by the second pair of appendages— the pedipalps, which may also be used for general sensing the environment as well as the manipulation of food. In some species, such as sea spiders, an additional pair of derived leg appendages, called ovigers, is present between the chelicerae and pedipalps. Ovigers are used for grooming and by males to carry eggs. In spiders, the chelicerae are often modified and terminate in fangs that inject venom into their prey before feeding (Figure 28.39).



Figure 28.38 Chelicerae. The chelicerae (first set of appendages) are well developed in the scorpion. (credit: Kevin Walsh)

Most chelicerates ingest food using a preoral cavity formed by the chelicerae and pedipalps. Some chelicerates may secrete digestive enzymes to pre-digest food before ingesting it. Parasitic chelicerates like ticks and mites have evolved blood-sucking apparatuses. Members of this subphylum have an open circulatory system with a heart that pumps blood into the hemocoel. Aquatic species, like horseshoe crabs, have gills, whereas terrestrial species have either tracheae or book lungs for gaseous exchange. Chelicerate hemolymph contains hemocyanin a copper-containing oxygen transport protein.



Figure 28.39 Spider. The trapdoor spider, like all spiders, is a member of the subphylum Chelicerata. (credit: Marshal Hedin)

The nervous system in chelicerates consists of a brain and two ventral nerve cords. Chelicerates are dioecious, meaning that the sexes are separate. These animals use external fertilization as well as internal fertilization strategies for reproduction, depending upon the species and its habitat. Parental care for the young ranges from absolutely none to relatively prolonged care.

Link to Learning

Link to Learning

Visit this site to click through a lesson on arthropods, including interactive habitat maps, and more.

Subphylum Myriapoda

Subphylum Myriapoda comprises arthropods with numerous legs. Although the name is misleading, suggesting that thousands of legs are present in these invertebrates, the number of legs typically varies from 10 to 750. This subphylum includes 16,000 species; the most commonly found examples are millipedes and centipedes. Virtually all myriapods are terrestrial animals and prefer a humid environment. Ancient myriapods (or myriapod-like arthropods) from the Silurian to the Devonian grew up to 10 feet in length (three meters). Unfortunately, they are all extinct!

Myriapods are typically found in moist soils, decaying biological material, and leaf litter. Subphylum Myriapoda is divided into four classes: Chilopoda, Symphyla, Diplopoda, and Pauropoda. Centipedes like *Scutigera coleoptrata* (Figure 28.40) are classified as chilopods. These animals bear one pair of legs per segment, mandibles as mouthparts, and are somewhat dorsoventrally flattened. The legs in the first segment are modified to form forcipules (poison claws) that deliver poison to prey like spiders and cockroaches, as these animals are all predatory. Symphyla are similar to centipedes, but lack the poison claws and are vegetarian. Millipedes bear two pairs of legs per diplosegment—a feature that results from the embryonic fusion of adjacent pairs of body segments. These arthropods are usually rounder in cross-section than centipedes, and are herbivores or detritivores. Millipedes have visibly more numbers of legs as compared to centipedes, although they do *not* have a thousand legs (Figure 28.40b). The Pauropods are similar to millipedes, but have fewer segments.



(a) (b)

Figure 28.40 Myriapods. The centipede *Scutigera coleoptrata* (a) has up to 15 pairs of legs. The North American millipede *Narceus americanus* (b) bears many legs, although not a thousand, as its name might suggest. (credit a: modification of work by Bruce Marlin; credit b: modification of work by Cory Zanker)

Subphylum Crustacea

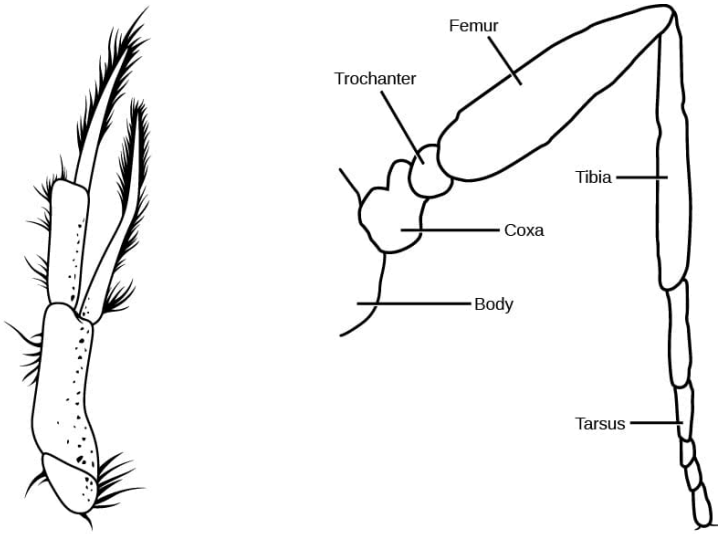
Crustaceans are the most dominant aquatic (both freshwater and marine) arthropods, with the total number of marine crustaceans standing at about 70,000 species. Krill, shrimp, lobsters, crabs, and crayfish are examples of crustaceans (Figure 28.41). However, there are also a number of terrestrial crustacean species as well: Terrestrial species like the wood lice (*Armadillidium* spp), also called pill bugs, roly-polies, potato bugs, or isopods, are also crustaceans. Nonetheless, the number of terrestrial species in this subphylum is relatively low.



(a) (b) (c)

Figure 28.41 Crustaceans. The (a) crab and (b) shrimp krill are both aquatic crustaceans. The pill bug *Armadillidium* is a terrestrial crustacean. (credit a: modification of work by William Warby; credit b: modification of work by Jon Sullivan credit c: modification of work by Franco Folini. https://commons.wikimedia.org/w/index.php?curid=789616)

Crustaceans typically possess two pairs of antennae, mandibles as mouthparts, and *biramous* (“two branched”) appendages, which means that their legs are formed in two parts called endopods and exopods, which appear superficially distinct from the *uniramous* (“one branched”) legs of myriapods and hexapods (Figure 28.42). Since biramous appendages are also seen in the trilobites, biramous appendages represent the ancestral condition in the arthropods. Currently, we describe various arthropods as having uniramous or biramous appendages, but these are descriptive only, and do not necessarily reflect evolutionary relationships other than that all jointed legs of arthropods share common ancestry.



(a) Biramous appendage (crayfish leg) (b) Uniramous appendage (insect leg)

Figure 28.42 Arthropod appendages. Arthropods may have (a) biramous (two-branched) appendages or (b) uniramous (one-branched) appendages. (credit b: modification of work by Nicholas W. Beeson)

In most crustaceans, the head and thorax is fused to form a cephalothorax (Figure 28.43), which is covered by a plate called the carapace, thus producing a body plan comprising two tagmata: cephalothorax and abdomen. Crustaceans have a chitinous exoskeleton that is shed by molting and ecdysis whenever the animal requires an increase in size or the next stage of development. The exoskeletons of many aquatic species are also infused with calcium carbonate, which makes them even stronger than those of other arthropods. Crustaceans have an open circulatory system where blood is pumped into the hemocoel by the dorsally located heart. Hemocyanin is the major respiratory pigment present in crustaceans, but hemoglobin is found in a few species and both are dissolved in the hemolymph rather than carried in cells.

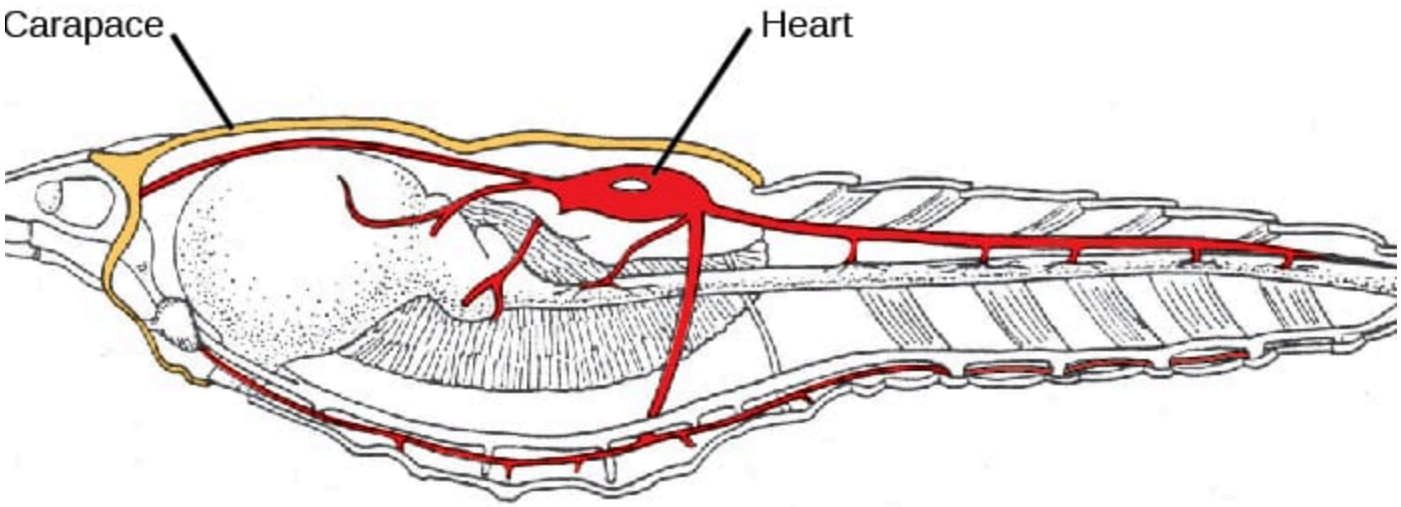
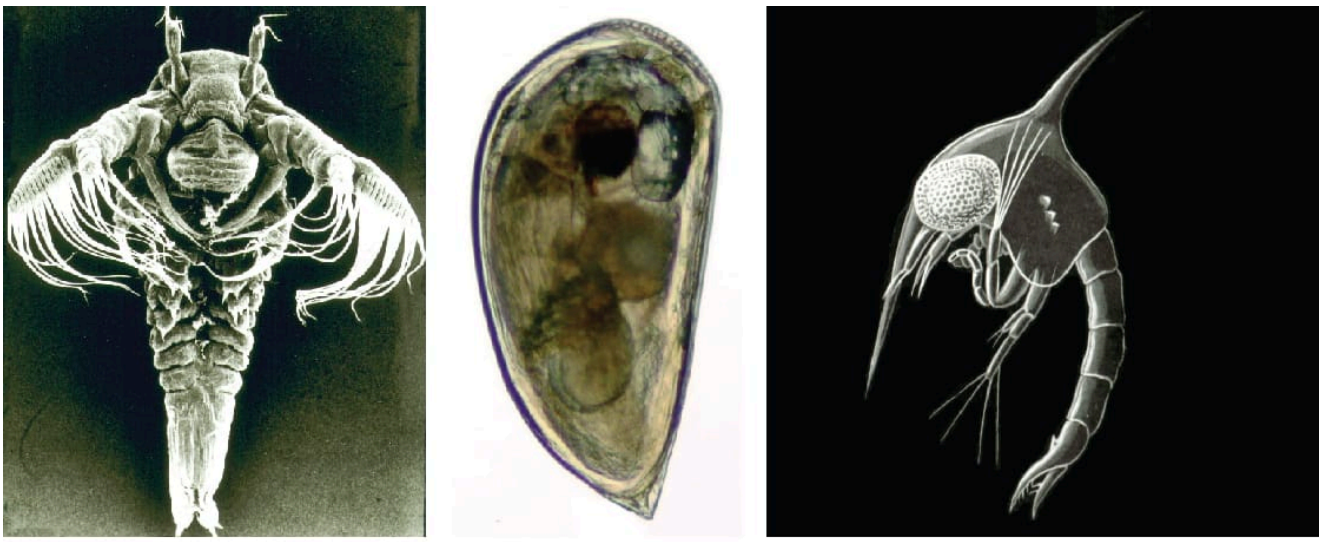


Figure 28.43 Crustacean anatomy. The crayfish is an example of a crustacean. It has a carapace around the cephalothorax and the heart in the dorsal thorax area. (credit: Jane Whitney)

As in the chelicerates, most crustaceans are dioecious. However, some species like barnacles may be hermaphrodites. Serial hermaphroditism, where the gonad can switch from producing sperm to ova, is also exhibited in some species. Fertilized eggs may be held within the female of the species or may be released in the water. Terrestrial crustaceans seek out damp spaces in their habitats to lay eggs.

Larval stages—nauplius or zoea—are seen in the early development of aquatic crustaceans. A cypris larva is also seen in the early development of barnacles (Figure 28.44).



(a) Nauplius larva of a tadpole shrimp (b) Cypris larva of a barnacle (c) Zoea larva of a green crab

Figure 28.44 Crustacean larvae. All crustaceans go through different larval stages. Shown are (a) the nauplius larval stage of a tadpole shrimp, (b) the cypris larval stage of a barnacle, and (c) the zoea larval stage of a green crab. (credit a: modification of work by USGS; credit b: modification of work by Mª. C. Mingorance Rodríguez; credit c: modification of work by B. Kimmel based on original work by Ernst Haeckel)

Crustaceans possess a brain formed by the fusion of the first three segmental ganglia, as well as two compound eyes. A ventral nerve cord connects additional segmental ganglia. Most crustaceans are carnivorous, but herbivorous and detritivorous species, and even endoparasitic species are known. A highly evolved endoparasitic species, such as *Sacculina* spp, parasitizes its crab host and ultimately destroys it after it forces the host to incubate the parasite's eggs! Crustaceans may also be cannibalistic when extremely high populations of these organisms are present.

Subphylum Hexapoda

The insects comprise the largest class of arthropods in terms of species diversity as well as in terms of biomass—at least in terrestrial habitats.

The name Hexapoda describes the presence of six legs (three pairs) in these animals, which differentiates them from other groups of arthropods that have different numbers of legs. In some cases, however, the number of legs has been evolutionarily reduced, or the legs have been highly modified to accommodate specific conditions, such as endoparasitism. Hexapod bodies are organized into three tagmata: head, thorax, and abdomen. Individual segments of the head have mouthparts derived from jointed legs, and the thorax has three pairs of jointed appendages, and also wings, in most derived groups. For example, in the pterygotes (winged insects), in addition to a pair of jointed legs on all three segments comprising the thorax—prothorax, mesothorax, and metathorax—there are veined wings on the mesothorax and metathorax.

Appendages found on other body segments are also evolutionarily derived from modified legs. Typically, the head bears an upper "lip" or labrum and mandibles (or derivation of mandibles) that serve as mouthparts; maxillae, and a lower "lip" called a labium: both of which manipulate food. The head also has one pair of sensory antennae, as well as sensory organs such as a pair of compound eyes, ocelli (simple eyes), and numerous sensory hairs. The abdomen usually has 11 segments and bears external reproductive apertures. The subphylum Hexapoda includes some insects that are winged (such as fruit flies) and others that are secondarily wingless (such as fleas). The only order of "primitively wingless" insects is the Thysanura, the bristletails. All other orders are winged or are descendants of formally winged insects.

The evolution of wings is a major, unsolved mystery. Unlike vertebrates, whose "wings" are simply preadaptations of "arms" that served as the structural foundations for the evolution of functional wings (this has occurred independently in pterosaurs, dinosaurs [birds], and bats), the evolution of wings in insects is a what we call a *de novo* (new) development that has given the pteryogotes domination over the Earth. Winged insects existed over 425 million years ago, and by the Carboniferous, several orders of winged insects (Paleoptera), most of which are now extinct, had evolved. There is good physical evidence that Paleozoic nymphs with thoracic winglets (perhaps hinged, former gill covers of semi-aquatic species) used these devices on land to elevate the thoracic temperature (the thorax is where the legs are located) to levels that would enable them to escape predators faster, find more food resources and mates, and disperse more easily. The thoracic winglets (which can be found on fossilized insects preceding the advent of truly winged insects) could have easily been selected for thermoregulatory purposes prior to reaching a size that would have allowed them the capacity for gliding or actual flapping flight. Even modern insects with broadly attached wings, such as butterflies, use the basal one-third of their wings (the area next to the thorax) for thermoregulation, and the outer two-thirds for flight, camouflage, and mate selection.

Many of the common insects we encounter on a daily basis—including ants, beetles, cockroaches, butterflies, crickets and flies—are examples of Hexapoda. Among these, adult ants, beetles, flies, and butterflies develop by complete metamorphosis from grub-like or caterpillar-like larvae, whereas adult cockroaches and crickets develop through a gradual or incomplete metamorphosis from wingless immatures. All growth occurs during the juvenile stages. Adults do not grow further (but may become larger) after their final molt. Variations in wing, leg, and mouthpart morphology all contribute to the enormous variety seen in the insects. Insect variability was also encouraged by their activity as pollinators and their coevolution with flowering plants. Some insects, especially termites, ants, bees, and wasps, are eusocial, meaning that they live in large groups with individuals assigned to specific roles or castes, like queen, drone, and worker. Social insects use pheromones—external chemical signals—to communicate and maintain group structure as well as a cohesive colony.

Visual Connection

Visual Connection

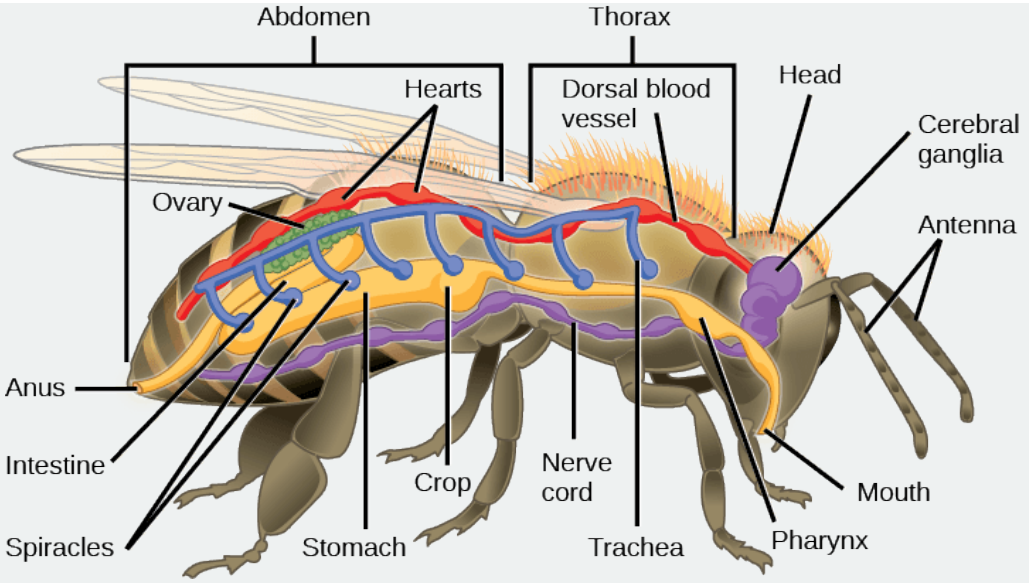


Figure 28.45 Insect anatomy. In this basic anatomy of a hexapod insect, note that insects have a well-developed digestive system (yellow), a respiratory system (blue), a circulatory system (red), and a nervous system (purple). Note the multiple "hearts" and the segmental ganglia.

Which of the following statements about insects is false?

a. Insects have both dorsal and ventral blood vessels.
b. Insects have spiracles, openings that allow air to enter into the tracheal system.
c. The trachea is part of the digestive system.
d. Most insects have a well-developed digestive system with a mouth, crop, and intestine.

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14: ECHINODERMS

14.1: Echinoderm Structure and Diversity

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14.1: Echinoderm Structure and Diversity

Learning Objectives

By the end of this section, you will be able to do the following:

- Describe the distinguishing characteristics of echinoderms
- Describe the distinguishing characteristics of chordates

The phyla Echinodermata and Chordata (the phylum that includes humans) both belong to the superphylum Deuterostomia. Recall that protostomes and deuterostomes differ in certain aspects of their embryonic development, and they are named based on which opening of the archenteron (primitive gut tube) develops first. The word deuterostome comes from the Greek word meaning "mouth second," indicating that the mouth develops as a secondary structure opposite the location of the blastopore, which becomes the anus. In protostomes ("mouth first"), the first embryonic opening becomes the mouth, and the second opening becomes the anus.

There are a series of other developmental characteristics that differ between protostomes and deuterostomes, including the type of early cleavage (embryonic cell division) and the mode of formation of the coelom of the embryo: Protosomes typically exhibit spiral mosaic cleavage whereas deuterostomes exhibit radial regulative cleavage. In deuterostomes, the endodermal lining of the archenteron usually forms buds called coelomic pouches that expand and ultimately obliterate the embryonic blastocoel (the cavity within the blastula and early gastrula) to become the embryonic mesoderm, the third germ layer. This happens when the mesodermal pouches become separated from the invaginating endodermal layer forming the archenteron, then expand and fuse to form the coelomic cavity. The resulting coelom is termed an enterocoelom. The archenteron develops into the alimentary canal, and a mouth opening is formed by invagination of ectoderm at the pole opposite the blastopore of the gastrula. The blastopore forms the anus of the alimentary system in the juvenile and adult forms. Cleavage in most deuterostomes is also *indeterminant*, meaning that the developmental fates of early embryonic cells are not decided at that point of embryonic development (this is why we could potentially clone most deuterostomes, including ourselves).

The deuterostomes consist of two major clades—the Chordata and the Ambulacraria. The Chordata include the vertebrates and two invertebrate subphyla, the urochordates and the cephalochordates. The Ambulacraria include the echinoderms and the hemichordates, which were once considered to be a chordate subphylum (Figure 28.46). The two clades, in addition to being deuterostomes, have some other interesting features in common. As we have seen, the vast majority of invertebrate animals do *not* possess a defined bony vertebral endoskeleton, or a bony cranium. However, one of the most ancestral groups of deuterostome invertebrates, the Echinodermata, do produce tiny skeletal "bones" called *ossicles* that make up a true endoskeleton, or internal skeleton, covered by an epidermis. The Hemichordata (acorn worms and pterobranchs) will not be covered here, but share with the echinoderms a three-part (tripartite) coelom, similar larval forms, and a derived metanephridium that rids the animals of nitrogenous wastes. They also share pharyngeal slits with the chordates (Figure 28.46). In addition, hemichordates have a dorsal nerve cord in the midline of the epidermis, but lack a neural tube, a true notochord and the endostyle and post-anal tail characteristic of chordates.

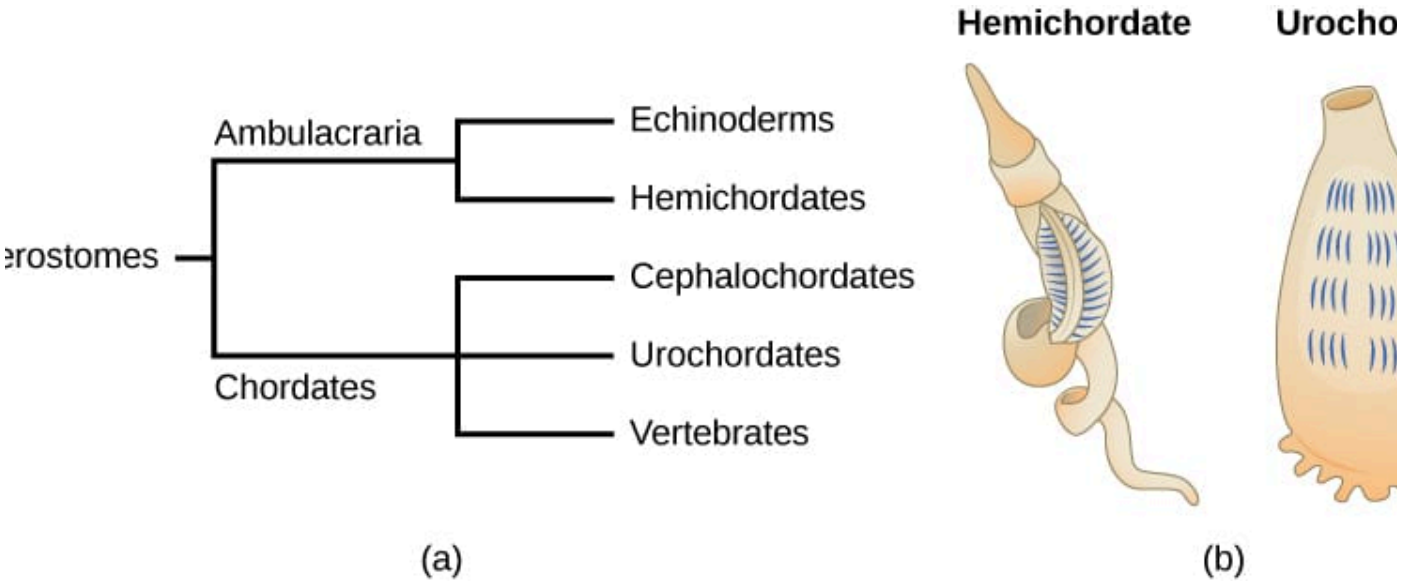


Figure 28.46 Ambulacraria and Chordata. (a) The major deuterostome taxa. (b) pharyngeal slits in hemichordates and urochordates. (credit a MAC; credit b modification of Gill Slits By Own work by Zebra.element [Public domain], via Wikimedia Commons)

Phylum Echinodermata

Echinodermata are named after their “prickly skin” (from the Greek “echinos” meaning “prickly” and “dermos” meaning “skin”). This phylum is a collection of about 7,000 described living species of exclusively marine, bottom-dwelling organisms. Sea stars (Figure 28.47), sea cucumbers, sea urchins, sand dollars, and brittle stars are all examples of echinoderms.

Morphology and Anatomy

Despite the adaptive value of bilaterality for most free-living cephalized animals, adult echinoderms exhibit pentaradial symmetry (with “arms” typically arrayed in multiples of five around a central axis). Echinoderms have an endoskeleton made of calcareous ossicles (small bony plates), covered by the epidermis. For this reason, it is an endoskeleton like our own, not an exoskeleton like that of arthropods. The ossicles may be fused together, embedded separately in the connective tissue of the dermis, or be reduced to minute spicules of bone as in sea cucumbers. The spines for which the echinoderms are named are connected to some of the plates. The spines may be moved by small muscles, but they can also be locked into place for defense. In some species, the spines are surrounded by tiny stalked claws called pedicellaria, which help keep the animal's surface clean of debris, protect *papulae* used in respiration, and sometimes aid in food capture.

The endoskeleton is produced by dermal cells, which also produce several kinds of pigments, imparting vivid colors to these animals. In sea stars, fingerlike projections (papillae) of dermal tissue extend through the endoskeleton and function as gills. Some cells are glandular, and may produce toxins. Each arm or section of the animal contains several different structures: for example, digestive glands, gonads, and the tube feet that are unique to the echinoderms. In echinoderms like sea stars, every arm bears two rows of *tube feet* on the oral side, running along an external ambulacral groove. These tube feet assist in locomotion, feeding, and chemical sensations, as well as serve to attach some species to the substratum.

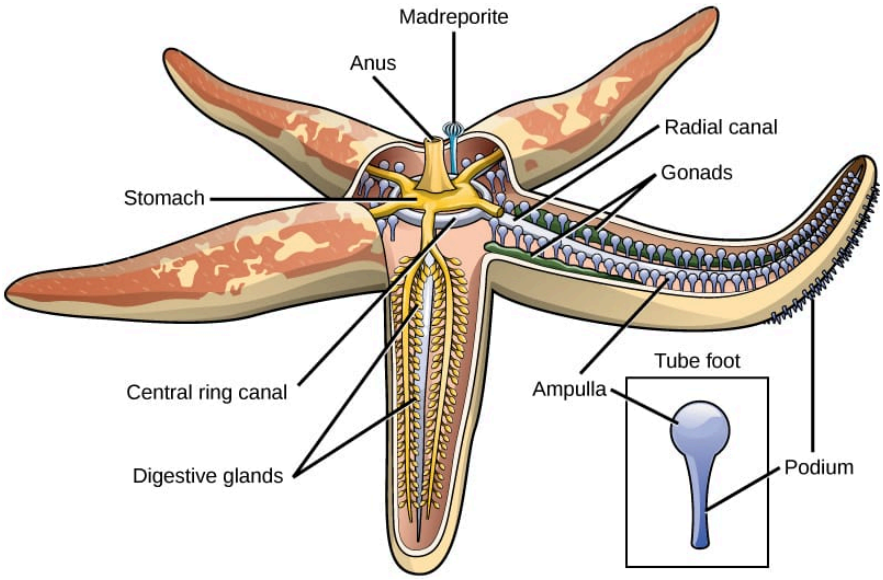


Figure 28.47 Anatomy of a sea star. This diagram of a sea star shows the pentaradial pattern typical of adult echinoderms, and the water vascular system that is their defining characteristic.

Water Vascular and Hemal Systems

Echinoderms have a unique ambulacral (water vascular) system, derived from part of the coelom, or "body cavity." The water vascular system consists of a central ring canal and radial canals that extend along each arm. Each radial canal is connected to a double row of tube feet, which project through holes in the endoskeleton, and function as tactile and ambulatory structures. These tube feet can extend or retract based on the volume of water present in the system of that arm, allowing the animal to move and also allowing it to capture prey with their suckerlike action. Individual tube feet are controlled by bulblike ampullae. Seawater enters the system through an aboral madreporite (opposite the oral area where the mouth is located) and passes to the ring canal through a short stone canal. Water circulating through these structures facilitates gaseous exchange and provides a hydrostatic source for locomotion and prey manipulation. A hemal system, consisting of oral, gastric, and aboral rings, as well as other vessels running roughly parallel to the water vascular system, circulates nutrients. Transport of nutrients and gases is shared by the water vascular and hemal systems in addition to the visceral body cavity that surrounds the major organs.

Nervous System

The nervous system in these animals is a relatively simple, comprising a circumoral nerve ring at the center and five radial nerves extending outward along the arms. In addition, several networks of nerves are located in different parts of the body. However, structures analogous to a brain or large ganglia are not present in these animals. Depending on the group, echinoderms may have well-developed sensory organs for touch and chemoreception (e.g., within the tube feet and on tentacles at the tips of the arms), as well as photoreceptors and statocysts.

Digestive and Excretory Systems

A mouth, located on the oral (ventral) side, opens through a short esophagus to a large, baglike stomach. The so-called "cardiac" stomach can be everted through the mouth during feeding (for example, when a starfish everts its stomach into a bivalve prey item to digest the animal—*alive*—within its own shell!) There are masses of digestive glands (pyloric caeca) in each arm, running dorsally along the arms and overlying the reproductive glands below them. After passing through the pyloric caeca in each arm, the digested food is channeled to a small anus, if one exists.

Podocytes—cells specialized for ultrafiltration of bodily fluids—are present near the center of the echinoderm disc, at the junction of the water vascular and hemal systems. These podocytes are connected by an internal system of canals to the madreporite, where water enters the stone canal. The adult echinoderm typically has a spacious and fluid-filled coelom. Cilia aid in circulating the fluid within the body cavity, and lead to the fluid-filled papulae, where the exchange of oxygen and carbon dioxide takes place, as well as the secretion of nitrogenous waste such as ammonia, by diffusion.

Reproduction

Echinoderms are dioecious, but males and females are indistinguishable apart from their gametes. Males and females release their gametes into water at the same time and fertilization is external. The early larval stages of all echinoderms (e.g., the *bipinnaria* of asteroid echinoderms such as sea stars) have bilateral symmetry, although each class of echinoderms has its own larval form. The radially symmetrical adult forms from a cluster of cells in the larva. Sea stars, brittle stars, and sea cucumbers may also reproduce asexually by fragmentation, as well as regenerate body parts lost in trauma, even when over 75 percent of their body mass is lost!

Classes of Echinoderms

This phylum is divided into five extant classes: Asteroidea (sea stars), Ophiuroidea (brittle stars), Echinoidea (sea urchins and sand dollars), Crinoidea (sea lilies or feather stars), and Holothuroidea (sea cucumbers) (Figure 28.48).

The most well-known echinoderms are members of class Asteroidea, or sea stars. They come in a large variety of shapes, colors, and sizes, with more than 1,800 species known so far. The key characteristic of sea stars that distinguishes them from other echinoderm classes includes thick arms that extend from a central disk from which various body organs branch into the arms. At the end of each arm are simple eye spots and tentacles that serve as touch receptors. Sea stars use their rows of tube feet not only for gripping surfaces but also for grasping prey. Most sea stars are carnivores and their major prey are in the phylum Mollusca. By manipulating its tube feet, a sea star can open molluscan shells. Sea stars have two stomachs, one of which can protrude through their mouths and secrete digestive juices into or onto prey, even before ingestion. A sea star eating a clam can partially open the shell, and then evert its stomach into the shell, introducing digestive enzymes into the interior of the mollusk. This process can both weaken the strong adductor (closing) muscles of a bivalve and begin the process of digestion.

Link to Learning

Link to Learning

Explore the sea star's body plan up close, watch one move across the sea floor, and see it devour a mussel.

Brittle stars belong to the class Ophiuroidea ("snake-tails"). Unlike sea stars, which have plump arms, brittle stars have long, thin, flexible arms that are sharply demarcated from the central disk. Brittle stars move by lashing out their arms or wrapping them around objects and pulling themselves forward. Their arms are also used for grasping prey. The water vascular system in ophiuroids is not used for locomotion.

Sea urchins and sand dollars are examples of Echinoidea ("prickly"). These echinoderms do not have arms, but are hemispherical or flattened with five rows of tube feet that extend through five rows of pores in a continuous internal shell called a *test*. Their tube feet are used to keep the body surface clean. Skeletal plates around the mouth are organized into a complex multipart feeding structure called "*Aristotle's lantern*." Most echinoids graze on algae, but some are suspension feeders, and others may feed on small animals or organic *detritus*—the fragmentary remains of plants or animals.

Sea lilies and feather stars are examples of Crinoidea. Sea lilies are *sessile*, with the body attached to a stalk, but the feather stars can actively move about using leglike *cirri* that emerge from the aboral surface. Both types of crinoid are suspension feeders, collecting small food organisms along the ambulacral grooves of their feather-like arms. The "feathers" consisted of branched arms lined with tube feet. The tube feet are used to move captured food toward the mouth. There are only about 600 extant species of crinoids, but they were far more numerous and abundant in ancient oceans. Many crinoids are deep-water species, but feather stars typically inhabit shallow areas, especially in substropical and tropical waters.

Sea cucumbers of class Holothuroidea exhibit an extended oral-aboral axis. These are the only echinoderms that demonstrate "functional" bilateral symmetry as adults, because the extended oral-aboral axis compels the animal to lie horizontally rather than stand vertically. The tube feet are reduced or absent, except on the side on which the animal lies. They have a single gonad and the digestive tract is more typical of a bilaterally symmetrical animal. A pair of gill-like structures called respiratory trees branch from the posterior gut; muscles around the cloaca pump water in and out of these trees. There are clusters of tentacles around the mouth. Some sea cucumbers feed on detritus, while others are suspension feeders, sifting out small organisms with their oral tentacles. Some species of sea cucumbers are unique among the echinoderms in that cells containing *hemoglobin* circulate in the coelomic fluid, the water vascular system and/or the hemal system.

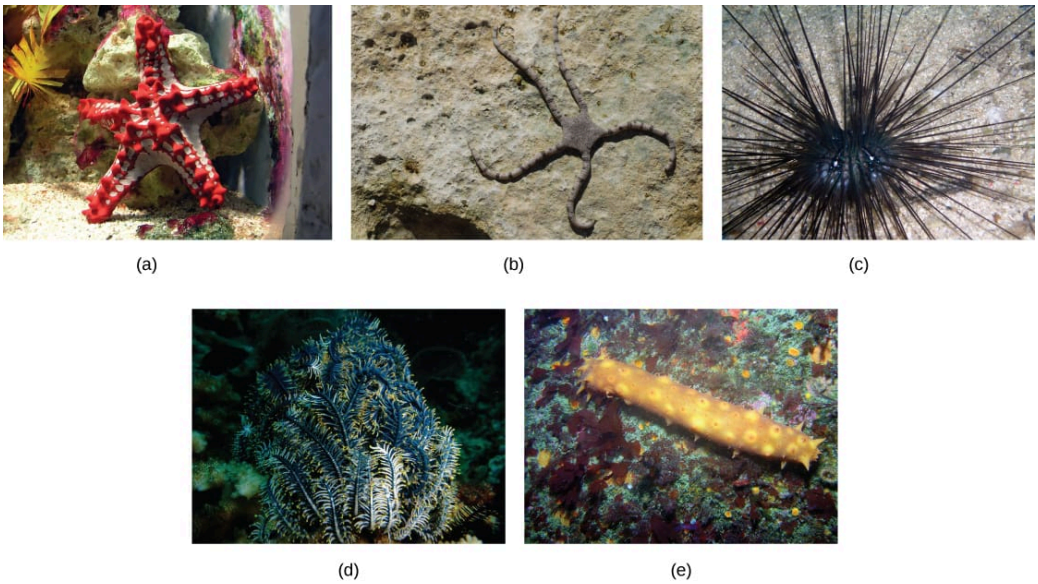


Figure 28.48 Classes of echinoderms. Different members of Echinodermata include the (a) sea star of class Asteroidea, (b) the brittle star of class Ophiuroidea, (c) the sea urchins of class Echinoidea, (d) the sea lilies belonging to class Crinoidea, and (e) sea cucumbers, representing class Holothuroidea. (credit a: modification of work by Adrian Pingstone; credit b: modification of work by Joshua Ganderson; credit c: modification of work by Samuel Chow; credit d: modification of work by Sarah Depper; credit e: modification of work by Ed Bierman)

Phylum Chordata

Animals in the phylum Chordata share five key features that appear at some stage of their development: a notochord, a dorsal hollow nerve cord, pharyngeal slits, a post-anal tail, and an endostyle/thyroid gland that secretes iodinated hormones. In some groups, some of these traits are present only during embryonic development. In addition to containing vertebrate classes, the phylum Chordata contains two clades of “invertebrates”: Urochordata (tunicates, salps, and larvaceans) and Cephalochordata (lancelets). Most tunicates live on the ocean floor and are suspension feeders. Lancelets are suspension feeders that feed on phytoplankton and other microorganisms. The invertebrate chordates will be discussed more extensively in the following chapter.

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15: CHORDATES & VERTEBRATE ORIGINS

15.1: Chordate Structure and Diversity

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15.1: Chordate Structure and Diversity

Learning Objectives

By the end of this section, you will be able to do the following:

- Describe the distinguishing characteristics of chordates
- Identify the derived characters of craniates that sets them apart from other chordates
- Describe the developmental fate of the notochord in vertebrates

The vertebrates exhibit two major innovations in their evolution from the invertebrate chordates. These innovations may be associated with the whole genome duplications that resulted in a quadruplication of the basic chordate genome, including the *Hox* gene loci that regulate the placement of structures along the three axes of the body. One of the first major steps was the emergence of the quadrupeds in the form of the amphibians. A second step was the evolution of the amniotic egg, which, similar to the evolution of pollen and seeds in plants, freed terrestrial animals from their dependence on water for fertilization and embryonic development. Within the amniotes, modifications of keratinous epidermal structures have given rise to scales, claws, hair, and feathers. The scales of reptiles sealed their skins against water loss, while hair and feathers provided insulation to support the evolution of endothermy, as well as served other functions such as camouflage and mate attraction in the vertebrate lineages that led to birds and mammals.

Currently, a number of vertebrate species face extinction primarily due to habitat loss and pollution. According to the International Union for the Conservation of Nature, more than 6,000 vertebrate species are classified as threatened. Amphibians and mammals are the classes with the greatest percentage of threatened species, with 29 percent of all amphibians and 21 percent of all mammals classified as threatened. Attempts are being made around the world to prevent the extinction of threatened species. For example, the Biodiversity Action Plan is an international program, ratified by 188 countries, which is designed to protect species and habitats.

Vertebrates are members of the kingdom Animalia and the phylum Chordata (Figure 29.2). Recall that animals that possess bilateral symmetry can be divided into two groups—protostomes and deuterostomes—based on their patterns of embryonic development. The deuterostomes, whose name translates as “second mouth,” consist of two major phyla: Echinodermata and Chordata. Echinoderms are invertebrate marine animals that have pentaradial symmetry and a spiny body covering, a group that includes sea stars, sea urchins, and sea cucumbers. The most conspicuous and familiar members of Chordata are vertebrates, but this phylum also includes two groups of invertebrate chordates.

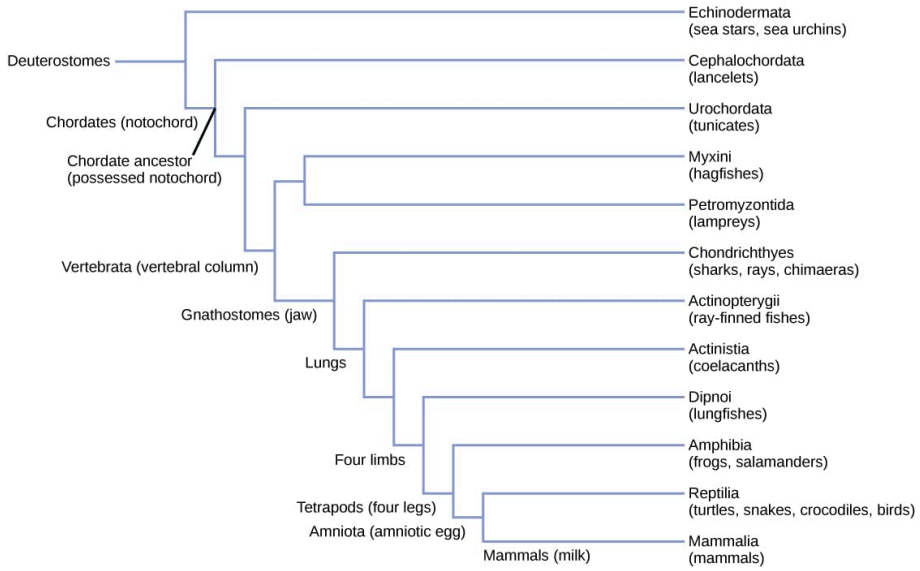


Figure 29.2 Deuterostome phylogeny. All chordates are deuterostomes possessing a notochord at some stage of their life cycle.

Characteristics of Chordata

Animals in the phylum Chordata share five key characteristics that appear at some stage during their development: a notochord, a dorsal hollow (tubular) nerve cord, pharyngeal gill arches or slits, a post-anal tail, and an endostyle/thyroid gland (Figure 29.3). In some groups, some of these key characteristics are present only during embryonic development.

The chordates are named for the notochord, which is a flexible, rod-shaped mesodermal structure that is found in the embryonic stage of all chordates and in the adult stage of some chordate species. It is strengthened with glycoproteins similar to cartilage and covered with a collagenous sheath. The notochord is located between the digestive tube and the nerve cord, and provides rigid skeletal support as well as a flexible location for attachment of axial muscles. In some chordates, the notochord acts as the primary axial support of the body throughout the animal's lifetime. However, in vertebrates (craniates), the notochord is present only during embryonic development, at which time it induces the development of the neural tube and serves as a support for the developing embryonic body. The notochord, however, is not found in the postembryonic stages of vertebrates; at this point, it has been replaced by the vertebral column (that is, the spine).

Visual Connection

Visual Connection

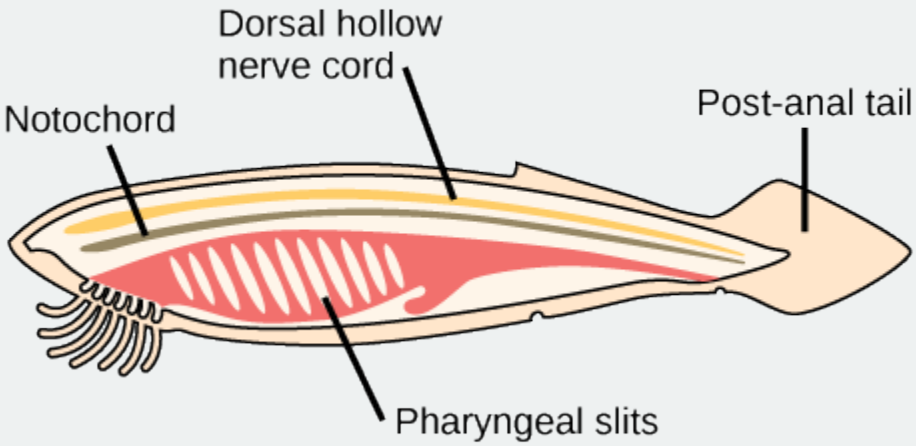


Figure 29.3 Chordate features. In chordates, four common features appear at some point during development: a notochord, a dorsal hollow nerve cord, pharyngeal slits, and a post-anal tail. The endostyle is embedded in the floor of the pharynx.

Which of the following statements about common features of chordates is true?

1. The dorsal hollow nerve cord is part of the chordate central nervous system.
2. In vertebrate fishes, the pharyngeal slits become the gills.
3. Humans are not chordates because humans do not have a tail.
4. Vertebrates do not have a notochord at any point in their development; instead, they have a vertebral column.
5. The endostyle secretes steroid hormones.

The dorsal hollow nerve cord is derived from ectoderm that rolls into a hollow tube during development. In chordates, it is located dorsally to the notochord. In contrast, the nervous system in protostome animal phyla is characterized by solid nerve cords that are located either ventrally and/or laterally to the gut. In vertebrates, the neural tube develops into the brain and spinal cord, which together comprise the central nervous system (CNS). The peripheral nervous system (PNS) refers to the peripheral nerves (including the cranial nerves) lying outside of the brain and spinal cord.

Pharyngeal slits are openings in the pharynx (the region just posterior to the mouth) that extend to the outside environment. In organisms that live in aquatic environments, pharyngeal slits allow for the exit of water that enters the mouth during feeding. Some invertebrate chordates use the pharyngeal slits to filter food out of the water that enters the mouth. The endostyle is a strip of ciliated mucus-producing tissue in the floor of the pharynx. Food particles trapped in the mucus are moved along the endostyle toward the gut. The endostyle also produces substances similar to thyroid hormones and is homologous with the thyroid gland in vertebrates. In vertebrate fishes, the pharyngeal slits are modified into gill supports, and in jawed fishes, into jaw supports. In tetrapods (land vertebrates), the slits are highly modified into components of the ear, and tonsils and thymus glands. In other vertebrates, pharyngeal arches, derived from all three germ layers, give rise to the oral jaw from the first pharyngeal arch, with the

second arch becoming the hyoid and jaw support.

The post-anal tail is a posterior elongation of the body, extending beyond the anus. The tail contains skeletal elements and muscles, which provide a source of locomotion in aquatic species, such as fishes. In some terrestrial vertebrates, the tail also helps with balance, courting, and signaling when danger is near. In humans and other great apes, the post-anal tail is reduced to a vestigial coccyx (“tail bone”) that aids in balance during sitting.

Link to Learning

Link to Learning

Click for a video discussing the evolution of chordates and five characteristics that they share.

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Chordates and the Evolution of Vertebrates

Two clades of chordates are invertebrates: Cephalochordata and Urochordata. Members of these groups also possess the five distinctive features of chordates at some point during their development.

Cephalochordata

Members of Cephalochordata possess a notochord, dorsal hollow tubular nerve cord, pharyngeal slits, endostyle/thyroid gland, and a post-anal tail in the adult stage (Figure 29.4). The notochord extends into the head, which gives the subphylum its name. Although the neural tube also extends into the head region, there is no well-defined brain, and the nervous system is centered around a hollow nerve cord lying above the notochord. Extinct members of this subphylum include *Pikaia*, which is the oldest known cephalochordate. Excellently preserved *Pikaia* fossils were recovered from the Burgess shales of Canada and date to the middle of the Cambrian age, making them more than 500 million years old. Its anatomy of *Pikaia* closely resembles that of the extant lancelet in the genus *Branchiostoma*.

The lancelets are named for their bladelike shape. Lancelets are only a few centimeters long and are usually found buried in sand at the bottom of warm temperate and tropical seas. Cephalochordates are suspension feeders. A water current is created by cilia in the mouth, and is filtered through oral tentacles. Water from the mouth then enters the pharyngeal slits, which filter out food particles. The filtered water collects in a gill chamber called the atrium and exits through the atriopore. Trapped food particles are caught in a stream of mucus produced by the endostyle in a ventral ciliated fold (or groove) of the pharynx and carried to the gut. Most gas exchange occurs across the body surface. Sexes are separate and gametes are released into the water through the atriopore for external fertilization.

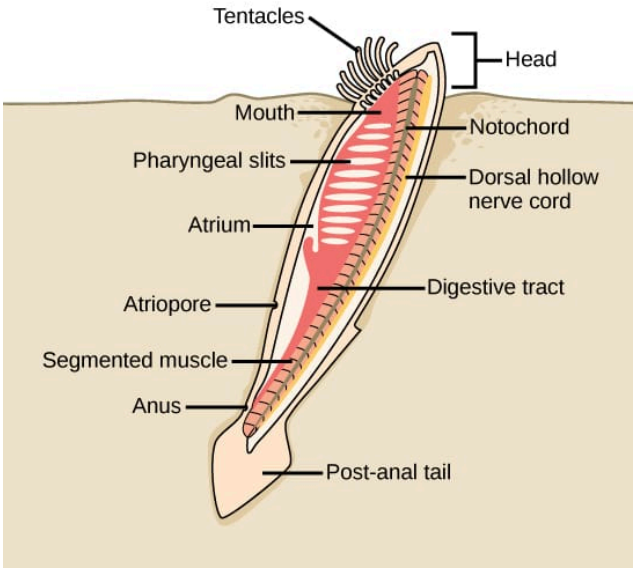


Figure 29.4 Cephalochordate anatomy. In the lancelet and other cephalochordates, the notochord extends into the head region. Adult lancelets retain all five key characteristics of chordates: a notochord, a dorsal hollow nerve cord, pharyngeal slits, an endostyle, and a post-anal tail.

Urochordata

The 1,600 species of Urochordata are also known as tunicates (Figure 29.5). The name tunicate derives from the cellulose-like carbohydrate material, called the **tunic**, which covers the outer body of tunicates. Although tunicates are classified as chordates, the adults do *not* have a notochord, a dorsal hollow nerve cord, or a post-anal tail, although they do have pharyngeal slits and an endostyle. The "tadpole" larval form, however, possesses all five structures. Most tunicates are hermaphrodites; their larvae hatch from eggs inside the adult tunicate's body. After hatching, a tunicate larva (possessing all five chordate features) swims for a few days until it finds a suitable surface on which it can attach, usually in a dark or shaded location. It then attaches via the head to the surface and undergoes metamorphosis into the adult form, at which point the notochord, nerve cord, and tail disappear, leaving the pharyngeal gill slits and the endostyle as the two remaining features of its chordate morphology.

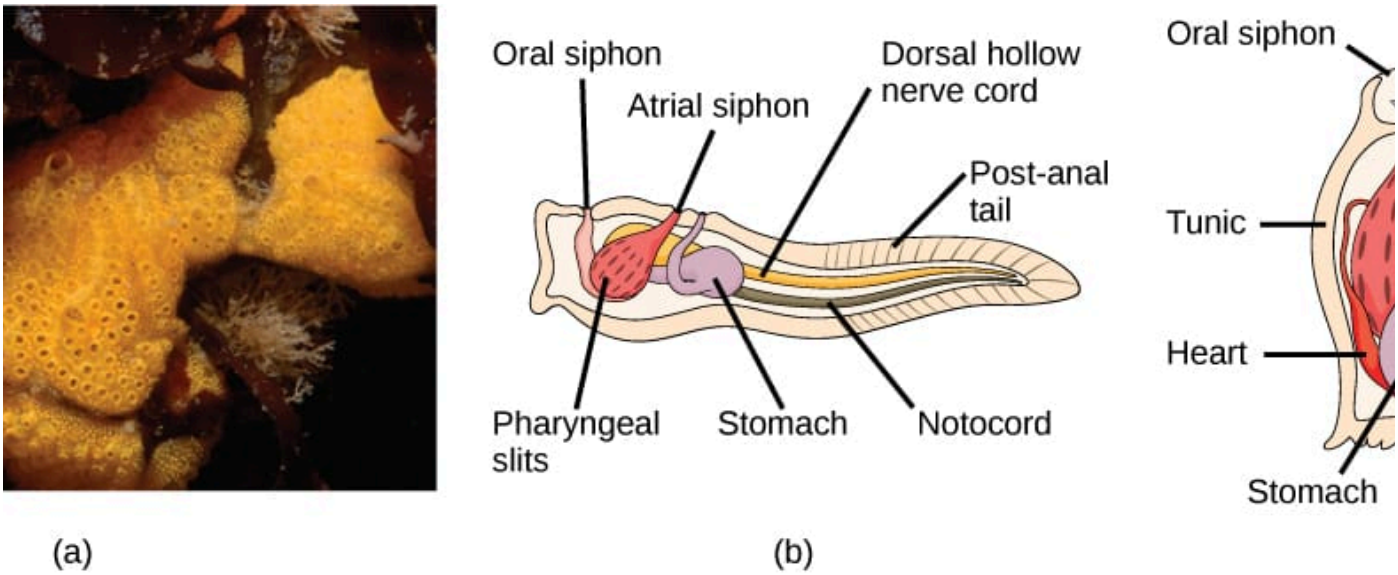


Figure 29.5 Urochordate anatomy. (a) This photograph shows a colony of the tunicate *Botrylloides violaceus*. (b) The larval stage of the tunicate possesses all of the features characteristic of chordates: a notochord, a dorsal hollow nerve cord, pharyngeal slits, an endostyle, and a post-anal tail. (c) In the adult stage, the notochord, nerve cord, and tail disappear, leaving just the pharyngeal slits and endostyle. (credit: modification of work by Dann Blackwood, USGS)

Adult tunicates may be either solitary or colonial forms, and some species may reproduce by budding. Most tunicates live a sessile existence on the ocean floor and are *suspension feeders*. However, chains of thaliacean tunicates called *salps* (Figure 29.6) can swim actively while feeding, propelling themselves as they move water through the pharyngeal slits. The primary foods of tunicates are plankton and detritus. Seawater enters the tunicate's body through its incurrent siphon. Suspended material is filtered out of this water by a mucous net produced by the endostyle and is passed into the intestine via the action of cilia. The anus empties into the excurrent siphon, which expels wastes and water. Tunicates are found in shallow ocean waters around the world.

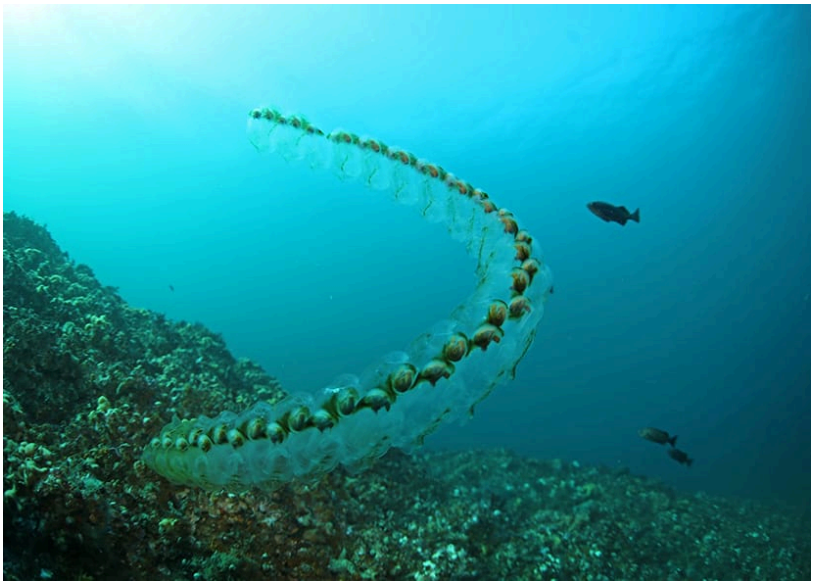


Figure 29.6 Salps. These colonial tunicates feed on phytoplankton. Salps are sequential hermaphrodites, with younger female colonies fertilized by older male colonies. (credit: Oregon Department of Fish & Wildlife via Wikimedia Commons)

Subphylum Vertebrata (Craniata)

A cranium is a bony, cartilaginous, or fibrous structure surrounding the brain, jaw, and facial bones (Figure 29.7). Most bilaterally symmetrical animals have a head; of these, those that have a cranium comprise the clade Craniata/Vertebrata, which includes the primitively jawless Myxini (hagfishes), Petromyzontida (lampreys), and all of the organisms called "vertebrates." (We should note that the Myxini have a cranium but lack a backbone.)

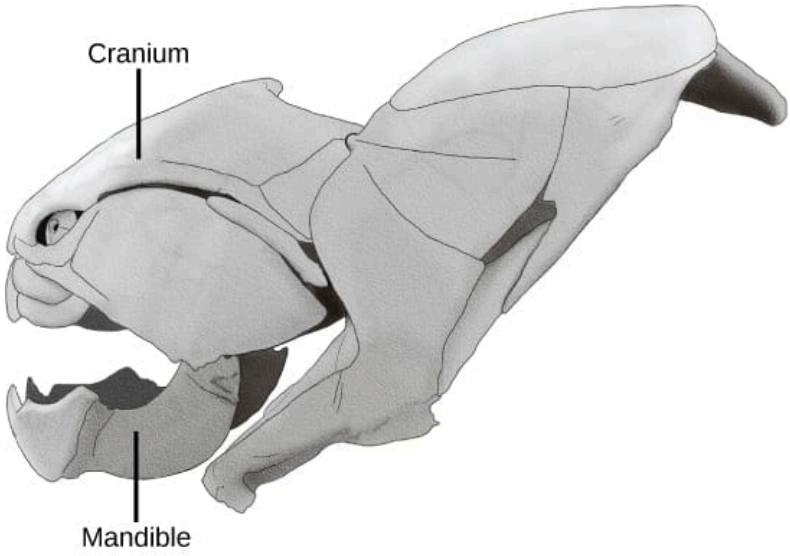


Figure 29.7 A craniate skull. The subphylum Craniata (or Vertebrata), including this placoderm fish (*Dunkleosteus* sp.), are

characterized by the presence of a cranium, mandible, and other facial bones. (credit: “Steveoc 86”/Wikimedia Commons)

Members of the phylum Craniata/Vertebrata display the five characteristic features of the chordates; however, members of this group also share derived characteristics that distinguish them from invertebrate chordates. Vertebrates are named for the vertebral column, composed of vertebrae—a series of separate, irregularly shaped bones joined together to form a backbone (Figure 29.8). Initially, the vertebrae form in segments around the embryonic notochord, but eventually replace it in adults. In most derived vertebrates, the notochord becomes the *nucleus pulposus* of the intervertebral discs that cushion and support adjacent vertebrae.

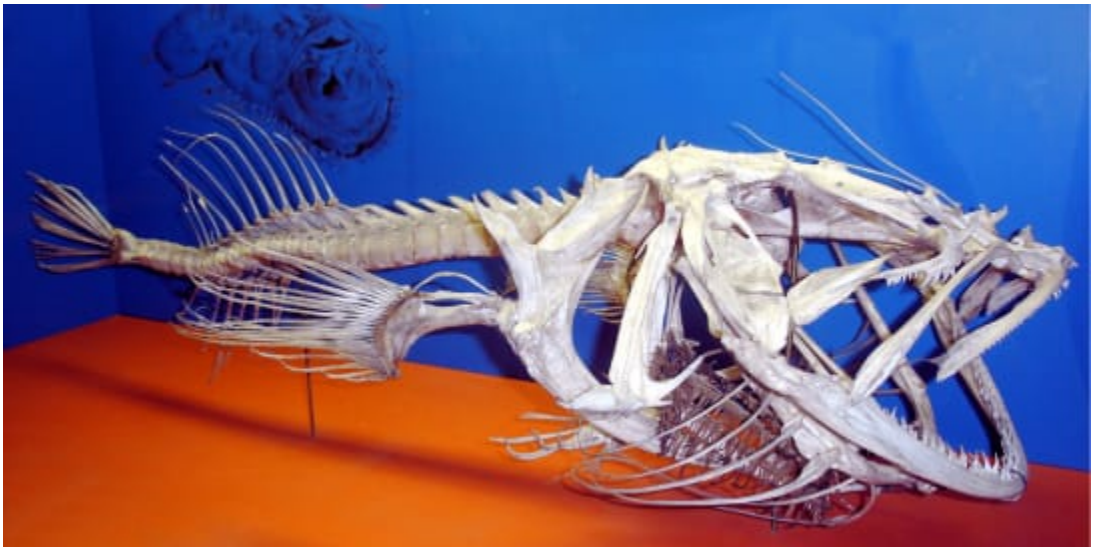


Figure 29.8 A vertebrate skeleton. Vertebrata are characterized by the presence of a backbone, such as the one that runs through the middle of this fish. All vertebrates are in the Craniata clade and have a cranium. (credit: Ernest V. More; taken at Smithsonian Museum of Natural History, Washington, D.C.)

The relationship of the vertebrates to the invertebrate chordates has been a matter of contention, but although these cladistic relationships are still being examined, it appears that the Craniata/Vertebrata are a monophyletic group that shares the five basic chordate characteristics with the other two subphyla, Urochordata and Cephalochordata. Traditional phylogenies place the cephalochordates as a sister clade to the chordates, a view that has been supported by most current molecular analyses. This hypothesis is further supported by the discovery of a fossil in China from the genus *Haikouella*. This organism seems to be an intermediate form between cephalochordates and vertebrates. The *Haikouella* fossils are about 530 million years old and appear similar to modern lancelets. These organisms had a brain and eyes, as do vertebrates, but lack the skull found in craniates.[1] This evidence suggests that vertebrates arose during the Cambrian explosion.

Vertebrates are the largest group of chordates, with more than 62,000 living species, which are grouped based on anatomical and physiological traits. More than one classification and naming scheme is used for these animals. Here we will consider the *traditional groups* Agnatha, Chondrichthyes, Osteichthyes, Amphibia, Reptilia, Aves, and Mammalia, which constitute classes in the subphylum Vertebrata/Craniata. Virtually all modern cladists classify birds within Reptilia, which correctly reflects their evolutionary heritage. Thus, we now have the nonavian reptiles and the avian reptiles in our reptilian classification. We consider them separately only for convenience. Further, we will consider hagfishes and lampreys together as jawless fishes, the Agnatha, although emerging classification schemes separate them into chordate jawless fishes (the hagfishes) and vertebrate jawless fishes (the lampreys).

Animals that possess jaws are known as gnathostomes, which means “jawed mouth.” Gnathostomes include fishes and tetrapods. Tetrapod literally means “four-footed,” which refers to the phylogenetic history of various land vertebrates, even though in some of the tetrapods, the limbs may have been modified for purposes other than walking. Tetrapods include amphibians, reptiles, birds, and mammals, and technically could also refer to the extinct fishlike groups that gave rise to the tetrapods. Tetrapods can be further divided into two groups: amphibians and amniotes. Amniotes are animals whose eggs contain four extraembryonic membranes (yolk sac, amnion, chorion, and allantois) that provide nutrition and a water-retaining environment for their embryos. Amniotes are adapted for terrestrial living, and include mammals, reptiles, and birds.

Footnotes

- 1Chen, J. Y., Huang, D. Y., and Li, C. W., “An early Cambrian craniate-like chordate,” *Nature* 402 (1999): 518–522, doi:10.1038/990080.

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16: FISHES

16.1: Fish Structure and Diversity

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16.1: Fish Structure and Diversity

Learning Objectives

By the end of this section, you will be able to do the following:

- Describe the difference between jawless and jawed fishes
- Discuss the distinguishing features of sharks and rays compared to other modern fishes

Modern fishes include an estimated 31,000 species, by far the most of all clades within the Vertebrata. Fishes were the earliest vertebrates, with jawless species being the earliest forms and jawed species evolving later. They are active feeders, rather than sessile, suspension feeders. The Agnatha (jawless fishes)—the hagfishes and lampreys—have a distinct cranium and complex sense organs including eyes, that distinguish them from the invertebrate chordates, the urochordates and cephalochordates.

Jawless Fishes: Superclass Agnatha

Jawless fishes (Agnatha) are craniates representing an ancient vertebrate lineage that arose over 550 million years ago. In the past, hagfishes and lampreys were sometimes recognized as separate clades within the Agnatha, primarily because lampreys were regarded as true vertebrates, whereas hagfishes were not. However, recent molecular data, both from rRNA and mtDNA, as well as embryological data, provide strong support for the hypothesis that living agnathans—previously called *cyclostomes*—are monophyletic, and thus share recent common ancestry. The discussion below, for convenience, separates the modern "cyclostomes" into the class Myxini and class Petromyzontida. The defining features of the living jawless fishes are the lack of jaws and lack of paired lateral appendages (fins). They also lack internal ossification and scales, although these are not defining features of the clade.

Some of the earliest jawless fishes were the armored ostracoderms (which translates to "shell-skin"): vertebrate fishes encased in bony armor—unlike present-day jawless fishes, which lack bone in their scales. Some ostracoderms, also unlike living jawless fishes, may have had paired fins. We should note, however, that the "ostracoderms" represent an assemblage of heavily armored extinct jawless fishes that may not form a natural evolutionary group. Fossils of the genus *Haikouichthys* from China, with an age of about 530 million years, show many typical vertebrate characteristics including paired eyes, auditory capsules, and rudimentary vertebrae.

Class Myxini: Hagfishes

The class Myxini includes at least 70 species of hagfishes—eel-like scavengers that live on the ocean floor and feed on living or dead invertebrates, fishes, and marine mammals (Figure 29.9). Although they are almost completely blind, sensory barbels around the mouth help them locate food by smell and touch. They feed using keratinized teeth on a movable cartilaginous plate in the mouth, which rasp pieces of flesh from their prey. These feeding structures allow the gills to be used exclusively for respiration, *not* for filter feeding as in the urochordates and cephalochordates. Hagfishes are entirely marine and are found in oceans around the world, except for the polar regions. Unique slime glands beneath the skin release a milky mucus (through surface pores) that upon contact with water becomes incredibly slippery, making the animal almost impossible to hold. This slippery mucus thus allows the hagfish to escape from the grip of predators. Hagfish can also twist their bodies into a knot, which provides additional leverage to feed. Sometimes hagfish enter the bodies of dead animals and eat carcasses from the inside out! Interestingly, they do not have a stomach!



Figure 29.9 Hagfish. Pacific hagfish are scavengers that live on the ocean floor. (credit: Linda Snook, NOAA/CBNMS)

Hagfishes have a cartilaginous skull, as well as a fibrous and cartilaginous skeleton, but the major supportive structure is the notochord that runs the length of the body. In hagfishes, the notochord is *not* replaced by the vertebral column, as it is in true vertebrates, and thus they may (morphologically) represent a sister group to the true vertebrates, making them the most basal clade among the skull-bearing chordates.

Class Petromyzontida: Lampreys

The class Petromyzontida includes approximately 40 species of lampreys, which are superficially similar to hagfishes in size and shape. However, lampreys possess extrinsic eye muscles, at least two semicircular canals, and a true cerebellum, as well as simple vertebral elements, called *arcualia*—cartilaginous structures arranged above the notochord. These features are also shared with the *gnathostomes*—vertebrates with jawed mouths and paired appendages (see below). Lampreys also have a dorsal tubular nerve cord with a well-differentiated brain, a small cerebellum, and 10 pairs of nerves. The classification of lampreys is still debated, but they clearly represent one of the oldest divergences of the vertebrate lineage. Lampreys lack paired appendages, as do the hagfishes, although they have one or two fleshy dorsal fins. As adults, lampreys are characterized by a rasping tongue within a toothed, funnel-like sucking mouth. Many species have a parasitic stage of their life cycle during which they are fish ectoparasites (some call them predators because they attack and eventually fall off) (Figure 29.10).



Figure 29.10 Lamprey. These parasitic sea lampreys, *Petromyzon marinus,* attach by suction to their lake trout host, and use their

rough tongues to rasp away flesh in order to feed on the trout's blood. (credit: USGS)

Lampreys live primarily in coastal and freshwater environments, and have a worldwide distribution, except for the tropics and polar regions. Some species are marine, but all species spawn in fresh water. Interestingly, northern lampreys in the family Petromyzontidae, have the highest number of chromosomes (164 to 174) among the vertebrates. Eggs are fertilized externally, and the larvae (called *ammocoetes*) differ greatly from the adult form, closely resembling the adult cephalocordate *amphioxus*. After spending three to 15 years as suspension feeders in rivers and streams, they attain sexual maturity. After one to three years of feeding on fish as ectoparasites during life in open water, the adults swim upstream, reproduce, and die within days.

Gnathostomes: Jawed Fishes

Gnathostomes, or "jaw-mouths," are vertebrates that possess true jaws—a milestone in the evolution of the vertebrates. In fact, one of the most significant developments in early vertebrate evolution was the development of the jaw: a hinged structure attached to the cranium that allows an animal to grasp and tear its food. Jaws were probably derived from the first pair of gill arches supporting the gills of jawless fishes.

Early gnathostomes also possessed two sets of paired fins, allowing the fishes to maneuver accurately. Pectoral fins are typically located on the anterior body, and pelvic fins on the posterior. Evolution of the jaw and paired fins permitted gnathostomes to expand their food options from the scavenging and suspension feeding of jawless fishes to active predation. The ability of gnathostomes to exploit new nutrient sources probably contributed to their replacing most jawless fishes during the Devonian period. Two early groups of gnathostomes were the *acanthodians* and *placoderms* (Figure 29.11), which arose in the late Silurian period and are now extinct. Most modern fishes are gnathostomes that belong to the clades Chondrichthyes and Osteichthyes (which include the class Actinoptertygii and class Sarcopterygii).



Figure 29.11 A placoderm. *Dunkleosteus* was an enormous placoderm from the Devonian period, 380 to 360 million years ago. It measured up to 10 meters in length and weighed up to 3.6 tons. Its head and neck were armored with heavy bony plates. Although *Dunkleosteus* had no true teeth, the edge of the jaw was armed with sharp bony blades. (credit: Nobu Tamura)

Class Chondrichthyes: Cartilaginous Fishes

The class Chondrichthyes (about 1,000 species) is a morphologically diverse clade, consisting of subclass Elasmobranchii (sharks [Figure 29.12], rays, and skates, together with the obscure and critically endangered sawfishes), and a few dozen species of fishes called *chimaeras*, or "ghost sharks" in the subclass Holocephali. Chondrichthyes are jawed fishes that possess paired fins and a skeleton made of cartilage. This clade arose approximately 370 million years ago in the early or middle Devonian. They are thought to be descended from the placoderms, which had endoskeletons made of bone; thus, the lighter cartilaginous skeleton of Chondrichthyes is a secondarily derived evolutionary development. Parts of shark skeleton are strengthened by granules of calcium carbonate, but this is not the same as bone.

Most cartilaginous fishes live in marine habitats, with a few species living in fresh water for a part or all of their lives. Most sharks are carnivores that feed on live prey, either swallowing it whole or using their jaws and teeth to tear it into smaller pieces. Sharks have abrasive skin covered with tooth-like scales called placoid scales. Shark teeth probably evolved from rows of these scales lining the mouth. A few species of sharks and rays, like the enormous whale shark (Figure 29.13), are suspension feeders that feed on plankton. The sawfishes have an extended rostrum that looks like a double-edged saw. The rostrum is covered with electrosensitive pores that allow the sawfish to detect slight movements of prey hiding in the muddy sea floor. The teeth in the rostrum are actually modified tooth-like structures called denticles, similar to scales.



Figure 29.12 Shark. Hammerhead sharks tend to school during the day and hunt prey at night. (credit: Masashi Sugawara)

Sharks have well-developed sense organs that aid them in locating prey, including a keen sense of smell and the ability to detect electromagnetic fields. Electroreceptors called ampullae of Lorenzini allow sharks to detect the electromagnetic fields that are produced by all living things, including their prey. (Electroreception has only been observed in aquatic or amphibious animals and sharks have perhaps the most sensitive electroreceptors of any animal.) Sharks, together with most fishes and aquatic and larval amphibians, also have a row of sensory structures called the lateral line, which is used to detect movement and vibration in the surrounding water, and is often considered to be functionally similar to the sense of “hearing” in terrestrial vertebrates. The lateral line is visible as a darker stripe that runs along the length of a fish’s body. Sharks have no mechanism for maintaining neutral buoyancy and must swim continuously to stay suspended in the water. Some must also swim in order to ventilate their gills but others have muscular pumps in their mouths to keep water flowing over the gills.

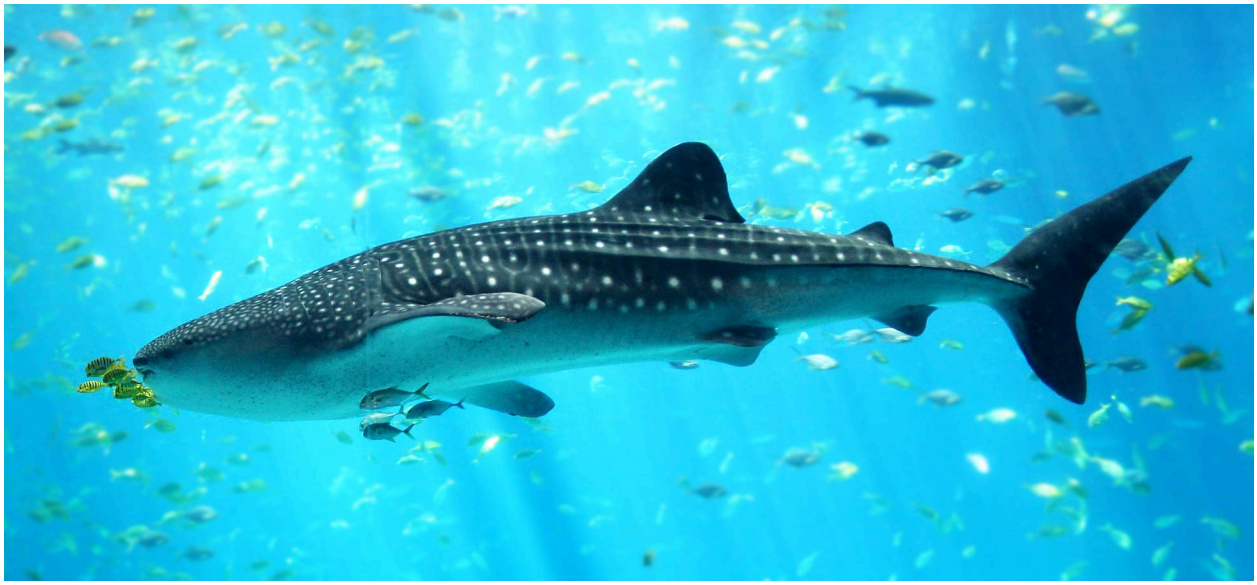


Figure 29.13 Whale shark in the Georgia Aquarium. Whale sharks are filter-feeders and can grow to be over 10 meters long. Whale sharks, like most other sharks, are ovoviviparous. (credit: modified from Zac Wolf [Own work] [CC BY-SA 2.5 (http://creativecommons.org/licenses/by-sa/2.5)], via Wikimedia Commons)

Sharks reproduce sexually, and eggs are fertilized internally. Most species are *ovoviviparous*: The fertilized egg is retained in the oviduct of the mother's body and the embryo is nourished by the egg yolk. The eggs hatch in the uterus, and young are born alive and fully functional. Some species of sharks are oviparous: They lay eggs that hatch outside of the mother's body. Embryos are protected by a shark egg case or "mermaid's purse" (Figure 29.14) that has the consistency of leather. The shark egg case has tentacles that snag in seaweed and give the newborn shark cover. A few species of sharks, e.g., tiger sharks and hammerheads, are viviparous: the yolk sac that initially contains the egg yolk and transfers its nutrients to the growing embryo becomes attached to the oviduct of the female, and nutrients are transferred directly from the mother to the growing embryo. In both viviparous and ovoviviparous sharks, gas exchange uses this yolk sac transport.

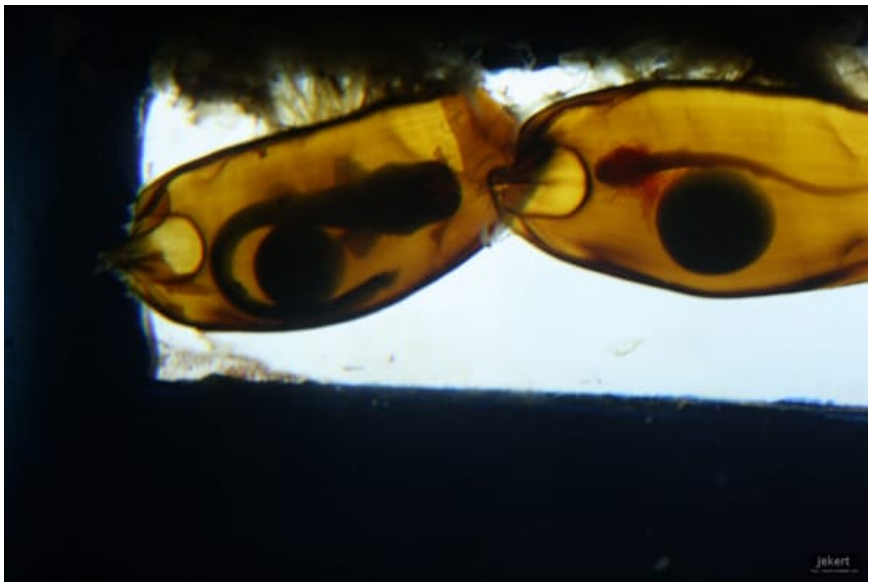


Figure 29.14 Shark egg cases. Shark embryos are clearly visible through these transparent egg cases. The round structure is the yolk that nourishes the growing embryo. (credit: Jek Bacarisas)

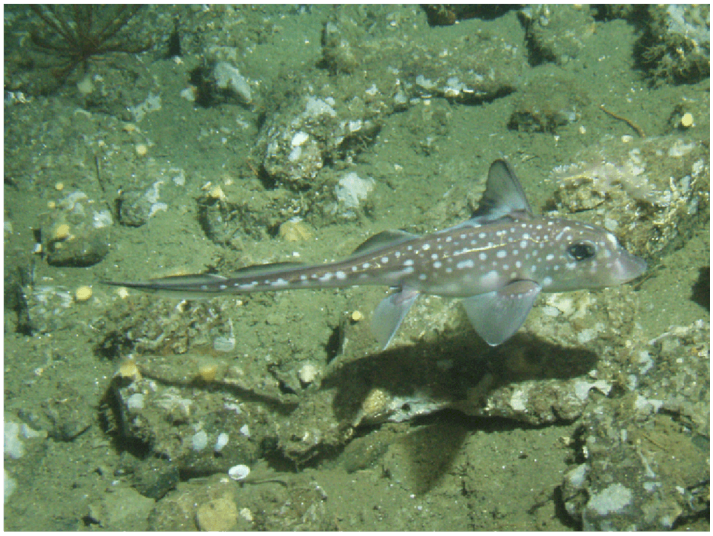
In general, the Chondrichthyes have a fusiform or dorsoventrally flattened body, a *heterocercal* caudal fin or tail (unequally sized fin lobes, with the tail vertebrae extending into the larger upper lobe) paired pectoral and pelvic fins (in males these may be modified as claspers), exposed gill slits (*elasmobranch*), and an intestine with a spiral valve that condenses the length of the intestine. They also have three pairs of semicircular canals, and excellent senses of smell, vibration, vision, and electroreception. A very large lobed liver produces *squalene oil* (a lightweight biochemical precursor to steroids) that serves to aid in buoyancy (because with a specific gravity of 0.855, it is lighter than that of water).

Rays and skates comprise more than 500 species. They are closely related to sharks but can be distinguished from sharks by their flattened bodies, pectoral fins that are enlarged and fused to the head, and gill slits on their ventral surface (Figure 29.15). Like sharks, rays and skates have a cartilaginous skeleton. Most species are marine and live on the sea floor, with nearly a worldwide distribution.

Unlike the stereotypical sharks and rays, the Holocephali (chimaeras or ratfish) have a *diphycercal* tail (equally sized fin lobes, with the tail vertebrae located between them), lack scales (lost secondarily in evolution), and have teeth modified as grinding plates that are used to feed on mollusks and other invertebrates (Figure 29.15b). Unlike sharks with elasmobranch or naked gills, chimaeras have four pairs of gills covered by an operculum. Many species have a pearly iridescence and are extremely pretty.



(a)



(b)

Figure 29.15 Cartilaginous fish. (a) Stingray. This stingray blends into the sandy bottom of the ocean floor. A spotted ratfish (b) Hydrolagus colliei credit a "Sailn1"/Flickr; (credit: a "Sailn1"/Flickr b: Linda Snook / MBNMS [Public domain], via Wikimedia Commons.)

Osteichthyes: Bony Fishes

Members of the clade Osteichthyes, also called bony fishes, are characterized by a bony skeleton. The vast majority of present-day fishes belong to this group, which consists of approximately 30,000 species, making it the largest class of vertebrates in existence today.

Nearly all bony fishes have an *ossified skeleton* with specialized bone cells (osteocytes) that produce and maintain a calcium phosphate matrix. This characteristic has been reversed only in a few groups of Osteichthyes, such as sturgeons and paddlefish, which have primarily cartilaginous skeletons. The skin of bony fishes is often covered by overlapping scales, and glands in the skin secrete mucus that reduces drag when swimming and aids the fish in osmoregulation. Like sharks, bony fishes have a lateral line system that detects vibrations in water.

All bony fishes use gills to breathe. Water is drawn over gills that are located in chambers covered and ventilated by a protective, muscular flap called the operculum. Many bony fishes also have a swim bladder, a gas-filled organ derived as a pouch from the gut. The swim bladder helps to control the buoyancy of the fish. In most bony fish, the gases of the swim bladder are exchanged directly with the blood. The swim bladder is believed to be homologous to the lungs of lungfish and the lungs of land vertebrates.

Bony fishes are further divided into two extant clades: Class Actinopterygii (ray-finned fishes) and Class Sarcopterygii (lobe-finned fishes).

Actinopterygii (Figure 29.16a), the ray-finned fishes, include many familiar fishes—tuna, bass, trout, and salmon among others—and represent about half of all vertebrate species. Ray-finned fishes are named for the fan of slender bones that supports their fins.

In contrast, the fins of Sarcopterygii (Figure 29.16b) are fleshy and lobed, supported by bones that are similar in type and arrangement to the bones in the limbs of early tetrapods. The few extant members of this clade include several species of lungfishes and the less familiar coelacanths, which were thought to be extinct until living specimens were discovered between Africa and Madagascar. Currently, two species of coelacanths have been described.

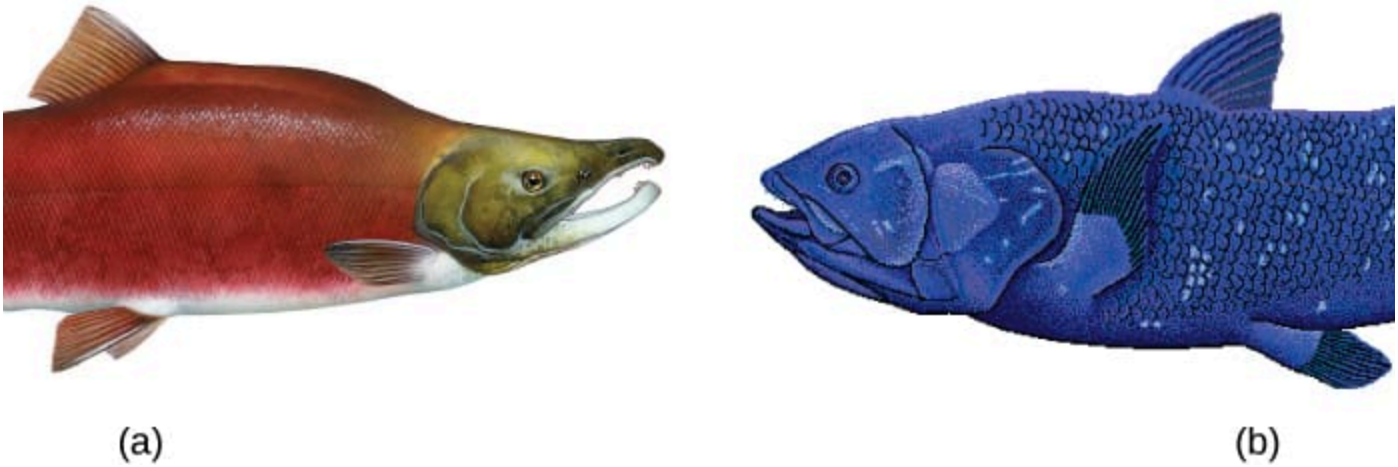


Figure 29.16 Osteichthyes. The (a) sockeye salmon and (b) coelacanth are both bony fishes of the Osteichthyes clade. The coelacanth, sometimes called a lobe-finned fish, was thought to have gone extinct in the Late Cretaceous period, 100 million years ago, until one was discovered in 1938 near the Comoros Islands between Africa and Madagascar. (credit a: modification of work by Timothy Knepp, USFWS; credit b: modification of work by Robbie Cada)

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17: AMPHIBIANS & REPTILES

17.1: Amphibian Structure and Diversity
17.2: Reptile Structure and Diversity

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17.1: Amphibian Structure and Diversity

Learning Objectives

By the end of this section, you will be able to do the following:

- Describe the important difference between the life cycle of amphibians and the life cycles of other vertebrates
- Distinguish between the characteristics of Urodela, Anura, and Apoda
- Describe the evolutionary history of amphibians

Amphibians are vertebrate tetrapods (“four limbs”), and include frogs, salamanders, and caecilians. The term “amphibian” loosely translates from the Greek as “dual life,” which is a reference to the metamorphosis that many frogs and salamanders undergo and the unique mix of aquatic and terrestrial phases that are required in their life cycle. In fact, they cannot stray far from water because their reproduction is intimately tied to aqueous environments. Amphibians evolved during the Devonian period and were the earliest terrestrial tetrapods. They represent an evolutionary transition from water to land that occurred over many millions of years. Thus, the Amphibia are the only living true vertebrates that have made a transition from water to land in both their ontogeny (life development) and phylogeny (evolution). They have not changed much in morphology over the past 350 million years!

Link to Learning

Link to Learning

Watch this series of four videos on tetrapod evolution:

- 1: The evolution from fish to earliest tetrapod
  Click to view content

Interactive Content

This interactive element is not available in this format. Visit the link or scan the QR code to access it online.

View this Interactive Content online

2: The discovery of coelacanth and *Acanthostega* fossils
Click to view content

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3: The number of fingers on “legs”
4: Reconstructing the environment of early tetrapods
Click to view content

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Characteristics of Amphibians

As tetrapods, most amphibians are characterized by four well-developed limbs. In some species of salamanders, hindlimbs are reduced or absent, but all caecilians are (secondarily) limbless. An important characteristic of extant amphibians is a moist, permeable skin that is achieved via mucus glands. Most water is taken in across the skin rather than by drinking. The skin is also one of three respiratory surfaces used by amphibians. The other two are the lungs and the buccal (mouth) cavity. Air is taken first into the mouth through the nostrils, and then pushed by positive pressure into the lungs by elevating the throat and closing the nostrils.

All extant adult amphibians are carnivorous, and some terrestrial amphibians have a sticky tongue used to capture prey. Amphibians also have multiple small teeth at the edge of the jaws. In salamanders and caecilians, teeth are present in both jaws, sometimes in multiple rows. In frogs and toads, teeth are seen only in the upper jaw. Additional teeth, called vomerine teeth, may be found in the roof of the mouth. Amphibian teeth are *pedicellate*, which means that the root and crown are calcified, separated by a zone of noncalcified tissue.

Amphibians have image-forming eyes and color vision. Ears are best developed in frogs and toads, which vocalize to communicate. Frogs use separate regions of the inner ear for detecting higher and lower sounds: the *papilla amphibiorum*, which is sensitive to frequencies below 10,000 hertz and unique to amphibians, and the *papilla basilaris*, which is sensitive to higher frequencies, including mating calls, transmitted from the eardrum through the stapes bone. Amphibians also have an extra bone in the ear, the operculum, which transmits low-frequency vibrations from the forelimbs and shoulders to the inner ear, and may be used for the detection of seismic signals.

Evolution of Amphibians

The fossil record provides evidence of the first tetrapods: now-extinct amphibian species dating to nearly 400 million years ago. Evolution of tetrapods from lobe-finned freshwater fishes (similar to coelacanths and lungfish) represented a significant change in body plan from one suited to organisms that respired and swam in water, to organisms that breathed air and moved onto land; these changes occurred over a span of 50 million years during the Devonian period.

Aquatic tetrapods of the Devonian period include *Ichthyostega* and *Acanthostega*. Both were aquatic, and may have had both gills and lungs. They also had four limbs, with the skeletal structure of limbs found in present-day tetrapods, including amphibians. However, the limbs could not be pulled in under the body and would not have supported their bodies well out of water. They probably lived in shallow freshwater environments, and may have taken brief terrestrial excursions, much like "walking" catfish do today in Florida. In *Ichthyostega*, the forelimbs were more developed than the hind limbs, so it might have dragged itself along when it ventured onto land. What preceded *Acanthostega* and *Ichthyostega*?

In 2006, researchers published news of their discovery of a fossil of a "tetrapod-like fish," *Tiktaalik roseae*, which seems to be a morphologically "intermediate form" between sarcopterygian fishes having feet-like fins and early tetrapods having true limbs (Figure 29.17). *Tiktaalik* likely lived in a shallow water environment about 375 million years ago.[2] Tiktaalik also had gills and lungs, but the loss of some gill elements gave it a neck, which would have allowed its head to move sideways for feeding. The eyes were on top of the head. It had fins, but the attachment of the fin bones to the shoulder suggested they might be weight-bearing. Tiktaalik preceded *Acanthostega* and *Ichthyostega*, with their four limbs, by about 10 million years and is considered to be a true intermediate clade between fish and amphibians.

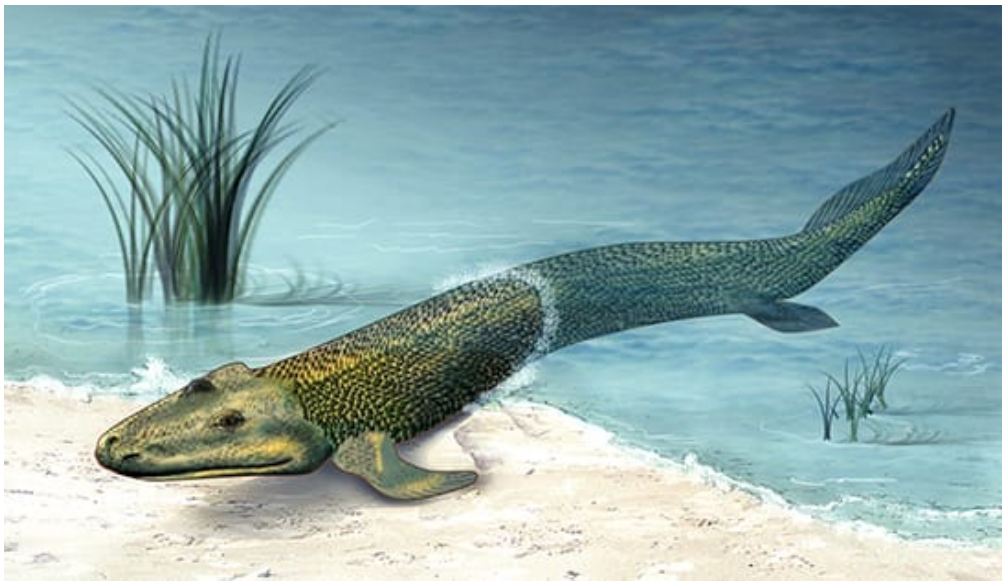


Figure 29.17 Tiktaalik. The recent fossil discovery of *Tiktaalik roseae* suggests evidence for an animal intermediate to finned fish and legged tetrapods, sometimes called a "fishapod." (credit: Zina Deretsky, National Science Foundation)

The early tetrapods that moved onto land had access to new nutrient sources and relatively few predators. This led to the widespread distribution of tetrapods during the early Carboniferous period, a period sometimes called the “age of the amphibians.”

Modern Amphibians

Amphibia comprises an estimated 6,770 extant species that inhabit tropical and temperate regions around the world. All living species are classified in the subclass Lissamphibia ("smooth-amphibian"), which is divided into three clades: Urodela (“tailed”), the salamanders; Anura (“tail-less”), the frogs; and Apoda (“legless ones”), the caecilians.

Urodela: Salamanders

Salamanders are amphibians that belong to the order Urodela (or Caudata). These animals are probably the most similar to ancestral amphibians. Living salamanders (Figure 29.18) include approximately 620 species, some of which are aquatic, others terrestrial, and some that live on land only as adults. Most adult salamanders have a generalized tetrapod body plan with four limbs and a tail. The placement of their legs makes it difficult to lift their bodies off the ground and they move by bending their bodies from side to side, called *lateral undulation*, in a fish-like manner while “walking” their arms and legs fore-and-aft. It is thought that their gait is similar to that used by early tetrapods. The majority of salamanders are lungless, and respiration occurs through the skin or through external gills in aquatic species. Some terrestrial salamanders have primitive lungs; a few species have both gills and lungs. The giant Japanese salamander, the largest living amphibian, has additional folds in its skin that enlarge its respiratory surface.

Most salamanders reproduce using an unusual process of internal fertilization of the eggs. Mating between salamanders typically involves an elaborate and often prolonged courtship. Such a courtship ends in the deposition of sperm by the males in a packet called a spermatophore, which is subsequently picked up by the female, thus ultimately fertilization is internal. All salamanders except one, the fire salamander, are oviparous. Aquatic salamanders lay their eggs in water, where they develop into legless larvae called *efts*. Terrestrial salamanders lay their eggs in damp nests, where the eggs are guarded by their mothers. These embryos go through the larval stage and complete metamorphosis before hatching into tiny adult forms. One aquatic salamander, the Mexican *axolotl*, never leaves the larval stage, becoming sexually mature without metamorphosis.



Figure 29.18 Salamander. Most salamanders have legs and a tail, but respiration varies among species. (credit: Valentina Storti)

Link to Learning

Link to Learning

View River Monsters: Fish With Arms and Hands? to see a video about an unusually large salamander species.

Anura: Frogs

Frogs (Figure 29.19) are amphibians that belong to the order Anura or Salientia ("jumpers"). Anurans are among the most diverse groups of vertebrates, with approximately 5,965 species that occur on all of the continents except Antarctica. Anurans, ranging from the minute New Guinea frog at 7 mm to the huge goliath frog at 32 cm from tropical Africa, have a body plan that is more specialized for movement. Adult frogs use their hind limbs and their arrow-like endoskeleton to jump accurately to capture prey on land. Tree frogs have hands adapted for grasping branches as they climb. In tropical areas, “flying frogs” can glide from perch to perch on the extended webs of their feet. Frogs have a number of modifications that allow them to avoid predators, including skin that acts as camouflage. Many species of frogs and salamanders also release defensive chemicals that are poisonous to predators from glands in the skin. Frogs with more toxic skins have bright warning (*aposematic*) coloration.



Figure 29.19 Tree frog. The Australian green tree frog is a nocturnal predator that lives in the canopies of trees near a water source.

Frog eggs are fertilized externally, and like other amphibians, frogs generally lay their eggs in moist environments. Although amphibian eggs are protected by a thick jelly layer, they would still dehydrate quickly in a dry environment. Frogs demonstrate a great diversity of parental behaviors, with some species laying many eggs and exhibiting little parental care, to species that carry eggs and tadpoles on their hind legs or embedded in their backs. The males of Darwin's frog carry tadpoles in their vocal sac. Many tree frogs lay their eggs off the ground in a folded leaf located over water so that the tadpoles can drop into the water as they hatch.

The life cycle of most frogs, as other amphibians, consists of two distinct stages: the larval stage followed by metamorphosis to an adult stage. However, the eggs of frogs in the genus *Eleutherodactylus* develop directly into little froglets, guarded by a parent. The larval stage of a frog, the tadpole, is often a filter-feeding herbivore. Tadpoles usually have gills, a lateral line system, longfinned tails, and lack limbs. At the end of the tadpole stage, frogs undergo metamorphosis into the adult form (Figure 29.20). During this stage, the gills, tail, and lateral line system disappear, and four limbs develop. The jaws become larger and are suited for carnivorous feeding, and the digestive system transforms into the typical short gut of a predator. An eardrum and air-breathing lungs also develop. These changes during metamorphosis allow the larvae to move onto land in the adult stage.



Figure 29.20 Amphibian metamorphosis. A juvenile frog metamorphoses into a frog. Here, the frog has started to develop limbs, but its tadpole tail is still evident.

Apoda: Caecilians

An estimated 185 species comprise the caecilians, a group of amphibians that belong to the order Apoda. They have no limbs, although they evolved from a legged vertebrate ancestor. The complete lack of limbs makes them resemble earthworms. This resemblance is enhanced by folds of skin that look like the segments of an earthworm. However, unlike earthworms, they have teeth in both jaws, and feed on a variety of small organisms found in soil, including earthworms! Caecilians are adapted for a burrowing or aquatic lifestyle, and they are nearly blind, with their tiny eyes sometimes covered by skin. Although they have a single lung, they also depend on cutaneous respiration. These animals are found in the tropics of South America, Africa, and Southern Asia. In the caecelians, the only amphibians in which the males have copulatory structures, fertilization is internal. Some caecilians are oviparous, but most bear live young. In these cases, the females help nourish their young with tissue from their oviduct before birth and from their skin after birth.

Evolution Connection

Evolution Connection

The Paleozoic Era and the Evolution of VertebratesWhen the vertebrates arose during the Paleozoic Era (542 to 251 MYA), the climate and geography of Earth was vastly different. The distribution of landmasses on Earth were also very different from that of today. Near the equator were two large supercontinents, Laurentia and Gondwana, which included most of today's continents, but in a radically different configuration (Figure 29.21). At this time, sea levels were very high, probably at a level that hasn't been reached since. As the Paleozoic progressed, glaciations created a cool global climate, but conditions warmed near the end of the first half of the Paleozoic. During the latter half of the Paleozoic, the landmasses began moving together, with the initial formation of a large northern block called Laurasia, which contained parts of what is now North America, along with Greenland, parts of Europe, and Siberia. Eventually, a single supercontinent, called Pangaea, was formed, starting in the latter third of the Paleozoic. Glaciations then began to affect Pangaea's climate and the distribution of vertebrate life.

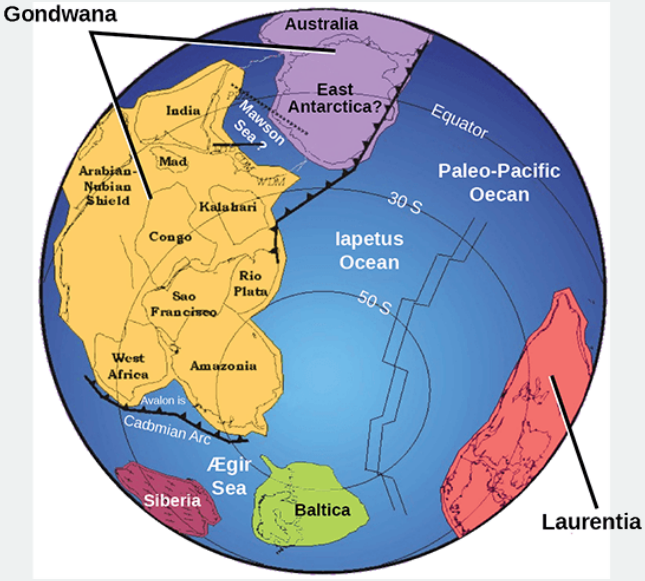


Figure 29.21 Paleozoic continents. During the Paleozoic Era, around 550 million years ago, the continent Gondwana formed. Both Gondwana and the continent Laurentia were located near the equator.

During the early Paleozoic, the amount of carbon dioxide in the atmosphere was much greater than it is today. This may have begun to change later, as land plants became more common. As the roots of land plants began to infiltrate rock and soil began to form, carbon dioxide was drawn out of the atmosphere and became trapped in the rock. This reduced the levels of carbon dioxide and increased the levels of oxygen in the atmosphere, so that by the end of the Paleozoic, atmospheric conditions were similar to those of today.

As plants became more common through the latter half of the Paleozoic, microclimates began to emerge and ecosystems began to change. As plants and ecosystems continued to grow and become more complex, vertebrates moved from the water to land. The presence of shoreline vegetation may have contributed to the movement of vertebrates onto land. One hypothesis suggests that the fins of aquatic vertebrates were used to maneuver through this vegetation, providing a precursor to the movement of fins on land and the further development of limbs. The late Paleozoic was a time of diversification of vertebrates, as amniotes emerged and became two different lines that gave rise, on one hand, to synapsids and mammals, and, on the other hand, to the codonts, reptiles, dinosaurs, and birds. Many marine vertebrates became extinct near the end of the Devonian period, which ended about 360 million years ago, and both marine and terrestrial vertebrates were decimated by a mass extinction in the early Permian period about 250 million years ago.

Link to Learning

Link to Learning

View Earth's Paleogeography: Continental Movements Through Time to see changes in Earth as life evolved.

Footnotes

- 2Daeschler, E. B., Shubin, N. H., and Jenkins, F. J. “A Devonian tetrapod-like fish and the evolution of the tetrapod body plan,” *Nature* 440 (2006): 757–763, doi:10.1038/nature04639, http://www.nature.com/nature/journal/v440/n7085/abs/nature04639.html.

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17.2: Reptile Structure and Diversity

Learning Objectives

By the end of this section, you will be able to do the following:

- Describe the main characteristics of amniotes
- Explain the difference between anapsids, synapsids, and diapsids, and give an example of each
- Identify the characteristics of reptiles
- Discuss the evolution of reptiles

The reptiles (including dinosaurs and birds) are distinguished from amphibians by their terrestrially adapted egg, which is supported by four *extraembryonic membrane*s: the yolk sac, the amnion, the chorion, and the allantois (Figure 29.22). The chorion and amnion develop from folds in the body wall, and the yolk sac and allantois are extensions of the midgut and hindgut respectively. The amnion forms a fluid-filled cavity that provides the embryo with its own internal aquatic environment. The evolution of the extraembryonic membranes led to less dependence on water for development and thus allowed the amniotes to branch out into drier environments.

In addition to these membranes, the eggs of birds, reptiles, and a few mammals have shells. An amniote embryo was then enclosed in the amnion, which was in turn encased in an extra-embryonic coelom contained within the chorion. Between the shell and the chorion was the albumin of the egg, which provided additional fluid and cushioning. This was a significant development that further distinguishes the amniotes from amphibians, which were and continue to be restricted to moist environments due their shell-less eggs. Although the shells of various reptilian amniotic species vary significantly, they all permit the retention of water and nutrients for the developing embryo. The egg shells of birds (avian reptiles) are hardened with calcium carbonate, making them rigid, but fragile. The shells of most nonavian reptile eggs, such as turtles, are leathery and require a moist environment. Most mammals do not lay eggs (except for monotremes such as the echidnas and platypuses). Instead, the embryo grows within the mother's body, with the placenta derived from two of the extraembryonic membranes.

Characteristics of Amniotes

The amniotic egg is the key characteristic of amniotes. In amniotes that lay eggs, the shell of the egg provides protection for the developing embryo while being permeable enough to allow for the exchange of carbon dioxide and oxygen. The *albumin*, or egg white, outside of the chorion provides the embryo with water and protein, whereas the fattier egg yolk contained in the yolk sac provides nutrients for the embryo, as is the case with the eggs of many other animals, such as amphibians. Here are the functions of the extraembryonic membranes:

1. Blood vessels in the yolk sac transport yolk nutrients to the circulatory system of the embryo.
2. The chorion facilitates exchange of oxygen and carbon dioxide between the embryo and the egg's external environment.
3. The allantois stores nitrogenous wastes produced by the embryo and also facilitates respiration.
4. The amnion protects the embryo from mechanical shock and supports hydration.

In mammals, the yolk sac is very reduced, but the embryo is still cushioned and enclosed within the amnion. The *placenta,* which transports nutrients and functions in gas exchange and waste management, is derived from the chorion and allantois.

Visual Connection

Visual Connection

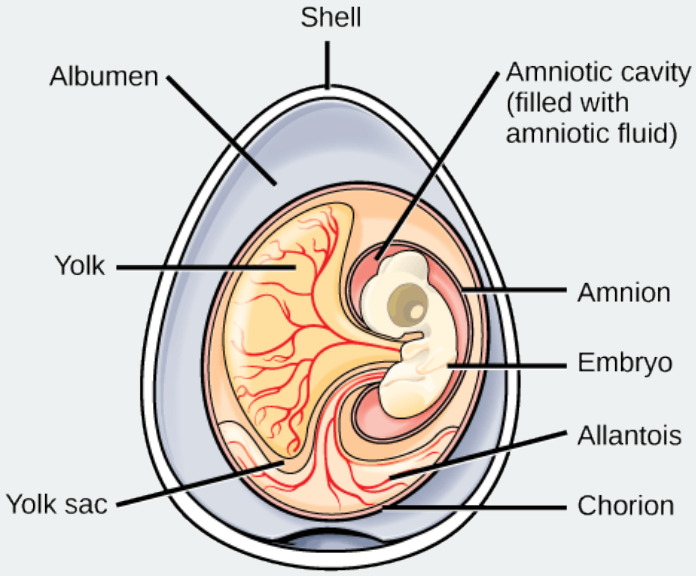


Figure 29.22 An amniotic egg. The key features of an amniotic egg are shown.

Which of the following statements about the parts of an egg are false?

1. The allantois stores nitrogenous waste and facilitates respiration.
2. The chorion facilitates gas exchange.
3. The yolk provides food for the growing embryo.
4. The amniotic cavity is filled with albumen.

Additional derived characteristics of amniotes include a waterproof skin, accessory keratinized structures, and costal (rib) ventilation of the lungs.

Evolution of Amniotes

The first amniotes evolved from tetrapod ancestors approximately 340 million years ago during the Carboniferous period. The early amniotes quickly diverged into two main lines: *synapsids* and *sauropsids*. Synapsids included the *therapsids*, a clade from which mammals evolved. Sauropsids were further divided into *anapsids* and *diapsids*. Diapsids gave rise to the reptiles, including the dinosaurs and birds. The key differences between the synapsids, anapsids, and diapsids are the structures of the skull and the number of *temporal fenestrae* ("windows") behind each eye (Figure 29.23). Temporal fenestrae are post-orbital openings in the skull that allow muscles to expand and lengthen. Anapsids have no temporal fenestrae, synapsids have one (fused ancestrally from two fenestrae), and diapsids have two (although many diapsids such as birds have highly modified diapsid skulls). Anapsids include extinct organisms and traditionally included turtles. However, more recent molecular and fossil evidence clearly shows that turtles arose within the diapsid line and secondarily lost the temporal fenestrae; thus they appear to be anapsids because modern turtles do not have fenestrae in the temporal bones of the skull. The canonical diapsids include dinosaurs, birds, and all other extinct and living reptiles.

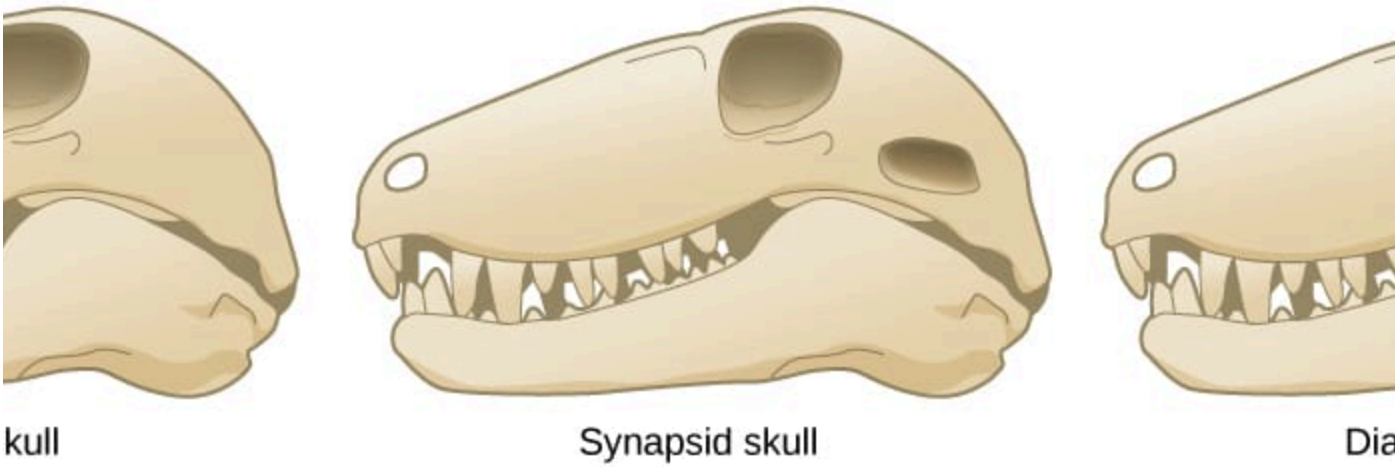


Figure 29.23 Amniote skulls. Compare the skulls and temporal fenestrae of anapsids, synapsids, and diapsids. Anapsids have no openings, synapsids have one opening, and diapsids have two openings.

The diapsids in turn diverged into two groups, the *Archosauromorpha* (“ancient lizard form”) and the *Lepidosauromorpha* (“scaly lizard form”) during the Mesozoic period (Figure 29.24). The lepidosaurs include modern lizards, snakes, and tuataras. The archosaurs include modern crocodiles and alligators, and the extinct ichthyosaurs (“fish lizards” superficially resembling dolphins), pterosaurs (“winged lizard”), dinosaurs (“terrible lizard”), and birds. (We should note that clade Dinosauria includes birds, which evolved from a branch of maniraptoran theropod dinosaurs in the Mesozoic.)

The evolutionarily derived characteristics of amniotes include the amniotic egg and its four extraembryonic membranes, a thicker and more waterproof skin, and rib ventilation of the lungs (ventilation is performed by drawing air into and out of the lungs by muscles such as the costal rib muscles and the diaphragm).

Visual Connection

Visual Connection

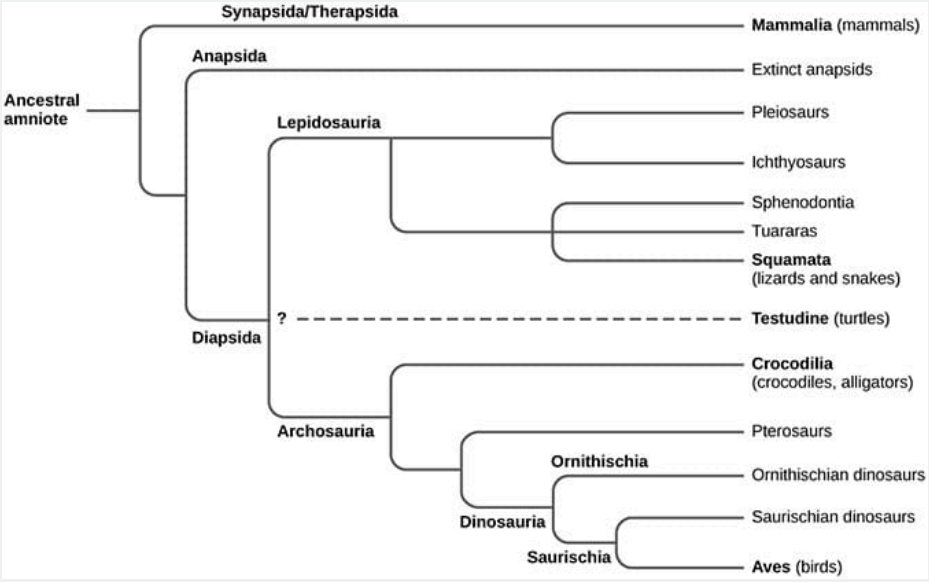


Figure 29.24 Amniote phylogeny. This chart shows the evolution of amniotes. The placement of Testudines (turtles) is currently still debated.

Question: Members of the order Testudines have an anapsid-like skull without obvious temporal fenestrae. However, molecular studies clearly indicate that turtles descended from a diapsid ancestor. Why might this be the case?

In the past, the most common division of amniotes has been into the classes Mammalia, Reptilia, and Aves. However, both birds

and mammals are descended from different amniote branches: the synapsids giving rise to the therapsids and mammals, and the diapsids giving rise to the lepidosaurs and archosaurs. We will consider both the birds and the mammals as groups distinct from reptiles for the purpose of this discussion with the understanding that this does not accurately reflect phylogenetic history and relationships.

Characteristics of Reptiles

Reptiles are tetrapods. Limbless reptiles—snakes and legless lizards—are classified as tetrapods because they are descended from four-limbed ancestors. Reptiles lay calcareous or leathery eggs enclosed in shells on land. Even aquatic reptiles return to the land to lay eggs. They usually reproduce sexually with internal fertilization. Some species display ovoviviparity, with the eggs remaining in the mother's body until they are ready to hatch. In ovoviviparous reptiles, most nutrients are supplied by the egg yolk, while the chorioallantois assists with respiration. Other species are viviparous, with the offspring born alive, with their development supported by a yolk sac-placenta, a chorioallantoic-placenta, or both.

One of the key adaptations that permitted reptiles to live on land was the development of their *scaly skin*, containing the protein keratin and waxy lipids, which reduced water loss from the skin. A number of keratinous epidermal structures have emerged in the descendants of various reptilian lineages and some have become defining characters for these lineages: scales, claws, nails, horns, feathers, and hair. Their occlusive skin means that reptiles cannot use their skin for respiration, like amphibians, and thus all amniotes breathe with lungs. All reptiles grow throughout their lives and regularly shed their skin, both to accommodate their growth and to rid themselves of ectoparasites. Snakes tend to shed the entire skin at one time, but other reptiles shed their skins in patches.

Reptiles ventilate their lungs using various muscular mechanisms to produce *negative pressure* (low pressure) within the lungs that allows them to expand and draw in air. In snakes and lizards, the muscles of the spine and ribs are used to expand or contract the rib cage. Since walking or running interferes with this activity, the squamates cannot breathe effectively while running. Some squamates can supplement rib movement with buccal pumping through the nose, with the mouth closed. In crocodilians, the lung chamber is expanded and contracted by moving the liver, which is attached to the pelvis. Turtles have a special problem with breathing, because their rib cage cannot expand. However, they can change the pressure around the lungs by pulling their limbs in and out of the shell, and by moving their internal organs. Some turtles also have a posterior respiratory sac that opens off the hindgut that aids in the diffusion of gases.

Most reptiles are ectotherms, animals whose main source of body heat comes from the environment; however, some crocodilians maintain elevated *thoracic* temperatures and thus appear to be at least regional endotherms. This is in contrast to true endotherms, which use heat produced by metabolism and muscle contraction to regulate body temperature over a very narrow temperature range, and thus are properly referred to as homeotherms. Reptiles have behavioral adaptations to help regulate body temperature, such as basking in sunny places to warm up through the absorption of solar radiation, or finding shady spots or going underground to minimize the absorption of solar radiation, which allows them to cool down and prevent overheating. The advantage of ectothermy is that metabolic energy from food is not required to heat the body; therefore, reptiles can survive on about 10 percent of the calories required by a similarly sized endotherm. In cold weather, some reptiles such as the garter snake *brumate*. Brumation is similar to hibernation in that the animal becomes less active and can go for long periods without eating, but differs from hibernation in that brumating reptiles are not asleep or living off fat reserves. Rather, their metabolism is slowed in response to cold temperatures, and the animal is very sluggish.

Evolution of Reptiles

Reptiles originated approximately 300 million years ago during the Carboniferous period. One of the oldest known amniotes is *Casineria*, which had both amphibian and reptilian characteristics. One of the earliest undisputed reptile fossils was *Hylonomus*, a lizardlike animal about 20 cm long. Soon after the first amniotes appeared, they diverged into three groups—synapsids, anapsids, and diapsids—during the Permian period. The Permian period also saw a second major divergence of diapsid reptiles into stem archosaurs (predecessors of thecodonts, crocodilians, dinosaurs, and birds) and lepidosaurs (predecessors of snakes and lizards). These groups remained inconspicuous until the Triassic period, when the archosaurs became the dominant terrestrial group possibly due to the extinction of large-bodied anapsids and synapsids during the Permian-Triassic extinction. About 250 million years ago, archosaurs radiated into the pterosaurs and both saurischian "lizard hip" and ornithischian "bird-hip" dinosaurs (see below).

Although they are sometimes mistakenly called dinosaurs, the pterosaurs were distinct from true dinosaurs (Figure 29.25). Pterosaurs had a number of adaptations that allowed for flight, including hollow bones (birds also exhibit hollow bones, a case

of convergent evolution). Their wings were formed by membranes of skin that attached to the long, fourth finger of each arm and extended along the body to the legs.



Figure 29.25 Pterosaurs. Pterosaurs, such as this *Quetzalcoatlus*, which existed from the late Triassic to the Cretaceous period (230 to 65.5 million years ago), possessed wings but are not believed to have been capable of powered flight. Instead, they may have been able to soar after launching from cliffs. (credit: Mark Witton, Darren Naish)

Archosaurs: Dinosaurs

Dinosaurs ("fearfully-great lizard") include the Saurischia ("lizard-hipped") with a simple, three-pronged pelvis, and Ornithischia ("bird-hipped") dinosaurs with a more complex pelvis, superficially similar to that of birds. However, it is a fact that birds evolved from the saurischian "lizard hipped" lineage, *not* the ornithischian "bird hip" lineage. Dinosaurs and their theropod descendants, the birds, are remnants of what was formerly a hugely diverse group of reptiles, some of which like *Argentinosaurus* were nearly 40 meters (130 feet) in length and weighed at least 80,000 kg (88 tons). They were the largest land animals to have lived, challenging and perhaps exceeding the great blue whale in size, but probably not weight—which could be greater than 200 tons.

Herrerasaurus, a bipedal dinosaur from Argentina, was one of the earliest dinosaurs that walked upright with the legs positioned directly below the pelvis, rather than splayed outward to the sides as in the crocodilians. The Ornithischia were all herbivores, and sometimes evolved into crazy shapes, such as ankylosaur "armored tanks" and horned dinosaurs such as *Triceratops*. Some, such as *Parasaurolophus*, lived in great herds and may have amplified their species-specific calls through elaborate crests on their heads.

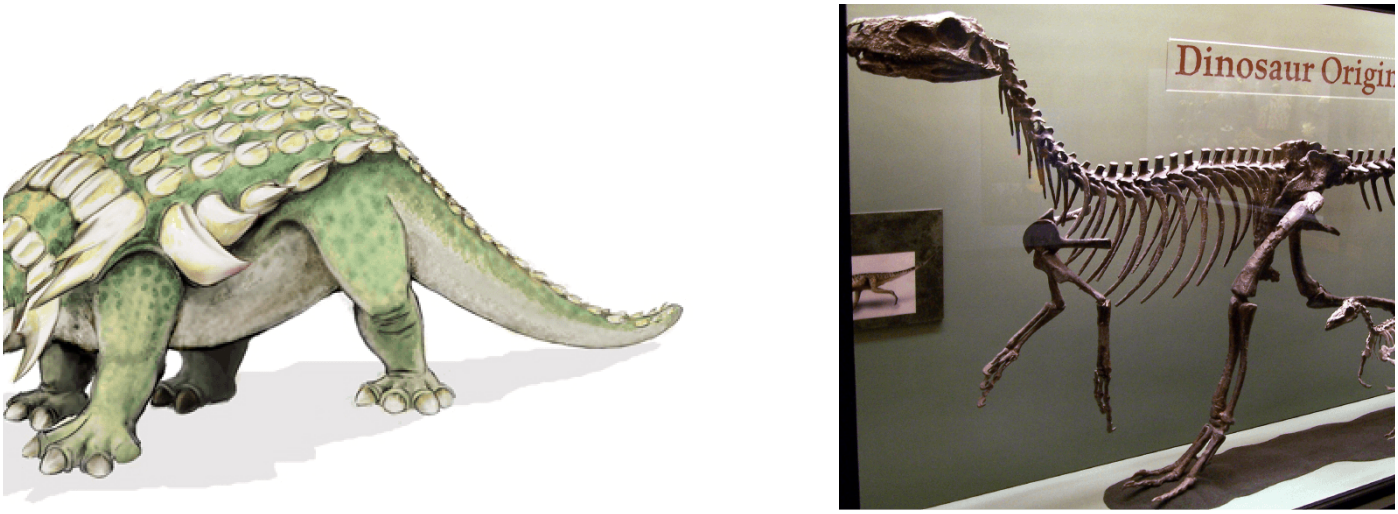
Both the ornithischian and saurischian dinosaurs provided parental care for their broods, just as crocodilians and birds do today. The end of the age of dinosaurs came about 65 million years ago, during the Mesozoic, coinciding with the impact of a large asteroid (that produced the Chicxulub crater) in what is now the Yucatan Peninsula of Mexico. Besides the immediate environmental disasters associated with this asteroid impacting the Earth at about 45,000 miles per hour, the impact may also have helped generate an enormous series of volcanic eruptions that changed the distribution and abundance of plant life worldwide, as well as its climate.

Archosaurs: Pterosaurs

More than 200 species of pterosaurs have been described, and in their day, beginning about 230 million years ago, they were the undisputed rulers of the Mesozoic skies for over 170 million years. Recent fossils suggest that hundreds of pterosaur species may have lived during any given period, dividing up the environment much like birds do today. Pterosaurs came in amazing sizes and shapes, ranging in size from that of a small song bird to that of the enormous *Quetzalcoatlus northropi*, which stood nearly 6 meters (19 feet) high and had a wingspan of nearly 14 meters (40 feet). This monstrous pterosaur, named after the Aztec god Quetzalcoatl, the feathered flying serpent that contributed largely to the creation of humankind, may have been the largest flying animal that ever evolved!

Some male pterosaurs apparently had brightly colored crests that may have served in sexual displays; some of these crests were much higher than the actual head! Pterosaurs had ultralight skeletons, with a *pteroid bone*, unique to pterosaurs, that strengthened the forewing membrane. Much of their wing span was exaggerated by a greatly elongated fourth finger that supported perhaps half of the wing. It is tempting to relate to them in terms of bird characteristics, but in reality, their proportions were decidedly not like birds at all. For example, it is common to find specimens, such as *Quetzalcoatlus*, with a head and neck region that together was three to four *times* as large as the torso. In addition, unlike the feathered bird wing, the reptilian wing had a layer of muscles, connective tissue, and blood vessels, all reinforced with a webbing of fibrous cords.

In contrast to the aerial pterosaurs, the dinosaurs were a diverse group of terrestrial reptiles with more than 1,000 species classified to date. Paleontologists continue to discover new species of dinosaurs. Some dinosaurs were quadrupeds (Figure 29.26); others were bipeds. Some were carnivorous, whereas others were herbivorous. Dinosaurs laid eggs, and a number of nests containing fossilized eggs, with intact embryos, have been found. It is not known with certainty whether dinosaurs were homeotherms or facultative endotherms. However, given that modern birds are endothermic, the dinosaurs that were the immediate ancestors to birds likely were endothermic as well. Some fossil evidence exists for dinosaurian parental care, and comparative biology supports this hypothesis since the archosaur birds and crocodilians both display extensive parental care.



(a) (b)

Figure 29.26 Ornithischian and saurischian Dinosaurs. *Edmontonia* was an armored dinosaur that lived in the Late Cretaceous period, 145.5 to 65.6 million years ago. Herrerasaurus and Eoraptor (b) were late Triassic saurischian dinosaurs dating to about 230 million years ago. (credit: a Mariana Ruiz Villareal b Zach Tirrell from Plymouth, USA, Dino Origins)

Dinosaurs dominated the Mesozoic era, which was known as the “Age of Reptiles.” The dominance of dinosaurs lasted until the end of the Cretaceous, the last period of the Mesozoic era. The Cretaceous-Tertiary extinction resulted in the loss of most of the large-bodied animals of the Mesozoic era. Birds are the only living descendants of one of the major clades of theropod dinosaurs.

Link to Learning

Link to Learning

Visit this site to see a video discussing the hypothesis that an asteroid caused the Cretaceous-Triassic (KT) extinction.

Modern Reptiles

Class Reptilia includes many diverse species that are classified into four living clades. There are the 25 species of Crocodilia, two species of Sphenodontia, approximately 9,200 Squamata species, and about 325 species of Testudines.

Crocodilia

Crocodilia (“small lizard”) arose as a distinct lineage by the middle Triassic; extant species include alligators, crocodiles, gharials, and caimans. Crocodilians (Figure 29.27) live throughout the tropics and subtropics of Africa, South America, Southern Florida, Asia, and Australia. They are found in freshwater, saltwater, and brackish habitats, such as rivers and lakes, and spend most of their time in water. Crocodiles are descended from terrestrial reptiles and can still walk and run well on land. They often move on their bellies in a swimming motion, propelled by alternate movements of their legs. However, some species can lift their bodies off the ground, pulling their legs in under the body with their feet rotated to face forward. This mode of locomotion takes a lot of energy, and seems to be used primarily to clear ground obstacles. Amazingly, some crocodiles can also gallop, pushing off with their hind legs and moving their hind and forelegs alternately in pairs. Galloping crocodiles have been clocked at speeds over 17 kph and, over short distances, in an ambush situation, they can easily chase down most humans if they are taken by surprise. However, they are short distance runners, not interested in a long chase, and most fit humans can probably outrun them in a sprint (assuming they respond quickly to the ambush!).



Figure 29.27 A crocodilian. Crocodilians, such as this Siamese crocodile (*Crocodylus siamensis*), provide parental care for their offspring. (credit: Keshav Mukund Kandhadai)

Sphenodontia

Sphenodontia (“wedge tooth”) arose in the early Mesozoic era, when they had a moderate radiation, but now are represented by only two living species: *Sphenodon punctatus* and *Sphenodon guntheri,* both found on offshore islands in New Zealand (Figure 29.28). The common name "tuatara" comes from a Maori word describing the crest along its back. Tuataras have a primitive diapsid skull with biconcave vertebrae. They measure up to 80 centimeters and weigh about 1 kilogram. Although superficially similar to an iguanid lizard, several unique features of the skull and jaws clearly define them and distinguish this group from the Squamata. They have no external ears. Tuataras briefly have a third (parietal) eye—with a lens, retina, and cornea—in the middle of the forehead. The eye is visible only in very young animals; it is soon covered with skin. Parietal eyes can sense light, but have limited color discrimination. Similar light-sensing structures are also seen in some other lizards. In their jaws, tuataras have two rows of teeth in the upper jaw that bracket a single row of teeth in the lower jaw. These teeth are actually projections from the jawbones, and are not replaced as they wear down.



Figure 29.28 A tuatara. This tuatara from New Zealand may resemble a lizard but belongs to a distinct lineage, the Sphenodontidae family. (credit: Sid Mosdell)

Squamata

The Squamata (“scaly or having scales”) arose in the late Permian, and extant species include lizards and snakes. Both are found on all continents except Antarctica. Lizards and snakes are most closely related to tuataras, both groups having evolved from a lepidosaurian ancestor. Squamata is the largest extant clade of reptiles (Figure 29.29).



Figure 29.29 A chameleon. This Jackson’s chameleon (*Trioceros jacksonii*) blends in with its surroundings.

Most lizards differ from snakes by having four limbs, although these have often been lost or significantly reduced in at least 60 lineages. Snakes lack eyelids and external ears, which are both present in lizards. There are about 6,000 species of lizards, ranging in size from tiny chameleons and geckos, some of which are only a few centimeters in length, to the Komodo dragon, which is about 3 meters in length.

Some lizards are extravagantly decorated with spines, crests, and frills, and many are brightly colored. Some lizards, like chameleons (Figure 29.29), can change their skin color by redistributing pigment within *chromatophores* in their skins. Chameleons change color both for camouflage and for social signaling. Lizards have multiple-colored oil droplets in their retinal cells that give them a good range of color vision. Lizards, unlike snakes, can focus their eyes by changing the shape of the lens.

The eyes of chameleons can move independently. Several species of lizards have a "hidden" *parietal eye*, similar to that in the tuatara. Both lizards and snakes use their tongues to sample the environment and a pit in the roof of the mouth, Jacobson's organ, is used to evaluate the collected sample.

Most lizards are carnivorous, but some large species, such as iguanas, are herbivores. Some predatory lizards are ambush predators, waiting quietly until their prey is close enough for a quick grab. Others are patient foragers, moving slowly through their environment to detect possible prey. Lizard tongues are long and sticky and can be extended at high speed for capturing insects or other small prey. Traditionally, the only venomous lizards are the Gila monster and the beaded lizard. However, venom glands have also been identified in several species of monitors and iguanids, but the venom is not injected directly and should probably be regarded as a toxin delivered with the bite.

Specialized features of the jaw are related to adaptations for feeding that have evolved to feed on relatively large prey (even though some current species have reversed this trend). Snakes are thought to have descended from either burrowing or aquatic lizards over 100 million years ago (Figure 29.30). They include about 3,600 species, ranging in size from 10 centimeter-long thread snakes to 10 meter-long pythons and anacondas. All snakes are legless, except for boids (e.g., boa constrictors), which have vestigial hindlimbs in the form of *pelvic spurs*. Like caecilian amphibians, the narrow bodies of most snakes have only a single functional lung. All snakes are carnivorous and eat small animals, birds, eggs, fish, and insects.



Figure 29.30 A nonvenomous snake. The garter snake belongs to the genus *Thamnophis*, the most widely distributed reptile genus in North America. (credit: Steve Jurvetson)

Most snakes have a skull that is very flexible, involving eight rotational joints. They also differ from other squamates by having mandibles (lower jaws) without either bony or ligamentous attachment anteriorly. Having this connection via skin and muscle allows for great dynamic expansion of the gape and independent motion of the two sides—both advantages in swallowing big prey. Most snakes are nonvenomous and simply swallow their prey alive, or subdue it by constriction before swallowing it. Venomous snakes use their venom both to kill or immobilize their prey, and to help digest it.

Although snakes have no eyelids, their eyes are protected with a transparent scale. Their retinas have both rods and cones, and like many animals, they do not have receptor pigments for red light. Some species, however, can see in the ultraviolet, which allows them to track ultraviolet signals in rodent trails. Snakes adjust focus by moving their heads. They have lost both external and middle ears, although their inner ears are sensitive to ground vibrations. Snakes have a number of sensory structures that assist in tracking prey. In pit vipers, like rattlesnakes, a sensory pit between the eye and nostrils is sensitive to infrared (“heat”) emissions from warm-blooded prey. A row of similar pits is located on the upper lip of boids. As noted above, snakes also use Jacobson's organ for detecting olfactory signals.

Testudines

The turtles, terrapins, and tortoises are members of the clade Testudines (“having a shell”) (Figure 29.31), and are characterized by a bony or cartilaginous shell. The shell in turtles is not just an epidermal covering, but is incorporated *into* the skeletal system.

The dorsal shell is called the carapace and includes the backbone and ribs; the ventral shell is called the plastron. Both shells are covered with keratinous plates or scutes, and the two shells are held together by a bridge. In some turtles, the plastron is hinged to allow the head and legs to be withdrawn under the shell.

The two living groups of turtles, Pleurodira and Cryptodira, have significant anatomical differences and are most easily recognized by how they retract their necks. The more common Cryptodira retract their neck in a vertical S-curve; they appear to simply pull their head backward when retracting. Less common Pleurodira ("side-neck") retract their neck with a horizontal curve, basically folding their neck to the side.

The Testudines arose approximately 200 million years ago, predating crocodiles, lizards, and snakes. There are about 325 living species of turtles and tortoises. Like other reptiles, turtles are ectotherms. All turtles are oviparous, laying their eggs on land, although many species live in or near water. None exhibit parental care. Turtles range in size from the speckled padloper tortoise at 8 centimeters (3.1 inches) to the leatherback sea turtle at 200 centimeters (over 6 feet). The term “turtle” is sometimes used to describe only those species of Testudines that live in the sea, with the terms “tortoise” and “terrapin” used to refer to species that live on land and in fresh water, respectively.



Figure 29.31 A tortoise. The African spurred tortoise (*Geochelone sulcata*) lives at the southern edge of the Sahara Desert. It is the third largest tortoise in the world. (credit: Jim Bowen)

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18: BIRDS & MAMMALS

18.1: Bird Structure and Diversity
18.2: Mammal Structure and Diversity
18.3: The Evolution of Primates

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18.1: Bird Structure and Diversity

Learning Objectives

By the end of this section, you will be able to do the following:

- Describe the evolutionary history of birds
- Describe the derived characteristics in birds that facilitate flight

With over 10,000 identified species, the birds are the most speciose of the land vertebrate classes. Abundant research has shown that birds are really an extant clade that evolved from maniraptoran theropod dinosaurs about 150 million years ago. Thus, even though the most obvious characteristic that *seems* to set birds apart from other extant vertebrates is the presence of feathers, we now know that feathers probably appeared in the common ancestor of both ornithischian and saurischian lineages of dinosaurs. Feathers in these clades are also homologous to reptilian scales and mammalian hair, according to the most recent research. While the wings of vertebrates like bats function without feathers, birds rely on feathers, and wings, along with other modifications of body structure and physiology, for flight, as we shall see.

Characteristics of Birds

Birds are endothermic, and more specifically, **homeothermic**—meaning that they usually maintain an elevated and constant body temperature, which is significantly above the average body temperature of most mammals. This is, in part, due to the fact that active flight—especially the hovering skills of birds such as hummingbirds—requires enormous amounts of energy, which in turn necessitates a high metabolic rate. Like mammals (which are also endothermic and homeothermic and covered with an insulating pelage), birds have several different types of feathers that together keep "heat" (infrared energy) within the core of the body, away from the surface where it can be lost by radiation and convection to the environment.

Modern birds produce two main types of feathers: *contour feathers* and *down feathers*. Contour feathers have a number of parallel *barbs* that branch from a *central shaft*. The barbs in turn have microscopic branches called *barbules* that are linked together by minute hooks, making the vane of a feather a strong, flexible, and uninterrupted surface. In contrast, the barbules of down feathers do not interlock, making these feathers especially good for insulation, trapping air in spaces between the loose, interlocking barbules of adjacent feathers to decrease the rate of heat loss by convection and radiation. Certain parts of a bird's body are covered in down feathers, and the base of other feathers has a downy portion, whereas newly hatched birds are covered almost entirely in down, which serves as an excellent coat of insulation, increasing the *thermal boundary layer* between the skin and the outside environment.

Feathers not only provide insulation, but also allow for flight, producing the lift and thrust necessary for flying birds to become and stay airborne. The feathers on a wing are *flexible,* so the feathers at the end of the wing separate as air moves over them, reducing the drag on the wing. Flight feathers are also asymmetrical and curved, so that air flowing over them generates lift. Two types of flight feathers are found on the wings, *primary feathers* and *secondary feathers* (Figure 29.32). Primary feathers are located at the tip of the wing and provide thrust as the bird moves its wings downward, using the pectoralis major muscles. Secondary feathers are located closer to the body, in the forearm portion of the wing, and provide lift. In contrast to primary and secondary feathers, contour feathers are found on the body, where they help reduce form drag produced by wind resistance against the body during flight. They create a smooth, aerodynamic surface so that air moves swiftly over the bird's body, preventing turbulence and creating ideal aerodynamic conditions for efficient flight.

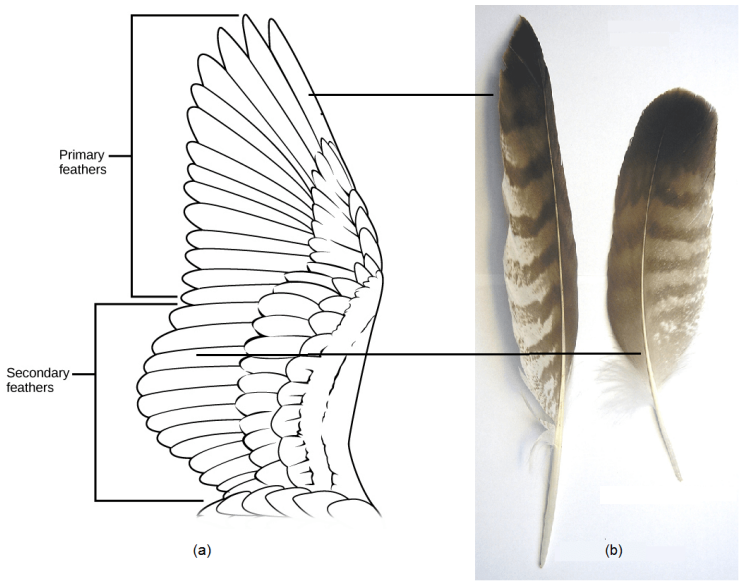


Figure 29.32 Flight feathers. (a) Primary feathers are located at the wing tip and provide thrust; secondary feathers are located close to the body and provide lift. (b) Primary and secondary feathers from a common buzzard (*Buteo buteo*). (Credit b: Mod. from S. Seyfert https://commons.wikimedia.org/w/index.php?curid=613813)

Flapping of the entire wing occurs primarily through the actions of the chest muscles: Specifically, the contraction of the pectoralis major muscles moves the wings downward (downstroke), whereas contraction of the supracoracoideus muscles moves the wings upward (upstroke) via a tough tendon that passes over the coracoid bone and the top of the humerus. Both muscles are attached to the keel of the sternum, and these are the muscles that humans eat on holidays (this is why the back of the bird offers little meat!). These muscles are highly developed in birds and account for a higher percentage of body mass than in most mammals. The flight muscles attach to a blade-shaped keel projecting ventrally from the sternum, like the keel of a boat. The sternum of birds is deeper than that of other vertebrates, which accommodates the large flight muscles. The flight muscles of birds who are active flyers are rich with oxygen-storing *myoglobin*. Another skeletal modification found in most birds is the fusion of the two clavicles (collarbones), forming the furcula or wishbone. The furcula is flexible enough to bend and provide support to the shoulder girdle during flapping.

An important requirement for flight is a low body weight. As body weight increases, the muscle output required for flying increases. The largest living bird is the ostrich, and while it is much smaller than the largest mammals, it is secondarily flightless. For birds that do fly, reduction in body weight makes flight easier. Several modifications are found in birds to reduce body weight, including *pneumatization of bones*. Pneumatic bones (Figure 29.33) are bones that are hollow, rather than filled with tissue; *cross struts* of bone called *trabeculae* provide structural reinforcement. Pneumatic bones are not found in all birds, and they are more extensive in large birds than in small birds. Not all bones of the skeleton are pneumatic, although the skulls of almost all birds are. The jaw is also lightened by the replacement of heavy jawbones and teeth with a beak made of keratin (just as hair, scales, and feathers are).



Figure 29.33 Pneumatic bone. Many birds have hollow, pneumatic bones, which make flight easier.

Other modifications that reduce weight include the lack of a urinary bladder. Birds possess a cloaca, an external body cavity into

which the intestinal, urinary, and genital orifices empty in reptiles, birds, and the monotreme mammals. The cloaca allows water to be reabsorbed from waste back into the bloodstream. Thus, uric acid is *not* eliminated as a liquid but is concentrated into urate salts, which are expelled along with fecal matter. In this way, water is not held in a urinary bladder, which would increase body weight. In addition, the females of most bird species only possess one functional (left) ovary rather than two, further reducing body mass.

The respiratory system of birds is dramatically different from that of reptiles and mammals, and is well adapted for the high metabolic rate required for flight. To begin, the air spaces of pneumatic bone are sometimes connected to air sacs in the body cavity, which replace coelomic fluid and also lighten the body. These air sacs are also connected to the path of airflow through the bird's body, and function in respiration. Unlike mammalian lungs in which air flows in two directions, as it is breathed in and out, diluting the concentration of oxygen, airflow through bird lungs is unidirectional (Figure 29.34). Gas exchange occurs in "air capillaries" or microscopic air passages within the lungs. The arrangement of air capillaries in the lungs creates a counter-current exchange system with the pulmonary blood. In a counter-current system, the air flows in one direction and the blood flows in the opposite direction, producing a favorable diffusion gradient and creating an efficient means of gas exchange. This very effective oxygen-delivery system of birds supports their higher metabolic activity. In effect, ventilation is provided by the parabronchi (minimally expandible lungs) with thin air sacs located among the visceral organs and the skeleton. A syrinx (voice box) resides near the junction of the trachea and bronchi. The syrinx, however, is *not* homologous to the mammalian larynx, which resides within the upper part of the trachea.

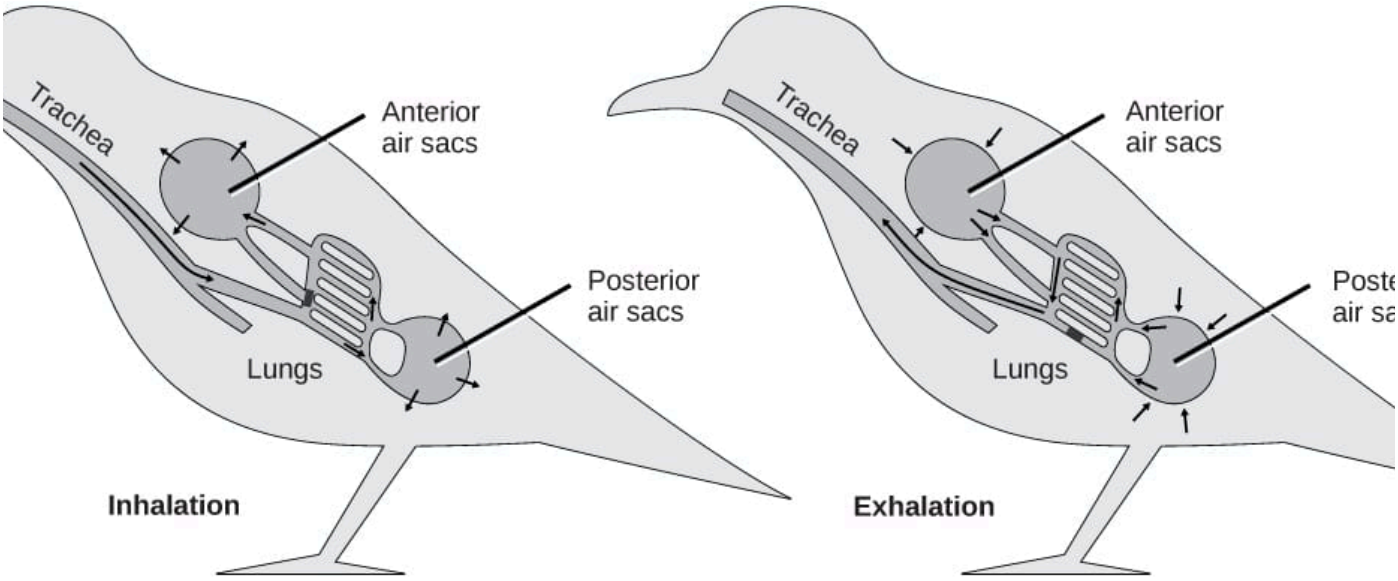


Figure 29.34 Air flow in bird lungs. Avian respiration is an efficient system of gas exchange with air flowing *unidirectionally*. A full ventilation cycle takes two breathing cycles. During the first inhalation, air passes from the trachea into posterior air sacs, then during the first exhalation into the lungs. The second inhalation moves the air in the lungs to the anterior air sacs, and the second exhalation moves the air in the anterior air sacs out of the body. Overall, each inhalation moves air into the air sacs, while each exhalation moves fresh air through the lungs and "used" air out of the body. The air sacs are connected to the hollow interior of bones. (credit: modification of work by L. Shyamal)

Beyond the unique characteristics discussed above, birds are also unusual vertebrates because of a number of other features. First, they typically have an elongate (very “dinosaurian”) S-shaped neck, but a short tail or *pygostyle*, produced from the fusion of the caudal vertebrae. Unlike mammals, birds have only one occipital condyle, allowing them extensive movement of the head and neck. They also have a very thin epidermis without sweat glands, and a specialized uropygial gland or sebaceous “preening gland” found at the dorsal base of the tail. This gland is an essential to preening (a virtually continuous activity) in most birds because it produces an oily substance that birds use to help waterproof their feathers as well as keep them flexible for flight. A number of birds, such as pigeons, parrots, hawks, and owls, lack a uropygial gland but have specialized feathers that “disintegrate” into a powdery down, which serves the same purpose as the oils of the uropygial gland.

Like mammals, birds have 12 pairs of cranial nerves, and a very large cerebellum and optic lobes, but only a single bone in the middle ear called the columella (the stapes in mammals). They have a closed circulatory system with two atria and two ventricles, but rather than a “left-bending” aortic arch like that of mammals, they have a “right-bending” aortic arch, and nucleated red blood cells (unlike the enucleated red blood cells of mammals).

All these unique and highly derived characteristics make birds one of the most conspicuous and successful groups of vertebrate animals, filling a range of ecological niches, and ranging in size from the tiny bee hummingbird of Cuba (about 2 grams) to the ostrich (about 140,000 grams). Their large brains, keen senses, and the abilities of many species to imitate vocalization and use tools make them some of the most intelligent vertebrates on Earth.

Evolution of Birds

Thanks to amazing new fossil discoveries in China, the evolutionary history of birds has become clearer, even though bird bones do not fossilize as well as those of other vertebrates. As we've seen earlier, birds are highly modified diapsids, but rather than having two fenestrations or openings in their skulls behind the eye, the skulls of modern birds are so specialized that it is difficult to see any trace of the original diapsid condition.

Birds belong to a group of diapsids called the archosaurs, which includes three other groups: living crocodilians, pterosaurs, and dinosaurs. Overwhelming evidence shows that birds evolved within the clade Dinosauria, which is further subdivided into two groups, the Saurischia ("lizard hips") and the Ornithischia ("bird hips"). Despite the names of these groups, it was not the bird-hipped dinosaurs that gave rise to modern birds. Rather, Saurischia diverged into two groups: One included the long-necked herbivorous dinosaurs, such as *Apatosaurus*. The second group, bipedal predators called theropods, gave rise to birds. This course of evolution is highlighted by numerous similarities between late (maniraptoran) theropod fossils and birds, specifically in the structure of the hip and wrist bones, as well as the presence of the wishbone, formed by the fusion of the clavicles.

The clade Neornithes includes the avian crown group, which comprises all living birds and the descendants from their most recent common maniraptoran ancestor. One well-known and important fossil of an animal that appears "intermediate" between dinosaurs and birds is *Archaeopteryx* (Figure 29.35), which is from the Jurassic period (200 to 145 MYA). *Archaeopteryx* has characteristics of both maniraptoran dinosaurs and modern birds. Some scientists propose classifying it as a bird, but others prefer to classify it as a dinosaur. Traits in skeletons of *Archaeopteryx* like those of a dinosaur included a jaw with teeth and a long bony tail. Like birds, it had feathers modified for flight, both on the forelimbs and on the tail, a trait associated only with birds among modern animals. Fossils of older feathered dinosaurs exist, but the feathers may not have had the characteristics of modern flight feathers.



(a) (b)

Figure 29.35 *Archaeopteryx*. (a) *Archaeopteryx* lived in the late Jurassic period around 150 million years ago. It had cuplike thecodont teeth like a dinosaur, but had (b) flight feathers like modern birds, which can be seen in this fossil. Note the claws on the wings, which are still found in a number of birds, such as the newborn chicks of the South American Hoatzin.

The Evolution of Flight in Birds

There are two basic hypotheses that explain how flight may have evolved in birds: the *arboreal ("tree") hypothesis* and the *terrestrial ("land") hypothesis*. The arboreal hypothesis posits that tree-dwelling precursors to modern birds jumped from branch to branch using their feathers for gliding before becoming fully capable of flapping flight. In contrast to this, the terrestrial

hypothesis holds that running (perhaps pursuing active prey such as small cursorial animals) was the stimulus for flight. In this scenario, wings could be used to capture prey and were preadapted for balance and flapping flight. Ostriches, which are large flightless birds, hold their wings out when they run, possibly for balance. However, this condition may represent a behavioral relict of the clade of flying birds that were their ancestors. It seems more likely that small feathered arboreal dinosaurs, were capable of gliding (and flapping) from tree to tree and branch to branch, improving the chances of escaping enemies, finding mates, and obtaining prey such as flying insects. This early flight behavior would have also greatly increased the opportunity for species dispersal.

Although we have a good understanding of how feathers and flight may have evolved, the question of how endothermy evolved in birds (and other lineages) remains unanswered. Feathers provide insulation, but this is only beneficial for *thermoregulatory purposes* if body heat is being produced internally. Similarly, internal heat production is only viable for the evolution of endothermy if *insulation is present* to retain that infrared energy. It has been suggested that one or the other—feathers or endothermy—evolved first in response to some other selective pressure (e.g., the ability to be active at night, provide camouflage, repel water, or serve as signals for mate selection). It seems probable that feathers and endothermy coevolved together, the improvement and evolutionary advancement of feathers reinforcing the evolutionary advancement of endothermy, and so on.

During the Cretaceous period (145 to 66 MYA), a group known as the Enantiornithes was the dominant bird type (Figure 29.36). Enantiornithes means “opposite birds,” which refers to the fact that certain bones of the shoulder are joined differently than the way the bones are joined in modern birds. Like *Archaeopteryx*, these birds retained teeth in their jaws, but did have a shortened tail, and at least some fossils have preserved “fans” of tail feathers. These birds formed an evolutionary lineage separate from that of modern birds, and they did not survive past the Cretaceous. Along with the Enantiornithes, however, another group of birds—the Ornithurae ("bird tails"), with a short, fused tail or pygostyle—emerged from the evolutionary line that includes modern birds. This clade was also present in the Cretaceous.

After the extinction of Enantiornithes, the Ornithurae became the dominant birds, with a large and rapid radiation occurring after the extinction of the dinosaurs during the Cenozoic era (66 MYA to the present). Molecular analysis based on very large data sets has produced our current understanding of the relationships among living birds. There are three major clades: the Paleognathae, the Galloanserae, and the Neoaves. The Paleognathae (“old jaw”) or ratites (polyphyletic) are a group of flightless birds including ostriches, emus, rheas, and kiwis. The Galloanserae include pheasants, ducks, geese and swans. The Neoaves ("new birds") includes all other birds. The Neoaves themselves have been distributed among five clades:[3] Strisores (nightjars, swifts, and hummingbirds), Columbaves (turacos, bustards, cuckoos, pigeons, and doves), Gruiformes (cranes), Aequorlitornithes (diving birds, wading birds, and shorebirds), and Inopinaves (a very large clade of land birds including hawks, owls, woodpeckers, parrots, falcons, crows, and songbirds). Despite the current classification scheme, it is important to understand that phylogenetic revisions, even for the extant birds, are still taking place.



Figure 29.36 Enantiornithean bird. *Shanweiniao cooperorum* was a species of Enantiornithes that did not survive past the Cretaceous period. (credit: Nobu Tamura)

Career Connection

Career Connection

VeterinarianVeterinarians are concerned with diseases, disorders, and injuries in animals, primarily vertebrates. They treat pets, livestock, and animals in zoos and laboratories. Veterinarians often treat dogs and cats, but also take care of birds, reptiles, rabbits, and other animals that are kept as pets. Veterinarians that work with farms and ranches care for pigs, goats, cows, sheep, and horses.

Veterinarians are required to complete a degree in veterinary medicine, which includes taking courses in comparative zoology, animal anatomy and physiology, microbiology, and pathology, among many other courses in chemistry, physics, and mathematics.

Veterinarians are also trained to perform surgery on many different vertebrate species, which requires an understanding of the vastly different anatomies of various species. For example, the stomach of ruminants like cows has four “compartments” versus one compartment for non-ruminants. As we have seen, birds also have unique anatomical adaptations that allow for flight, which requires additional training and care.

Some veterinarians conduct research in academic settings, broadening our knowledge of animals and medical science. One area of research involves understanding the transmission of animal diseases to humans, called zoonotic diseases. For example, one area of great concern is the transmission of the avian flu virus to humans. One type of avian flu virus, H5N1, is a highly pathogenic strain that has been spreading in birds in Asia, Europe, Africa, and the Middle East. Although the virus does not cross over easily to humans, there have been cases of bird-to-human transmission. More research is needed to understand how this virus can cross the species barrier and how its spread can be prevented.

Footnotes

- 3Prum, RO et al. 2015. A comprehensive phylogeny of birds (Aves) using targeted next-generation DNA sequencing. Nature 526: 569 - 573. http://dx.doi.org/10.1038/nature15697

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18.2: Mammal Structure and Diversity

Learning Objectives

By the end of this section, you will be able to do the following:

- Name and describe the distinguishing features of the three main groups of mammals
- Describe the likely line of evolutionary descent that produced mammals
- List some derived features that may have arisen in response to mammals' need for constant, high-level metabolism
- Identify the major clades of eutherian mammals

Mammals, comprising about 5,200 species, are vertebrates that possess hair and mammary glands. Several other characteristics are distinctive to mammals, including certain features of the jaw, skeleton, integument, and internal anatomy. Modern mammals belong to three clades: monotremes, marsupials, and eutherians (or placental mammals).

Characteristics of Mammals

The presence of hair, composed of the protein keratin, is one of the most obvious characteristics of mammals. Although it is not very extensive or obvious on some species (such as whales), hair has many important functions for most mammals. Mammals are endothermic, and hair traps a boundary layer of air close to the body, retaining heat generated by metabolic activity. Along with insulation, hair can serve as a sensory mechanism via specialized hairs called *vibrissae*, better known as whiskers. Vibrissae attach to nerves that transmit information about tactile vibration produced by sound sensation, which is particularly useful to nocturnal or burrowing mammals. Hair can also provide protective coloration or be part of social signaling, such as when an animal's hair stands "on end" to warn enemies, or possibly to make the mammal "look bigger" to predators.

Unlike the skin of birds, the integument (skin) of mammals, includes a number of different types of secretory glands. Sebaceous glands produce a lipid mixture called *sebum* that is secreted onto the hair and skin, providing water resistance and lubrication for hair. Sebaceous glands are located over most of the body. Eccrine glands produce sweat, or perspiration, which is mainly composed of water, but also contains metabolic waste products, and sometimes compounds with antibiotic activity. In most mammals, eccrine glands are limited to certain areas of the body, and some mammals do not possess them at all. However, in primates, especially humans, sweat glands are located over most of the body surface and figure prominently in regulating the body temperature through evaporative cooling. Apocrine glands, or *scent glands*, secrete substances that are used for chemical communication, such as in skunks. Mammary glands produce milk that is used to feed newborns. In both monotremes and eutherians, both males and females possess mammary glands, while in some marsupials, mammary glands are found only in females, with exception of some opossums. Mammary glands likely are modified sebaceous or eccrine glands, but their evolutionary origin is not entirely clear.

The skeletal system of mammals possesses many unique features. The lower jaw of mammals consists of only one bone, the dentary, and the jaw hinge connects the dentary to the squamosal (flat) part of the temporal bone in the skull. The jaws of other vertebrates are composed of several bones, including the quadrate bone at the back of the skull and the articular bone at the back of the jaw, with the jaw connected between the quadrate and articular bones. In the ear of other vertebrates, vibrations are transmitted to the inner ear by a single bone, the *stapes*. In mammals, the quadrate and articular bones have moved into the middle ear (Figure 29.37). The malleus is derived from the articular bone, whereas the incus originated from the quadrate bone. This arrangement of jaw and ear bones aids in distinguishing fossil mammals from fossils of other synapsids.

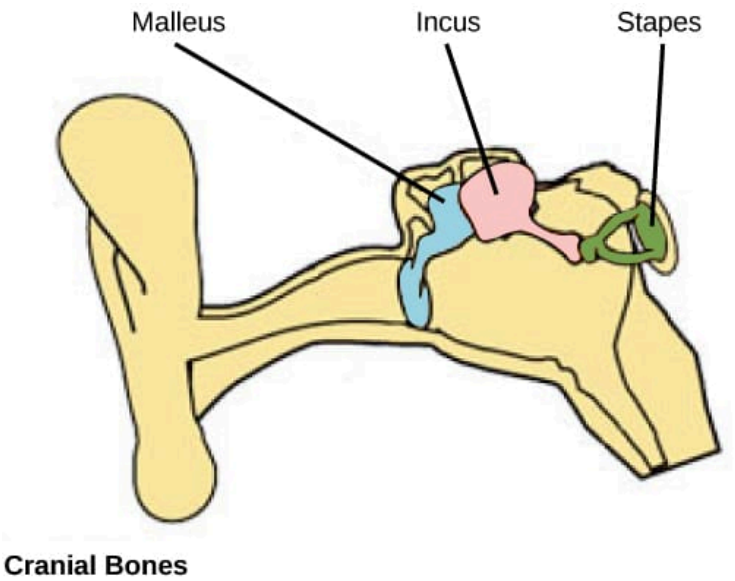


Figure 29.37 Mammalian ear bones. Bones of the mammalian middle ear are modified from bones of the jaw and skull in reptiles. The stapes is found in other vertebrates (e.g., the columella of birds) whereas in mammals, the malleus and incus are derived from the articular and quadrate bones, respectively. (credit: NCI)

The adductor muscles that close the jaw comprise two major muscles in mammals: the *temporalis* and the *masseter*. Working together, these muscles permit up-and-down and side-to-side movements of the jaw, making chewing possible—which is unique to mammals. Most mammals have *heterodont teeth*, meaning that they have different types and shapes of teeth (incisors, canines, premolars, and molars) rather than just one type and shape of tooth. Most mammals are also diphyodonts, meaning that they have two sets of teeth in their lifetime: deciduous or "baby" teeth, and permanent teeth. Most other vertebrates with teeth are *polyphyodonts*, that is, their teeth are replaced throughout their entire life.

Mammals, like birds, possess a four-chambered heart; however, the hearts of birds and mammals are an example of convergent evolution, since mammals clearly arose independently from different groups of tetrapod ancestors. Mammals also have a specialized group of cardiac cells (fibers) located in the walls of their right atrium called the sinoatrial node, or pacemaker, which determines the rate at which the heart beats. Mammalian erythrocytes (red blood cells) do *not* have nuclei, whereas the erythrocytes of other vertebrates are nucleated.

The kidneys of mammals have a portion of the nephron called the loop of Henle or nephritic loop, which allows mammals to produce urine with a high concentration of solutes—higher than that of the blood. Mammals lack a renal portal system, which is a system of veins that moves blood from the hind or lower limbs and region of the tail to the kidneys. Renal portal systems are present in all other vertebrates except jawless fishes. A urinary bladder is present in all mammals.

Unlike birds, the skulls of mammals have two occipital condyles, bones at the base of the skull that articulate with the first vertebra, as well as a secondary palate at the rear of the pharynx that helps to separate the pathway of swallowing from that of breathing. Turbinate bones (conchae in humans) are located along the sides of the nasal cavity, and help warm and moisten air as it is inhaled. The pelvic bones are fused in mammals, and there are typically seven cervical vertebrae (except for some edentates and manatees). Mammals have movable eyelids and fleshy external ears (pinnae), quite unlike the naked external auditory openings of birds. Mammals also have a muscular diaphragm that is lacking in birds.

Mammalian brains also have certain characteristics that differ from the brains of other vertebrates. In some, but not all mammals, the *cerebral cortex*, the outermost part of the cerebrum, is highly convoluted and folded, allowing for a greater surface area than is possible with a smooth cortex. The optic lobes, located in the midbrain, are divided into two parts in mammals, while other vertebrates possess a single, undivided lobe. Eutherian mammals also possess a specialized structure, the corpus callosum, which links the two cerebral hemispheres together. The corpus callosum functions to integrate motor, sensory, and cognitive functions between the left and right cerebral cortexes.

Evolution of Mammals

Mammals are synapsids, meaning they have a single, ancestrally fused, postorbital opening in the skull. They are the only living

synapsids, as earlier forms became extinct by the Jurassic period. The early non-mammalian synapsids can be divided into two groups, the pelycosaurs and the therapsids. Within the therapsids, a group called the cynodonts are thought to have been the ancestors of mammals (Figure 29.38).



Figure 29.38 Cynodont. Cynodonts ("dog teeth"), which first appeared in the Late Permian period 260 million years ago, are thought to be the ancestors of modern mammals. Holes in the upper jaws of cynodonts suggest that they had whiskers, which might also indicate the presence of hair. (credit: Nobu Tamura)

As with birds, a key characteristic of synapsids is endothermy, rather than the ectothermy seen in many other vertebrates (such as fish, amphibians, and most reptiles). The increased metabolic rate required to internally modify body temperature likely went hand-in-hand with changes to certain skeletal structures that improved food processing and ambulation. The later synapsids, which had more evolved characteristics unique to mammals, possess cheeks for holding food and heterodont teeth, which are specialized for chewing, mechanically breaking down food to speed digestion, and releasing the energy needed to produce heat. Chewing also requires the ability to breathe at the same time, which is facilitated by the presence of a *secondary palate* (comprising the bony palate and the posterior continuation of the soft palate). The secondary palate separates the area of the mouth where chewing occurs from the area above where respiration occurs, allowing breathing to proceed uninterrupted while the animal is chewing. A secondary palate is not found in pelycosaurs but *is* present in cynodonts and mammals. The jawbone also shows changes from early synapsids to later ones. The zygomatic arch, or cheekbone, is present in mammals and advanced therapsids such as cynodonts, but is not present in pelycosaurs. The presence of the zygomatic arch suggests the presence of masseter muscles, which close the jaw and function in chewing.

In the appendicular skeleton, the shoulder girdle of therian mammals is modified from that of other vertebrates in that it does not possess a procoracoid bone or an interclavicle, and the scapula is the dominant bone.

Mammals evolved from therapsids in the late Triassic period, as the earliest known mammal fossils are from the early Jurassic period, some 205 million years ago. One group of transitional mammals was the morganucodonts, small nocturnal insectivores. The jaws of morganucodonts were “transitional,” with features of both reptilian and mammalian jaws (Figure 29.39). Like modern mammals, the morganucodonts had differentiated teeth and were diphyodonts. Mammals first began to diversify in the Mesozoic era, from the Jurassic to the Cretaceous periods. Even some small gliding mammals appear in the fossil record during this time period. However, most of the Jurassic mammals were extinct by the end of the Mesozoic. During the Cretaceous period, another radiation of mammals began and continued through the Cenozoic era, about 65 million years ago.



Figure 29.39 A morganucodont. This morganucodont *Megazotrodon*, an extinct basal mammal, may have been nocturnal and insectivorous. Inset: Jaw of a morganucodont, showing a double hinge, one between the dentary and squamosal and one between the articular (yellow) and quadrate (blue) bones. In living mammals, the articular and quadrate bones have been incorporated into the middle ear. (Credit: By Nordelch [Megazostrodon Natural History Museum] Wikimedia Commons. Credit inset: Mod from Philcha. https://commons.wikimedia.org/w/index.php? curid=3631949)

Living Mammals

There are three major groups of living mammals: *monotremes* (*prototheria*), *marsupials* (*metatheria*), and *placental* (*eutheria*) mammals. The eutherians and the marsupials together comprise a clade of therian mammals, with the monotremes forming a sister clade to both metatherians and eutherians.

There are very few living species of monotremes: the platypus and four species of echidnas, or spiny anteaters. The leathery-beaked platypus belongs to the family Ornithorhynchidae (“bird beak”), whereas echidnas belong to the family Tachyglossidae (“sticky tongue”) (Figure 29.40). The platypus and one species of echidna are found in Australia, and the other species of echidna are found in New Guinea. Monotremes are unique among mammals because they lay eggs, rather than giving birth to live young. The shells of their eggs are not like the hard shells of birds, but have a leathery shell, similar to the shells of reptile eggs. Monotremes retain their eggs through about two-thirds of the developmental period, and then lay them in nests. A yolk-sac placenta helps support development. The babies hatch in a fetal state and complete their development in the nest, nourished by milk secreted by mammary glands opening directly to the skin. Monotremes, except for young platypuses, do not have teeth. Body temperature in the monotreme species is maintained at about 30°C, considerably lower than the average body temperature of marsupial and placental mammals, which are typically between 35 and 38°C.



(a) (b)

Figure 29.40 Egg-laying mammals. (a) The platypus, a monotreme, possesses a leathery beak and lays eggs rather than giving birth to live young. (b) The echidna is another monotreme, with long hairs modified into spines. (credit b: modification of work by Barry Thomas)

Over 2/3 of the approximately 330 living species of marsupials are found in Australia, New Guinea, and surrounding islands, with the rest, nearly all various types of opossum, found in the Americas, especially South America. Australian marsupials include the kangaroo, koala, bandicoot, Tasmanian devil (Figure 29.41), and several other species. Like monotremes, the embryos of marsupials are nourished during a short gestational period (about a month in kangaroos) by a yolk-sac placenta, but with no intervening egg shell. Some marsupial embryos can enter an embryonic diapause, and delay implantation, suspending development until implantation is completed. Marsupial young are also effectively fetal at birth. Most, but not all, species of marsupials possess a pouch in which the very premature young reside, receiving milk and continuing their development. In kangaroos, the young joeys continue to nurse for about a year and a half.



Figure 29.41 A marsupial mammal. The Tasmanian devil is one of several marsupials native to Australia. (credit: Wayne McLean)

Eutherians (placentals) are the most widespread and numerous of the mammals, occurring throughout the world. Eutherian mammals are sometimes called “placental mammals” because all species possess a complex chorioallantoic placenta that connects a fetus to the mother, allowing for gas, fluid, and nutrient exchange. There are about 4,000 species of placental mammals in 18 to 20 orders with various adaptations for burrowing, flying, swimming, hunting, running, and climbing. In the evolutionary sense, they have been incredibly successful in form, diversity, and abundance. The eutherian mammals are

classified in two major clades, the Atlantogenata and the Boreoeutheria. The Atlantogeneta include the Afrotheria (e.g., elephants, hyraxes, and manatees) and the Xenarthra (anteaters, armadillos, and sloths). The Boreoeutheria contain two large groups, the Euarchontoglires and the Laurasiatheria. Familiar orders in the Euarchontoglires are the Scandentia (tree shrews), Rodentia (rats, mice, squirrels, porcupines), Lagomorpha (rabbits and hares), and the Primates (including humans). Major Laurasiatherian orders include the Perissodactyla (e.g., horses and rhinos), the Cetartiodactyla (e.g., cows, giraffes, pigs, hippos, and whales), the Carnivora (e.g., cats, dogs, and bears), and the Chiroptera (bats and flying foxes). The two largest orders are the rodents (2,000 species) and bats (about 1,000 species), which together constitute approximately 60 percent of all eutherian species.

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18.3: The Evolution of Primates

Learning Objectives

By the end of this section, you will be able to do the following:

- Describe the derived features that distinguish primates from other animals
- Describe the defining features of the major groups of primates
- Identify the major hominin precursors to modern humans
- Explain why scientists are having difficulty determining the true lines of descent in hominids

Order Primates of class Mammalia includes lemurs, tarsiers, monkeys, apes, and humans. Non-human primates live primarily in the tropical or subtropical regions of South America, Africa, and Asia. They range in size from the mouse lemur at 30 grams (1 ounce) to the mountain gorilla at 200 kilograms (441 pounds). The characteristics and evolution of primates are of particular interest to us as they allow us to understand the evolution of our own species.

Characteristics of Primates

All primate species possess adaptations for climbing trees, as they all descended from tree-dwellers. This arboreal heritage of primates has resulted in hands and feet that are adapted for climbing, or brachiation (swinging through trees using the arms). These adaptations include, but are not limited to: 1) a rotating shoulder joint, 2) a big toe that is widely separated from the other toes (except humans) and thumbs sufficiently separated from fingers to allow for gripping branches, and 3) stereoscopic vision, two overlapping fields of vision from the eyes, which allows for the perception of depth and gauging distance. Other characteristics of primates are brains that are larger than those of most other mammals, claws that have been modified into flattened nails, typically only one offspring per pregnancy, and a trend toward holding the body upright.

Order Primates is divided into two groups: Strepsirrhini (“turned-nosed”) and Haplorhini (“simple-nosed”) primates. Strepsirrhines, also called the wet-nosed primates, include prosimians like the bush babies and pottos of Africa, the lemurs of Madagascar, and the lorises of Southeast Asia. Haplorhines, or dry-nosed primates, include tarsiers (Figure 29.42) and simians (New World monkeys, Old World monkeys, apes, and humans). In general, strepsirrhines tend to be nocturnal, have larger olfactory centers in the brain, and exhibit a smaller size and smaller brain than anthropoids. Haplorhines, with a few exceptions, are diurnal, and depend more on their vision. Another interesting difference between the strepsirrhines and haplorhines is that strepsirrhines have the enzymes for making vitamin C, while haplorhines have to get it from their food.



Figure 29.42 A Philippine tarsier. This tarsier, *Carlito syrichta*, is one of the smallest primates—about 5 inches long, from nose

to the base of the tail. The tail is not shown, but is about twice the length of the body. Note the large eyes, each of which is about the same size as the animal's brain, and the long hind legs. (credit: mtoz (http://creativecommons.org/licenses/by-sa/2.0), via Wikimedia Commons)

Evolution of Primates

The first primate-like mammals are referred to as proto-primates. They were roughly similar to squirrels and tree shrews in size and appearance. The existing fossil evidence (mostly from North Africa) is very fragmented. These proto-primates remain largely mysterious creatures until more fossil evidence becomes available. Although genetic evidence suggests that primates diverged from other mammals about 85 MYA, the oldest known primate-like mammals with a relatively robust fossil record date to about 65 MYA. Fossils like the proto-primate *Plesiadapis* (although some researchers do not agree that *Plesiadapis* was a proto-primate) had some features of the teeth and skeleton in common with true primates. They were found in North America and Europe in the Cenozoic and went extinct by the end of the Eocene.

The first true primates date to about 55 MYA in the Eocene epoch. They were found in North America, Europe, Asia, and Africa. These early primates resembled present-day prosimians such as lemurs. Evolutionary changes continued in these early primates, with larger brains and eyes, and smaller muzzles being the trend. By the end of the Eocene epoch, many of the early prosimian species went extinct due either to cooler temperatures or competition from the first monkeys.

Anthropoid monkeys evolved from prosimians during the Oligocene epoch. By 40 million years ago, evidence indicates that monkeys were present in the New World (South America) and the Old World (Africa and Asia). New World monkeys are also called Platyrrhini—a reference to their broad noses (Figure 29.43). Old World monkeys are called Catarrhini—a reference to their narrow, downward-pointed noses. There is still quite a bit of uncertainty about the origins of the New World monkeys. At the time the platyrrhines arose, the continents of South American and Africa had drifted apart. Therefore, it is thought that monkeys arose in the Old World and reached the New World either by drifting on log rafts or by crossing land bridges. Due to this reproductive isolation, New World monkeys and Old World monkeys underwent separate adaptive radiations over millions of years. The New World monkeys are all arboreal, whereas Old World monkeys include both arboreal and ground-dwelling species. The arboreal habits of the New World monkeys are reflected in the possession of prehensile or grasping tails by most species. The tails of Old World monkeys are never prehensile and are often reduced, and some species have ischial callosities—thickened patches of skin on their seats.



Figure 29.43 A New World monkey. The howler monkey is native to Central and South America. It makes a call that sounds like a lion roaring. (credit: Xavi Talleda)

Apes evolved from the catarrhines in Africa midway through the Cenozoic, approximately 25 million years ago. Apes are generally larger than monkeys and they do not possess a tail. All apes are capable of moving through trees, although many species spend most their time on the ground. When walking quadrupedally, monkeys walk on their palms, while apes support the upper body on their knuckles. Apes are more intelligent than monkeys, and they have larger brains relative to body size. The apes are divided into two groups. The lesser apes comprise the family Hylobatidae, including gibbons and siamangs. The great apes include the

genera *Pan* (chimpanzees and bonobos) *Gorilla* (gorillas), *Pongo* (orangutans), and *Homo* (humans) (Figure 29.44).

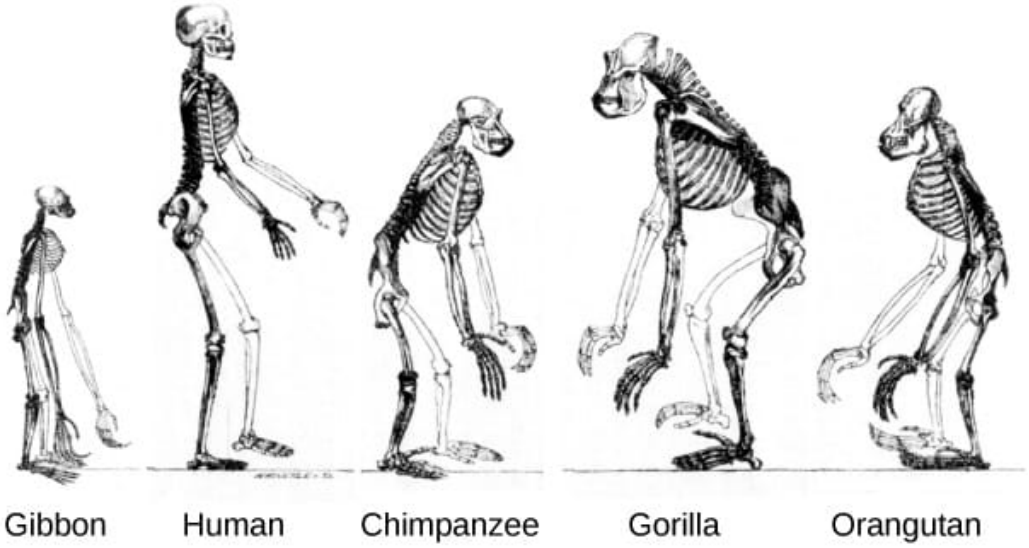


Figure 29.44 Primate skeletons. All great apes have a similar skeletal structure. (credit: modification of work by Tim Vickers)

The very arboreal gibbons are smaller than the great apes; they have low sexual dimorphism (that is, the sexes are not markedly different in size), although in some species, the sexes differ in color; and they have relatively longer arms used for swinging through trees (Figure 29.45a). Two species of orangutan are native to different islands in Indonesia: Borneo (*P. pygmaeus*) and Sumatra (*P. abelii*). A third orangutan species, *Pongo tapanuliensis*, was reported in 2017 from the Batang Toru forest in Sumatra. Orangutans are arboreal and solitary. Males are much larger than females and have cheek and throat pouches when mature. Gorillas all live in Central Africa. The eastern and western populations are recognized as separate species, *G. berengei* and *G. gorilla*. Gorillas are strongly sexually dimorphic, with males about twice the size of females. In older males, called silverbacks, the hair on the back turns white or gray. Chimpanzees (Figure 29.45b) are the species considered to be most closely related to humans. However, the species most closely related to the chimpanzee is the bonobo. Genetic evidence suggests that chimpanzee and human lineages separated 5 to 7 MYA, while chimpanzee (*Pan troglodytes*) and bonobo (*Pan paniscus*) lineages separated about 2 MYA. Chimpanzees and bonobos both live in Central Africa, but the two species are separated by the Congo River, a significant geographic barrier. Bonobos are slighter than chimpanzees, but have longer legs and more hair on their heads. In chimpanzees, white tail tufts identify juveniles, while bonobos keep their white tail tufts for life. Bonobos also have higher-pitched voices than chimpanzees. Chimpanzees are more aggressive and sometimes kill animals from other groups, while bonobos are not known to do so. Both chimpanzees and bonobos are omnivorous. Orangutan and gorilla diets also include foods from multiple sources, although the predominant food items are fruits for orangutans and foliage for gorillas.



Figure 29.45 Lesser and great apes. This white-cheeked gibbon (a) is a lesser ape. In gibbons of this species, females and infants are buff and males are black. This young chimpanzee (b) is one of the great apes. It possesses a relatively large brain and has no tail. (credit a: MAC. credit b: modification of work by Aaron Logan)

Human Evolution

The family Hominidae of order Primates includes the hominoids: the great apes and humans (Figure 29.46). Evidence from the fossil record and from a comparison of human and chimpanzee DNA suggests that humans and chimpanzees diverged from a common hominoid ancestor approximately six million years ago. Several species evolved from the evolutionary branch that includes humans, although our species is the only surviving member. The term hominin is used to refer to those species that evolved after this split of the primate line, thereby designating species that are more closely related to humans than to chimpanzees. A number of marker features differentiate humans from the other hominoids, including bipedalism or upright posture, increase in the size of the brain, and a fully opposable thumb that can touch the little finger. Bipedal hominins include several groups that were probably part of the modern human lineage—*Australopithecus*, *Homo habilis*, and *Homo erectus*—and several non-ancestral groups that can be considered "cousins" of modern humans, such as Neanderthals and Denisovans.

Determining the true lines of descent in hominins is difficult. In years past, when relatively few hominin fossils had been recovered, some scientists believed that considering them in order, from oldest to youngest, would demonstrate the course of evolution from early hominins to modern humans. In the past several years, however, many new fossils have been found, and it is clear that there was often more than one species alive at any one time and that many of the fossils found (and species named) represent hominin species that died out and are not ancestral to modern humans.

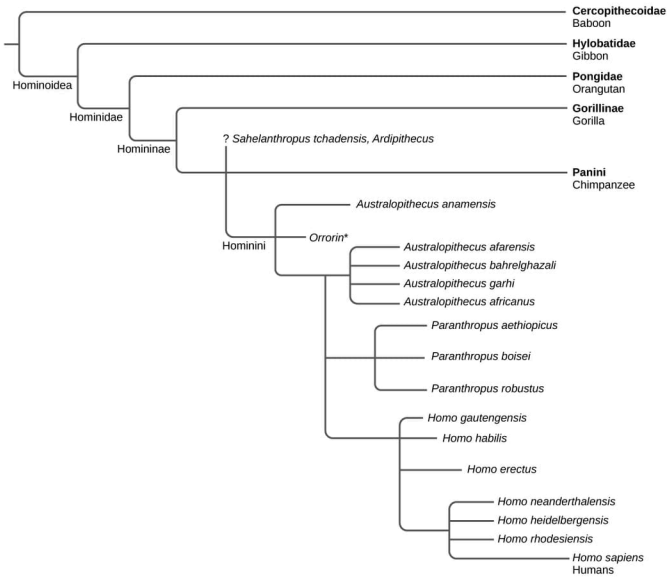


Figure 29.46 Hominin phylogeny. This chart shows evolutionary relationship among Hominins and hypothesized relation to modern humans. (*still debated phylogeny position).

Very Early Hominins

Three species of very early hominids have made news in the late 20th and early 21st centuries: *Ardipithecus*, *Sahelanthropus*, and *Orrorin*. The youngest of the three species, *Ardipithecus*, was discovered in the 1990s, and dates to about 4.4 MYA. Although the bipedality of the early specimens was uncertain, several more specimens of *Ardipithecus* were discovered in the intervening years and demonstrated that the organism was bipedal. Two different species of *Ardipithecus* have been identified, *A. ramidus* and *A. kadabba*, whose specimens are older, dating to 5.6 MYA. However, the status of this genus as a human ancestor is uncertain.

The oldest of the three, *Sahelanthropus tchadensis*, was discovered in 2001-2002 and has been dated to nearly seven million years ago. There is a single specimen of this genus, a skull that was a surface find in Chad. The fossil, informally called "Toumai," is a mosaic of primitive and evolved characteristics, and it is unclear how this fossil fits with the picture given by molecular data, namely that the line leading to modern humans and modern chimpanzees apparently bifurcated about six million years ago. It is not thought at this time that this species was an ancestor of modern humans.

A younger (c. 6 MYA) species, *Orrorin tugenensis*, is also a relatively recent discovery, found in 2000. There are several specimens of *Orrorin*. Some features of *Orrorin* are more similar to those of modern humans than are the australopithicenes, although *Orrorin* is much older. If *Orrorin* is a human ancestor, then the australopithicenes may not be in the direct human lineage. Additional specimens of these species may help to clarify their role.

Early Hominins: Genus *Australopithecus*

Australopithecus ("southern ape") is a genus of hominin that evolved in eastern Africa approximately four million years ago and went extinct about two million years ago. This genus is of particular interest to us as it is thought that our genus, genus *Homo*, evolved from a common ancestor shared with *Australopithecus* about two million years ago (after likely passing through some transitional states). *Australopithecus* had a number of characteristics that were more similar to the great apes than to modern humans. For example, sexual dimorphism was more exaggerated than in modern humans. Males were up to 50 percent larger than females, a ratio that is similar to that seen in modern gorillas and orangutans. In contrast, modern human males are approximately 15 to 20 percent larger than females. The brain size of *Australopithecus* relative to its body mass was also smaller than in modern humans and more similar to that seen in the great apes. A key feature that *Australopithecus* had in common with modern humans was bipedalism, although it is likely that *Australopithecus* also spent time in trees. Hominin footprints, similar to those of modern humans, were found in Laetoli, Tanzania and dated to 3.6 million years ago. They showed that hominins at the time of *Australopithecus* were walking upright.

There were a number of *Australopithecus* species, which are often referred to as *australopiths*. *Australopithecus anamensis* lived about 4.2 million years ago. More is known about another early species, *Australopithecus afarensis*, which lived between 3.9 and 2.9 million years ago. This species demonstrates a trend in human evolution: the reduction of the dentition and jaw in size. *A. afarensis* (Figure 29.47a) had smaller canines and molars compared to apes, but these were larger than those of modern humans. Its brain size was 380 to 450 cubic centimeters, approximately the size of a modern chimpanzee brain. It also had prognathic jaws, which is a relatively longer jaw than that of modern humans. In the mid-1970s, the fossil of an adult female *A. afarensis* was found in the Afar region of Ethiopia and dated to 3.24 million years ago (Figure 29.48). The fossil, which is informally called "Lucy," is significant because it was the most complete australopith fossil found, with 40 percent of the skeleton recovered.



(a) (b)

Figure 29.47 Australopithicene and modern human skulls. The skull of (a) *Australopithecus afarensis*, an early hominid that lived between two and three million years ago, resembled that of (b) modern humans but was smaller with a sloped forehead, larger teeth, and a prominent jaw.



Figure 29.48 Lucy. This adult female *Australopithecus afarensis* skeleton, nicknamed Lucy, was discovered in the mid-1970s. (credit: "120"/Wikimedia Commons)

Australopithecus africanus lived between two and three million years ago. It had a slender build and was bipedal, but had robust arm bones and, like other early hominids, may have spent significant time in trees. Its brain was larger than that of *A. afarensis* at 500 cubic centimeters, which is slightly less than one-third the size of modern human brains. Two other species, *Australopithecus bahrelghazali* and *Australopithecus garhi*, have been added to the roster of australopiths in recent years. A. *bahrelghazali* is unusual in being the only australopith found in Central Africa.

A Dead End: Genus *Paranthropus*

The australopiths had a relatively slender build and teeth that were suited for soft food. In the past several years, fossils of hominids of a different body type have been found and dated to approximately 2.5 million years ago. These hominids, of the genus *Paranthropus*, were muscular, stood 1.3 to 1.4 meters tall, and had large grinding teeth. Their molars showed heavy wear, suggesting that they had a coarse and fibrous vegetarian diet as opposed to the partially carnivorous diet of the australopiths. *Paranthropus* includes *Paranthropus robustus* of South Africa, and *Paranthropus aethiopicus* and *Paranthropus boisei* of East Africa. The hominids in this genus went extinct more than one million years ago and are not thought to be ancestral to modern humans, but rather members of an evolutionary branch on the hominin tree that left no descendants.

Early Hominins: Genus *Homo*

The human genus, *Homo*, first appeared between 2.5 and three million years ago. For many years, fossils of a species called *H. habilis* were the oldest examples in the genus *Homo*, but in 2010, a new species called *Homo gautengensis* was discovered and may be older. Compared to *A. africanus*, *H. habilis* had a number of features more similar to modern humans. *H. habilis* had a jaw that was less prognathic than the australopiths and a larger brain, at 600 to 750 cubic centimeters. However, *H. habilis* retained some features of older hominin species, such as long arms. The name *H. habilis* means "handy man," which is a reference to the stone tools that have been found with its remains.

Link to Learning

Link to Learning

Watch this video about Smithsonian paleontologist Briana Pobiner explaining the link between hominin eating of meat and evolutionary trends.

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H. erectus appeared approximately 1.8 million years ago (Figure 29.49). It is believed to have originated in East Africa and was the first hominin species to migrate out of Africa. Fossils of *H. erectus* have been found in India, China, Java, and Europe, and were known in the past as "Java Man" or "Peking Man." *H. erectus* had a number of features that were more similar to modern humans than those of *H. habilis*. *H. erectus* was larger in size than earlier hominins, reaching heights up to 1.85 meters and weighing up to 65 kilograms, which are sizes similar to those of modern humans. Its degree of sexual dimorphism was less than in earlier species, with males being 20 to 30 percent larger than females, which is close to the size difference seen in our own species. *H. erectus* had a larger brain than earlier species at 775 to 1,100 cubic centimeters, which compares to the 1,130 to 1,260 cubic centimeters seen in modern human brains. *H. erectus* also had a nose with downward-facing nostrils similar to modern humans, rather than the forward-facing nostrils found in other primates. Longer, downward-facing nostrils allow for the warming of cold air before it enters the lungs and may have been an adaptation to colder climates. Artifacts found with fossils of *H. erectus* suggest that it was the first hominin to use fire, hunt, and have a home base. *H. erectus* is generally thought to have lived until about 50,000 years ago.



Figure 29.49 *Homo erectus*. *Homo erectus* had a prominent brow and a nose that pointed downward rather than forward.

Humans: *Homo sapiens*

A number of species, sometimes called archaic *Homo sapiens*, apparently evolved from *H. erectus* starting about 500,000 years ago. These species include *Homo heidelbergensis*, *Homo rhodesiensis*, and *Homo neanderthalensis*. These archaic *H. sapiens* had a brain size similar to that of modern humans, averaging 1,200 to 1,400 cubic centimeters. They differed from modern humans by having a thick skull, a prominent brow ridge, and a receding chin. Some of these species survived until 30,000 to 10,000 years ago, overlapping with modern humans (Figure 29.50).



Figure 29.50 Neanderthal. The *Homo neanderthalensis* used tools and may have worn clothing.

There is considerable debate about the origins of anatomically modern humans or *Homo sapiens sapiens*. As discussed earlier, *H. erectus* migrated out of Africa and into Asia and Europe in the first major wave of migration about 1.5 million years ago. It is thought that modern humans arose in Africa from *H. erectus* and migrated out of Africa about 100,000 years ago in a second major migration wave. Then, modern humans replaced *H. erectus* species that had migrated into Asia and Europe in the first wave.

This evolutionary timeline is supported by molecular evidence. One approach to studying the origins of modern humans is to examine mitochondrial DNA (mtDNA) from populations around the world. Because a fetus develops from an egg containing its mother's mitochondria (which have their own, non-nuclear DNA), mtDNA is passed entirely through the maternal line. Mutations in mtDNA can now be used to estimate the timeline of genetic divergence. The resulting evidence suggests that all modern humans have mtDNA inherited from a common ancestor that lived in Africa about 160,000 years ago. Another approach to the molecular understanding of human evolution is to examine the Y chromosome, which is passed from male parent to male offspring. This evidence suggests that all males today inherited a Y chromosome from a male that lived in Africa about 140,000 years ago.

The study of mitochondrial DNA led to the identification of another human species or subspecies, the Denisovans. DNA from teeth and finger bones suggested two things. First, the mitochondrial DNA was different from that of both modern humans and Neanderthals. Second, the genomic DNA suggested that the Denisovans shared a common ancestor with the Neanderthals. Genes from both Neanderthals and Denisovans have been identified in modern human populations, indicating that interbreeding among the three groups occurred over part of their range.

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19: ANIMAL ECOLOGY & CONSERVATION

19.1: Population Ecology
19.2: Population Growth and Regulation
19.3: Community Ecology
19.4: Energy Flow through Ecosystems
19.5: Importance of Biodiversity
19.6: Threats to Biodiversity
19.7: Preserving Biodiversity

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19.1: Population Ecology

Populations are dynamic entities. Their size and composition fluctuate in response to numerous factors, including seasonal and yearly changes in the environment, natural disasters such as forest fires and volcanic eruptions, and competition for resources between and within species. The statistical study of populations is called demography: a set of mathematical tools designed to describe populations and investigate how they change. Many of these tools were actually designed to study human populations. For example, life tables, which detail the life expectancy of individuals within a population, were initially developed by life insurance companies to set insurance rates. In fact, while the term “demographics” is sometimes assumed to mean a study of human populations, all living populations can be studied using this approach.

Population Size and Density

Populations are characterized by their population size (total number of individuals) and their population density (number of individuals per unit area). A population may have a large number of individuals that are distributed densely, or sparsely. There are also populations with small numbers of individuals that may be dense or very sparsely distributed in a local area. Population size can affect potential for adaptation because it affects the amount of genetic variation present in the population. Density can have effects on interactions within a population such as competition for food and the ability of individuals to find a mate. Smaller organisms tend to be more densely distributed than larger organisms (Figure 19.1.1).

ART CONNECTION

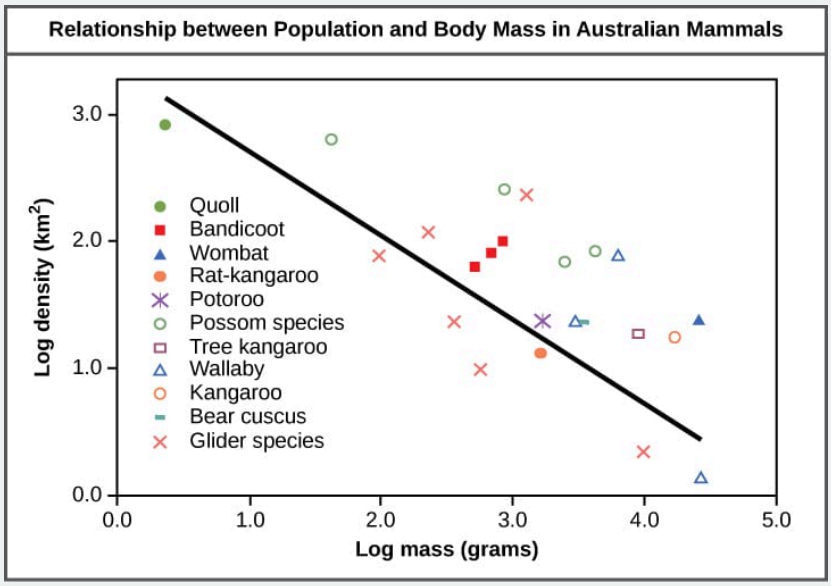


Figure 19.1.1**:** Australian mammals show a typical inverse relationship between population density and body size.

As this graph shows, population density typically decreases with increasing body size. Why do you think this is the case?

Estimating Population Size

The most accurate way to determine population size is to count all of the individuals within the area. However, this method is usually not logistically or economically feasible, especially when studying large areas. Thus, scientists usually study populations by sampling a representative portion of each habitat and use this sample to make inferences about the population as a whole. The methods used to sample populations to determine their size and density are typically tailored to the characteristics of the organism being studied. For immobile organisms such as plants, or for very small and slow-moving organisms, a quadrat may be used. A quadrat is a wood, plastic, or metal square that is randomly located on the ground and used to count the number of individuals that lie within its boundaries. To obtain an accurate count using this method, the square must be placed at random

locations within the habitat enough times to produce an accurate estimate. This counting method will provide an estimate of both population size and density. The number and size of quadrat samples depends on the type of organisms and the nature of their distribution.

For smaller mobile organisms, such as mammals, a technique called mark and recapture is often used. This method involves marking a sample of captured animals in some way and releasing them back into the environment to mix with the rest of the population; then, a new sample is captured and scientists determine how many of the marked animals are in the new sample. This method assumes that the larger the population, the lower the percentage of marked organisms that will be recaptured since they will have mixed with more unmarked individuals. For example, if 80 field mice are captured, marked, and released into the forest, then a second trapping 100 field mice are captured and 20 of them are marked, the population size (*N*) can be determined using the following equation:

$$\frac{\text{number marked first catch} \times \text{total number second catch}}{\text{number marked second catch}} = N$$

Using our example, the population size would be 400.

$$\frac{80 \times 100}{20} = 400$$

These results give us an estimate of 400 total individuals in the original population. The true number usually will be a bit different from this because of chance errors and possible bias caused by the sampling methods.

Species Distribution

In addition to measuring density, further information about a population can be obtained by looking at the distribution of the individuals throughout their range. A species distribution pattern is the distribution of individuals within a habitat at a particular point in time—broad categories of patterns are used to describe them.

Individuals within a population can be distributed at random, in groups, or equally spaced apart (more or less). These are known as random, clumped, and uniform distribution patterns, respectively (Figure 19.1.2). Different distributions reflect important aspects of the biology of the species; they also affect the mathematical methods required to estimate population sizes. An example of random distribution occurs with dandelion and other plants that have wind-dispersed seeds that germinate wherever they happen to fall in favorable environments. A clumped distribution, may be seen in plants that drop their seeds straight to the ground, such as oak trees; it can also be seen in animals that live in social groups (schools of fish or herds of elephants). Uniform distribution is observed in plants that secrete substances inhibiting the growth of nearby individuals (such as the release of toxic chemicals by sage plants). It is also seen in territorial animal species, such as penguins that maintain a defined territory for nesting. The territorial defensive behaviors of each individual create a regular pattern of distribution of similar-sized territories and individuals within those territories. Thus, the distribution of the individuals within a population provides more information about how they interact with each other than does a simple density measurement. Just as lower density species might have more difficulty finding a mate, solitary species with a random distribution might have a similar difficulty when compared to social species clumped together in groups.

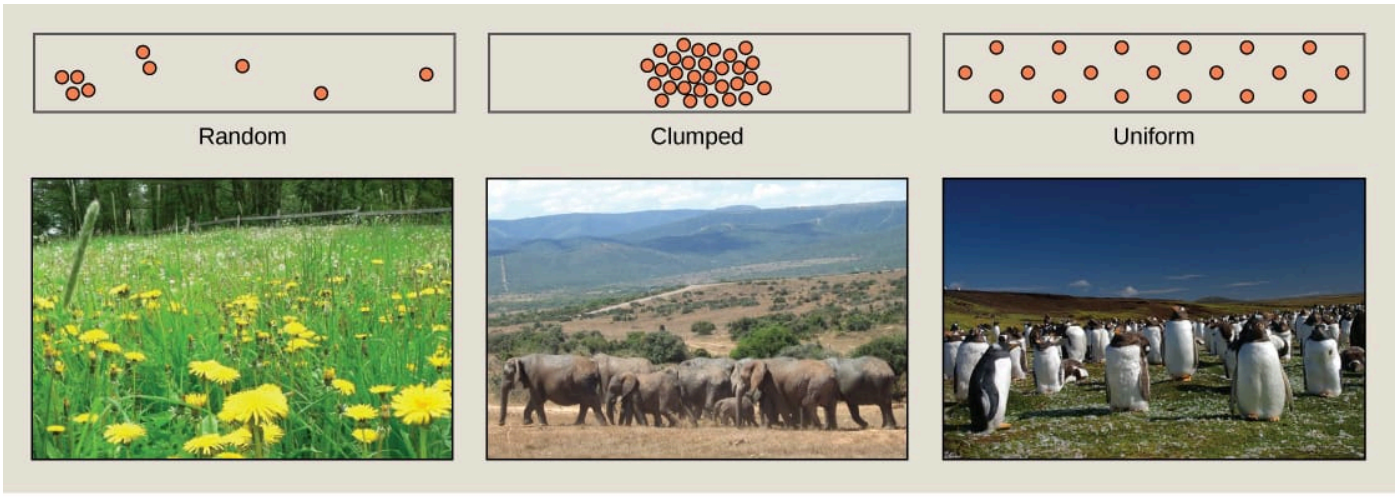


Figure 19.1.2**:** Species may have a random, clumped, or uniform distribution. Plants such as (a) dandelions with wind-dispersed seeds tend to be randomly distributed. Animals such as (b) elephants that travel in groups exhibit a clumped distribution. Territorial birds such as (c) penguins tend to have a uniform distribution. (credit a: modification of work by Rosendahl; credit b: modification of work by Rebecca Wood; credit c: modification of work by Ben Tubby)

Demography

While population size and density describe a population at one particular point in time, scientists must use demography to study the dynamics of a population. Demography is the statistical study of population changes over time: birth rates, death rates, and life expectancies. These population characteristics are often displayed in a life table.

Life Tables

Life tables provide important information about the life history of an organism and the life expectancy of individuals at each age. They are modeled after actuarial tables used by the insurance industry for estimating human life expectancy. Life tables may include the probability of each age group dying before their next birthday, the percentage of surviving individuals dying at a particular age interval (their mortality rate, and their life expectancy at each interval. An example of a life table is shown in Table 19.1.1 from a study of Dall mountain sheep, a species native to northwestern North America. Notice that the population is divided into age intervals (column A). The mortality rate (per 1000) shown in column D is based on the number of individuals dying during the age interval (column B), divided by the number of individuals surviving at the beginning of the interval (Column C) multiplied by 1000.

$$\text{mortality rate} = \frac{\text{number of individuals dying}}{\text{number of individuals surviving}} \times 1000$$

For example, between ages three and four, 12 individuals die out of the 776 that were remaining from the original 1000 sheep. This number is then multiplied by 1000 to give the mortality rate per thousand.

$$\text{mortality rate} = \frac{12}{776} \times 1000 \approx 15.5$$

As can be seen from the mortality rate data (column D), a high death rate occurred when the sheep were between six months and a year old, and then increased even more from 8 to 12 years old, after which there were few survivors. The data indicate that if a sheep in this population were to survive to age one, it could be expected to live another 7.7 years on average, as shown by the life-expectancy numbers in column E.

This life table of Ovis dalli shows the number of deaths, number of survivors, mortality rate, and life expectancy at each age interval for Dall mountain sheep.

Table 19.1.1: Life Table of Dall Mountain Sheep[1]

A	B	C	D	E
Age interval (years)	Number dying in age interval out of 1000 born	Number surviving at beginning of age interval out of 1000 born	Mortality rate per 1000 alive at beginning of age interval	Life expectancy or mean lifetime remaining to those attaining age interval
0–0.5	54	1000	54.0	7.06
0.5–1	145	946	153.3	—
1–2	12	801	15.0	7.7
2–3	13	789	16.5	6.8
3–4	12	776	15.5	5.9
4–5	30	764	39.3	5.0
5–6	46	734	62.7	4.2
6–7	48	688	69.8	3.4
7–8	69	640	107.8	2.6
8–9	132	571	231.2	1.9
9–10	187	439	426.0	1.3
10–11	156	252	619.0	0.9
11–12	90	96	937.5	0.6
12–13	3	6	500.0	1.2
13–14	3	3	1000	0.7

Survivorship Curves

Another tool used by population ecologists is a survivorship curve, which is a graph of the number of individuals surviving at each age interval versus time. These curves allow us to compare the life histories of different populations (Figure 19.1.3). There are three types of survivorship curves. In a type I curve, mortality is low in the early and middle years and occurs mostly in older individuals. Organisms exhibiting a type I survivorship typically produce few offspring and provide good care to the offspring increasing the likelihood of their survival. Humans and most mammals exhibit a type I survivorship curve. In type II curves, mortality is relatively constant throughout the entire life span, and mortality is equally likely to occur at any point in the life span. Many bird populations provide examples of an intermediate or type II survivorship curve. In type III survivorship curves, early ages experience the highest mortality with much lower mortality rates for organisms that make it to advanced years. Type III organisms typically produce large numbers of offspring, but provide very little or no care for them. Trees and marine invertebrates exhibit a type III survivorship curve because very few of these organisms survive their younger years, but those that do make it to an old age are more likely to survive for a relatively long period of time.

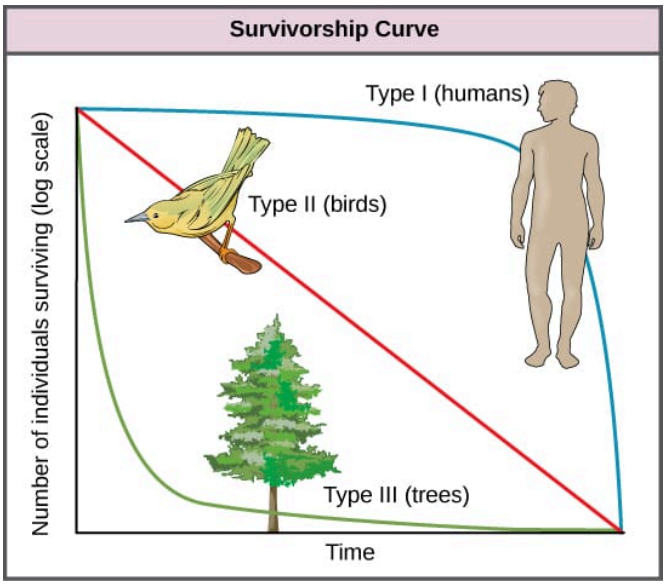


Figure 19.1.3**:** Survivorship curves show the distribution of individuals in a population according to age. Humans and most mammals have a Type I survivorship curve, because death primarily occurs in the older years. Birds have a Type II survivorship curve, as death at any age is equally probable. Trees have a Type III survivorship curve because very few survive the younger years, but after a certain age, individuals are much more likely to survive.

Section Summary

Populations are individuals of a species that live in a particular habitat. Ecologists measure characteristics of populations: size, density, and distribution pattern. Life tables are useful to calculate life expectancies of individual population members. Survivorship curves show the number of individuals surviving at each age interval plotted versus time.

Art Connections

Figure 19.1.1: As this graph shows, population density typically decreases with increasing body size. Why do you think this is the case?

Answer

Smaller animals require less food and others resources, so the environment can support more of them per unit area.

Footnotes

1. 1 Data Adapted from Edward S. Deevey, Jr., “Life Tables for Natural Populations of Animals,” *The Quarterly Review of Biology* 22, no. 4 (December 1947): 283-314.

Glossary

demography
the statistical study of changes in populations over time

life table
a table showing the life expectancy of a population member based on its age

mark and recapture
a method used to determine population size in mobile organisms

mortality rate
: the proportion of population surviving to the beginning of an age interval that dies during that age interval

population density
: the number of population members divided by the area being measured

population size
: the number of individuals in a population

quadrat
: a square within which a count of individuals is made that is combined with other such counts to determine population size and density in slow moving or stationary organisms

species distribution pattern
: the distribution of individuals within a habitat at a given point in time

survivorship curve
: a graph of the number of surviving population members versus the relative age of the member

Contributors and Attributions

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

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19.2: Population Growth and Regulation

Population ecologists make use of a variety of methods to model population dynamics. An accurate model should be able to describe the changes occurring in a population and predict future changes.

Population Growth

The two simplest models of population growth use deterministic equations (equations that do not account for random events) to describe the rate of change in the size of a population over time. The first of these models, exponential growth, describes theoretical populations that increase in numbers without any limits to their growth. The second model, logistic growth, introduces limits to reproductive growth that become more intense as the population size increases. Neither model adequately describes natural populations, but they provide points of comparison.

Exponential Growth

Charles Darwin, in developing his theory of natural selection, was influenced by the English clergyman Thomas Malthus. Malthus published his book in 1798 stating that populations with abundant natural resources grow very rapidly; however, they limit further growth by depleting their resources. The early pattern of accelerating population size is called exponential growth.

The best example of exponential growth in organisms is seen in bacteria. Bacteria are prokaryotes that reproduce largely by binary fission. This division takes about an hour for many bacterial species. If 1000 bacteria are placed in a large flask with an abundant supply of nutrients (so the nutrients will not become quickly depleted), the number of bacteria will have doubled from 1000 to 2000 after just an hour. In another hour, each of the 2000 bacteria will divide, producing 4000 bacteria. After the third hour, there should be 8000 bacteria in the flask. The important concept of exponential growth is that the growth rate—the number of organisms added in each reproductive generation—is itself increasing; that is, the population size is increasing at a greater and greater rate. After 24 of these cycles, the population would have increased from 1000 to more than 16 billion bacteria. When the population size, *N*, is plotted over time, a J-shaped growth curve is produced (Figure 19.2.1**a**).

The bacteria-in-a-flask example is not truly representative of the real world where resources are usually limited. However, when a species is introduced into a new habitat that it finds suitable, it may show exponential growth for a while. In the case of the bacteria in the flask, some bacteria will die during the experiment and thus not reproduce; therefore, the growth rate is lowered from a maximal rate in which there is no mortality. The growth rate of a population is largely determined by subtracting the death rate, *D*, (number organisms that die during an interval) from the birth rate, *B*, (number organisms that are born during an interval). The growth rate can be expressed in a simple equation that combines the birth and death rates into a single factor: *r*. This is shown in the following formula:

$$\text{Population growth} = rN$$

The value of *r* can be positive, meaning the population is increasing in size (the rate of change is positive); or negative, meaning the population is decreasing in size; or zero, in which case the population size is unchanging, a condition known as zero population growth.

Logistic Growth

Extended exponential growth is possible only when infinite natural resources are available; this is not the case in the real world. Charles Darwin recognized this fact in his description of the “struggle for existence,” which states that individuals will compete (with members of their own or other species) for limited resources. The successful ones are more likely to survive and pass on the traits that made them successful to the next generation at a greater rate (natural selection). To model the reality of limited resources, population ecologists developed the logistic growth model.

Carrying Capacity and the Logistic Model

In the real world, with its limited resources, exponential growth cannot continue indefinitely. Exponential growth may occur in

environments where there are few individuals and plentiful resources, but when the number of individuals gets large enough, resources will be depleted and the growth rate will slow down. Eventually, the growth rate will plateau or level off (Figure 19.2.1 **b**). This population size, which is determined by the maximum population size that a particular environment can sustain, is called the carrying capacity, or *K*. In real populations, a growing population often overshoots its carrying capacity, and the death rate increases beyond the birth rate causing the population size to decline back to the carrying capacity or below it. Most populations usually fluctuate around the carrying capacity in an undulating fashion rather than existing right at it.

The formula used to calculate logistic growth adds the carrying capacity as a moderating force in the growth rate. The expression "*K* – *N*" is equal to the number of individuals that may be added to a population at a given time, and "*K* – *N*" divided by "*K*" is the fraction of the carrying capacity available for further growth. Thus, the exponential growth model is restricted by this factor to generate the logistic growth equation:

$$\text{Population growth} = rN\left[\frac{K-N}{K}\right]$$

Notice that when *N* is almost zero the quantity in brackets is almost equal to 1 (or *K*/*K*) and growth is close to exponential. When the population size is equal to the carrying capacity, or *N* = *K*, the quantity in brackets is equal to zero and growth is equal to zero. A graph of this equation (logistic growth) yields the S-shaped curve (Figure 19.2.1**b**). It is a more realistic model of population growth than exponential growth. There are three different sections to an S-shaped curve. Initially, growth is exponential because there are few individuals and ample resources available. Then, as resources begin to become limited, the growth rate decreases. Finally, the growth rate levels off at the carrying capacity of the environment, with little change in population number over time.

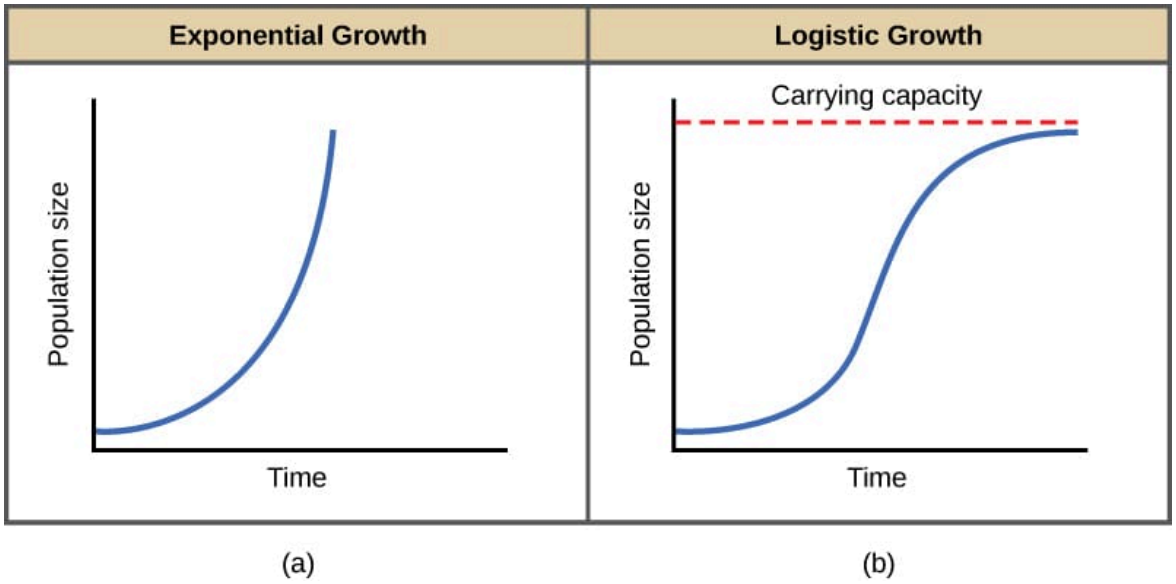


Figure 19.2.1**:** When resources are unlimited, populations exhibit (a) exponential growth, shown in a J-shaped curve. When resources are limited, populations exhibit (b) logistic growth. In logistic growth, population expansion decreases as resources become scarce, and it levels off when the carrying capacity of the environment is reached. The logistic growth curve is S-shaped.

Role of Intraspecific Competition

The logistic model assumes that every individual within a population will have equal access to resources and, thus, an equal chance for survival. For plants, the amount of water, sunlight, nutrients, and space to grow are the important resources, whereas in animals, important resources include food, water, shelter, nesting space, and mates.

In the real world, phenotypic variation among individuals within a population means that some individuals will be better adapted to their environment than others. The resulting competition for resources among population members of the same species is termed intraspecific competition. Intraspecific competition may not affect populations that are well below their carrying capacity, as resources are plentiful and all individuals can obtain what they need. However, as population size increases, this competition intensifies. In addition, the accumulation of waste products can reduce carrying capacity in an environment.

Examples of Logistic Growth

Yeast, a microscopic fungus used to make bread and alcoholic beverages, exhibits the classical S-shaped curve when grown in a test tube (Figure 19.2.2**a**). Its growth levels off as the population depletes the nutrients that are necessary for its growth. In the real world, however, there are variations to this idealized curve. Examples in wild populations include sheep and harbor seals (Figure 19.2.2**b**). In both examples, the population size exceeds the carrying capacity for short periods of time and then falls below the carrying capacity afterwards. This fluctuation in population size continues to occur as the population oscillates around its carrying capacity. Still, even with this oscillation, the logistic model is confirmed.

ART CONNECTION

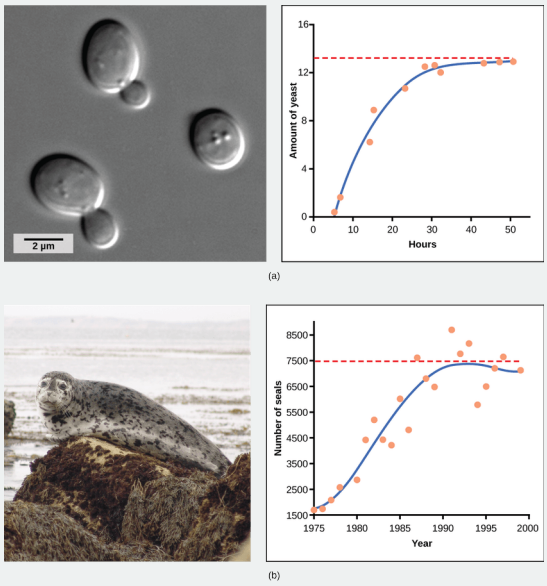


Figure 19.2.2**:** (a) Yeast grown in ideal conditions in a test tube shows a classical S-shaped logistic growth curve, whereas (b) a natural population of seals shows real-world fluctuation. The yeast is visualized using differential interference contrast light micrography. (credit a: scale-bar data from Matt Russell)

If the major food source of seals declines due to pollution or overfishing, which of the following would likely occur?

A. The carrying capacity of seals would decrease, as would the seal population.
B. The carrying capacity of seals would decrease, but the seal population would remain the same.
C. The number of seal deaths would increase, but the number of births would also increase, so the population size would remain the same.
D. The carrying capacity of seals would remain the same, but the population of seals would decrease.

Population Dynamics and Regulation

The logistic model of population growth, while valid in many natural populations and a useful model, is a simplification of real-world population dynamics. Implicit in the model is that the carrying capacity of the environment does not change, which is not the case. The carrying capacity varies annually. For example, some summers are hot and dry whereas others are cold and wet; in many areas, the carrying capacity during the winter is much lower than it is during the summer. Also, natural events such as earthquakes, volcanoes, and fires can alter an environment and hence its carrying capacity. Additionally, populations do not usually exist in isolation. They share the environment with other species, competing with them for the same resources (interspecific competition). These factors are also important to understanding how a specific population will grow.

Population growth is regulated in a variety of ways. These are grouped into density-dependent factors, in which the density of the population affects growth rate and mortality, and density-independent factors, which cause mortality in a population regardless of population density. Wildlife biologists, in particular, want to understand both types because this helps them manage populations and prevent extinction or overpopulation.

Density-dependent Regulation

Most density-dependent factors are biological in nature and include predation, inter- and intraspecific competition, and parasites. Usually, the denser a population is, the greater its mortality rate. For example, during intra- and interspecific competition, the reproductive rates of the species will usually be lower, reducing their populations' rate of growth. In addition, low prey density increases the mortality of its predator because it has more difficulty locating its food source. Also, when the population is denser, diseases spread more rapidly among the members of the population, which affect the mortality rate.

Density dependent regulation was studied in a natural experiment with wild donkey populations on two sites in Australia.[1] On one site the population was reduced by a population control program; the population on the other site received no interference. The high-density plot was twice as dense as the low-density plot. From 1986 to 1987 the high-density plot saw no change in donkey density, while the low-density plot saw an increase in donkey density. The difference in the growth rates of the two populations was caused by mortality, not by a difference in birth rates. The researchers found that numbers of offspring birthed by each mother was unaffected by density. Growth rates in the two populations were different mostly because of juvenile mortality caused by the mother's malnutrition due to scarce high-quality food in the dense population. Figure 19.2.3 shows the difference in age-specific mortalities in the two populations.

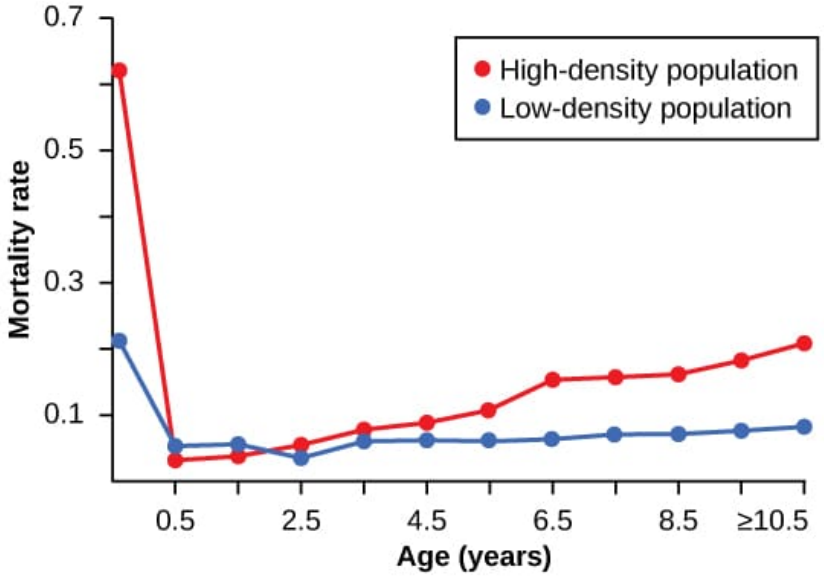


Figure 19.2.3**:** This graph shows the age-specific mortality rates for wild donkeys from high- and low-density populations. The juvenile mortality is much higher in the high-density population because of maternal malnutrition caused by a shortage of high-quality food.

Density-independent Regulation and Interaction with Density-dependent Factors

Many factors that are typically physical in nature cause mortality of a population regardless of its density. These factors include weather, natural disasters, and pollution. An individual deer will be killed in a forest fire regardless of how many deer happen to be in that area. Its chances of survival are the same whether the population density is high or low. The same holds true for cold winter weather.

In real-life situations, population regulation is very complicated and density-dependent and independent factors can interact. A dense population that suffers mortality from a density-independent cause will be able to recover differently than a sparse population. For example, a population of deer affected by a harsh winter will recover faster if there are more deer remaining to reproduce.

EVOLUTION IN ACTION: Why Did the Woolly Mammoth Go Extinct?



Figure 19.2.4**:** The three images include: (a) 1916 mural of a mammoth herd from the American Museum of Natural History, (b) the only stuffed mammoth in the world is in the Museum of Zoology located in St. Petersburg, Russia, and (c) a one-month-old baby mammoth, named Lyuba, discovered in Siberia in 2007. (credit a: modification of work by Charles R. Knight; credit b: modification of work by "Tanapon"/Flickr; credit c: modification of work by Matt Howry)

Woolly mammoths began to go extinct about 10,000 years ago, soon after paleontologists believe humans able to hunt them began to colonize North America and northern Eurasia (Figure 19.2.4). A mammoth population survived on Wrangel Island, in the East Siberian Sea, and was isolated from human contact until as recently as 1700 BC. We know a lot about these animals from carcasses found frozen in the ice of Siberia and other northern regions.

It is commonly thought that climate change and human hunting led to their extinction. A 2008 study estimated that climate change reduced the mammoth's range from 3,000,000 square miles 42,000 years ago to 310,000 square miles 6,000 years ago.[2] Through archaeological evidence of kill sites, it is also well documented that humans hunted these animals. A 2012 study concluded that no single factor was exclusively responsible for the extinction of these magnificent creatures.[3] In addition to climate change and reduction of habitat, scientists demonstrated another important factor in the mammoth's extinction was the migration of human hunters across the Bering Strait to North America during the last ice age 20,000 years ago.

The maintenance of stable populations was and is very complex, with many interacting factors determining the outcome. It is important to remember that humans are also part of nature. Once we contributed to a species' decline using primitive hunting technology only.

Demographic-Based Population Models

Population ecologists have hypothesized that suites of characteristics may evolve in species that lead to particular adaptations to their environments. These adaptations impact the kind of population growth their species experience. Life history characteristics such as birth rates, age at first reproduction, the numbers of offspring, and even death rates evolve just like anatomy or behavior, leading to adaptations that affect population growth. Population ecologists have described a continuum of life-history "strategies" with *K*-selected species on one end and *r*-selected species on the other. *K*-selected species are adapted to stable, predictable environments. Populations of *K*-selected species tend to exist close to their carrying capacity. These species tend to have larger, but fewer, offspring and contribute large amounts of resources to each offspring. Elephants would be an example of a *K*-selected species. *r*-selected species are adapted to unstable and unpredictable environments. They have large numbers of small offspring. Animals that are *r*-selected do not provide a lot of resources or parental care to offspring, and the offspring are relatively self-sufficient at birth. Examples of *r*-selected species are marine invertebrates such as jellyfish and plants such as the dandelion. The two extreme strategies are at two ends of a continuum on which real species life histories will exist. In addition,

life history strategies do not need to evolve as suites, but can evolve independently of each other, so each species may have some characteristics that trend toward one extreme or the other.

Section Summary

Populations with unlimited resources grow exponentially—with an accelerating growth rate. When resources become limiting, populations follow a logistic growth curve in which population size will level off at the carrying capacity.

Populations are regulated by a variety of density-dependent and density-independent factors. Life-history characteristics, such as age at first reproduction or numbers of offspring, are characteristics that evolve in populations just as anatomy or behavior can evolve over time. The model of *r*- and *K*-selection suggests that characters, and possibly suites of characters, may evolve adaptations to population stability near the carrying capacity (*K*-selection) or rapid population growth and collapse (*r*-selection). Species will exhibit adaptations somewhere on a continuum between these two extremes.

Art Exercise

Figure 19.2.2: If the major food source of seals declines due to pollution or overfishing, which of the following would likely occur?

A. The carrying capacity of seals would decrease, as would the seal population.
B. The carrying capacity of seals would decrease, but the seal population would remain the same.
C. The number of seal deaths would increase, but the number of births would also increase, so the population size would remain the same.
D. The carrying capacity of seals would remain the same, but the population of seals would decrease.

Answer

A: The carrying capacity of seals would decrease, as would the seal population.

Footnotes

1. 1 David Choquenot, "Density-Dependent Growth, Body Condition, and Demography in Feral Donkeys: Testing the Food Hypothesis," *Ecology* 72, no. 3 (June 1991):805–813.
2. 2 David Nogués-Bravo et al., "Climate Change, Humans, and the Extinction of the Woolly Mammoth." *PLoS Biol* 6 (April 2008): e79, doi:10.1371/journal.pbio.0060079.
3. 3 G.M. MacDonald et al., "Pattern of Extinction of the Woolly Mammoth in Beringia." *Nature Communications* 3, no. 893 (June 2012), doi:10.1038/ncomms1881.

Glossary

birth rate
the number of births within a population at a specific point in time

carrying capacity
the maximum number of individuals of a population that can be supported by the limited resources of a habitat

death rate
the number of deaths within a population at a specific point in time

density-dependent regulation
the regulation of population in which birth and death rates are dependent on population size

density-independent regulation
the regulation of population in which the death rate is independent of the population size

exponential growth
an accelerating growth pattern seen in populations where resources are not limiting

intraspecific competition
: the competition among members of the same species

J-shaped growth curve
: the shape of an exponential growth curve

***K*-selected species**
: a species suited to stable environments that produce a few, relatively large offspring and provide parental care

logistic growth
: the leveling off of exponential growth due to limiting resources

***r*-selected species**
: a species suited to changing environments that produce many offspring and provide little or no parental care

S-shaped growth curve
: the shape of a logistic growth curve

zero population growth
: the steady population size where birth rates and death rates are equal

Contributors and Attributions

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19.3: Community Ecology

In general, populations of one species never live in isolation from populations of other species. The interacting populations occupying a given habitat form an ecological community. The number of species occupying the same habitat and their relative abundance is known as the diversity of the community. Areas with low species diversity, such as the glaciers of Antarctica, still contain a wide variety of living organisms, whereas the diversity of tropical rainforests is so great that it cannot be accurately assessed. Scientists study ecology at the community level to understand how species interact with each other and compete for the same resources.

Predation and Herbivory

Perhaps the classical example of species interaction is the predator-prey relationship. The narrowest definition of the predator-prey interaction describes individuals of one population that kill and then consume the individuals of another population. Population sizes of predators and prey in a community are not constant over time, and they may vary in cycles that appear to be related. The most often cited example of predator-prey population dynamics is seen in the cycling of the lynx (predator) and the snowshoe hare (prey), using 100 years of trapping data from North America (Figure 19.3.1). This cycling of predator and prey population sizes has a period of approximately ten years, with the predator population lagging one to two years behind the prey population. An apparent explanation for this pattern is that as the hare numbers increase, there is more food available for the lynx, allowing the lynx population to increase as well. When the lynx population grows to a threshold level, however, they kill so many hares that hare numbers begin to decline, followed by a decline in the lynx population because of scarcity of food. When the lynx population is low, the hare population size begins to increase due, in part, to low predation pressure, starting the cycle anew.

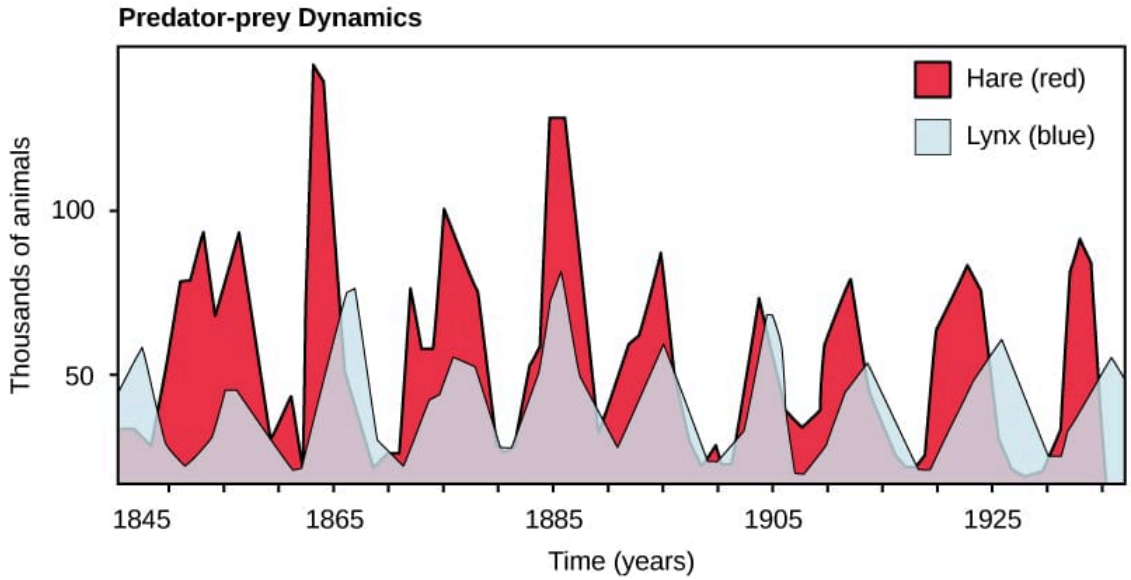


Figure 19.3.1**:** The cycling of snowshoe hare and lynx populations in Northern Ontario is an example of predator-prey dynamics.

Defense Mechanisms against Predation and Herbivory

Predation and predator avoidance are strong selective agents. Any heritable character that allows an individual of a prey population to better evade its predators will be represented in greater numbers in later generations. Likewise, traits that allow a predator to more efficiently locate and capture its prey will lead to a greater number of offspring and an increase in the commonness of the trait within the population. Such ecological relationships between specific populations lead to adaptations that are driven by reciprocal evolutionary responses in those populations. Species have evolved numerous mechanisms to escape predation and herbivory (the consumption of plants for food). Defenses may be mechanical, chemical, physical, or behavioral.

Mechanical defenses, such as the presence of armor in animals or thorns in plants, discourage predation and herbivory by discouraging physical contact (Figure 19.3.2**a**). Many animals produce or obtain chemical defenses from plants and store them to

prevent predation. Many plant species produce secondary plant compounds that serve no function for the plant except that they are toxic to animals and discourage consumption. For example, the foxglove produces several compounds, including digitalis, that are extremely toxic when eaten (Figure 19.3.2**b**). (Biomedical scientists have purposed the chemical produced by foxglove as a heart medication, which has saved lives for many decades.)



(a) (b)

Figure 19.3.2**:** The (a) honey locust tree uses thorns, a mechanical defense, against herbivores, while the (b) foxglove uses a chemical defense: toxins produces by the plant can cause nausea, vomiting, hallucinations, convulsions, or death when consumed. (credit a: modification of work by Huw Williams; credit b: modification of work by Philip Jägenstedt)

Many species use their body shape and coloration to avoid being detected by predators. The tropical walking stick is an insect with the coloration and body shape of a twig, which makes it very hard to see when it is stationary against a background of real twigs (Figure 19.3.3**a**). In another example, the chameleon can change its color to match its surroundings (Figure 19.3.3**b**).



(a) (b)

Figure 19.3.3**:** (a) The tropical walking stick and (b) the chameleon use their body shape and/or coloration to prevent detection by predators. (credit a: modification of work by Linda Tanner; credit b: modification of work by Frank Vassen)

Some species use coloration as a way of warning predators that they are distasteful or poisonous. For example, the monarch butterfly caterpillar sequesters poisons from its food (plants and milkweeds) to make itself poisonous or distasteful to potential predators. The caterpillar is bright yellow and black to advertise its toxicity. The caterpillar is also able to pass the sequestered toxins on to the adult monarch, which is also dramatically colored black and red as a warning to potential predators. Fire-bellied toads produce toxins that make them distasteful to their potential predators. They have bright red or orange coloration on their bellies, which they display to a potential predator to advertise their poisonous nature and discourage an attack. These are only two examples of warning coloration, which is a relatively common adaptation. Warning coloration only works if a predator uses eyesight to locate prey and can learn—a naïve predator must experience the negative consequences of eating one before it will

avoid other similarly colored individuals (Figure 19.3.4).



Figure 19.3.4: The fire-bellied toad has bright coloration on its belly that serves to warn potential predators that it is toxic. (credit: modification of work by Roberto Verzo)

While some predators learn to avoid eating certain potential prey because of their coloration, other species have evolved mechanisms to mimic this coloration to avoid being eaten, even though they themselves may not be unpleasant to eat or contain toxic chemicals. In some cases of mimicry, a harmless species imitates the warning coloration of a harmful species. Assuming they share the same predators, this coloration then protects the harmless ones. Many insect species mimic the coloration of wasps, which are stinging, venomous insects, thereby discouraging predation (Figure 19.3.5).



Figure 19.3.5: One form of mimicry is when a harmless species mimics the coloration of a harmful species, as is seen with the (a) wasp (*Polistes* sp.) and the (b) hoverfly (*Syrphus* sp.). (credit: modification of work by Tom Ings)

In other cases of mimicry, multiple species share the same warning coloration, but all of them actually have defenses. The commonness of the signal improves the compliance of all the potential predators. Figure 19.3.6 shows a variety of foul-tasting butterflies with similar coloration.



Figure 19.3.6**:** Several unpleasant-tasting *Heliconius* butterfly species share a similar color pattern with better-tasting varieties, an example of mimicry. (credit: Joron M, Papa R, Beltrán M, Chamberlain N, Mavárez J, et al.)

Competitive Exclusion Principle

Resources are often limited within a habitat and multiple species may compete to obtain them. Ecologists have come to understand that all species have an ecological niche. A niche is the unique set of resources used by a species, which includes its interactions with other species. The competitive exclusion principle states that two species cannot occupy the same niche in a habitat: in other words, different species cannot coexist in a community if they are competing for all the same resources. This principle works because if there is an overlap in resource use and therefore competition between two species, then traits that lessen reliance on the shared resource will be selected for leading to evolution that reduces the overlap. If either species is unable to evolve to reduce competition, then the species that most efficiently exploits the resource will drive the other species to extinction. An experimental example of this principle is shown in Figure 19.3.7 with two protozoan species: *Paramecium aurelia* and *Paramecium caudatum*. When grown individually in the laboratory, they both thrive. But when they are placed together in the same test tube (habitat), *P. aurelia* outcompetes *P. caudatum* for food, leading to the latter's eventual extinction.

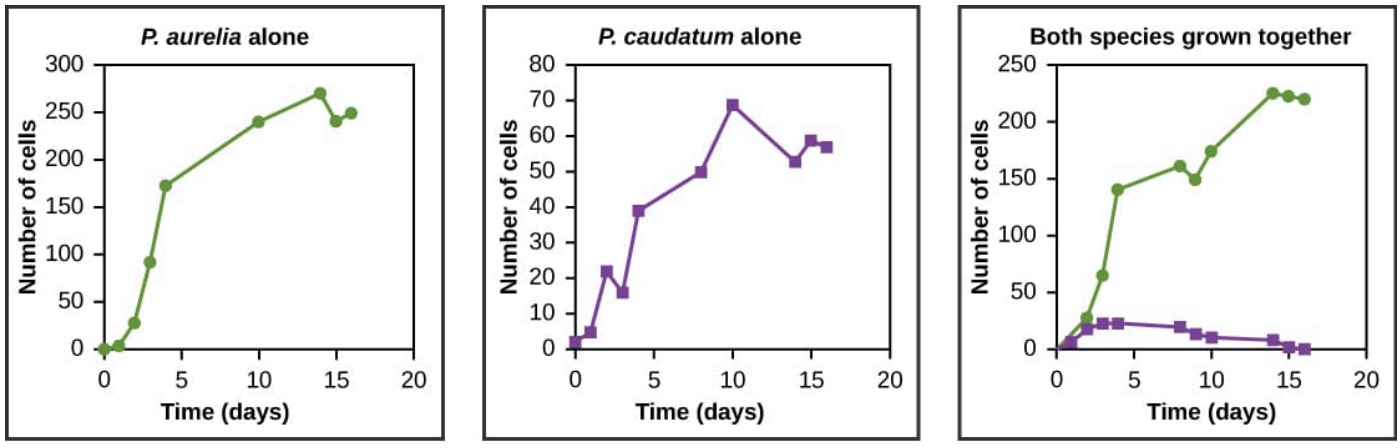


Figure 19.3.7**:** *Paramecium aurelia* and *Paramecium caudatum* grow well individually, but when they compete for the same resources, the *P. aurelia* outcompetes the *P. caudatum*.

Symbiosis

Symbiotic relationships are close, long-term interactions between individuals of different species. Symbioses may be commensal,

in which one species benefits while the other is neither harmed nor benefited; mutualistic, in which both species benefit; or parasitic, in which the interaction harms one species and benefits the other.

Commensalism

A commensal relationship occurs when one species benefits from a close prolonged interaction, while the other neither benefits nor is harmed. Birds nesting in trees provide an example of a commensal relationship (Figure 19.3.8). The tree is not harmed by the presence of the nest among its branches. The nests are light and produce little strain on the structural integrity of the branch, and most of the leaves, which the tree uses to get energy by photosynthesis, are above the nest so they are unaffected. The bird, on the other hand, benefits greatly. If the bird had to nest in the open, its eggs and young would be vulnerable to predators. Many potential commensal relationships are difficult to identify because it is difficult to prove that one partner does not derive some benefit from the presence of the other.



Figure 19.3.8: The southern masked-weaver is starting to make a nest in a tree in Zambezi Valley, Zambia. This is an example of a commensal relationship, in which one species (the bird) benefits, while the other (the tree) neither benefits nor is harmed. (credit: "Hanay"/Wikimedia Commons)

Mutualism

A second type of symbiotic relationship is called mutualism, in which two species benefit from their interaction. For example, termites have a mutualistic relationship with protists that live in the insect's gut (Figure 19.3.9**a**). The termite benefits from the ability of the protists to digest cellulose. However, the protists are able to digest cellulose only because of the presence of symbiotic bacteria within their cells that produce the cellulase enzyme. The termite itself cannot do this: without the protozoa, it would not be able to obtain energy from its food (cellulose from the wood it chews and eats). The protozoa benefit by having a protective environment and a constant supply of food from the wood chewing actions of the termite. In turn, the protists benefit from the enzymes provided by their bacterial endosymbionts, while the bacteria benefit from a doubly protective environment and a constant source of nutrients from two hosts. Lichen are a mutualistic relationship between a fungus and photosynthetic algae or cyanobacteria (Figure 19.3.9**b**). The glucose produced by the algae provides nourishment for both organisms, whereas the physical structure of the lichen protects the algae from the elements and makes certain nutrients in the atmosphere more available to the algae. The algae of lichens can live independently given the right environment, but many of the fungal partners are unable to live on their own.



(a) (b)

Figure 19.3.9**:** (a) Termites form a mutualistic relationship with symbiotic protozoa in their guts, which allow both organisms to obtain energy from the cellulose the termite consumes. (b) Lichen is a fungus that has symbiotic photosynthetic algae living in close association. (credit a: modification of work by Scott Bauer, USDA; credit b: modification of work by Cory Zanker)

Parasitism

A parasite is an organism that feeds off another without immediately killing the organism it is feeding on. In this relationship, the parasite benefits, but the organism being fed upon, the host, is harmed. The host is usually weakened by the parasite as it siphons resources the host would normally use to maintain itself. Parasites may kill their hosts, but there is usually selection to slow down this process to allow the parasite time to complete its reproductive cycle before it or its offspring are able to spread to another host.

The reproductive cycles of parasites are often very complex, sometimes requiring more than one host species. A tapeworm causes disease in humans when contaminated, undercooked meat such as pork, fish, or beef is consumed (Figure 19.3.10). The tapeworm can live inside the intestine of the host for several years, benefiting from the host's food, and it may grow to be over 50 feet long by adding segments. The parasite moves from one host species to a second host species in order to complete its life cycle. *Plasmodium falciparum* is another parasite: the protists that cause malaria, a significant disease in many parts of the world. Living inside human liver and red blood cells, the organism reproduces asexually in the human host and then sexually in the gut of blood-feeding mosquitoes to complete its life cycle. Thus malaria is spread from human to mosquito and back to human, one of many arthropod-borne infectious diseases of humans.

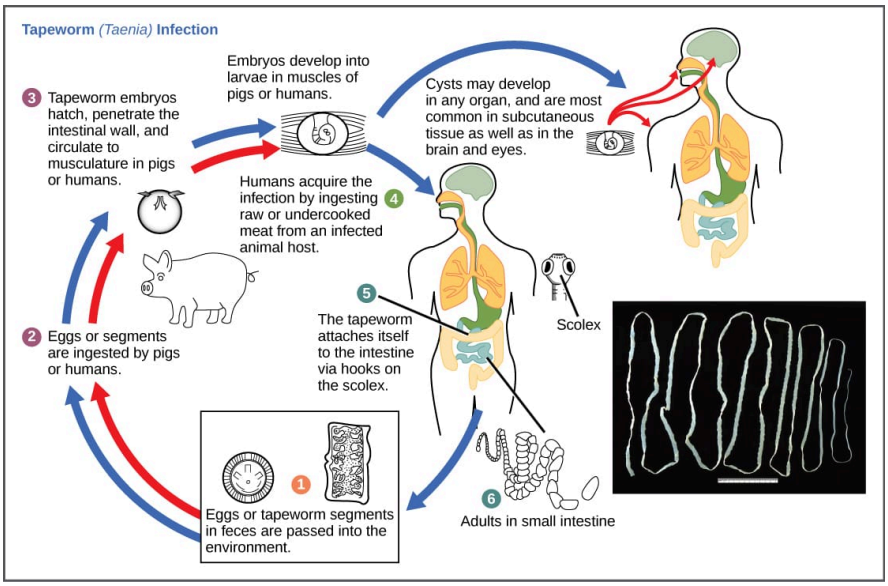


Figure 19.3.10**:** This diagram shows the life cycle of the tapeworm, a human worm parasite. (credit: modification of work by CDC)

CONCEPT IN ACTION

This interactive element is not available in this format. Visit the link or scan the QR code to access it online.

View this YouTube Video online

To learn more about "Symbiosis in the Sea," watch this webisode of Jonathan Bird's Blue World.

Characteristics of Communities

Communities are complex systems that can be characterized by their structure (the number and size of populations and their interactions) and dynamics (how the members and their interactions change over time). Understanding community structure and dynamics allows us to minimize impacts on ecosystems and manage ecological communities we benefit from.

Biodiversity

Ecologists have extensively studied one of the fundamental characteristics of communities: biodiversity. One measure of biodiversity used by ecologists is the number of different species in a particular area and their relative abundance. The area in question could be a habitat, a biome, or the entire biosphere. Species richness is the term used to describe the number of species living in a habitat or other unit. Species richness varies across the globe (Figure 19.3.11). Ecologists have struggled to understand the determinants of biodiversity. Species richness is related to latitude: the greatest species richness occurs near the equator and the lowest richness occurs near the poles. Other factors influence species richness as well. Island biogeography attempts to explain the great species richness found in isolated islands, and has found relationships between species richness, island size, and distance from the mainland.

Relative species abundance is the number individuals in a species relative to the total number of individuals in all species within a system. Foundation species, described below, often have the highest relative abundance of species.

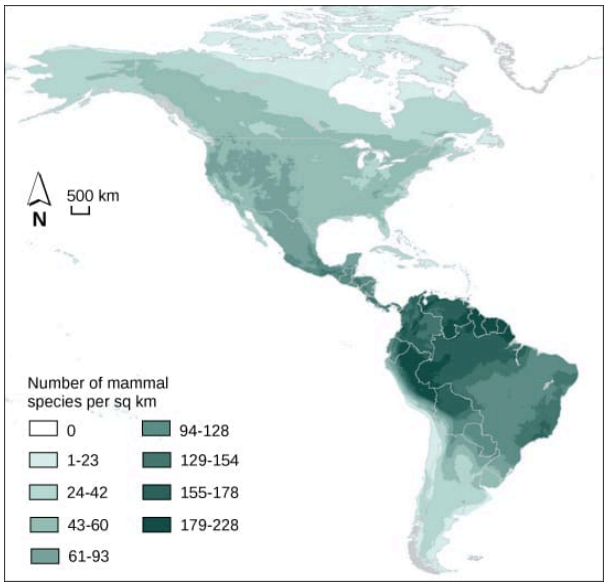


Figure 19.3.11**:** The greatest species richness for mammals in North America is associated in the equatorial latitudes. (credit: modification of work by NASA, CIESIN, Columbia University)

Foundation Species

Foundation species are considered the “base” or “bedrock” of a community, having the greatest influence on its overall structure. They are often primary producers, and they are typically an abundant organism. For example, kelp, a species of brown algae, is a foundation species that forms the basis of the kelp forests off the coast of California.

Foundation species may physically modify the environment to produce and maintain habitats that benefit the other organisms that use them. Examples include the kelp described above or tree species found in a forest. The photosynthetic corals of the coral reef also provide structure by physically modifying the environment (Figure 19.3.12). The exoskeletons of living and dead coral make up most of the reef structure, which protects many other species from waves and ocean currents.



Figure 19.3.12: Coral is the foundation species of coral reef ecosystems. (credit: Jim E. Maragos, USFWS)

Keystone Species

A keystone species is one whose presence has inordinate influence in maintaining the prevalence of various species in an ecosystem, the ecological community’s structure, and sometimes its biodiversity. *Pisaster ochraceus*, the intertidal sea star, is a keystone species in the northwestern portion of the United States (Figure 19.3.13). Studies have shown that when this organism is removed from communities, mussel populations (their natural prey) increase, which completely alters the species composition and reduces biodiversity. Another keystone species is the banded tetra, a fish in tropical streams, which supplies nearly all of the phosphorus, a necessary inorganic nutrient, to the rest of the community. The banded tetra feeds largely on insects from the terrestrial ecosystem and then excretes phosphorus into the aquatic ecosystem. The relationships between populations in the community, and possibly the biodiversity, would change dramatically if these fish were to become extinct.



Figure 19.3.13**:** The *Pisaster ochraceus* sea star is a keystone species. (credit: Jerry Kirkhart)

BIOLOGY IN ACTION: Invasive Species

Invasive species are non-native organisms that, when introduced to an area out of its native range, alter the community they invade. In the United States, invasive species like the purple loosestrife (*Lythrum salicaria*) and the zebra mussel (*Dreissena polymorpha*) have altered aquatic ecosystems, and some forests are threatened by the spread of common buckthorn (*Rhamnus cathartica*) and garlic mustard (*Alliaria petiolata*). Some well-known invasive animals include the emerald ash borer (*Agrilus planipennis*) and the European starling (*Sturnus vulgaris*). Whether enjoying a forest hike, taking a summer boat trip, or simply walking down an urban street, you have likely encountered an invasive species.

One of the many recent proliferations of an invasive species concerns the Asian carp in the United States. Asian carp were introduced to the United States in the 1970s by fisheries (commercial catfish ponds) and by sewage treatment facilities that used the fish's excellent filter feeding abilities to clean their ponds of excess plankton. Some of the fish escaped, and by the 1980s they had colonized many waterways of the Mississippi River basin, including the Illinois and Missouri Rivers.

Voracious feeders and rapid reproducers, Asian carp may outcompete native species for food and could lead to their extinction. One species, the grass carp, feeds on phytoplankton and aquatic plants. It competes with native species for these resources and alters nursery habitats for other fish by removing aquatic plants. Another species, the silver carp, competes with native fish that feed on zooplankton. In some parts of the Illinois River, Asian carp constitute 95 percent of the community's biomass. Although edible, the fish is bony and not desired in the United States. Moreover, their presence now threatens the native fish and fisheries of the Great Lakes, which are important to local economies and recreational anglers. Asian carp have even injured humans. The fish, frightened by the sound of approaching motorboats, thrust themselves into the air, often landing in the boat or directly hitting boaters.

The Great Lakes and their prized salmon and lake trout fisheries are being threatened by Asian carp. The carp are not yet present in the Great Lakes, and attempts are being made to prevent its access to the lakes through the Chicago Ship and Sanitary Canal, which is the only connection between the Mississippi River and Great Lakes basins. To prevent the Asian carp from leaving the canal, a series of electric barriers have been used to discourage their migration; however, the threat is significant enough that several states and Canada have sued to have the Chicago channel permanently cut off from Lake Michigan. Local and national politicians have weighed in on how to solve the problem. In general, governments have been ineffective in preventing or slowing the introduction of invasive species.

The issues associated with Asian carp show how population and community ecology, fisheries management, and politics intersect on issues of vital importance to the human food supply and economy. Socio-political issues like the Asian carp make extensive use of the sciences of population ecology, the study of members of a particular species occupying a habitat; and community ecology, the study of the interaction of all species within a habitat.

Community Dynamics

Community dynamics are the changes in community structure and composition over time, often following environmental disturbances such as volcanoes, earthquakes, storms, fires, and climate change. Communities with a relatively constant number of species are said to be at equilibrium. The equilibrium is dynamic with species identities and relationships changing over time, but maintaining relatively constant numbers. Following a disturbance, the community may or may not return to the equilibrium state.

Succession describes the sequential appearance and disappearance of species in a community over time after a severe disturbance. In primary succession, newly exposed or newly formed rock is colonized by living organisms; in secondary succession, a part of an ecosystem is disturbed and remnants of the previous community remain. In both cases, there is a sequential change in species until a more or less permanent community develops.

Primary Succession and Pioneer Species

Primary succession occurs when new land is formed, for example, following the eruption of volcanoes, such as those on the Big Island of Hawaii. As lava flows into the ocean, new land is continually being formed. On the Big Island, approximately 32 acres of land is added to it its size each year. Weathering and other natural forces break down the rock enough for the establishment of hearty species such as lichens and some plants, known as pioneer species(Figure 19.3.14). These species help to further break down the mineral-rich lava into soil where other, less hardy but more competitive species, such as grasses, shrubs, and trees, will grow and eventually replace the pioneer species. Over time the area will reach an equilibrium state, with a set of organisms quite different from the pioneer species.



Figure 19.3.14**:** During primary succession in lava on Maui, Hawaii, succulent plants are the pioneer species. (credit: Forest and Kim Starr)

Secondary succession

A classic example of secondary succession occurs in oak and hickory forests cleared by wildfire (Figure 19.3.15). Wildfires will burn most vegetation, and unless the animals can flee the area, they are killed. Their nutrients, however, are returned to the ground in the form of ash. Thus, although the community has been dramatically altered, there is a soil ecosystem present that provides a foundation for rapid recolonization.

Before the fire, the vegetation was dominated by tall trees with access to the major plant energy resource: sunlight. Their height gave them access to sunlight while also shading the ground and other low-lying species. After the fire, though, these trees are no longer dominant. Thus, the first plants to grow back are usually annual plants followed within a few years by quickly growing and spreading grasses and other pioneer species. Due, at least in part, to changes in the environment brought on by the growth of grasses and forbs, over many years, shrubs emerge along with small pine, oak, and hickory trees. These organisms are called intermediate species. Eventually, over 150 years, the forest will reach its equilibrium point and resemble the community before

the fire. This equilibrium state is referred to as the climax community, which will remain until the next disturbance. The climax community is typically characteristic of a given climate and geology. Although the community in equilibrium looks the same once it is attained, the equilibrium is a dynamic one with constant changes in abundance and sometimes species identities. The return of a natural ecosystem after agricultural activities is also a well-documented secondary succession process.

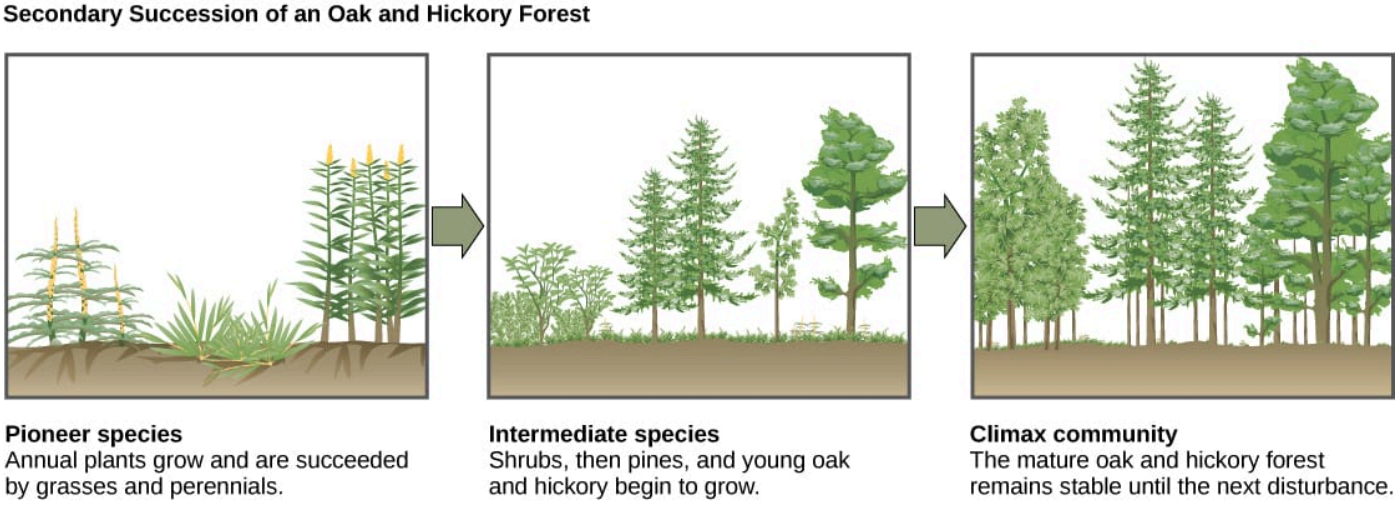


Figure 19.3.15**:** Secondary succession is seen in an oak and hickory forest after a forest fire. A sequence of the community present at three successive times at the same location is depicted.

Section Summary

Communities include all the different species living in a given area. The variety of these species is referred to as biodiversity. Many organisms have developed defenses against predation and herbivory, including mechanical defenses, warning coloration, and mimicry. Two species cannot exist indefinitely in the same habitat competing directly for the same resources. Species may form symbiotic relationships such as commensalism, mutualism, or parasitism. Community structure is described by its foundation and keystone species. Communities respond to environmental disturbances by succession: the predictable appearance of different types of plant species, until a stable community structure is established.

Glossary

climax community
: the final stage of succession, where a stable community is formed by a characteristic assortment of plant and animal species

competitive exclusion principle
: no two species within a habitat can coexist indefinitely when they compete for the same resources at the same time and place

environmental disturbance
: a change in the environment caused by natural disasters or human activities

foundation species
: a species which often forms the major structural portion of the habitat

host
: an organism a parasite lives on

island biogeography
: the study of life on island chains and how their geography interacts with the diversity of species found there

keystone species
: a species whose presence is key to maintaining biodiversity in an ecosystem and to upholding an ecological community's structure

mimicry
an adaptation in which an organism looks like another organism that is dangerous, toxic, or distasteful to its predators

mutualism
a symbiotic relationship between two species where both species benefit

parasite
an organism that uses resources from another species: the host

pioneer species
the first species to appear in primary and secondary succession

primary succession
the succession on land that previously has had no life

relative species abundance
the absolute population size of a particular species relative to the population size of other species within the community

secondary succession
the succession in response to environmental disturbances that move a community away from its equilibrium

species richness
the number of different species in a community

Contributors and Attributions

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19.4: Energy Flow through Ecosystems

An ecosystem is a community of living organisms and their abiotic (non-living) environment. Ecosystems can be small, such as the tide pools found near the rocky shores of many oceans, or large, such as those found in the tropical rainforest of the Amazon in Brazil (Figure 19.4.1).



Figure 19.4.1: A (a) tidal pool ecosystem in Matinicus Island, Maine, is a small ecosystem, while the (b) Amazon rainforest in Brazil is a large ecosystem. (credit a: modification of work by Jim Kuhn; credit b: modification of work by Ivan Mlinaric)

There are three broad categories of ecosystems based on their general environment: freshwater, marine, and terrestrial. Within these three categories are individual ecosystem types based on the environmental habitat and organisms present.

Ecology of Ecosystems

Life in an ecosystem often involves competition for limited resources, which occurs both within a single species and between different species. Organisms compete for food, water, sunlight, space, and mineral nutrients. These resources provide the energy for metabolic processes and the matter to make up organisms' physical structures. Other critical factors influencing community dynamics are the components of its physical environment: a habitat's climate (seasons, sunlight, and rainfall), elevation, and geology. These can all be important environmental variables that determine which organisms can exist within a particular area.

Freshwater ecosystems are the least common, occurring on only 1.8 percent of Earth's surface. These systems comprise lakes, rivers, streams, and springs; they are quite diverse, and support a variety of animals, plants, fungi, protists and prokaryotes.

Marine ecosystems are the most common, comprising 75 percent of Earth's surface and consisting of three basic types: shallow ocean, deep ocean water, and deep ocean bottom. Shallow ocean ecosystems include extremely biodiverse coral reef ecosystems, yet the deep ocean water is known for large numbers of plankton and krill (small crustaceans) that support it. These two environments are especially important to aerobic respirators worldwide, as the phytoplankton perform 40 percent of all photosynthesis on Earth. Although not as diverse as the other two, deep ocean bottom ecosystems contain a wide variety of marine organisms. Such ecosystems exist even at depths where light is unable to penetrate through the water.

Terrestrial ecosystems, also known for their diversity, are grouped into large categories called biomes. A biome is a large-scale community of organisms, primarily defined on land by the dominant plant types that exist in geographic regions of the planet with similar climatic conditions. Examples of biomes include tropical rainforests, savannas, deserts, grasslands, temperate forests, and tundras. Grouping these ecosystems into just a few biome categories obscures the great diversity of the individual ecosystems within them. For example, the saguaro cacti (*Carnegiea gigantean*) and other plant life in the Sonoran Desert, in the United States, are relatively diverse compared with the desolate rocky desert of Boa Vista, an island off the coast of Western Africa (Figure 19.4.2

).



(a) (b)

Figure 19.4.2**:** Desert ecosystems, like all ecosystems, can vary greatly. The desert in (a) Saguaro National Park, Arizona, has abundant plant life, while the rocky desert of (b) Boa Vista island, Cape Verde, Africa, is devoid of plant life. (credit a: modification of work by Jay Galvin; credit b: modification of work by Ingo Wölbern)

Ecosystems and Disturbance

Ecosystems are complex with many interacting parts. They are routinely exposed to various disturbances: changes in the environment that affect their compositions, such as yearly variations in rainfall and temperature. Many disturbances are a result of natural processes. For example, when lightning causes a forest fire and destroys part of a forest ecosystem, the ground is eventually populated with grasses, followed by bushes and shrubs, and later mature trees: thus, the forest is restored to its former state. This process is so universal that ecologists have given it a name—succession. The impact of environmental disturbances caused by human activities is now as significant as the changes wrought by natural processes. Human agricultural practices, air pollution, acid rain, global deforestation, overfishing, oil spills, and illegal dumping on land and into the ocean all have impacts on ecosystems.

Equilibrium is a dynamic state of an ecosystem in which, despite changes in species numbers and occurrence, biodiversity remains somewhat constant. In ecology, two parameters are used to measure changes in ecosystems: resistance and resilience. The ability of an ecosystem to remain at equilibrium in spite of disturbances is called resistance. The speed at which an ecosystem recovers equilibrium after being disturbed is called resilience. Ecosystem resistance and resilience are especially important when considering human impact. The nature of an ecosystem may change to such a degree that it can lose its resilience entirely. This process can lead to the complete destruction or irreversible altering of the ecosystem.

Food Chains and Food Webs

A food chain is a linear sequence of organisms through which nutrients and energy pass as one organism eats another; the levels in the food chain are producers, primary consumers, higher-level consumers, and finally decomposers. These levels are used to describe ecosystem structure and dynamics. There is a single path through a food chain. Each organism in a food chain occupies a specific trophic level (energy level), its position in the food chain or food web.

In many ecosystems, the base, or foundation, of the food chain consists of photosynthetic organisms (plants or phytoplankton), which are called producers. The organisms that consume the producers are herbivores: the primary consumers. Secondary consumers are usually carnivores that eat the primary consumers. Tertiary consumers are carnivores that eat other carnivores. Higher-level consumers feed on the next lower trophic levels, and so on, up to the organisms at the top of the food chain: the apex consumers. In the Lake Ontario food chain, shown in Figure 19.4.3, the Chinook salmon is the apex consumer at the top of this food chain.

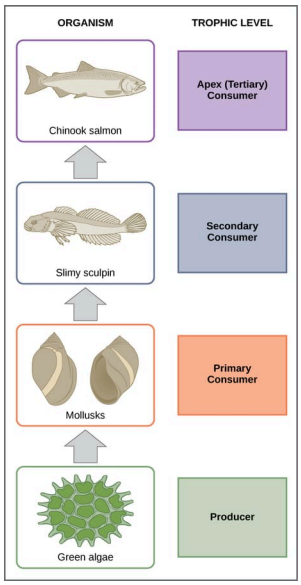


Figure 19.4.3**:** These are the trophic levels of a food chain in Lake Ontario at the United States–Canada border. Energy and nutrients flow from photosynthetic green algae at the base to the top of the food chain: the Chinook salmon. (credit: modification of work by National Oceanic and Atmospheric Administration/NOAA)

One major factor that limits the number of steps in a food chain is energy. Energy is lost at each trophic level and between trophic levels as heat and in the transfer to decomposers (Figure 19.4.4). Thus, after a limited number of trophic energy transfers, the amount of energy remaining in the food chain may not be great enough to support viable populations at yet a higher trophic level.

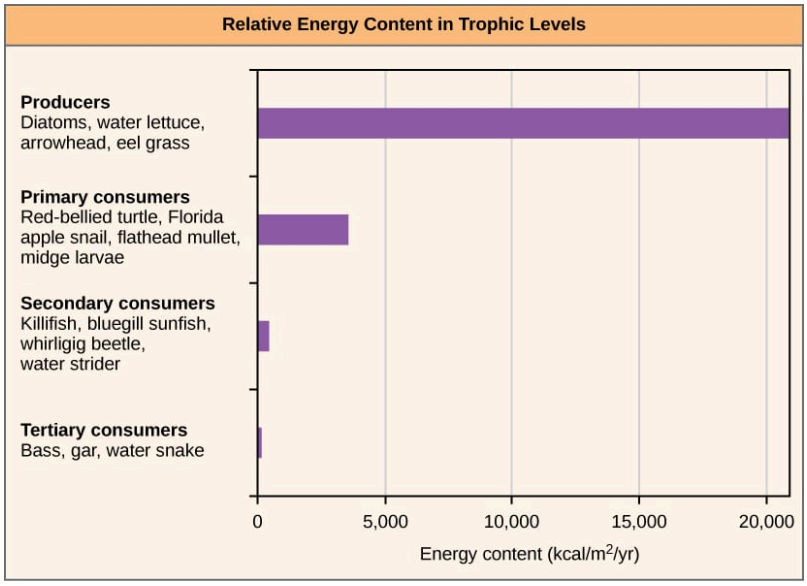


Figure 19.4.4**:** The relative energy in trophic levels in a Silver Springs, Florida, ecosystem is shown. Each trophic level has less energy available, and usually, but not always, supports a smaller mass of organisms at the next level.

There is a one problem when using food chains to describe most ecosystems. Even when all organisms are grouped into appropriate trophic levels, some of these organisms can feed on more than one trophic level; likewise, some of these organisms can also be fed on from multiple trophic levels. In addition, species feed on and are eaten by more than one species. In other words, the linear model of ecosystems, the food chain, is a hypothetical, overly simplistic representation of ecosystem structure. A holistic model—which includes all the interactions between different species and their complex interconnected relationships with each other and with the environment—is a more accurate and descriptive model for ecosystems. A food web is a concept that accounts for the multiple trophic (feeding) interactions between each species and the many species it may feed on, or that feed on it. In a food web, the several trophic connections between each species and the other species that interact with it may cross multiple trophic levels. The matter and energy movements of virtually all ecosystems are more accurately described by food webs (Figure 19.4.5).

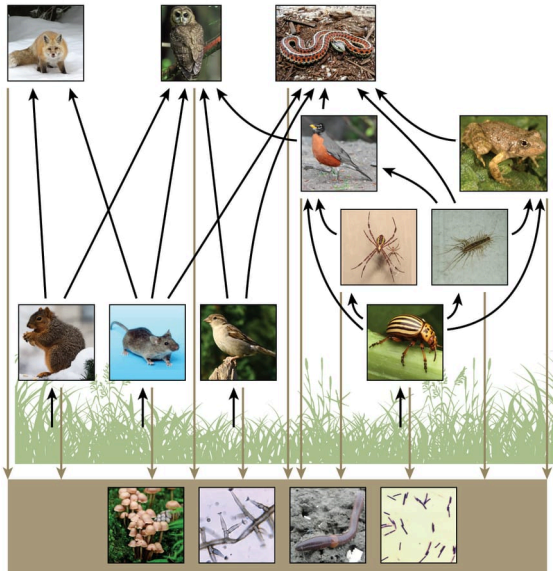


Figure 19.4.5**:** This food web shows the interactions between organisms across trophic levels. Arrows point from an organism that is consumed to the organism that consumes it. All the producers and consumers eventually become nourishment for the decomposers (fungi, mold, earthworms, and bacteria in the soil). (credit "fox": modification of work by Kevin Bacher, NPS; credit "owl": modification of work by John and Karen Hollingsworth, USFWS; credit "snake": modification of work by Steve Jurvetson; credit "robin": modification of work by Alan Vernon; credit "frog": modification of work by Alessandro Catenazzi; credit "spider": modification of work by "Sanba38"/Wikimedia Commons; credit "centipede": modification of work by “Bauerph”/Wikimedia Commons; credit "squirrel": modification of work by Dawn Huczek; credit "mouse": modification of work by NIGMS, NIH; credit "sparrow": modification of work by David Friel; credit "beetle": modification of work by Scott Bauer, USDA Agricultural Research Service; credit "mushrooms": modification of work by Chris Wee; credit "mold": modification of work by Dr. Lucille Georg, CDC; credit "earthworm": modification of work by Rob Hille; credit "bacteria": modification of work by Don Stalons, CDC)

CONCEPT IN ACTION

openstax COLLEGE™

Head to this online interactive simulator to investigate food web function. In the *Interactive Labs* box, under Food Web, click **Step 1**. Read the instructions first, and then click **Step 2** for additional instructions. When you are ready to create a simulation, in the upper-right corner of the *Interactive Labs* box, click **OPEN SIMULATOR**.

Two general types of food webs are often shown interacting within a single ecosystem. A grazing food web has plants or other photosynthetic organisms at its base, followed by herbivores and various carnivores. A detrital food web consists of a base of organisms that feed on decaying organic matter (dead organisms), including decomposers (which break down dead and decaying

organisms) and detritivores (which consume organic detritus). These organisms are usually bacteria, fungi, and invertebrate animals that recycle organic material back into the biotic part of the ecosystem as they themselves are consumed by other organisms. As ecosystems require a method to recycle material from dead organisms, grazing food webs have an associated detrital food web. For example, in a meadow ecosystem, plants may support a grazing food web of different organisms, primary and other levels of consumers, while at the same time supporting a detrital food web of bacteria and fungi feeding off dead plants and animals. Simultaneously, a detrital food web can contribute energy to a grazing food web, as when a robin eats an earthworm.

How Organisms Acquire Energy in a Food Web

All living things require energy in one form or another. Energy is used by most complex metabolic pathways (usually in the form of ATP), especially those responsible for building large molecules from smaller compounds. Living organisms would not be able to assemble macromolecules (proteins, lipids, nucleic acids, and complex carbohydrates) from their monomers without a constant energy input.

Food-web diagrams illustrate how energy flows directionally through ecosystems. They can also indicate how efficiently organisms acquire energy, use it, and how much remains for use by other organisms of the food web. Energy is acquired by living things in two ways: autotrophs harness light or chemical energy and heterotrophs acquire energy through the consumption and digestion of other living or previously living organisms.

Photosynthetic and chemosynthetic organisms are autotrophs, which are organisms capable of synthesizing their own food (more specifically, capable of using inorganic carbon as a carbon source). Photosynthetic autotrophs (photoautotrophs) use sunlight as an energy source, and chemosynthetic autotrophs (chemoautotrophs) use inorganic molecules as an energy source. Autotrophs are critical for most ecosystems: they are the producer trophic level. Without these organisms, energy would not be available to other living organisms, and life itself would not be possible.

Photoautotrophs, such as plants, algae, and photosynthetic bacteria, are the energy source for a majority of the world's ecosystems. These ecosystems are often described by grazing and detrital food webs. Photoautotrophs harness the Sun's solar energy by converting it to chemical energy in the form of ATP (and NADP). The energy stored in ATP is used to synthesize complex organic molecules, such as glucose. The rate at which photosynthetic producers incorporate energy from the Sun is called gross primary productivity. However, not all of the energy incorporated by producers is available to the other organisms in the food web because producers must also grow and reproduce, which consumes energy. Net primary productivity is the energy that remains in the producers after accounting for these organisms' respiration and heat loss. The net productivity is then available to the primary consumers at the next trophic level.

Chemoautotrophs are primarily bacteria and archaea that are found in rare ecosystems where sunlight is not available, such as those associated with dark caves or hydrothermal vents at the bottom of the ocean (Figure 19.4.6). Many chemoautotrophs in hydrothermal vents use hydrogen sulfide (H_2S), which is released from the vents as a source of chemical energy; this allows them to synthesize complex organic molecules, such as glucose, for their own energy and, in turn, supplies energy to the rest of the ecosystem.

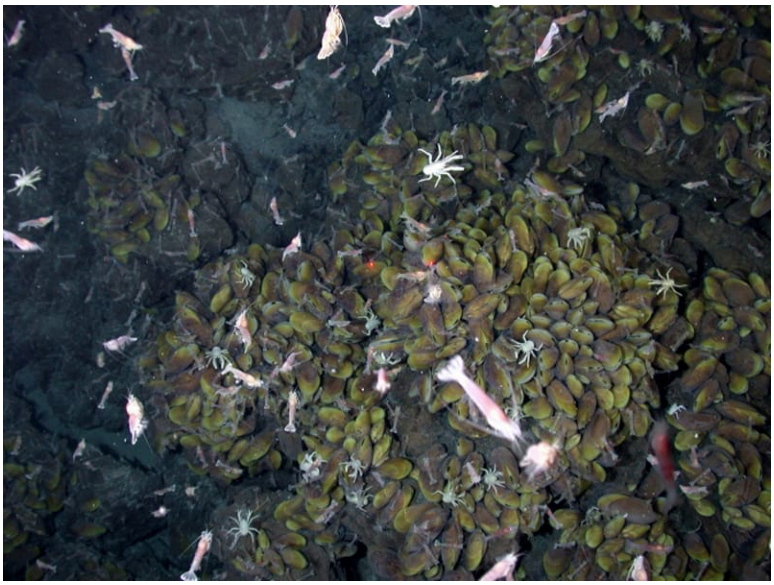


Figure 19.4.6**:** Swimming shrimp, a few squat lobsters, and hundreds of vent mussels are seen at a hydrothermal vent at the bottom of the ocean. As no sunlight penetrates to this depth, the ecosystem is supported by chemoautotrophic bacteria and organic material that sinks from the ocean's surface. This picture was taken in 2006 at the submerged NW Eifuku volcano off the coast of Japan by the National Oceanic and Atmospheric Administration (NOAA). The summit of this highly active volcano lies 1535 m below the surface.

Consequences of Food Webs: Biological Magnification

One of the most important consequences of ecosystem dynamics in terms of human impact is biomagnification. Biomagnification is the increasing concentration of persistent, toxic substances in organisms at each successive trophic level. These are substances that are fat soluble, not water soluble, and are stored in the fat reserves of each organism. Many substances have been shown to biomagnify, including classical studies with the pesticide dichlorodiphenyltrichloroethane (DDT), which were described in the 1960s bestseller, *Silent Spring* by Rachel Carson. DDT was a commonly used pesticide before its dangers to apex consumers, such as the bald eagle, became known. In aquatic ecosystems, organisms from each trophic level consumed many organisms in the lower level, which caused DDT to increase in birds (apex consumers) that ate fish. Thus, the birds accumulated sufficient amounts of DDT to cause fragility in their eggshells. This effect increased egg breakage during nesting and was shown to have devastating effects on these bird populations. The use of DDT was banned in the United States in the 1970s.

Other substances that biomagnify are polychlorinated biphenyls (PCB), which were used as coolant liquids in the United States until their use was banned in 1979, and heavy metals, such as mercury, lead, and cadmium. These substances are best studied in aquatic ecosystems, where predatory fish species accumulate very high concentrations of toxic substances that are at quite low concentrations in the environment and in producers. As illustrated in a study performed by the NOAA in the Saginaw Bay of Lake Huron of the North American Great Lakes (Figure 19.4.7), PCB concentrations increased from the producers of the ecosystem (phytoplankton) through the different trophic levels of fish species. The apex consumer, the walleye, has more than four times the amount of PCBs compared to phytoplankton. Also, based on results from other studies, birds that eat these fish may have PCB levels at least one order of magnitude higher than those found in the lake fish.

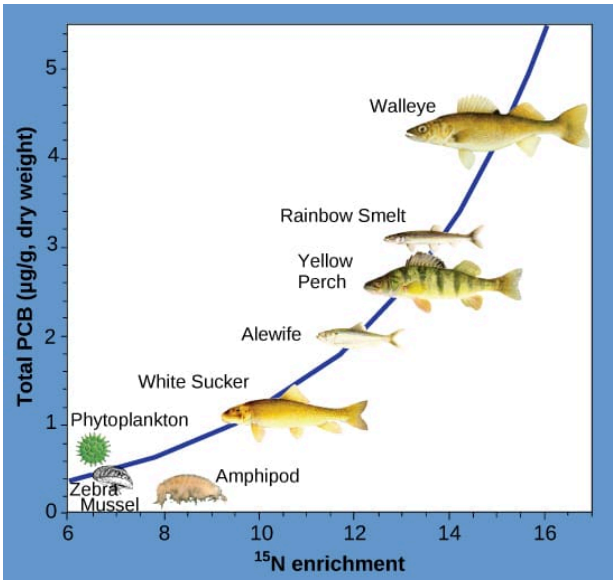


Figure 19.4.7**:** This chart shows the PCB concentrations found at the various trophic levels in the Saginaw Bay ecosystem of Lake Huron. Notice that the fish in the higher trophic levels accumulate more PCBs than those in lower trophic levels. (credit: Patricia Van Hoof, NOAA)

Other concerns have been raised by the biomagnification of heavy metals, such as mercury and cadmium, in certain types of seafood. The United States Environmental Protection Agency recommends that pregnant women and young children should not consume any swordfish, shark, king mackerel, or tilefish because of their high mercury content. These individuals are advised to eat fish low in mercury: salmon, shrimp, pollock, and catfish. Biomagnification is a good example of how ecosystem dynamics can affect our everyday lives, even influencing the food we eat.

Section Summary

Ecosystems exist underground, on land, at sea, and in the air. Organisms in an ecosystem acquire energy in a variety of ways, which is transferred between trophic levels as the energy flows from the base to the top of the food web, with energy being lost at each transfer. There is energy lost at each trophic level, so the lengths of food chains are limited because there is a point where not enough energy remains to support a population of consumers. Fat soluble compounds biomagnify up a food chain causing damage to top consumers. even when environmental concentrations of a toxin are low.

Glossary

autotroph
: an organism capable of synthesizing its own food molecules from smaller inorganic molecules

apex consumer
: an organism at the top of the food chain

biomagnification
: an increasing concentration of persistent, toxic substances in organisms at each trophic level, from the producers to the apex consumers

biome
: a large-scale community of organisms, primarily defined on land by the dominant plant types that exist in geographic regions of the planet with similar climatic conditions

chemoautotroph
: an organism capable of synthesizing its own food using energy from inorganic molecules

detrital food web
: a type of food web that is supported by dead or decaying organisms rather than by living autotrophs; these are often associated with grazing food webs within the same ecosystem

ecosystem
a community of living organisms and their interactions with their abiotic environment

equilibrium
the steady state of a system in which the relationships between elements of the system do not change

food chain
a linear sequence of trophic (feeding) relationships of producers, primary consumers, and higher level consumers

food web
a web of trophic (feeding) relationships among producers, primary consumers, and higher level consumers in an ecosystem

grazing food web
a type of food web in which the producers are either plants on land or phytoplankton in the water; often associated with a detrital food web within the same ecosystem

gross primary productivity
the rate at which photosynthetic producers incorporate energy from the Sun

net primary productivity
the energy that remains in the producers after accounting for the organisms' respiration and heat loss

photoautotroph
an organism that uses sunlight as an energy source to synthesize its own food molecules

primary consumer
the trophic level that obtains its energy from the producers of an ecosystem

producer
the trophic level that obtains its energy from sunlight, inorganic chemicals, or dead or decaying organic material

resilience (ecological)
the speed at which an ecosystem recovers equilibrium after being disturbed

resistance (ecological)
the ability of an ecosystem to remain at equilibrium in spite of disturbances

secondary consumer
a trophic level in an ecosystem, usually a carnivore that eats a primary consumer

tertiary consumer
a trophic level in an ecosystem, usually carnivores that eat other carnivores

trophic level
the position of a species or group of species in a food chain or a food web

Contributors and Attributions

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19.5: Importance of Biodiversity

Biodiversity is a broad term for biological variety, and it can be measured at a number of organizational levels. Traditionally, ecologists have measured biodiversity by taking into account both the number of species and the number of individuals in each of those species. However, biologists are using measures of biodiversity at several levels of biological organization (including genes, populations, and ecosystems) to help focus efforts to preserve the biologically and technologically important elements of biodiversity.

When biodiversity loss through extinction is thought of as the loss of the passenger pigeon, the dodo, or, even, the woolly mammoth there seems to be no reason to care about it because these events happened long ago. How is the loss practically important for the welfare of the human species? Would these species have made our lives any better? From the perspective of evolution and ecology, the loss of a particular individual species, with some exceptions, may seem unimportant, but the current accelerated extinction rate means the loss of tens of thousands of species within our lifetimes. Much of this loss is occurring in tropical rainforests like the one pictured in Figure 19.5.1, which are especially high-diversity ecosystems that are being cleared for timber and agriculture. This is likely to have dramatic effects on human welfare through the collapse of ecosystems and in added costs to maintain food production, clean air and water, and improve human health.



Figure 19.5.1**:** This tropical lowland rainforest in Madagascar is an example of a high biodiversity habitat. This particular location is protected within a national forest, yet only 10 percent of the original coastal lowland forest remains, and research suggests half the original biodiversity has been lost. (credit: Frank Vassen)

Biologists recognize that human populations are embedded in ecosystems and are dependent on them, just as is every other species on the planet. Agriculture began after early hunter-gatherer societies first settled in one place and heavily modified their immediate environment: the ecosystem in which they existed. This cultural transition has made it difficult for humans to recognize their dependence on living things other than crops and domesticated animals on the planet. Today our technology smoothes out the extremes of existence and allows many of us to live longer, more comfortable lives, but ultimately the human species cannot exist without its surrounding ecosystems. Our ecosystems provide our food. This includes living plants that grow in soil ecosystems and the animals that eat these plants (or other animals) as well as photosynthetic organisms in the oceans and the other organisms that eat them. Our ecosystems have provided and will provide many of the medications that maintain our health, which are commonly made from compounds found in living organisms. Ecosystems provide our clean water, which is held in lake and river ecosystems or passes through terrestrial ecosystems on its way into groundwater.

Types of Biodiversity

A common meaning of biodiversity is simply the number of species in a location or on Earth; for example, the American Ornithologists' Union lists 2078 species of birds in North and Central America. This is one measure of the bird biodiversity on the

continent. More sophisticated measures of diversity take into account the relative abundances of species. For example, a forest with 10 equally common species of trees is more diverse than a forest that has 10 species of trees wherein just one of those species makes up 95 percent of the trees rather than them being equally distributed. Biologists have also identified alternate measures of biodiversity, some of which are important in planning how to preserve biodiversity.

Genetic and Chemical Biodiversity

Genetic diversity is one alternate concept of biodiversity. Genetic diversity (or variation) is the raw material for adaptation in a species. A species' future potential for adaptation depends on the genetic diversity held in the genomes of the individuals in populations that make up the species. The same is true for higher taxonomic categories. A genus with very different types of species will have more genetic diversity than a genus with species that look alike and have similar ecologies. The genus with the greatest potential for subsequent evolution is the most genetically diverse one.

Most genes code for proteins, which in turn carry out the metabolic processes that keep organisms alive and reproducing. Genetic diversity can also be conceived of as chemical diversity in that species with different genetic makeups produce different assortments of chemicals in their cells (proteins as well as the products and byproducts of metabolism). This chemical diversity is important for humans because of the potential uses for these chemicals, such as medications. For example, the drug eptifibatide is derived from rattlesnake venom and is used to prevent heart attacks in individuals with certain heart conditions.

At present, it is far cheaper to discover compounds made by an organism than to imagine them and then synthesize them in a laboratory. Chemical diversity is one way to measure diversity that is important to human health and welfare. Through selective breeding, humans have domesticated animals, plants, and fungi, but even this diversity is suffering losses because of market forces and increasing globalism in human agriculture and migration. For example, international seed companies produce only a very few varieties of a given crop and provide incentives around the world for farmers to buy these few varieties while abandoning their traditional varieties, which are far more diverse. The human population depends on crop diversity directly as a stable food source and its decline is troubling to biologists and agricultural scientists.

Ecosystems Diversity

It is also useful to define ecosystem diversity: the number of different ecosystems on Earth or in a geographical area. Whole ecosystems can disappear even if some of the species might survive by adapting to other ecosystems. The loss of an ecosystem means the loss of the interactions between species, the loss of unique features of coadaptation, and the loss of biological productivity that an ecosystem is able to create. An example of a largely extinct ecosystem in North America is the prairie ecosystem (Figure 19.5.2). Prairies once spanned central North America from the boreal forest in northern Canada down into Mexico. They are now all but gone, replaced by crop fields, pasture lands, and suburban sprawl. Many of the species survive, but the hugely productive ecosystem that was responsible for creating our most productive agricultural soils is now gone. As a consequence, their soils are now being depleted unless they are maintained artificially at greater expense. The decline in soil productivity occurs because the interactions in the original ecosystem have been lost; this was a far more important loss than the relatively few species that were driven extinct when the prairie ecosystem was destroyed.



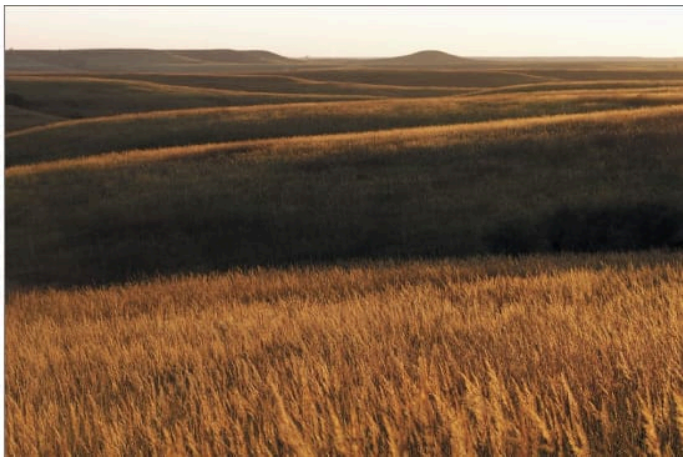


Figure 19.5.2: The variety of ecosystems on Earth—from coral reef to prairie—enables a great diversity of species to exist. (credit "coral reef": modification of work by Jim Maragos, USFWS; credit: "prairie": modification of work by Jim Minnerath, USFWS)

Current Species Diversity

Despite considerable effort, knowledge of the species that inhabit the planet is limited. A recent estimate suggests that the eukaryote species for which science has names, about 1.5 million species, account for less than 20 percent of the total number of eukaryote species present on the planet (8.7 million species, by one estimate). Estimates of numbers of prokaryotic species are largely guesses, but biologists agree that science has only just begun to catalog their diversity. Even with what is known, there is no centralized repository of names or samples of the described species; therefore, there is no way to be sure that the 1.5 million descriptions is an accurate number. It is a best guess based on the opinions of experts on different taxonomic groups. Given that Earth is losing species at an accelerating pace, science knows little about what is being lost. Table 19.5.1 presents recent estimates of biodiversity in different groups.

***Table** 19.5.1**:** Estimated Numbers of Described and Predicted species*

	Source: Mora et al 2011		Source: Chapman 2009		Source: Groombridge and Jenkins 2002	
	Described	Predicted	Described	Predicted	Described	Predicted
Animals	1,124,516	9,920,000	1,424,153	6,836,330	1,225,500	10,820,000
Photosynthetic protists	17,892	34,900	25,044	200,500	—	—
Fungi	44,368	616,320	98,998	1,500,000	72,000	1,500,000
Plants	224,244	314,600	310,129	390,800	270,000	320,000
Non-photosynthetic protists	16,236	72,800	28,871	1,000,000	80,000	600,000
Prokaryotes	—	—	10,307	1,000,000	10,175	—
Total	1,438,769	10,960,000	1,897,502	10,897,630	1,657,675	13,240,000

***Table** 19.5.1**:** This table shows the estimated number of species by taxonomic group—including both described (named and studied) and predicted (yet to be named) species.*

There are various initiatives to catalog described species in accessible and more organized ways, and the internet is facilitating that effort. Nevertheless, at the current rate of species description, which according to the State of Observed Species[1] reports is 17,000–20,000 new species a year, it would take close to 500 years to describe all of the species currently in existence. The task, however, is becoming increasingly impossible over time as extinctionremoves species from Earth faster than they can be described.

Naming and counting species may seem an unimportant pursuit given the other needs of humanity, but it is not simply an accounting. Describing species is a complex process by which biologists determine an organism's unique characteristics and whether or not that organism belongs to any other described species. It allows biologists to find and recognize the species after the initial discovery to follow up on questions about its biology. That subsequent research will produce the discoveries that make the species valuable to humans and to our ecosystems. Without a name and description, a species cannot be studied in depth and in a coordinated way by multiple scientists.

Patterns of Biodiversity

Biodiversity is not evenly distributed on the planet. Lake Victoria contained almost 500 species of cichlids (only one family of fishes present in the lake) before the introduction of an exotic species in the 1980s and 1990s caused a mass extinction. All of these species were found only in Lake Victoria, which is to say they were endemic. Endemic species are found in only one location. For example, the blue jay is endemic to North America, while the Barton Springs salamander is endemic to the mouth of one spring in Austin, Texas. Endemics with highly restricted distributions, like the Barton Springs salamander, are particularly vulnerable to extinction. Higher taxonomic levels, such as genera and families, can also be endemic.

Lake Huron contains about 79 species of fish, all of which are found in many other lakes in North America. What accounts for the difference in diversity between Lake Victoria and Lake Huron? Lake Victoria is a tropical lake, while Lake Huron is a temperate lake. Lake Huron in its present form is only about 7,000 years old, while Lake Victoria in its present form is about 15,000 years old. These two factors, latitude and age, are two of several hypotheses biogeographers have suggested to explain biodiversity patterns on Earth.

CAREER IN ACTION: Biogeography

Biogeography is the study of the distribution of the world's species both in the past and in the present. The work of biogeographers is critical to understanding our physical environment, how the environment affects species, and how changes in environment impact the distribution of a species.

There are three main fields of study under the heading of biogeography: ecological biogeography, historical biogeography (called paleobiogeography), and conservation biogeography. Ecological biogeography studies the current factors affecting the distribution of plants and animals. Historical biogeography, as the name implies, studies the past distribution of species. Conservation biogeography, on the other hand, is focused on the protection and restoration of species based upon the known historical and current ecological information. Each of these fields considers both zoogeography and phytogeography—the past and present distribution of animals and plants.

One of the oldest observed patterns in ecology is that biodiversity in almost every taxonomic group of organism increases as latitude declines. In other words, biodiversity increases closer to the equator (Figure 19.5.3).

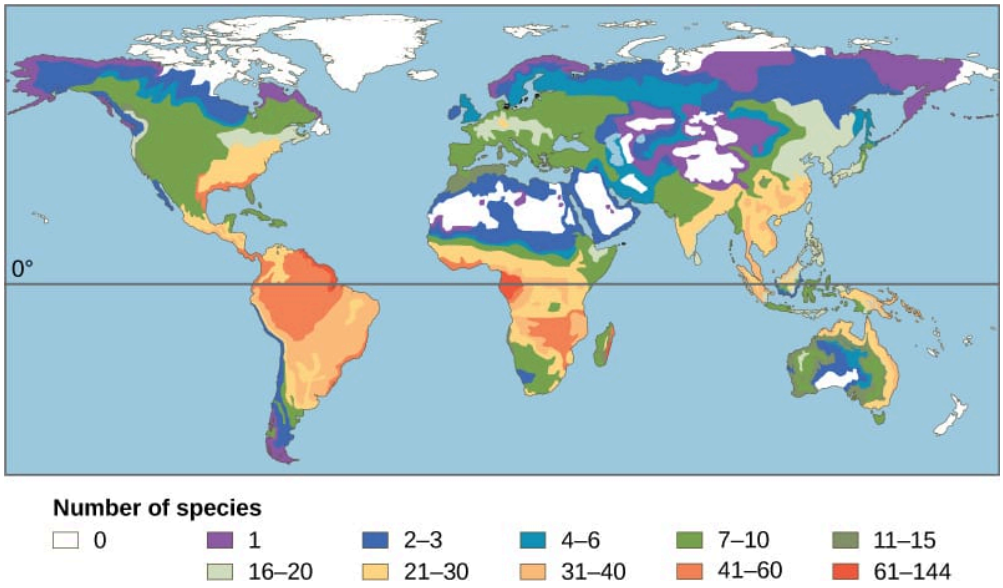


Figure 19.5.3: This map illustrates the number of amphibian species across the globe and shows the trend toward higher biodiversity at lower latitudes. A similar pattern is observed for most taxonomic groups.

It is not yet clear why biodiversity increases closer to the equator, but hypotheses include the greater age of the ecosystems in the tropics versus temperate regions, which were largely devoid of life or drastically impoverished during the last ice age. The greater age provides more time for speciation. Another possible explanation is the greater energy the tropics receive from the sun versus the lesser energy input in temperate and polar regions. But scientists have not been able to explain how greater energy input could translate into more species. The complexity of tropical ecosystems may promote speciation by increasing the habitat heterogeneity, or number of ecological niches, in the tropics relative to higher latitudes. The greater heterogeneity provides more opportunities for coevolution, specialization, and perhaps greater selection pressures leading to population differentiation. However, this hypothesis suffers from some circularity—ecosystems with more species encourage speciation, but how did they get more species to begin with? The tropics have been perceived as being more stable than temperate regions, which have a pronounced climate and day-length seasonality. The tropics have their own forms of seasonality, such as rainfall, but they are generally assumed to be more stable environments and this stability might promote speciation.

Regardless of the mechanisms, it is certainly true that biodiversity is greatest in the tropics. The number of endemic species is higher in the tropics. The tropics also contain more biodiversity hotspots. At the same time, our knowledge of the species living in the tropics is lowest and because of recent, heavy human activity the potential for biodiversity loss is greatest.

Importance of Biodiversity

Loss of biodiversity eventually threatens other species we do not impact directly because of their interconnectedness; as species disappear from an ecosystem other species are threatened by the changes in available resources. Biodiversity is important to the survival and welfare of human populations because it has impacts on our health and our ability to feed ourselves through agriculture and harvesting populations of wild animals.

Human Health

Many medications are derived from natural chemicals made by a diverse group of organisms. For example, many plants produce secondary plant compounds, which are toxins used to protect the plant from insects and other animals that eat them. Some of these secondary plant compounds also work as human medicines. Contemporary societies that live close to the land often have a broad knowledge of the medicinal uses of plants growing in their area. For centuries in Europe, older knowledge about the medical uses of plants was compiled in herbals—books that identified the plants and their uses. Humans are not the only animals to use plants for medicinal reasons. The other great apes, orangutans, chimpanzees, bonobos, and gorillas have all been observed self-medicating with plants.

Modern pharmaceutical science also recognizes the importance of these plant compounds. Examples of significant medicines derived from plant compounds include aspirin, codeine, digoxin, atropine, and vincristine (Figure 19.5.4). Many medications were once derived from plant extracts but are now synthesized. It is estimated that, at one time, 25 percent of modern drugs contained at least one plant extract. That number has probably decreased to about 10 percent as natural plant ingredients are replaced by synthetic versions of the plant compounds. Antibiotics, which are responsible for extraordinary improvements in health and lifespans in developed countries, are compounds largely derived from fungi and bacteria.



Figure 19.5.4: Catharanthus roseus, the Madagascar periwinkle, has various medicinal properties. Among other uses, it is a source of vincristine, a drug used in the treatment of lymphomas. (credit: Forest and Kim Starr)

In recent years, animal venoms and poisons have excited intense research for their medicinal potential. By 2007, the FDA had approved five drugs based on animal toxins to treat diseases such as hypertension, chronic pain, and diabetes. Another five drugs are undergoing clinical trials and at least six drugs are being used in other countries. Other toxins under investigation come from mammals, snakes, lizards, various amphibians, fish, snails, octopuses, and scorpions.

Aside from representing billions of dollars in profits, these medications improve people's lives. Pharmaceutical companies are actively looking for new natural compounds that can function as medicines. It is estimated that one third of pharmaceutical research and development is spent on natural compounds and that about 35 percent of new drugs brought to market between 1981 and 2002 were from natural compounds.

Finally, it has been argued that humans benefit psychologically from living in a biodiverse world. The chief proponent of this idea is entomologist E. O. Wilson. He argues that human evolutionary history has adapted us to living in a natural environment

and that built environments generate stresses that affect human health and well-being. There is considerable research into the psychologically regenerative benefits of natural landscapes that suggest the hypothesis may hold some truth.

Agricultural

Since the beginning of human agriculture more than 10,000 years ago, human groups have been breeding and selecting crop varieties. This crop diversity matched the cultural diversity of highly subdivided populations of humans. For example, potatoes were domesticated beginning around 7,000 years ago in the central Andes of Peru and Bolivia. The people in this region traditionally lived in relatively isolated settlements separated by mountains. The potatoes grown in that region belong to seven species and the number of varieties likely is in the thousands. Each variety has been bred to thrive at particular elevations and soil and climate conditions. The diversity is driven by the diverse demands of the dramatic elevation changes, the limited movement of people, and the demands created by crop rotation for different varieties that will do well in different fields.

Potatoes are only one example of agricultural diversity. Every plant, animal, and fungus that has been cultivated by humans has been bred from original wild ancestor species into diverse varieties arising from the demands for food value, adaptation to growing conditions, and resistance to pests. The potato demonstrates a well-known example of the risks of low crop diversity: during the tragic Irish potato famine (1845–1852 AD), the single potato variety grown in Ireland became susceptible to a potato blight—wiping out the crop. The loss of the crop led to famine, death, and mass emigration. Resistance to disease is a chief benefit to maintaining crop biodiversity and lack of diversity in contemporary crop species carries similar risks. Seed companies, which are the source of most crop varieties in developed countries, must continually breed new varieties to keep up with evolving pest organisms. These same seed companies, however, have participated in the decline of the number of varieties available as they focus on selling fewer varieties in more areas of the world replacing traditional local varieties.

The ability to create new crop varieties relies on the diversity of varieties available and the availability of wild forms related to the crop plant. These wild forms are often the source of new gene variants that can be bred with existing varieties to create varieties with new attributes. Loss of wild species related to a crop will mean the loss of potential in crop improvement. Maintaining the genetic diversity of wild species related to domesticated species ensures our continued supply of food.

Since the 1920s, government agriculture departments have maintained seed banks of crop varieties as a way to maintain crop diversity. This system has flaws because over time seed varieties are lost through accidents and there is no way to replace them. In 2008, the Svalbard Global seed Vault, located on Spitsbergen island, Norway, (Figure 19.5.5) began storing seeds from around the world as a backup system to the regional seed banks. If a regional seed bank stores varieties in Svalbard, losses can be replaced from Svalbard should something happen to the regional seeds. The Svalbard seed vault is deep into the rock of the arctic island. Conditions within the vault are maintained at ideal temperature and humidity for seed survival, but the deep underground location of the vault in the arctic means that failure of the vault's systems will not compromise the climatic conditions inside the vault.

ART CONNECTION



Figure 19.5.5**:** The Svalbard Global Seed Vault is a storage facility for seeds of Earth's diverse crops. (credit: Mari Tefre, Svalbard Global Seed Vault)

The Svalbard seed vault is located on Spitsbergen island in Norway, which has an arctic climate. Why might an arctic climate be good for seed storage?

Although crops are largely under our control, our ability to grow them is dependent on the biodiversity of the ecosystems in which they are grown. That biodiversity creates the conditions under which crops are able to grow through what are known as ecosystem services—valuable conditions or processes that are carried out by an ecosystem. Crops are not grown, for the most part, in built environments. They are grown in soil. Although some agricultural soils are rendered sterile using controversial pesticide treatments, most contain a huge diversity of organisms that maintain nutrient cycles—breaking down organic matter into nutrient compounds that crops need for growth. These organisms also maintain soil texture that affects water and oxygen dynamics in the soil that are necessary for plant growth. Replacing the work of these organisms in forming arable soil is not practically possible. These kinds of processes are called ecosystem services. They occur within ecosystems, such as soil ecosystems, as a result of the diverse metabolic activities of the organisms living there, but they provide benefits to human food production, drinking water availability, and breathable air.

Other key ecosystem services related to food production are plant pollination and crop pest control. It is estimated that honeybee pollination within the United States brings in $1.6 billion per year; other pollinators contribute up to $6.7 billion. Over 150 crops in the United States require pollination to produce. Many honeybee populations are managed by beekeepers who rent out their hives' services to farmers. Honeybee populations in North America have been suffering large losses caused by a syndrome known as colony collapse disorder, a new phenomenon with an unclear cause. Other pollinators include a diverse array of other bee species and various insects and birds. Loss of these species would make growing crops requiring pollination impossible, increasing dependence on other crops.

Finally, humans compete for their food with crop pests, most of which are insects. Pesticides control these competitors, but these are costly and lose their effectiveness over time as pest populations adapt. They also lead to collateral damage by killing non-pest species as well as beneficial insects like honeybees, and risking the health of agricultural workers and consumers. Moreover, these pesticides may migrate from the fields where they are applied and do damage to other ecosystems like streams, lakes, and even the ocean. Ecologists believe that the bulk of the work in removing pests is actually done by predators and parasites of those pests, but the impact has not been well studied. A review found that in 74 percent of studies that looked for an effect of landscape complexity (forests and fallow fields near to crop fields) on natural enemies of pests, the greater the complexity, the greater the effect of pest-suppressing organisms. Another experimental study found that introducing multiple enemies of pea aphids (an important alfalfa pest) increased the yield of alfalfa significantly. This study shows that a diversity of pests is more effective at control than one single pest. Loss of diversity in pest enemies will inevitably make it more difficult and costly to grow food. The world's growing human population faces significant challenges in the increasing costs and other difficulties associated with producing food.

Wild Food Sources

In addition to growing crops and raising food animals, humans obtain food resources from wild populations, primarily wild fish populations. For about one billion people, aquatic resources provide the main source of animal protein. But since 1990, production from global fisheries has declined. Despite considerable effort, few fisheries on Earth are managed sustainability.

Fishery extinctions rarely lead to complete extinction of the harvested species, but rather to a radical restructuring of the marine ecosystem in which a dominant species is so over-harvested that it becomes a minor player, ecologically. In addition to humans losing the food source, these alterations affect many other species in ways that are difficult or impossible to predict. The collapse of fisheries has dramatic and long-lasting effects on local human populations that work in the fishery. In addition, the loss of an inexpensive protein source to populations that cannot afford to replace it will increase the cost of living and limit societies in other ways. In general, the fish taken from fisheries have shifted to smaller species and the larger species are overfished. The ultimate outcome could clearly be the loss of aquatic systems as food sources.

Summary

Biodiversity exists at multiple levels of organization, and is measured in different ways depending on the goals of those taking the measurements. These include numbers of species, genetic diversity, chemical diversity, and ecosystem diversity. The number of described species is estimated to be 1.5 million with about 17,000 new species being described each year. Estimates for the total number of eukaryotic species on Earth vary but are on the order of 10 million. Biodiversity is negatively correlated with latitude for most taxa, meaning that biodiversity is higher in the tropics. The mechanism for this pattern is not known with certainty, but several plausible hypotheses have been advanced.

Humans use many compounds that were first discovered or derived from living organisms as medicines: secondary plant compounds, animal toxins, and antibiotics produced by bacteria and fungi. More medicines are expected to be discovered in nature. Loss of biodiversity will impact the number of pharmaceuticals available to humans. Biodiversity may provide important psychological benefits to humans.

Crop diversity is a requirement for food security, and it is being lost. The loss of wild relatives to crops also threatens breeders' abilities to create new varieties. Ecosystems provide ecosystem services that support human agriculture: pollination, nutrient cycling, pest control, and soil development and maintenance. Loss of biodiversity threatens these ecosystem services and risks making food production more expensive or impossible. Wild food sources are mainly aquatic, but few are being managed for sustainability. Fisheries' ability to provide protein to human populations is threatened when extinction occurs.

Art Connections

Figure 19.5.5: The Svalbard seed vault is located on Spitsbergen island in Norway, which has an arctic climate. Why might an arctic climate be good for seed storage?

Answer

The ground is permanently frozen so the seeds will keep, even if the electricity fails.

Footnotes

1. 1 International Institute for Species Exploration (IISE), *2011 State of Observed Species (SOS)*. Tempe, AZ: IISE, 2011. Accessed May, 20, 2012. species.asu.edu/SOS.

Glossary

biodiversity
the variety of a biological system, typically conceived as the number of species, but also applying to genes, biochemistry, and ecosystems

chemical diversity
the variety of metabolic compounds in an ecosystem

ecosystem diversity
: the variety of ecosystems

endemic species
: a species native to one place

extinction
: the disappearance of a species from Earth; local extinction is the disappearance of a species from a region

genetic diversity
: the variety of genes and alleles in a species or other taxonomic group or ecosystem; the term can refer to allelic diversity or genome-wide diversity

habitat heterogeneity
: the number of ecological niches

secondary plant compound
: a compound produced as a byproduct of plant metabolic processes that is typically toxic, but is sequestered by the plant to defend against herbivores

Contributors and Attributions

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19.6: Threats to Biodiversity

The core threat to biodiversity on the planet, and therefore a threat to human welfare, is the combination of human population growth and the resources used by that population. The human population requires resources to survive and grow, and those resources are being removed unsustainably from the environment. The three greatest proximate threats to biodiversity are habitat loss, overharvesting, and introduction of exotic species. The first two of these are a direct result of human population growth and resource use. The third results from increased mobility and trade. A fourth major cause of extinction, anthropogenic (human-caused) climate change, has not yet had a large impact, but it is predicted to become significant during this century. Global climate change is also a consequence of human population needs for energy and the use of fossil fuels to meet those needs (Figure 19.6.1). Environmental issues, such as toxic pollution, have specific targeted effects on species, but are not generally seen as threats at the magnitude of the others.

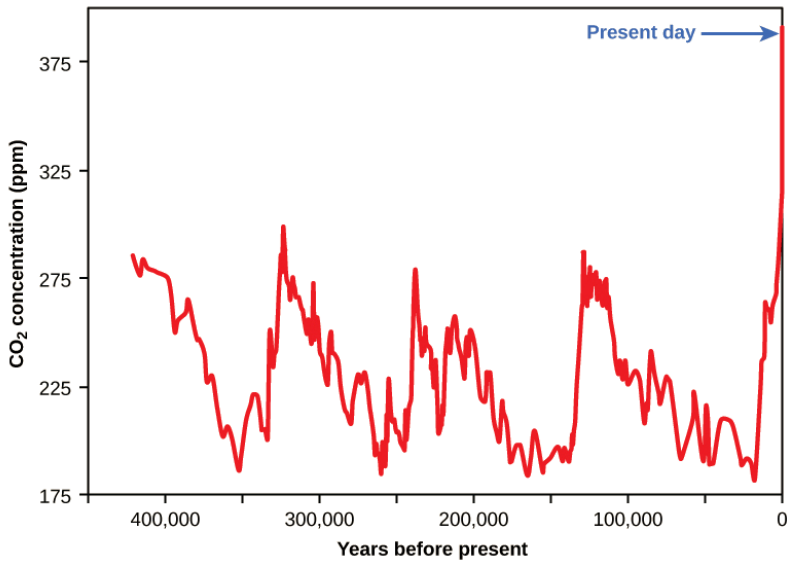


Figure 19.6.1**:** Atmospheric carbon dioxide levels fluctuate in a cyclical manner. However, the burning of fossil fuels in recent history has caused a dramatic increase in the levels of carbon dioxide in the Earth's atmosphere, which have now reached levels never before seen recently on Earth. Scientists predict that the addition of this "greenhouse gas" to the atmosphere is resulting in climate change that will significantly impact biodiversity in the coming century.

Habitat Loss

Humans rely on technology to modify their environment and replace certain functions that were once performed by the natural ecosystem. Other species cannot do this. Elimination of their habitat—whether it is a forest, coral reef, grassland, or flowing river—will kill the individuals in the species. Remove the entire habitat within the range of a species and, unless they are one of the few species that do well in human-built environments, the species will become extinct. Human destruction of habitats (habitats generally refer to the part of the ecosystem required by a particular species) accelerated in the latter half of the twentieth century. Consider the exceptional biodiversity of Sumatra: it is home to one species of orangutan, a species of critically endangered elephant, and the Sumatran tiger, but half of Sumatra's forest is now gone. The neighboring island of Borneo, home to the other species of orangutan, has lost a similar area of forest. Forest loss continues in protected areas of Borneo. The orangutan in Borneo is listed as endangered by the International Union for Conservation of Nature (IUCN), but it is simply the most visible of thousands of species that will not survive the disappearance of the forests of Borneo. The forests are removed for timber and to plant palm oil plantations (Figure 19.6.2). Palm oil is used in many products including food products, cosmetics, and biodiesel in Europe. A 5-year estimate of global forest cover loss for the years from 2000 to 2005 was 3.1 percent. Much loss (2.4 percent) occurred in the humid tropics where forest loss is primarily from timber extraction. These losses certainly also represent the extinction of species unique to those areas.



Figure 19.6.2**:** An oil palm plantation in Sabah province Borneo, Malaysia, replaces native forest habitat that a variety of species depended on to live. (credit: Lian Pin Koh)

BIOLOGY IN ACTION: Preventing Habitat Destruction with Wise Wood Choices

Most consumers do not imagine that the home improvement products they buy might be contributing to habitat loss and species extinctions. Yet the market for illegally harvested tropical timber is huge, and the wood products often find themselves in building supply stores in the United States. One estimate is that 10 percent of the imported timber stream in the United States, which is the world's largest consumer of wood products, is potentially illegally logged. In 2006, this amounted to $3.6 billion in wood products. Most of the illegal products are imported from countries that act as intermediaries and are not the originators of the wood.

How is it possible to determine if a wood product, such as flooring, was harvested sustainably or even legally? The Forest Stewardship Council (FSC) certifies sustainably harvested forest products; therefore, looking for their certification on flooring and other hardwood products is one way to ensure that the wood has not been taken illegally from a tropical forest. Certification applies to specific products, not to a producer; some producers' products may not have certification while other products are certified. There are certifications other than the FSC, but these are run by timber companies creating a conflict of interest. Another approach is to buy domestic wood species. While it would be great if there was a list of legal versus illegal woods, it is not that simple. Logging and forest management laws vary from country to country; what is illegal in one country may be legal in another. Where and how a product is harvested and whether the forest from which it comes is being sustainably maintained all factor into whether a wood product will be certified by the FSC. It is always a good idea to ask questions about where a wood product came from and how the supplier knows that it was harvested legally.

Habitat destruction can affect ecosystems other than forests. Rivers and streams are important ecosystems and are frequently the target of habitat modification through building and from damming or water removal. Damming of rivers affects flows and access to all parts of a river. Altering a flow regime can reduce or eliminate populations that are adapted to seasonal changes in flow. For example, an estimated 91 percent of river lengths in the United States have been modified with damming or bank modifications. Many fish species in the United States, especially rare species or species with restricted distributions, have seen declines caused by river damming and habitat loss. Research has confirmed that species of amphibians that must carry out parts of their life cycles in both aquatic and terrestrial habitats are at greater risk of population declines and extinction because of the increased likelihood that one of their habitats or access between them will be lost. This is of particular concern because amphibians have been declining in numbers and going extinct more rapidly than many other groups for a variety of possible reasons.

Overharvesting

Overharvesting is a serious threat to many species, but particularly to aquatic species. There are many examples of regulated fisheries (including hunting of marine mammals and harvesting of crustaceans and other species) monitored by fisheries

scientists that have nevertheless collapsed. The western Atlantic cod fishery is the most spectacular recent collapse. While it was a hugely productive fishery for 400 years, the introduction of modern factory trawlers in the 1980s and the pressure on the fishery led to it becoming unsustainable. The causes of fishery collapse are both economic and political in nature. Most fisheries are managed as a common resource, available to anyone willing to fish, even when the fishing territory lies within a country's territorial waters. Common resources are subject to an economic pressure known as the tragedy of the commons, in which fishers have little motivation to exercise restraint in harvesting a fishery when they do not own the fishery. The general outcome of harvests of resources held in common is their overexploitation. While large fisheries are regulated to attempt to avoid this pressure, it still exists in the background. This overexploitation is exacerbated when access to the fishery is open and unregulated and when technology gives fishers the ability to overfish. In a few fisheries, the biological growth of the resource is less than the potential growth of the profits made from fishing if that time and money were invested elsewhere. In these cases—whales are an example—economic forces will drive toward fishing the population to extinction.

CONCEPT IN ACTION

Explore a U.S. Fish & Wildlife Service interactive map of critical habitat for endangered and threatened species in the United States. To begin, select "Visit the online mapper."

For the most part, fishery extinction is not equivalent to biological extinction—the last fish of a species is rarely fished out of the ocean. But there are some instances in which true extinction is a possibility. Whales have slow-growing populations and are at risk of complete extinction through hunting. Also, there are some species of sharks with restricted distributions that are at risk of extinction. The groupers are another population of generally slow-growing fishes that, in the Caribbean, includes a number of species that are at risk of extinction from overfishing.

Coral reefs are extremely diverse marine ecosystems that face peril from several processes. Reefs are home to 1/3 of the world's marine fish species—about 4000 species—despite making up only one percent of marine habitat. Most home marine aquaria house coral reef species that are wild-caught organisms—not cultured organisms. Although no marine species is known to have been driven extinct by the pet trade, there are studies showing that populations of some species have declined in response to harvesting, indicating that the harvest is not sustainable at those levels. There are also concerns about the effect of the pet trade on some terrestrial species such as turtles, amphibians, birds, plants, and even the orangutans.

Bush meat is the generic term used for wild animals killed for food. Hunting is practiced throughout the world, but hunting practices, particularly in equatorial Africa and parts of Asia, are believed to threaten several species with extinction. Traditionally, bush meat in Africa was hunted to feed families directly; however, recent commercialization of the practice now has bush meat available in grocery stores, which has increased harvest rates to the level of unsustainability. Additionally, human population growth has increased the need for protein foods that are not being met from agriculture. Species threatened by the bush meat trade are mostly mammals including many monkeys and the great apes living in the Congo basin.

Exotic Species

Exotic species are species that have been intentionally or unintentionally introduced by humans into an ecosystem in which they did not evolve. Human transportation of people and goods, including the intentional transport of organisms for trade, has dramatically increased the introduction of species into new ecosystems. These new introductions are sometimes at distances that are well beyond the capacity of the species to ever travel itself and outside the range of the species' natural predators.

Most exotic species introductions probably fail because of the low number of individuals introduced or poor adaptation to the ecosystem they enter. Some species, however, have characteristics that can make them especially successful in a new ecosystem. These exotic species often undergo dramatic population increases in their new habitat and reset the ecological conditions in the new environment, threatening the species that exist there. When this happens, the exotic species also becomes an invasive species. Invasive species can threaten other species through competition for resources, predation, or disease.

CONCEPT IN ACTION

Explore this interactive global database of exotic or invasive species.

Lakes and islands are particularly vulnerable to extinction threats from introduced species. In Lake Victoria, the intentional

introduction of the Nile perch was largely responsible for the extinction of about 200 species of cichlids. The accidental introduction of the brown tree snake via aircraft (Figure 19.6.3) from the Solomon Islands to Guam in 1950 has led to the extinction of three species of birds and three to five species of reptiles endemic to the island. Several other species are still threatened. The brown tree snake is adept at exploiting human transportation as a means to migrate; one was even found on an aircraft arriving in Corpus Christi, Texas. Constant vigilance on the part of airport, military, and commercial aircraft personnel is required to prevent the snake from moving from Guam to other islands in the Pacific, especially Hawaii. Islands do not make up a large area of land on the globe, but they do contain a disproportionate number of endemic species because of their isolation from mainland ancestors.



Figure 19.6.3**:** The brown tree snake, Boiga irregularis, is an exotic species that has caused numerous extinctions on the island of Guam since its accidental introduction in 1950. (credit: NPS)

Many introductions of aquatic species, both marine and freshwater, have occurred when ships have dumped ballast water taken on at a port of origin into waters at a destination port. Water from the port of origin is pumped into tanks on a ship empty of cargo to increase stability. The water is drawn from the ocean or estuary of the port and typically contains living organisms such as plant parts, microorganisms, eggs, larvae, or aquatic animals. The water is then pumped out before the ship takes on cargo at the destination port, which may be on a different continent. The zebra mussel was introduced to the Great Lakes from Europe prior to 1988 in ship ballast. The zebra mussels in the Great Lakes have cost the industry millions of dollars in clean up costs to maintain water intakes and other facilities. The mussels have also altered the ecology of the lakes dramatically. They threaten native mollusk populations, but have also benefited some species, such as smallmouth bass. The mussels are filter feeders and have dramatically improved water clarity, which in turn has allowed aquatic plants to grow along shorelines, providing shelter for young fish where it did not exist before. The European green crab, *Carcinus maenas*, was introduced to San Francisco Bay in the late 1990s, likely in ship ballast water, and has spread north along the coast to Washington. The crabs have been found to dramatically reduce the abundance of native clams and crabs with resulting increases in the prey of native crabs.

Invading exotic species can also be disease organisms. It now appears that the global decline in amphibian species recognized in the 1990s is, in some part, caused by the fungus *Batrachochytrium dendrobatidis*, which causes the disease chytridiomycosis (Figure 19.6.4). There is evidence that the fungus is native to Africa and may have been spread throughout the world by transport of a commonly used laboratory and pet species: the African clawed frog, *Xenopus laevis*. It may well be that biologists themselves are responsible for spreading this disease worldwide. The North American bullfrog, *Rana catesbeiana*, which has also been widely introduced as a food animal but which easily escapes captivity, survives most infections of *B. dendrobatidis* and can act as a reservoir for the disease.



Figure 19.6.4**:** This Limosa harlequin frog (Atelopus limosus), an endangered species from Panama, died from a fungal disease called chytridiomycosis. The red lesions are symptomatic of the disease. (credit: Brian Gratwicke)

Early evidence suggests that another fungal pathogen, *Geomyces destructans*, introduced from Europe is responsible for white-nose syndrome, which infects cave-hibernating bats in eastern North America and has spread from a point of origin in western New York State (Figure 19.6.5). The disease has decimated bat populations and threatens extinction of species already listed as endangered: the Indiana bat, *Myotis sodalis*, and potentially the Virginia big-eared bat, *Corynorhinus townsendii virginianus*. How the fungus was introduced is unknown, but one logical presumption would be that recreational cavers unintentionally brought the fungus on clothes or equipment from Europe.



Figure 19.6.5**:** This little brown bat in Greeley Mine, Vermont, March 26, 2009, was found to have white-nose syndrome. (credit: modification of work by Marvin Moriarty, USFWS)

Climate Change

Climate change, and specifically the anthropogenic warming trend presently underway, is recognized as a major extinction threat, particularly when combined with other threats such as habitat loss. Anthropogenic warming of the planet has been observed and is hypothesized to continue due to past and continuing emission of greenhouse gases, primarily carbon dioxide and methane, into the atmosphere caused by the burning of fossil fuels and deforestation. These gases decrease the degree to which Earth is able to radiate heat energy created by the sunlight that enters the atmosphere. The changes in climate and energy balance

caused by increasing greenhouse gases are complex and our understanding of them depends on predictions generated from detailed computer models. Scientists generally agree the present warming trend is caused by humans and some of the likely effects include dramatic and dangerous climate changes in the coming decades. However, there is still debate and a lack of understanding about specific outcomes. Scientists disagree about the likely magnitude of the effects on extinction rates, with estimates ranging from 15 to 40 percent of species committed to extinction by 2050. Scientists do agree that climate change will alter regional climates, including rainfall and snowfall patterns, making habitats less hospitable to the species living in them. The warming trend will shift colder climates toward the north and south poles, forcing species to move with their adapted climate norms, but also to face habitat gaps along the way. The shifting ranges will impose new competitive regimes on species as they find themselves in contact with other species not present in their historic range. One such unexpected species contact is between polar bears and grizzly bears. Previously, these two species had separate ranges. Now, their ranges are overlapping and there are documented cases of these two species mating and producing viable offspring. Changing climates also throw off the delicate timing adaptations that species have to seasonal food resources and breeding times. Scientists have already documented many contemporary mismatches to shifts in resource availability and timing.

Range shifts are already being observed: for example, on average, European bird species ranges have moved 91 km (56.5 mi) northward. The same study suggested that the optimal shift based on warming trends was double that distance, suggesting that the populations are not moving quickly enough. Range shifts have also been observed in plants, butterflies, other insects, freshwater fishes, reptiles, amphibians, and mammals.

Climate gradients will also move up mountains, eventually crowding species higher in altitude and eliminating the habitat for those species adapted to the highest elevations. Some climates will completely disappear. The rate of warming appears to be accelerated in the arctic, which is recognized as a serious threat to polar bear populations that require sea ice to hunt seals during the winter months: seals are the only source of protein available to polar bears. A trend to decreasing sea ice coverage has occurred since observations began in the mid-twentieth century. The rate of decline observed in recent years is far greater than previously predicted by climate models (Figure 19.6.6).



Figure 19.6.6: The effect of global warming can be seen in the continuing retreat of Grinnell Glacier. The mean annual temperature in Glacier National Park has increased 1.33°C since 1900. The loss of a glacier results in the loss of summer meltwaters, sharply reducing seasonal water supplies and severely affecting local ecosystems. (credit: USGS, GNP Archives)

Finally, global warming will raise ocean levels due to meltwater from glaciers and the greater volume occupied by warmer water. Shorelines will be inundated, reducing island size, which will have an effect on some species, and a number of islands will disappear entirely. Additionally, the gradual melting and subsequent refreezing of the poles, glaciers, and higher elevation mountains—a cycle that has provided freshwater to environments for centuries—will be altered. This could result in an overabundance of salt water and a shortage of fresh water.

Summary

The core threats to biodiversity are human population growth and unsustainable resource use. To date, the most significant causes of extinction are habitat loss, introduction of exotic species, and overharvesting. Climate change is predicted to be

a significant cause of extinction in the coming century. Habitat loss occurs through deforestation, damming of rivers, and other activities. Overharvesting is a threat particularly to aquatic species, but the taking of bush meat in the humid tropics threatens many species in Asia, Africa, and the Americas. Exotic species have been the cause of a number of extinctions and are especially damaging to islands and lakes. Exotic species' introductions are increasing because of the increased mobility of human populations and growing global trade and transportation. Climate change is forcing range changes that may lead to extinction. It is also affecting adaptations to the timing of resource availability that negatively affects species in seasonal environments. The impacts of climate change are currently greatest in the arctic. Global warming will also raise sea levels, eliminating some islands and reducing the area of all others.

Glossary

bush meat
: a wild-caught animal used as food (typically mammals, birds, and reptiles); usually referring to hunting in the tropics of sub-Saharan Africa, Asia, and the Americas

chytridiomycosis
: a disease of amphibians caused by the fungus *Batrachochytrium dendrobatidis;* thought to be a major cause of the global amphibian decline

exotic species
: (also, invasive species) a species that has been introduced to an ecosystem in which it did not evolve

tragedy of the commons
: an economic principle that resources held in common will inevitably be over-exploited

white-nose syndrome
: a disease of cave-hibernating bats in the eastern United States and Canada associated with the fungus *Geomyces destructans*

Contributors and Attributions

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19.7: Preserving Biodiversity

Preserving biodiversity is an extraordinary challenge that must be met by greater understanding of biodiversity itself, changes in human behavior and beliefs, and various preservation strategies.

Change in Biodiversity through Time

The number of species on the planet, or in any geographical area, is the result of an equilibrium of two evolutionary processes that are ongoing: speciation and extinction. Both are natural “birth” and “death” processes of macroevolution. When speciation rates begin to outstrip extinction rates, the number of species will increase; likewise, the reverse is true when extinction rates begin to overtake speciation rates. Throughout the history of life on Earth, as reflected in the fossil record, these two processes have fluctuated to a greater or lesser extent, sometimes leading to dramatic changes in the number of species on the planet as reflected in the fossil record (Figure 19.7.1).

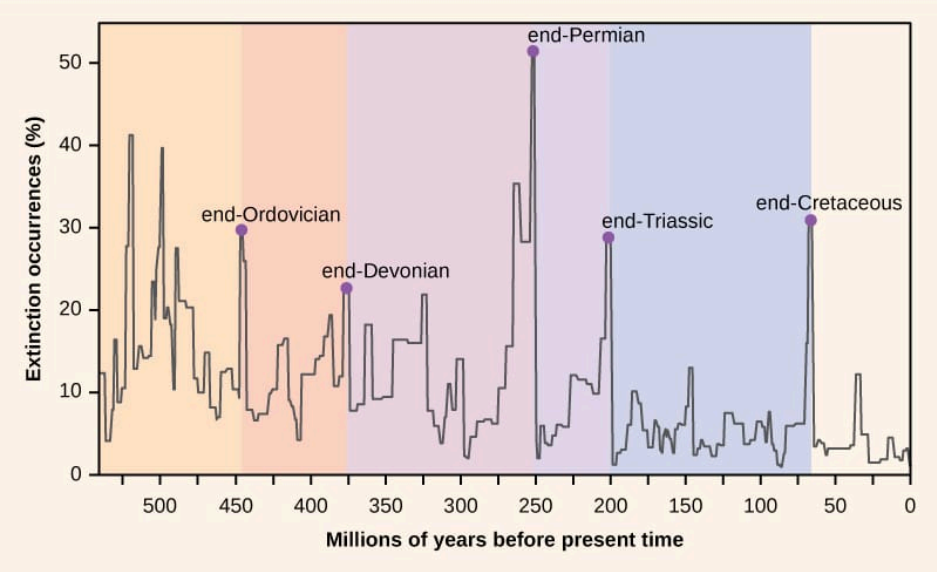


Figure 19.7.1: Extinction intensity as reflected in the fossil record has fluctuated throughout Earth’s history. Sudden and dramatic losses of biodiversity, called mass extinctions, have occurred five times.

Paleontologists have identified five strata in the fossil record that appear to show sudden and dramatic (greater than half of all extant species disappearing from the fossil record) losses in biodiversity. These are called mass extinctions. There are many lesser, yet still dramatic, extinction events, but the five mass extinctions have attracted the most research into their causes. An argument can be made that the five mass extinctions are only the five most extreme events in a continuous series of large extinction events throughout the fossil record (since 542 million years ago). In most cases, the hypothesized causes are still controversial; in one, the most recent, the cause seems clear. The most recent extinction in geological time, about 65 million years ago, saw the disappearance of the dinosaurs and many other species. Most scientists now agree the cause of this extinction was the impact of a large asteroid in the present-day Yucatán Peninsula and the subsequent energy release and global climate changes caused by dust ejected into the atmosphere.

Recent and Current Extinction Rates

A sixth, or Holocene, mass extinction has mostly to do with the activities of *Homo sapiens*. There are numerous recent extinctions of individual species that are recorded in human writings. Most of these are coincident with the expansion of the European colonies since the 1500s.

One of the earlier and popularly known examples is the dodo bird. The dodo bird lived in the forests of Mauritius, an island in the Indian Ocean. The dodo bird became extinct around 1662. It was hunted for its meat by sailors and was easy prey because

the dodo, which did not evolve with humans, would approach people without fear. Introduced pigs, rats, and dogs brought to the island by European ships also killed dodo young and eggs (Figure 19.7.2).



Figure 19.7.2: The dodo bird was hunted to extinction around 1662. (credit: Ed Uthman, taken in Natural History Museum, London, England)

Steller's sea cow became extinct in 1768; it was related to the manatee and probably once lived along the northwest coast of North America. Steller's sea cow was discovered by Europeans in 1741, and it was hunted for meat and oil. A total of 27 years elapsed between the sea cow's first contact with Europeans and extinction of the species. The last Steller's sea cow was killed in 1768. In another example, the last living passenger pigeon died in a zoo in Cincinnati, Ohio, in 1914. This species had once migrated in the millions but declined in numbers because of overhunting and loss of habitat through the clearing of forests for farmland.

These are only a few of the recorded extinctions in the past 500 years. The International Union for Conservation of Nature (IUCN) keeps a list of extinct and endangered species called the Red List. The list is not complete, but it describes 380 vertebrates that became extinct after 1500 AD, 86 of which were driven extinct by overhunting or overfishing.

Estimates of Present-day Extinction Rates

Estimates of extinction rates are hampered by the fact that most extinctions are probably happening without being observed. The extinction of a bird or mammal is often noticed by humans, especially if it has been hunted or used in some other way. But there are many organisms that are less noticeable to humans (not necessarily of less value) and many that are undescribed.

The background extinction rate is estimated to be about 1 per million species years (E/MSY). One "species year" is one species in existence for one year. One million species years could be one species persisting for one million years, or a million species persisting for one year. If it is the latter, then one extinction per million species years would be one of those million species becoming extinct in that year. For example, if there are 10 million species in existence, then we would expect 10 of those species to become extinct in a year. This is the background rate.

One contemporary extinction-rate estimate uses the extinctions in the written record since the year 1500. For birds alone, this method yields an estimate of 26 E/MSY, almost three times the background rate. However, this value may be underestimated for three reasons. First, many existing species would not have been described until much later in the time period and so their loss would have gone unnoticed. Second, we know the number is higher than the written record suggests because now extinct species are being described from skeletal remains that were never mentioned in written history. And third, some species are probably already extinct even though conservationists are reluctant to name them as such. Taking these factors into account raises the estimated extinction rate to nearer 100 E/MSY. The predicted rate by the end of the century is 1500 E/MSY.

A second approach to estimating present-time extinction rates is to correlate species loss with habitat loss, and it is based on measuring forest-area loss and understanding species–area relationships. The species-area relationship is the rate at which new species are seen when the area surveyed is increased (Figure 19.7.3). Likewise, if the habitat area is reduced, the number of

species seen will also decline. This kind of relationship is also seen in the relationship between an island's area and the number of species present on the island: as one increases, so does the other, though not in a straight line. Estimates of extinction rates based on habitat loss and species–area relationships have suggested that with about 90 percent of habitat loss an expected 50 percent of species would become extinct. Figure 19.7.3 shows that reducing forest area from 100 km^2 to 10 km^2, a decline of 90 percent, reduces the number of species by about 50 percent. Species–area estimates have led to estimates of present-day species extinction rates of about 1000 E/MSY and higher. In general, actual observations do not show this amount of loss and one explanation put forward is that there is a delay in extinction. According to this explanation, it takes some time for species to fully suffer the effects of habitat loss and they linger on for some time after their habitat is destroyed, but eventually they will become extinct. Recent work has also called into question the applicability of the species-area relationship when estimating the loss of species. This work argues that the species–area relationship leads to an overestimate of extinction rates. Using an alternate method would bring estimates down to around 500 E/MSY in the coming century. Note that this value is still 500 times the background rate.

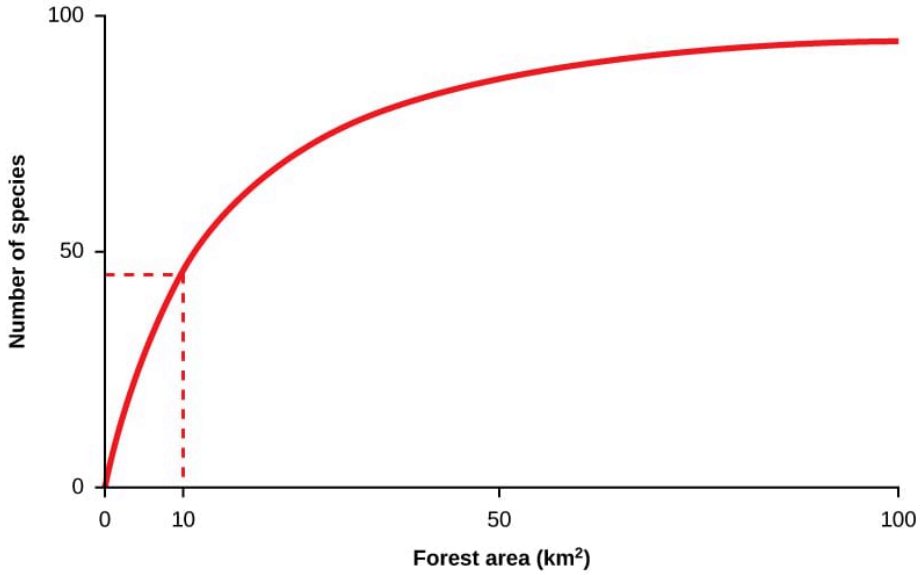


Figure 19.7.3**:** A typical species-area curve shows the cumulative number of species found as more and more area is sampled. The curve has also been interpreted to show the effect on species numbers of destroying habitat; a reduction in habitat of 90 percent from 100 km^2 to 10 km^2 reduces the number of species supported by about 50 percent.

CONCEPT IN ACTION



Go to this website for an interactive exploration of endangered and extinct species, their ecosystems, and the causes of their endangerment or extinction.

Conservation of Biodiversity

The threats to biodiversity at the genetic, species, and ecosystem levels have been recognized for some time. In the United States, the first national park with land set aside to remain in a wilderness state was Yellowstone Park in 1890. However, attempts to preserve nature for various reasons have occurred for centuries. Today, the main efforts to preserve biodiversity involve legislative approaches to regulate human and corporate behavior, setting aside protected areas, and habitat restoration.

Changing Human Behavior

Legislation has been enacted to protect species throughout the world. The legislation includes international treaties as well as national and state laws. The Convention on International Trade in Endangered Species of Wild Fauna and Flora (CITES) treaty came into force in 1975. The treaty, and the national legislation that supports it, provides a legal framework for preventing "listed" species from being transported across nations' borders, thus protecting them from being caught or killed in the first place when the purpose involves international trade. The listed species that are protected to one degree or another by the treaty number some 33,000. The treaty is limited in its reach because it only deals with international movement of organisms or their parts. It is also limited by various countries' ability or willingness to enforce the treaty and supporting legislation. The illegal trade in organisms and their parts is probably a market in the hundreds of millions of dollars.

Within many countries there are laws that protect endangered species and that regulate hunting and fishing. In the United States, the Endangered Species Act was enacted in 1973. When an at-risk species is listed by the Act, the U.S. Fish & Wildlife Service is required by law to develop a management plan to protect the species and bring it back to sustainable numbers. The Act, and others like it in other countries, is a useful tool, but it suffers because it is often difficult to get a species listed, or to get an effective management plan in place once a species is listed. Additionally, species may be controversially taken off the list without necessarily having had a change in their situation. More fundamentally, the approach to protecting individual species rather than entire ecosystems (although the management plans commonly involve protection of the individual species' habitat) is both inefficient and focuses efforts on a few highly visible and often charismatic species, perhaps at the expense of other species that go unprotected.

The Migratory Bird Treaty Act (MBTA) is an agreement between the United States and Canada that was signed into law in 1918 in response to declines in North American bird species caused by hunting. The Act now lists over 800 protected species. It makes

it illegal to disturb or kill the protected species or distribute their parts (much of the hunting of birds in the past was for their feathers). Examples of protected species include northern cardinals, the red-tailed hawk, and the American black vulture.

Global warming is expected to be a major driver of biodiversity loss. Many governments are concerned about the effects of anthropogenic global warming, primarily on their economies and food resources. Since greenhouse gas emissions do not respect national boundaries, the effort to curb them is an international one. The international response to global warming has been mixed. The Kyoto Protocol, an international agreement that came out of the United Nations Framework Convention on Climate Change that committed countries to reducing greenhouse gas emissions by 2012, was ratified by some countries, but spurned by others. Two countries that were especially important in terms of their potential impact that did not ratify the Kyoto protocol were the United States and China. Some goals for reduction in greenhouse gasses were met and exceeded by individual countries, but, worldwide, the effort to limit greenhouse gas production is not succeeding. The intended replacement for the Kyoto Protocol has not materialized because governments cannot agree on timelines and benchmarks. Meanwhile, the resulting costs to human societies and biodiversity predicted by a majority of climate scientists will be high.

As already mentioned, the non-profit, non-governmental sector plays a large role in conservation effort both in North America and around the world. The approaches range from species-specific organizations to the broadly focused IUCN and Trade Records Analysis of Flora and Fauna in Commerce (TRAFFIC). The Nature Conservancy takes a novel approach. It purchases land and protects it in an attempt to set up preserves for ecosystems. Ultimately, human behavior will change when human values change. At present, the growing urbanization of the human population is a force that mitigates against valuing biodiversity, because many people no longer come in contact with natural environments and the species that inhabit them.

Conservation in Preserves

Establishment of wildlife and ecosystem preserves is one of the key tools in conservation efforts (Figure 19.7.4). A preserve is an area of land set aside with varying degrees of protection for the organisms that exist within the boundaries of the preserve. Preserves can be effective for protecting both species and ecosystems, but they have some serious drawbacks.



Figure 19.7.4: National parks, such as Grand Teton National Park in Wyoming, help conserve biodiversity. (credit: Don DeBold)

A simple measure of success in setting aside preserves for biodiversity protection is to set a target percentage of land or marine habitat to protect. However, a more detailed preserve design and choice of location is usually necessary because of the way protected lands are allocated and how biodiversity is distributed: protected lands tend to contain less economically valuable resources rather than being set aside specifically for the species or ecosystems at risk. In 2003, the IUCN World Parks Congress estimated that 11.5 percent of Earth's land surface was covered by preserves of various kinds. This area is greater than previous goals; however, it only represents 9 out of 14 recognized major biomes and research has shown that 12 percent of all species live outside preserves; these percentages are much higher when threatened species are considered and when only high quality preserves are considered. For example, high quality preserves include only about 50 percent of threatened amphibian species. The conclusion must be that either the percentage of area protected must be increased, the percentage of high quality preserves must be increased, or preserves must be targeted with greater attention to biodiversity protection. Researchers argue that more

attention to the latter solution is required.

A biodiversity hotspot is a conservation concept developed by Norman Myers in 1988. Hotspots are geographical areas that contain high numbers of endemic species. The purpose of the concept was to identify important locations on the planet for conservation efforts, a kind of conservation triage. By protecting hotspots, governments are able to protect a larger number of species. The original criteria for a hotspot included the presence of 1500 or more species of endemic plants and 70 percent of the area disturbed by human activity. There are now 34 biodiversity hotspots (Figure 19.7.5) that contain large numbers of endemic species, which include half of Earth's endemic plants.

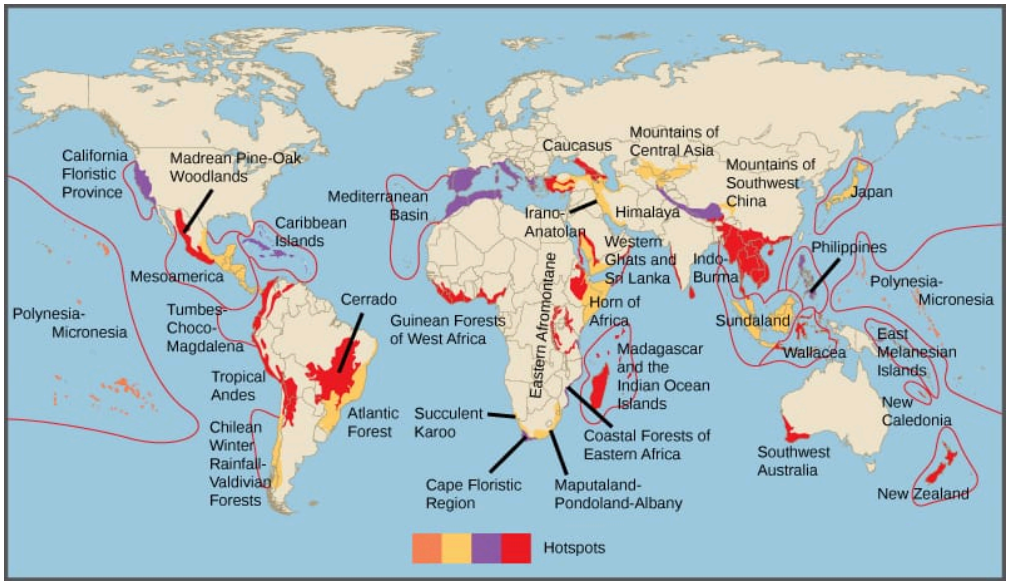


Figure 19.7.5**:** Conservation International has identified 34 biodiversity hotspots. Although these cover only 2.3 percent of the Earth's surface, 42 percent of the terrestrial vertebrate species and 50 percent of the world's plants are endemic to those hotspots.

There has been extensive research into optimal preserve designs for maintaining biodiversity. The fundamental principles behind much of the research have come from the seminal theoretical work of Robert H. MacArthur and Edward O. Wilson published in 1967 on island biogeography.[1] This work sought to understand the factors affecting biodiversity on islands. Conservation preserves can be seen as "islands" of habitat within "an ocean" of non-habitat. In general, large preserves are better because they support more species, including species with large home ranges; they have more core area of optimal habitat for individual species; they have more niches to support more species; and they attract more species because they can be found and reached more easily.

Preserves perform better when there are partially protected buffer zones around them of suboptimal habitat. The buffer allows organisms to exit the boundaries of the preserve without immediate negative consequences from hunting or lack of resources. One large preserve is better than the same area of several smaller preserves because there is more core habitat unaffected by less hospitable ecosystems outside the preserve boundary. For this same reason, preserves in the shape of a square or circle will be better than a preserve with many thin "arms." If preserves must be smaller, then providing wildlife corridors between them so that species and their genes can move between the preserves; for example, preserves along rivers and streams will make the smaller preserves behave more like a large one. All of these factors are taken into consideration when planning the nature of a preserve before the land is set aside.

In addition to the physical specifications of a preserve, there are a variety of regulations related to the use of a preserve. These can include anything from timber extraction, mineral extraction, regulated hunting, human habitation, and nondestructive human recreation. Many of the decisions to include these other uses are made based on political pressures rather than conservation considerations. On the other hand, in some cases, wildlife protection policies have been so strict that subsistence-living indigenous populations have been forced from ancestral lands that fell within a preserve. In other cases, even if a preserve is designed to protect wildlife, if the protections are not or cannot be enforced, the preserve status will have little meaning in the face of illegal poaching and timber extraction. This is a widespread problem with preserves in the tropics.

Some of the limitations on preserves as conservation tools are evident from the discussion of preserve design. Political and economic pressures typically make preserves smaller, never larger, so setting aside areas that are large enough is difficult.

Enforcement of protections is also a significant issue in countries without the resources or political will to prevent poaching and illegal resource extraction.

Climate change will create inevitable problems with the location of preserves as the species within them migrate to higher latitudes as the habitat of the preserve becomes less favorable. Planning for the effects of global warming on future preserves, or adding new preserves to accommodate the changes expected from global warming is in progress, but will only be as effective as the accuracy of the predictions of the effects of global warming on future habitats.

Finally, an argument can be made that conservation preserves reinforce the cultural perception that humans are separate from nature, can exist outside of it, and can only operate in ways that do damage to biodiversity. Creating preserves reduces the pressure on human activities outside the preserves to be sustainable and non-damaging to biodiversity. Ultimately, the political, economic, and human demographic pressures will degrade and reduce the size of conservation preserves if the activities outside them are not altered to be less damaging to biodiversity.

CONCEPT IN ACTION



Check out this interactive global data system of protected areas. Review data about specific protected areas by location or study statistics on protected areas by country or region.

Habitat Restoration

Habitat restoration holds considerable promise as a mechanism for maintaining or restoring biodiversity. Of course once a species has become extinct, its restoration is impossible. However, restoration can improve the biodiversity of degraded ecosystems. Reintroducing wolves, a top predator, to Yellowstone National Park in 1995 led to dramatic changes in the ecosystem that increased biodiversity. The wolves (Figure 19.7.6) function to suppress elk and coyote populations and provide more abundant resources to the guild of carrion eaters. Reducing elk populations has allowed revegetation of riparian (the areas along the banks of a stream or river) areas, which has increased the diversity of species in that habitat. Suppression of coyotes has increased the species previously suppressed by this predator. The number of species of carrion eaters has increased because of the predatory activities of the wolves. In this habitat, the wolf is a keystone species, meaning a species that is instrumental in maintaining diversity within an ecosystem. Removing a keystone species from an ecological community causes a collapse in diversity. The results from the Yellowstone experiment suggest that restoring a keystone species effectively can have the effect of restoring biodiversity in the community. Ecologists have argued for the identification of keystone species where possible and for focusing protection efforts on these species. It makes sense to return the keystone species to the ecosystems where they have been removed.



Figure 19.7.6**:** This photograph shows the Gibbon wolf pack in Yellowstone National Park, March 1, 2007. Wolves have been identified as a keystone species. (credit: Doug Smith, NPS)

Other large-scale restoration experiments underway involve dam removal. In the United States, since the mid-1980s, many aging dams are being considered for removal rather than replacement because of shifting beliefs about the ecological value of free-flowing rivers. The measured benefits of dam removal include restoration of naturally fluctuating water levels (often the purpose of dams is to reduce variation in river flows), which leads to increased fish diversity and improved water quality. In the Pacific Northwest, dam removal projects are expected to increase populations of salmon, which is considered a keystone species because it transports nutrients to inland ecosystems during its annual spawning migrations. In other regions, such as the Atlantic coast, dam removal has allowed the return of other spawning anadromous fish species (species that are born in fresh water, live most of their lives in salt water, and return to fresh water to spawn). Some of the largest dam removal projects have yet to occur or have happened too recently for the consequences to be measured. The large-scale ecological experiments that these removal projects constitute will provide valuable data for other dam projects slated either for removal or construction.

The Role of Zoos and Captive Breeding

Zoos have sought to play a role in conservation efforts both through captive breeding programs and education (Figure 19.7.7). The transformation of the missions of zoos from collection and exhibition facilities to organizations that are dedicated to conservation is ongoing. In general, it has been recognized that, except in some specific targeted cases, captive breeding programs for endangered species are inefficient and often prone to failure when the species are reintroduced to the wild. Zoo facilities are far too limited to contemplate captive breeding programs for the numbers of species that are now at risk. Education, on the other hand, is a potential positive impact of zoos on conservation efforts, particularly given the global trend to urbanization and the consequent reduction in contacts between people and wildlife. A number of studies have been performed to look at the effectiveness of zoos on people's attitudes and actions regarding conservation; at present, the results tend to be mixed.



Figure 19.7.7**:** Zoos and captive breeding programs help preserve many endangered species, such as this golden lion tamarin. (credit: Garrett Ziegler)

Summary

Five mass extinctions with losses of more than 50 percent of extant species are observable in the fossil record. Recent extinctions are recorded in written history and are the basis for one method of estimating contemporary extinction rates. The other method uses measures of habitat loss and species-area relationships. Estimates of contemporary extinction rates vary but are as high as 500 times the background rate, as determined from the fossil record, and are predicted to rise.

There is a legislative framework for biodiversity protection. International treaties such as CITES regulate the transportation of endangered species across international borders. Legislation within individual countries protecting species and agreements on global warming have had limited success; there is at present no international agreement on targets for greenhouse gas emissions. In the United States, the Endangered Species Act protects listed species but is hampered by procedural difficulties and a focus on individual species. The Migratory Bird Act is an agreement between Canada and the United States to protect migratory birds. The non-profit sector is also very active in conservation efforts in a variety of ways.

Conservation preserves are a major tool in biodiversity protection. Presently, 11 percent of Earth's land surface is protected in some way. The science of island biogeography has informed the optimal design of preserves; however, preserves have limitations imposed by political and economic forces. In addition, climate change will limit the effectiveness of present preserves in the future. A downside of preserves is that they may lessen the pressure on human societies to function more sustainably outside the preserves.

Habitat restoration has the potential to restore ecosystems to previous biodiversity levels before species become extinct. Examples of restoration include reintroduction of keystone species and removal of dams on rivers. Zoos have attempted to take a more active role in conservation and can have a limited role in captive breeding programs. Zoos also have a useful role in education.

Footnotes

1. 1 Robert H. MacArthur and Edward O. Wilson, E. O., *The Theory of Island Biogeography* (Princeton, N.J.: Princeton University Press, 1967).

Glossary

biodiversity hotspot
: a concept originated by Norman Myers to describe a geographical region with a large number of endemic species and a large percentage of degraded habitat

extinction rate
: the number of species becoming extinct over time, sometimes defined as extinctions per million species–years to make numbers manageable (E/MSY)

species-area relationship
: the relationship between area surveyed and number of species encountered; typically measured by incrementally increasing the area of a survey and determining the cumulative numbers of species

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hominoid
18.3: The Evolution of Primates
Homo
18.3: The Evolution of Primates
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18.3: The Evolution of Primates
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18.3: The Evolution of Primates
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Law of Independent Assortment
4.6: Patterns of Inheritance
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2.2: Eukaryotic Cells
nucleus
2.2: Eukaryotic Cells

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1.1: The Study of Life
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1.1: The Study of Life
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S

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