GENERAL BIOLOGY



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1: THE STUDY OF LIFE

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1.1: The Science of Biology - Introduction to the Study of Biology

Learning Objectives

- Describe the field of biological science

The Study of Life

Biology is a natural science concerned with the study of life and living organisms. Modern biology is a vast and eclectic field composed of many specialized disciplines that study the structure, function, growth, distribution, evolution, or other features of living organisms. However, despite the broad scope of biology, there are certain general and unifying concepts that govern all study and research:

- the cell is the basic unit of life
- genes (consisting of DNA or RNA) are the basic unit of heredity
- evolution accounts for the unity and diversity seen among living organisms
- all organisms survive by consuming and transforming energy
- all organisms maintain a stable internal environment



Figure 1.1.1: Biology: The Study of Life: A collection of organisms clockwise from top left: bacteria, koala, fern, toadstool, tree frog, tarantula.

Biological research indicates the first forms of life on Earth were microorganisms that existed for billions of years before the evolution of larger organisms. The mammals, birds, and flowers so familiar to us are all relatively recent, originating within the last 200 million years. Modern-appearing humans, *Homo sapiens*, are a relatively new species, having inhabited this planet for only the last 200,000 years (approximately).



Figure 1.1.1: Stromatolites: Stromatolites, sedimentary accretions formed by the actions of cyanobacteria, provide fossil evidence of life on Earth about 3.5 billion years ago.

History of Biological Science

Although modern biology is a relatively recent development, sciences related to and included within it have been studied since ancient times. Natural philosophy was studied as early as the ancient civilizations of Mesopotamia, Egypt, the Indian subcontinent, and China. However, the origins of modern biology and its approach to the study of nature are most often traced back to ancient Greece. (Biology is derived from the Greek word “bio” meaning “life” and the suffix “ology” meaning “study of.”)

Advances in microscopy also had a profound impact on biological thinking. In the early 19th century, a number of biologists pointed to the central importance of the cell and in 1838, Schleiden and Schwann began promoting the now universal ideas of the cell theory. Jean-Baptiste Lamarck was the first to present a coherent theory of evolution, although it was the British naturalist Charles Darwin who spread the theory of natural selection throughout the scientific community. In 1953, the discovery of the double helical structure of DNA marked the transition to the era of molecular genetics.



Figure 1.1.1: Phrenology: Dr. Spurzheim’s divisions of the organs of phrenology marked externally: Phrenology is a pseudoscience that attempted to determine brain function and personality by analyzing an individual’s skull.

Science and Pseudoscience

Science is a process for learning about the natural world. Most scientific investigations involve the testing of potential answers to important research questions. For example, oncologists (cancer doctors) are interested in finding out why some cancers respond well to chemotherapy while others are unaffected. Based on their growing knowledge of molecular biology, some doctors suspect a connection between a patient's genetics and their response to chemotherapy. Many years of research have produced numerous scientific papers documenting the evidence for a connection between cancer, genetics, and treatment response. Once published, scientific information is available for anyone to read, learn from, or even question/dispute. This makes science an iterative, or cumulative, process, where previous research is used as the foundation for new research. Our current understanding of any issue in the sciences is the culmination of all previous work.

Pseudoscience is a belief presented as scientific although it is not a product of scientific investigation. Pseudoscience is often known as fringe or alternative science. It usually lacks the carefully-controlled and thoughtfully-interpreted experiments which provide the foundation of the natural sciences and which contribute to their advancement.

Key Points

- Biology has evolved as a field of science since it was first studied in ancient civilizations, although modern biology is a relatively recent field.
- Science is a process that requires the testing of ideas using evidence gathered from the natural world. Science is iterative in nature and involves critical thinking, careful data collection, rigorous peer review, and the communication of results.
- Science also refers to the body of knowledge produced by scientific investigation.
- Pseudoscience is a belief presented as scientific although it is not a product of scientific investigation.

Key Terms

- **pseudoscience**: Any belief purported to be scientific or supported by science that is not a product of scientific investigation.
- **science**: A process for learning about the natural world that tests ideas using evidence gathered from nature.
- **Biology**: A natural science concerned with the study of life and living organisms.

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1.2: The Science of Biology - Scientific Reasoning

Learning Objectives

- Compare and contrast theories and hypotheses

The Process of Science

Science (from the Latin scientia, meaning “knowledge”) can be defined as knowledge that covers general truths or the operation of general laws, especially when acquired and tested by the scientific method. 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 (testable statements) by means of repeatable experiments. Although using the scientific method is inherent to science, it is inadequate in determining what science is. This is because it is relatively easy to apply the scientific method to disciplines such as physics and chemistry, but when it comes to disciplines like archaeology, paleoanthropology, psychology, and geology, the scientific method becomes less applicable as it becomes more difficult to repeat experiments.

These areas of study are still sciences, however. Consider archaeology: even though one cannot perform repeatable experiments, hypotheses may still be supported. For instance, an archaeologist can hypothesize that an ancient culture existed based on finding a piece of pottery. Further hypotheses could be made about various characteristics of this culture. These hypotheses may be found to be plausible (supported by data) and tentatively accepted, or may be falsified and rejected altogether (due to contradictions from data and other findings). A group of related hypotheses, that have not been disproven, may eventually lead to the development of a verified theory. A theory is a tested and confirmed explanation for observations or phenomena that is supported by a large body of evidence. Science may be better defined as fields of study that attempt to comprehend the nature of the universe.

Scientific Reasoning

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. To do this, they use two methods of logical thinking: inductive reasoning and deductive reasoning.

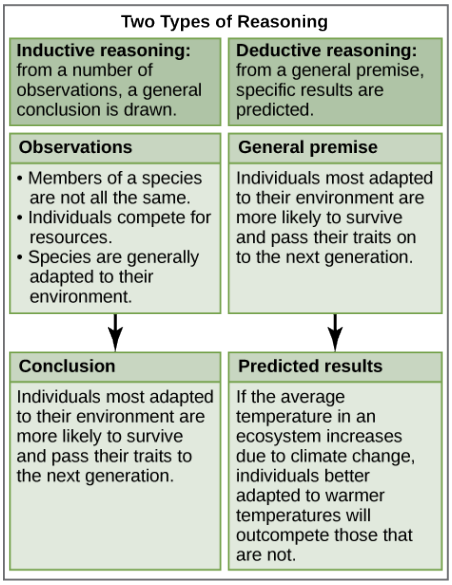


Figure 1.2.1: Scientific Reasoning: Scientists use two types of reasoning, inductive and deductive, to advance scientific knowledge.

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 or quantitative 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 provide an example. In this type of research, many live brains are observed while people are doing a specific activity, such as viewing images of food. The part of the brain that "lights up" during this activity is then predicted to be the part controlling the response to the selected stimulus; in this case, images of food. The "lighting up" of the various areas of the brain is caused by excess absorption of radioactive sugar derivatives by active areas of the brain. The resultant increase in radioactivity is observed by a scanner. Then researchers can stimulate that part of the brain to see if similar responses result.

Deductive reasoning or deduction is the type of logic used in hypothesis-based science. In deductive reason, 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. Studies in climate change can illustrate this type of reasoning. For example, scientists may predict that if the climate becomes warmer in a particular region, then the distribution of plants and animals should change. These predictions have been written and tested, and many such predicted changes have been observed, such as the modification of arable areas for agriculture correlated with changes in the average temperatures.

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, which is usually inductive, aims to observe, explore, and discover, while hypothesis-based science, which is usually deductive, 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 and most scientific endeavors combine both approaches. The fuzzy boundary becomes apparent when thinking about how easily observation can lead to specific questions. For example, a gentleman in the 1940s observed that the burr seeds that stuck to his clothes and his dog's fur had a tiny hook structure. Upon closer inspection, he discovered that the burrs' gripping device was more reliable than a zipper. He eventually developed a company and produced the hook-and-loop fastener popularly known today as Velcro. Descriptive science and hypothesis-based science are in continuous dialogue.



Figure 1.2.1: A Burr: This fruit attaches to animal fur via the hooks on its surface to improve distribution. Velcro is an example of a biomimetic invention which has copied burrs and uses small flexible hooks to reversibly attach to fluffy surfaces.

Key Points

- A hypothesis is a statement/prediction that can be tested by experimentation.
- A theory is an explanation for a set of observations or phenomena that is supported by extensive research and that can be used as the basis for further research.
- Inductive reasoning draws on observations to infer logical conclusions based on the evidence.
- Deductive reasoning is hypothesis-based logical reasoning that deduces conclusions from test results.

Key Terms

- **theory**: a well-substantiated explanation of some aspect of the natural world based on knowledge that has been repeatedly confirmed through observation and experimentation
- **hypothesis**: a tentative conjecture explaining an observation, phenomenon, or scientific problem that can be tested by further observation, investigation, and/or experimentation

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1.3: The Science of Biology - The Scientific Method

Learning Objectives

- Discuss hypotheses and the components of a scientific experiment as part of the scientific method

The Scientific Method

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) who set up inductive methods for scientific inquiry. The scientific method can be applied to almost all fields of study as a logical, rational, problem-solving method.



Figure 1.3.1: Sir Francis Bacon: Sir Francis Bacon (1561–1626) is credited with being the first to define 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. A teenager notices that his friend is really tall and wonders why. So his question might be, "Why is my friend so tall? "

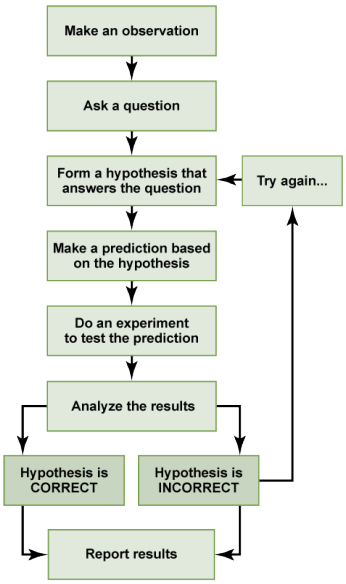


Figure 1.3.1: The Scientific Method: The scientific method consists of a series of well-defined steps. If a hypothesis is not supported by experimental data, a new hypothesis can be proposed.

Proposing a Hypothesis

Recall that a hypothesis is an educated guess that can be tested. Hypotheses often also include an explanation for the educated guess. To solve one problem, several hypotheses may be proposed. For example, the student might believe that his friend is tall because he drinks a lot of milk. So his hypothesis might be "If a person drinks a lot of milk, then they will grow to be very tall because milk is good for your bones." Generally, hypotheses have the format "If...then..." Keep in mind that there could be other responses to the question; therefore, other hypotheses may be proposed. A second hypothesis might be, "If a person has tall parents, then they will also be tall, because they have the genes to be tall. "

Once a hypothesis has been selected, the student can make a prediction. A prediction is similar to a hypothesis but it is truly a guess. For instance, they might predict that their friend is tall because he drinks a lot of milk.

Testing a Hypothesis

A valid hypothesis must be testable. It should also be falsifiable, meaning that it can be disproven by experimental results. Importantly, science does not claim to "prove" anything because scientific understandings are always subject to modification with further information. This step—openness to disproving ideas—is what distinguishes sciences from non-sciences. The presence of the supernatural, for instance, is neither testable nor falsifiable. To test a hypothesis, a researcher will conduct one or more experiments designed to eliminate one or more of the hypotheses. 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. The control group contains every feature of the experimental group except it is not given the manipulation that is hypothesized. For example, a control group could be a group of varied teenagers that did not drink milk and they could be compared to the experimental group, a group of varied teenagers that did drink milk. Thus, if the results of the experimental group differ from the control group, the difference must be due to the hypothesized manipulation rather than some outside factor. To test the first hypothesis, the student would find out if drinking milk affects height. If drinking milk has no affect on height, then there must be another reason for the height of the friend. To test the second hypothesis, the student could check whether or not his friend has tall parents. Each hypothesis should be tested by carrying out appropriate experiments. 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. Using the scientific method, the hypotheses that are inconsistent with experimental data are rejected.

While this "tallness" example is based on observational results, other hypotheses and experiments might have clearer controls. For instance, a student might attend class on Monday and realize she had difficulty concentrating on the lecture. One hypothesis to explain this occurrence might be, "If I eat breakfast before class, then I am better able to pay attention." The student could then design an experiment with a control to test this hypothesis.

The scientific method may seem too rigid and structured. It is important to keep in mind that although scientists often follow this sequence, there is flexibility. 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.

Key Points

- In the scientific method, observations lead to questions that require answers.
- In the scientific method, the hypothesis is a testable statement proposed to answer a question.
- In the scientific method, experiments (often with controls and variables) are devised to test hypotheses.
- In the scientific method, analysis of the results of an experiment will lead to the hypothesis being accepted or rejected.

Key Terms

- **scientific method**: a way of discovering knowledge based on making falsifiable predictions (hypotheses), testing them, and developing theories based on collected data
- **hypothesis**: an educated guess that usually is found in an “if...then...” format
- **control group**: a group that contains every feature of the experimental group except it is not given the manipulation that is hypothesized

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1.4: The Science of Biology - Basic and Applied Science

Learning Objectives

- Differentiate between basic and applied science

Two Types of Science: Basic Science 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 to 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 goal of basic science is knowledge for knowledge's sake; though this does not mean that, in the end, it may not result in a practical application.

In contrast, applied science or "technology" aims to use science to solve real-world problems such as improving crop yields, finding a cure for a particular disease, or saving animals threatened by a natural disaster. In applied science, the problem is usually defined for the researcher.



Figure 1.4.1: Example of Applied Science: After Hurricane Ike struck the Gulf Coast in 2008, the U.S. Fish and Wildlife Service rescued this brown pelican. Thanks to applied science, scientists knew how to rehabilitate the bird.

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 wide knowledge foundation generated through basic science.

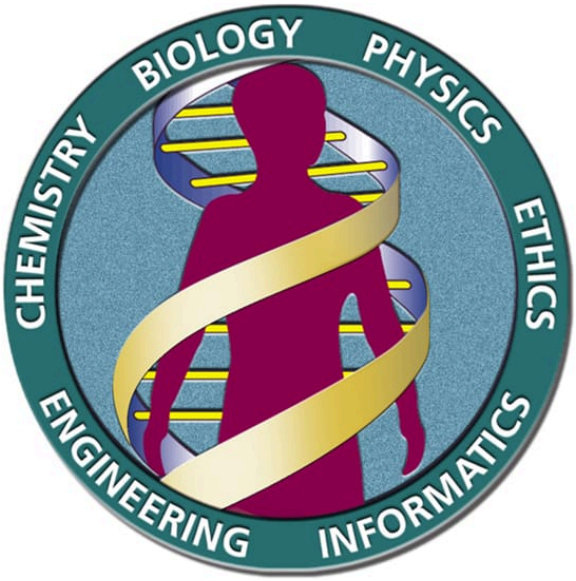


Figure 1.4.2: A Link Between Basic and Applied Science: The Human Genome Project was a 13-year collaborative effort among researchers working in several different fields of science. The project, which sequenced the entire human genome, was completed in 2003.

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, DNA makes new copies of itself shortly before a cell divides. 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 less complex organisms have also been studied as part of this project in order to gain a better understanding of human chromosomes. The Human Genome Project relied on basic research carried out with simple organisms and, later, with the human genome. An important end goal eventually became using the data for applied research to seek cures and early diagnoses for genetically-related diseases.

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 on the dish, 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.

Key Points

- The only goal of basic science research is to increase the knowledge base of a particular field of study.
- Applied science uses the knowledge base supplied by basic science to devise solutions, often technological, to specific problems.
- The basic science involved in mapping the human genome is leading to applied science techniques that will diagnose and treat genetic diseases.

Key Terms

- **basic science**: research done solely to expand the knowledge base
- **applied science**: The discipline dealing with the art or science of applying scientific knowledge to practical problems.

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1.5: The Science of Biology - Publishing Scientific Work

Learning Objectives

- Describe the role played by peer-reviewed scientific articles

Reporting Scientific Work

Scientists must share their findings in order for other researchers to expand and build upon their discoveries. Collaboration with other scientists—when planning, conducting, and analyzing results—are all important for scientific research. For this reason, a major aspect of a scientist's work is communicating with peers and disseminating results to peers. Scientists can share results by presenting them at a scientific meeting or conference, but this approach can reach only the select few who are present. Instead, most scientists present their results in peer-reviewed manuscripts that are published in scientific journals. Peer-reviewed manuscripts are scientific papers that are reviewed 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.



Figure 1.5.1: Scientific Journal: Scientific research is published in peer-reviewed scientific journals.

A scientific paper is very different from creative writing. Although creativity is required to design experiments, there are fixed guidelines when it comes to presenting scientific results. Scientific writing must be brief, concise, and accurate. It needs to be succinct but detailed-enough to allow peers to reproduce the experiments.

The scientific paper consists of several specific sections: introduction, materials and methods, results, and discussion. This structure is sometimes called the "IMRaD" format. There are usually acknowledgment and reference sections, as well as an abstract (a concise summary) at the beginning of the paper. There might be additional sections depending on the type of paper and the journal where it will be published; for example, some review papers require an outline.

The introduction starts with brief, but broad, background information about what is known in the field. A good introduction also gives the rationale and justification for the work. The introduction refers to the published scientific work of others and, therefore, requires citations following the style of the journal. Using the work or ideas of others without proper citation is considered plagiarism.

The materials and methods section includes a complete and accurate description of the substances and the techniques used by the researchers to gather data. The description should be thorough, yet concise, while providing enough information to allow another researcher to repeat the experiment and obtain similar results. This section will also include information on how measurements were made and what types of calculations and statistical analyses were used to examine raw data. Although the materials and methods section gives an accurate description of the experiments, it does not discuss them.

Journals may require separate results and discussion sections, or it may combine them in one section. If the journal does not allow the combination of both sections, the results section simply narrates the findings without any further interpretation. The results are presented by means of tables or graphs, but no duplicate information should be presented. In the discussion section, the researcher will interpret the results, describe how variables may be related, and attempt to explain the observations. It is indispensable to conduct an extensive literature search to put the results in the context of previously-published scientific research. Therefore, proper citations are included in this section as well.

Finally, the conclusion section summarizes the importance of the experimental findings. While the scientific paper almost certainly answered one or more scientific questions that were stated, any good research should lead to more questions. A well-written scientific paper leaves doors open for the researcher and others to continue and expand on the findings.

Review articles do not follow the IMRAD format because they do not present original scientific findings or primary literature. Instead, they summarize and comment on findings that were published as primary literature. They typically include extensive reference sections.

Key Points

- The body of scientific knowledge is recorded in peer-reviewed science journals which allow other scientists to determine what has been done previously and where their own research fits in the larger field of study.
- A scientific article generally follows the steps of the scientific method: introduction (background, observations, question), materials and methods (hypothesis and experimental plan), results (analysis of collected data), and discussion (conclusions drawn from analysis).
- Peer reviewers are other researchers in that field of study who carefully dissect, analyze, and critique a research article submitted for publication.
- Review articles (summaries and commentaries on prior research in a field of study) also go through the peer-review process.

Key Terms

- **peer review**: The scholarly process whereby manuscripts intended to be published in an academic journal are reviewed by independent researchers to evaluate the contribution, importance, and accuracy of the manuscript's contents.

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1.6: The Science of Biology - Branches and Subdisciplines of Biology

Learning Objectives

- Recognize the various subfields of biology; e.g. microbiology, genetics, evolutionary, etc.

Branches of Biological Study

The scope of biology is broad and therefore contains many branches and subdisciplines. Biologists may pursue one of those subdisciplines and work in a more focused field. The biological branches are divided according to the focus of the discipline and can even be divided based on the types of techniques and tools used to study that specific focus. However, with the increasing amount of basic biological information growing due to advances in technology and databases, there is often cross-discipline and collaboration between branches. For instance, molecular biology and biochemistry study biological processes at the molecular and chemical level, respectively, including interactions among molecules such as DNA, RNA, and proteins, as well as the way they are regulated. Microbiology, the study of microorganisms, is the study of the structure and function of single-celled organisms. It is quite a broad branch itself, and depending on the subject of study, there are also microbial physiologists, ecologists, and geneticists, among others.

Biological Disciplines and Careers

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 materials associated with crimes.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, including the processing of DNA found in many different environments and materials associated with the crime scenes.



Figure 1.6.1: Forensic Science: This forensic scientist works in a DNA extraction room at the U.S. Army Criminal Investigation Laboratory at Fort Gillem, GA.

Another field of biological study, neurobiology, is the study 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 subdiscipline focuses on different functions of the nervous system using molecular, cellular, developmental, medical, and

computational approaches.

Additional branches of biology include paleontology, which uses fossils to study life's history; zoology, which studies animals; and botany, which studies plants. Biologists can also specialize as biotechnologists, ecologists, or physiologists. This is just a small sample of the many fields that biologists can pursue.



Figure 1.6.1: Paleontology: Researchers work on excavating dinosaur fossils at a site in Castellón, Spain.

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

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Key Points

- Biology is broad and focuses on the study of life from various perspectives.
- The branches and subdisciplines of biology, which are highly focused areas, have resulted in the development of careers that are specific to these branches and subdisciplines.
- Branches of biological study include microbiology, physiology, ecology and genetics; subdisciplines within these branches can include: microbial physiology, microbial ecology and microbial genetics.

Key Terms

- **genetic engineering**: the deliberate modification of the genetic structure of an organism
- **forensic**: Relating to the use of science and technology in the investigation and establishment of facts or evidence in a court of law.

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1.7: Themes and Concepts of Biology - Properties of Life

Learning Objectives

- Describe the properties of life

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



Figure 1.7.1: Multicellular Organisms: A toad represents a highly organized structure consisting of cells, tissues, organs, and organ systems.

Order

Organisms are highly organized, coordinated 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 organelles and other cellular inclusions. In multicellular organisms, similar cells form tissues. Tissues, in turn, collaborate to create organs (body structures with a distinct function). Organs work together to form organ systems.



Figure 1.7.2: Response to Stimuli: The leaves of this sensitive plant (Mimosa pudica) will instantly droop and fold when touched. After a few minutes, the plant returns to normal.

Sensitivity or Response to Stimuli

Organisms can respond to diverse stimuli. For example, plants can grow toward a source of light, climb on fences and walls, or respond to touch. 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.

Reproduction

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



Figure 1.7.3: Reproduction: Although no two look alike, these kittens have inherited genes from both parents and share many of the same characteristics.

Growth and Development

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

Regulation

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



Figure 1.7.4: Homeostasis: Polar bears (Ursus maritimus) 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.

Homeostasis

In order to function properly, cells need to have appropriate conditions such as proper temperature, pH, and appropriate concentration 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 homeostasis (literally, "steady state")—the ability of an organism to maintain constant internal conditions. For example, an organism needs to regulate body temperature through a process known as thermoregulation. Organisms that live in cold climates, such as the polar bear, have body structures that help them withstand low temperatures and conserve body heat. Structures that aid in this type of insulation include fur, feathers, blubber, and fat. In hot climates, organisms have methods (such as perspiration in humans or panting in dogs) that help them to shed excess body heat.



Figure 1.7.5: Energy Processing: The California condor (Gymnogyps californianus) uses chemical energy derived from food to power flight.

Energy Processing

All organisms 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 in molecules they take in as food.



Figure 1.7.6: Adaptation in the flat-tailed horned lizard: This lizard exhibits a flattened body and coloring that helps camouflage it, both of which are adaptive traits that help it avoid predators.

Evolution

As a population of organisms interacts with the environment, individuals with traits that contribute to reproduction and survival in that particular environment will leave more offspring. Over time those advantageous traits (called adaptations) will become more common in the population. This process, change over time, is called evolution, and it is one of the processes that explain the diverse species seen in biology. Adaptations help organisms survive in their ecological niches, and adaptive traits may be structural, behavioral, or physiological; as such, adaptations frequently involve other properties of organisms such as homeostasis, reproduction, and growth and development.

Key Points

- Order can include highly organized structures such as cells, tissues, organs, and organ systems.
- Interaction with the environment is shown by response to stimuli.
- The ability to reproduce, grow and develop are defining features of life.
- The concepts of biological regulation and maintenance of homeostasis are key to survival and define major properties of life.
- Organisms use energy to maintain their metabolic processes.
- Populations of organisms evolve to produce individuals that are adapted to their specific environment.

Key Terms

- **phototaxis**: The movement of an organism either towards or away from a source of light
- **gene**: a unit of heredity; the functional units of chromosomes that determine specific characteristics by coding for specific proteins
- **chemotaxis**: the movement of a cell or an organism in response to a chemical stimulant

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1.8: Themes and Concepts of Biology - Levels of Organization of Living Things

Learning Objectives

- Describe the biological levels of organization from the smallest to highest level

Living things are highly organized and structured, following a hierarchy that can be examined 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 which are chemical structures consisting of at least two atoms held together by one or more chemical bonds. Many molecules that are biologically important are macromolecules, large molecules that are typically formed by polymerization (a polymer is a large molecule that is made by combining smaller units called monomers, which are simpler than macromolecules). An example of a macromolecule is deoxyribonucleic acid (DNA), which contains the instructions for the structure and functioning of all living organisms.

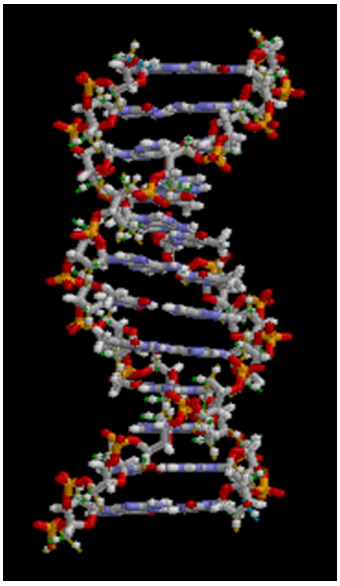


Figure 1.8.1: DNA: All molecules, including this DNA molecule, are composed of atoms.

From Organelles to Biospheres

Macromolecules can form aggregates within a cell that are surrounded by membranes; these are called organelles. Organelles are small structures that exist within cells. Examples of these include: mitochondria and chloroplasts, which carry out indispensable functions. Mitochondria produce energy to power the cell while chloroplasts enable green plants to utilize the energy in sunlight to make sugars. All living things are made of cells, and the cell itself 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 the reproductive mechanism of 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 or colonial organisms that do not have membrane-bound nuclei; in contrast, the cells of eukaryotes do have membrane-bound organelles and a membrane-bound nucleus.

In larger organisms, cells combine to make tissues, which are groups of similar cells carrying out similar or related functions. Organs are collections of tissues grouped together performing 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. Mammals have many organ systems. For instance, the circulatory system transports blood through the body and to and from the lungs; it includes organs such as the heart and blood vessels. Furthermore, 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.

All the individuals of a species living within a specific area are collectively called a population. For example, a forest may include many pine trees. All of these pine trees represent the population of 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 sum 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, non-living parts of that environment such as nitrogen in the soil or rain water. At the highest level of organization, the biosphere is the collection of all ecosystems, and it represents the zones of life on earth. It includes land, water, and even the atmosphere to a certain extent. Taken together, all of these levels comprise the biological levels of organization, which range from organelles to the biosphere.

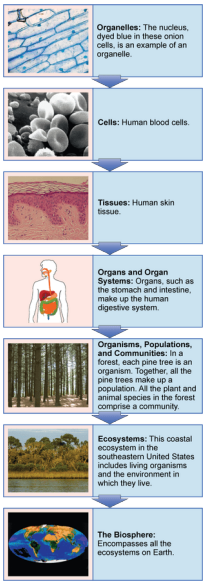


Figure 1.8.1: Biological Levels of Organization: The biological levels of organization of living things follow a hierarchy, such as the one shown. From a single organelle to the entire biosphere, living organisms are part of a highly structured hierarchy.

Key Points

- The atom is the smallest and most fundamental unit of matter. The bonding of at least two atoms or more form molecules.
- The simplest level of organization for living things is a single organelle, which is composed of aggregates of macromolecules.
- The highest level of organization for living things is the biosphere; it encompasses all other levels.
- The biological levels of organization of living things arranged from the simplest to most complex are: organelle, cells, tissues, organs, organ systems, organisms, populations, communities, ecosystem, and biosphere.

Key Terms

- **molecule**: The smallest particle of a specific compound that retains the chemical properties of that compound; two or more atoms held together by chemical bonds.
- **macromolecule**: a very large molecule, especially used in reference to large biological polymers (e.g. nucleic acids and proteins)
- **polymerization**: The chemical process, normally with the aid of a catalyst, to form a polymer by bonding together multiple identical units (monomers).

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1.9: Themes and Concepts of Biology - The Diversity of Life

Learning Objectives

- Recognize the three major domains used for classification

The fact that biology has such a broad scope as a science has to do with the 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.

The evolution of various life forms on Earth can be summarized in a phylogenetic tree using phylogeny. 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 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 is proportional to the time elapsed since the split.

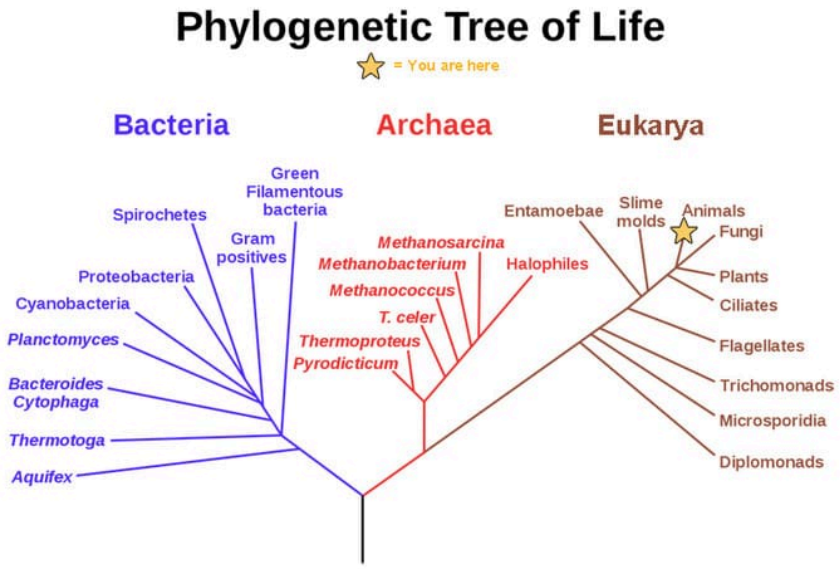


Figure 1.9.1: Phylogenetic Tree of Life: This phylogenetic tree was constructed by microbiologist Carl Woese using data obtained from sequencing ribosomal RNA genes. The tree shows the separation of living organisms into three domains: Bacteria, Archaea, and Eukarya. Bacteria and Archaea are prokaryotes, single-celled organisms lacking intracellular organelles.

Carl Woese and the Phylogenetic Tree

In the past, biologists grouped living organisms into five kingdoms: animals, plants, fungi, protists, and bacteria. The organizational scheme was based mainly on physical features, as opposed to physiology, biochemistry, or molecular biology, all of which are used by modern systematics. 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. The first two are prokaryotic cells with microbes that lack membrane-enclosed nuclei and organelles. The third domain contains the eukaryotes and includes unicellular microorganisms together with the four original kingdoms (excluding bacteria). Woese defined Archaea as a new domain, and this resulted in a new taxonomic tree. 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).

Woese's tree was constructed from comparative sequencing of the genes that are universally distributed, present in every organism, and conserved (meaning that these genes have remained essentially unchanged throughout evolution). Woese's approach was revolutionary because comparisons of physical features are insufficient to differentiate between the prokaryotes

that appear fairly similar in spite of their tremendous biochemical diversity and genetic variability. The comparison of homologous DNA and RNA sequences provided Woese with a sensitive device that revealed the extensive variability of prokaryotes, and which justified the separation of the prokaryotes into two domains: bacteria and archaea. DNA, the universal genetic material, contains the instructions for the structure and function of all living organisms and can be divided into genes whose expression varies between organisms. The RNA, which is transcribed from DNA, varies between organisms as well based on the expression of specific genes. Thus, to examine differences at this molecular level provides a more accurate depiction of the diversity which exists.

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Key Points

- The three major Domains of Life include: Domain Bacteria, Domain Eukarya and Domain Archaea.
- Domain Bacteria and Domain Archaea include prokaryotic cells that lack membrane-enclosed nuclei and organelles.
- Domain Eukarya include eukaryotes and more complex organisms that contain membrane-bound nuclei and organelles.
- Carl Woese defined Archaea as a new domain and constructed the phylogentic tree of life which shows separation of all living organisms.
- The phylogenetic tree of life was constructed by Carl Woese using sequencing data of ribosomal RNA genes. Therefore, genetics classification surpassed morphological cataloguing, which was the traditional way of organizing living beings.

Key Terms

- **phylogeny**: the evolutionary history of an organism
- **extremophile**: an organism that lives under extreme conditions of temperature, salinity, etc; commercially important as a source of enzymes that operate under similar conditions
- **DNA**: a biopolymer of deoxyribonucleic acids (a type of nucleic acid) that has four different chemical groups, called bases: adenine, guanine, cytosine, and thymine

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2: THE CHEMICAL FOUNDATION OF LIFE

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2.4: Atoms, Isotopes, Ions, and Molecules - The Periodic Table

2.5: Atoms, Isotopes, Ions, and Molecules - Electron Shells and the Bohr Model

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2.1: Atoms, Isotopes, Ions, and Molecules - Overview of Atomic Structure

Learning Objectives

- Discuss the electronic and structural properties of an atom

An atom is the smallest unit of matter that retains all of the chemical properties of an element. Atoms combine to form molecules, which then interact to form solids, gases, or liquids. For example, water is composed of hydrogen and oxygen atoms that have combined to form water molecules. Many biological processes are devoted to breaking down molecules into their component atoms so they can be reassembled into a more useful molecule.

Atomic Particles

Atoms consist of three basic particles: protons, electrons, and neutrons. The nucleus (center) of the atom contains the protons (positively charged) and the neutrons (no charge). The outermost regions of the atom are called electron shells and contain the electrons (negatively charged). Atoms have different properties based on the arrangement and number of their basic particles.

The hydrogen atom (H) contains only one proton, one electron, and no neutrons. This can be determined using the atomic number and the mass number of the element (see the concept on atomic numbers and mass numbers).

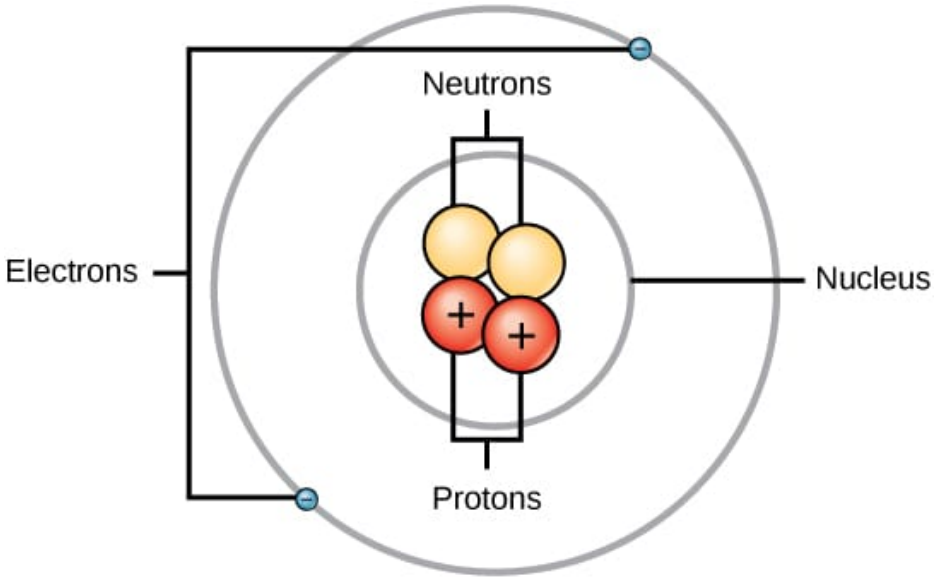


Figure 2.1.1: Structure of an atom: Elements, such as helium, depicted here, are made up of atoms. Atoms are made up of protons and neutrons located within the nucleus, with electrons in orbitals surrounding the nucleus.

Atomic Mass

Protons and neutrons have approximately the same mass, about 1.67×10^{-24} grams. Scientists define this amount of mass as one atomic mass unit (amu) or one Dalton. Although similar in mass, protons are positively charged, while neutrons have no charge. Therefore, the number of neutrons in an atom contributes significantly to its mass, but not to its charge.

Electrons are much smaller in mass than protons, weighing only 9.11×10^{-28} grams, or about 1/1800 of an atomic mass unit. Therefore, they do not contribute much to an element's overall atomic mass. When considering atomic mass, it is customary to ignore the mass of any electrons and calculate the atom's mass based on the number of protons and neutrons alone.

Electrons contribute greatly to the atom's charge, as each electron has a negative charge equal to the positive charge of a proton. Scientists define these charges as "+1" and "-1. " In an uncharged, neutral atom, the number of electrons orbiting the nucleus is equal to the number of protons inside the nucleus. In these atoms, the positive and negative charges cancel each other out, leading to an atom with no net charge.

Table 2.1.1: Protons, neutrons, and electrons: Both protons and neutrons have a mass of 1 amu and are found in the nucleus. However, protons have a charge of +1, and neutrons are uncharged. Electrons have a mass of approximately 0 amu, orbit the nucleus, and have a charge of -1.

	Charge	Mass (amu)	Location
proton	+1	1	nucleus
neutron	0	1	nucles
electron	-1	0	orbitals

Exploring Electron Properties: Compare the behavior of electrons to that of other charged particles to discover properties of electrons such as charge and mass.

Volume of Atoms

Accounting for the sizes of protons, neutrons, and electrons, most of the volume of an atom—greater than 99 percent—is, in fact, empty space. Despite all this empty space, solid objects do not just pass through one another. The electrons that surround all atoms are negatively charged and cause atoms to repel one another, preventing atoms from occupying the same space. These intermolecular forces prevent you from falling through an object like your chair.

Interactive Element

Interactive: Build an Atom: Build an atom out of protons, neutrons, and electrons, and see how the element, charge, and mass change. Then play a game to test your ideas!

Key Points

- An atom is composed of two regions: the nucleus, which is in the center of the atom and contains protons and neutrons, and the outer region of the atom, which holds its electrons in orbit around the nucleus.
- Protons and neutrons have approximately the same mass, about 1.67 × 10-24 grams, which scientists define as one atomic mass unit (amu) or one Dalton.
- Each electron has a negative charge (-1) equal to the positive charge of a proton (+1).
- Neutrons are uncharged particles found within the nucleus.

Key Terms

- **atom**: The smallest possible amount of matter which still retains its identity as a chemical element, consisting of a nucleus surrounded by electrons.
- **proton**: Positively charged subatomic particle forming part of the nucleus of an atom and determining the atomic number of an element. It weighs 1 amu.
- **neutron**: A subatomic particle forming part of the nucleus of an atom. It has no charge. It is equal in mass to a proton or it weighs 1 amu.

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2.2: Atoms, Isotopes, Ions, and Molecules - Atomic Number and Mass Number

Learning Objectives

- Determine the relationship between the mass number of an atom, its atomic number, its atomic mass, and its number of subatomic particles

Atomic Number

Neutral atoms of an element contain an equal number of protons and electrons. The number of protons determines an element's atomic number (Z) and distinguishes one element from another. For example, carbon's atomic number (Z) is 6 because it has 6 protons. The number of neutrons can vary to produce isotopes, which are atoms of the same element that have different numbers of neutrons. The number of electrons can also be different in atoms of the same element, thus producing ions (charged atoms). For instance, iron, Fe, can exist in its neutral state, or in the +2 and +3 ionic states.

Mass Number

An element's mass number (A) is the sum of the number of protons and the number of neutrons. The small contribution of mass from electrons is disregarded in calculating the mass number. This approximation of mass can be used to easily calculate how many neutrons an element has by simply subtracting the number of protons from the mass number. Protons and neutrons both weigh about one atomic mass unit or amu. Isotopes of the same element will have the same atomic number but different mass numbers.

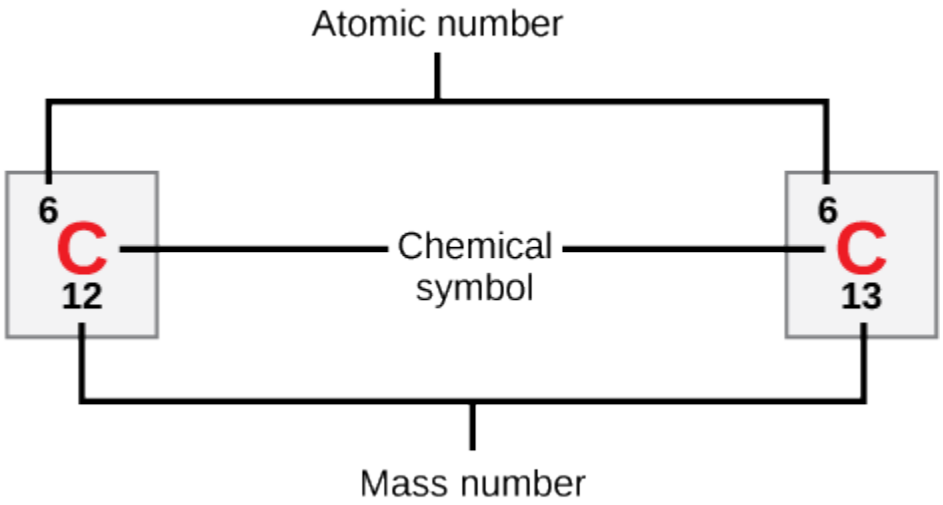


Figure 2.2.1: Atomic number, chemical symbol, and mass number: Carbon has an atomic number of six, and two stable isotopes with mass numbers of twelve and thirteen, respectively. Its average atomic mass is 12.11.

Scientists determine the atomic mass by calculating the mean of the mass numbers for its naturally-occurring isotopes. Often, the resulting number contains a decimal. For example, the atomic mass of chlorine (Cl) is 35.45 amu because chlorine is composed of several isotopes, some (the majority) with an atomic mass of 35 amu (17 protons and 18 neutrons) and some with an atomic mass of 37 amu (17 protons and 20 neutrons).

Given an atomic number (Z) and mass number (A), you can find the number of protons, neutrons, and electrons in a neutral atom. For example, a lithium atom (Z=3, A=7 amu) contains three protons (found from Z), three electrons (as the number of protons is equal to the number of electrons in an atom), and four neutrons (7 – 3 = 4).

Key Points

- Neutral atoms of each element contain an equal number of protons and electrons.
- The number of protons determines an element's atomic number and is used to distinguish one element from another.
- The number of neutrons is variable, resulting in isotopes, which are different forms of the same atom that vary only in the number of neutrons they possess.
- Together, the number of protons and the number of neutrons determine an element's mass number.
- Since an element's isotopes have slightly different mass numbers, the atomic mass is calculated by obtaining the mean of the mass numbers for its isotopes.

Key Terms

- **mass number**: The sum of the number of protons and the number of neutrons in an atom.
- **atomic number**: The number of protons in an atom.
- **atomic mass**: The average mass of an atom, taking into account all its naturally occurring isotopes.

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2.3: Atoms, Isotopes, Ions, and Molecules - Isotopes

Learning Objectives

- Discuss the properties of isotopes and their use in radiometric dating

What is an Isotope?

Isotopes are various forms of an element that have the same number of protons but a different number of neutrons. Some elements, such as carbon, potassium, and uranium, have multiple naturally-occurring isotopes. Isotopes are defined first by their element and then by the sum of the protons and neutrons present.

- Carbon-12 (or ^{12}C) contains six protons, six neutrons, and six electrons; therefore, it has a mass number of 12 amu (six protons and six neutrons).
- Carbon-14 (or ^{14}C) contains six protons, eight neutrons, and six electrons; its atomic mass is 14 amu (six protons and eight neutrons).

While the mass of individual isotopes is different, their physical and chemical properties remain mostly unchanged.

Isotopes do differ in their stability. Carbon-12 (^{12}C) is the most abundant of the carbon isotopes, accounting for 98.89% of carbon on Earth. Carbon-14 (^{14}C) is unstable and only occurs in trace amounts. Unstable isotopes most commonly emit alpha particles (He^{2+}) and electrons. Neutrons, protons, and positrons can also be emitted and electrons can be captured to attain a more stable atomic configuration (lower level of potential energy) through a process called radioactive decay. The new atoms created may be in a high energy state and emit gamma rays which lowers the energy but alone does not change the atom into another isotope. These atoms are called radioactive isotopes or radioisotopes.

Radiocarbon Dating

Carbon is normally present in the atmosphere in the form of gaseous compounds like carbon dioxide and methane. Carbon-14 (^{14}C) is a naturally-occurring radioisotope that is created from atmospheric ^{14}N (nitrogen) by the addition of a neutron and the loss of a proton, which is caused by cosmic rays. This is a continuous process so more ^{14}C is always being created in the atmosphere. Once produced, the ^{14}C often combines with the oxygen in the atmosphere to form carbon dioxide. Carbon dioxide produced in this way diffuses in the atmosphere, is dissolved in the ocean, and is incorporated by plants via photosynthesis. Animals eat the plants and, ultimately, the radiocarbon is distributed throughout the biosphere.

In living organisms, the relative amount of ^{14}C in their body is approximately equal to the concentration of ^{14}C in the atmosphere. When an organism dies, it is no longer ingesting ^{14}C, so the ratio between ^{14}C and ^{12}C will decline as ^{14}C gradually decays back to ^{14}N. This slow process, which is called beta decay, releases energy through the emission of electrons from the nucleus or positrons.

After approximately 5,730 years, half of the starting concentration of ^{14}C will have been converted back to ^{14}N. This is referred to as its half-life, or the time it takes for half of the original concentration of an isotope to decay back to its more stable form. Because the half-life of ^{14}C is long, it is used to date formerly-living objects such as old bones or wood. Comparing the ratio of the ^{14}C concentration found in an object to the amount of ^{14}C in the atmosphere, the amount of the isotope that has not yet decayed can be determined. On the basis of this amount, the age of the material can be accurately calculated, as long as the material is believed to be less than 50,000 years old. This technique is called radiocarbon dating, or carbon dating for short.



Figure 2.3.1: Application of carbon dating: The age of carbon-containing remains less than 50,000 years old, such as this pygmy mammoth, can be determined using carbon dating.

Other elements have isotopes with different half lives. For example, ^{40}K (potassium-40) has a half-life of 1.25 billion years, and ^{235}U (uranium-235) has a half-life of about 700 million years. Scientists often use these other radioactive elements to date objects that are older than 50,000 years (the limit of carbon dating). Through the use of radiometric dating, scientists can study the age of fossils or other remains of extinct organisms.

Key Points

- Isotopes are atoms of the same element that contain an identical number of protons, but a different number of neutrons.
- Despite having different numbers of neutrons, isotopes of the same element have very similar physical properties.
- Some isotopes are unstable and will undergo radioactive decay to become other elements.
- The predictable half-life of different decaying isotopes allows scientists to date material based on its isotopic composition, such as with Carbon-14 dating.

Key Terms

- **isotope**: Any of two or more forms of an element where the atoms have the same number of protons, but a different number of neutrons within their nuclei.
- **half-life**: The time it takes for half of the original concentration of an isotope to decay back to its more stable form.
- **radioactive isotopes**: an atom with an unstable nucleus, characterized by excess energy available that undergoes radioactive decay and creates most commonly gamma rays, alpha or beta particles.
- **radiocarbon dating**: Determining the age of an object by comparing the ratio of the 14C concentration found in it to the amount of 14C in the atmosphere.

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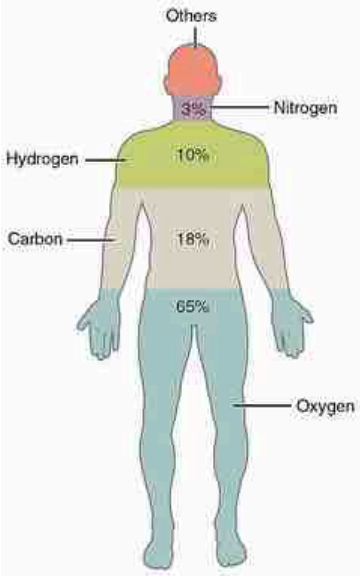
2.4: Atoms, Isotopes, Ions, and Molecules - The Periodic Table

Learning Objectives

- Discuss the organization of the periodic table

Matter and Elements

Matter comprises all of the physical objects in the universe, those that take up space and have mass. All matter is composed of atoms of one or more elements, pure substances with specific chemical and physical properties. There are 98 elements that naturally occur on earth, yet living systems use a relatively small number of these. Living creatures are composed mainly of just four elements: carbon, hydrogen, oxygen, and nitrogen (often remembered by the acronym CHON). As elements are bonded together they form compounds that often have new emergent properties that are different from the properties of the individual elements. Life is an example of an emergent property that arises from the specific collection of molecules found in cells.



Element	Symbol	Percentage in Body
Oxygen	O	65.0
Carbon	C	18.5
Hydrogen	H	9.5
Nitrogen	N	3.2
Calcium	Ca	1.5
Phosphorus	P	1.0
Potassium	K	0.4
Sulfur	S	0.3
Sodium	Na	0.2
Chlorine	Cl	0.2
Magnesium	Mg	0.1
Trace elements include boron (B), chromium (Cr), cobalt (Co), copper (Cu), fluorine (F), iodine (I), iron (Fe), manganese (Mn), molybdenum (Mo), selenium (Se), silicon (Si), tin (Sn), vanadium (V), and zinc (Zn).		less than 1.0

Elements of the human body arranged by percent of total mass: There are 25 elements believed to play an active role in human health. Carbon, hydrogen, oxygen, and nitrogen make up approximately 96% of the mass in a human body.

The Periodic Table

The different elements are organized and displayed in the periodic table. Devised by Russian chemist Dmitri Mendeleev (1834–1907) in 1869, the table groups elements that, although unique, share certain chemical properties with other elements. In the periodic table the elements are organized and displayed according to their atomic number and are arranged in a series of rows (periods) and columns (groups) based on shared chemical and physical properties. If you look at a periodic table, you will see the groups numbered at the top of each column from left to right starting with 1 and ending with 18. In addition to providing the atomic number for each element, the periodic table also displays the element's atomic mass. Looking at carbon, for example, its symbol (C) and name appear, as well as its atomic number of six (in the upper left-hand corner) and its atomic mass of 12.11.

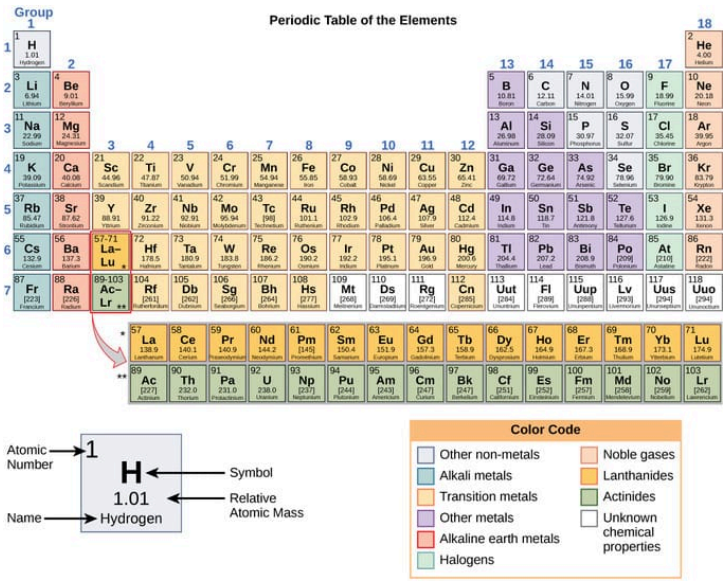


Figure 2.4.1: The periodic table: The periodic table shows the atomic mass and atomic number of each element. The atomic number appears above the symbol for the element and the approximate atomic mass appears below it.

The arrangement of the periodic table allows the elements to be grouped according to their chemical properties. Within the main group elements (Groups 1-2, 13-18), there are some general trends that we can observe. The further down a given group, the elements have an increased metallic character: they are good conductors of both heat and electricity, solids at room temperature, and shiny in appearance. Moving from left to right across a period, the elements have greater non-metallic character. These elements are insulators, poor heat conductors, and can exist in different phases at room temperature (brittle solid, liquid, or gas). The elements at the boundary between the metallic elements (grey elements) and nonmetal elements (green elements) are metalloid in character (pink elements). They have low electrical conductivity that increases with temperature. They also share properties with both the metals and the nonmetals.

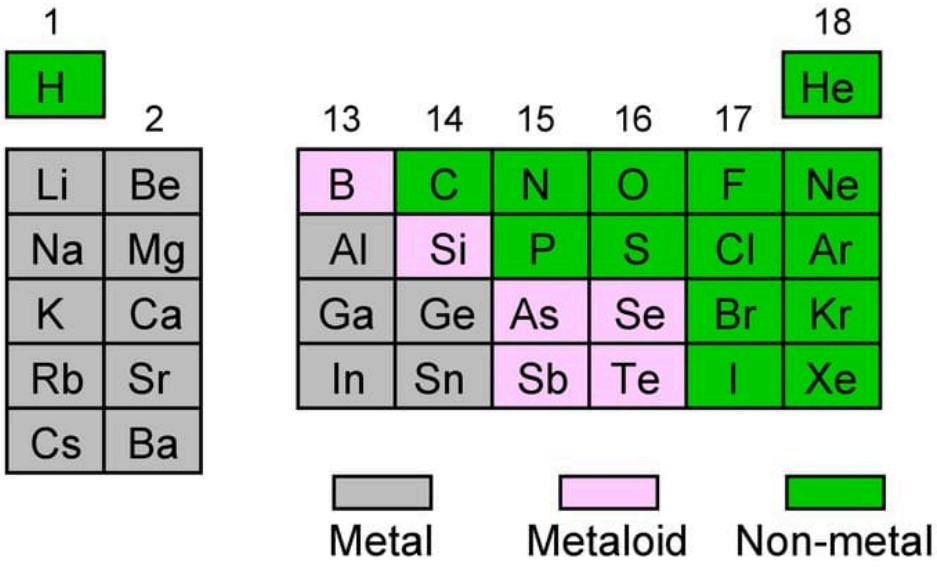


Figure 2.4.1: The main group elements: Within the p-block at the boundary between the metallic elements (grey elements) and nonmetal elements (green elements) there is positioned boron and silicon that are metalloid in character (pink elements), i.e., they have low electrical conductivity that increases with temperature.

Today, the periodic table continues to expand as heavier and heavier elements are synthesized in laboratories. These large elements are extremely unstable and, as such, are very difficult to detect; but their continued creation is an ongoing challenge undertaken by scientists around the world.

Key Points

- All matter is made from atoms of one or more elements. Living creatures consist mainly of carbon, hydrogen, oxygen, and nitrogen (CHON).
- Combining elements creates compounds that may have emergent properties.
- The periodic table is a listing of the elements according to increasing atomic number that is further organized into columns based on similar physical and chemical properties and electron configuration.
- As one moves down a column or across a row, there are some general trends for the properties of the elements.
- The periodic table continues to expand today as heavier and heavier elements are created in laboratories around the world.

Key Terms

- **element**: Pure chemical substances consisting of only one type of atom with a defined set of chemical and physical properties.
- **emergent properties**: Properties found in compound structures that are different from those of the individual components and would not be predicted based on the properties of the individual components.
- **periodic table**: A tabular chart of the chemical elements according to their atomic numbers so that elements with similar properties are in the same column.

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2.5: Atoms, Isotopes, Ions, and Molecules - Electron Shells and the Bohr Model

Learning Objectives

- Construct an atom according to the Bohr model

Electron Shells and the Bohr Model

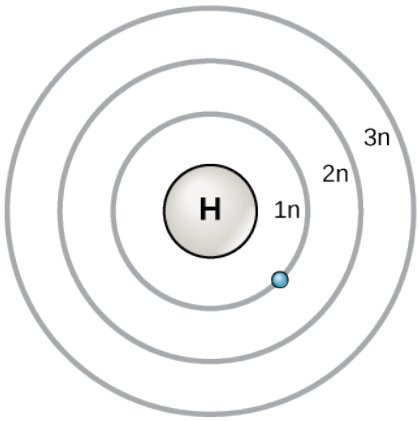


Figure 2.5.1: Orbitals in the Bohr model: The Bohr model was developed by Niels Bohr in 1913. In this model, electrons exist within principal shells. An electron normally exists in the lowest energy shell available, which is the one closest to the nucleus. Energy from a photon of light can bump it up to a higher energy shell, but this situation is unstable and the electron quickly decays back to the ground state. In the process, a photon of light is released.

As previously discussed, there is a connection between the number of protons in an element, the atomic number that distinguishes one element from another, and the number of electrons it has. In all electrically-neutral atoms, the number of electrons is the same as the number of protons. Each element, when electrically neutral, has a number of electrons equal to its atomic number.

An early model of the atom was developed in 1913 by Danish scientist Niels Bohr (1885–1962). The Bohr model shows the atom as a central nucleus containing protons and neutrons with the electrons in circular orbitals at specific distances from the nucleus. These orbits form electron shells or energy levels, which are a way of visualizing the number of electrons in the various shells. These energy levels are designated by a number and the symbol “n.” For example, 1n represents the first energy level located closest to the nucleus.

Electrons fill orbit shells in a consistent order. Under standard conditions, atoms fill the inner shells (closer to the nucleus) first, often resulting in a variable number of electrons in the outermost shell. The innermost shell has a maximum of two electrons, but the next two electron shells can each have a maximum of eight electrons. This is known as the octet rule which states that, with the exception of the innermost shell, atoms are more stable energetically when they have eight electrons in their valence shell, the outermost electron shell. Examples of some neutral atoms and their electron configurations are shown in. As shown, helium has a complete outer electron shell, with two electrons filling its first and only shell. Similarly, neon has a complete outer 2n shell containing eight electrons. In contrast, chlorine and sodium have seven and one electrons in their outer shells, respectively. Theoretically, they would be more energetically stable if they followed the octet rule and had eight.

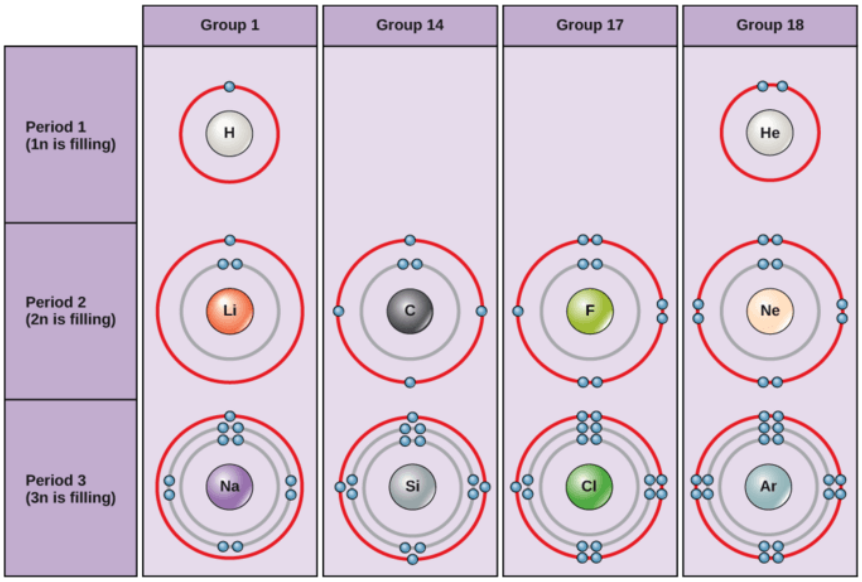


Figure 2.5.1: Bohr diagrams: Bohr diagrams indicate how many electrons fill each principal shell. Group 18 elements (helium, neon, and argon are shown) have a full outer, or valence, shell. A full valence shell is the most stable electron configuration. Elements in other groups have partially-filled valence shells and gain or lose electrons to achieve a stable electron configuration.

An atom may gain or lose electrons to achieve a full valence shell, the most stable electron configuration. The periodic table is arranged in columns and rows based on the number of electrons and where these electrons are located, providing a tool to understand how electrons are distributed in the outer shell of an atom. As shown in, the group 18 atoms helium (He), neon (Ne), and argon (Ar) all have filled outer electron shells, making it unnecessary for them to gain or lose electrons to attain stability; they are highly stable as single atoms. Their non-reactivity has resulted in their being named the inert gases (or noble gases). In comparison, the group 1 elements, including hydrogen (H), lithium (Li), and sodium (Na), all have one electron in their outermost shells. This means that they can achieve a stable configuration and a filled outer shell by donating or losing an electron. As a result of losing a negatively-charged electron, they become positively-charged ions. When an atom loses an electron to become a positively-charged ion, this is indicated by a plus sign after the element symbol; for example, Na^{+}. Group 17 elements, including fluorine and chlorine, have seven electrons in their outermost shells; they tend to fill this shell by gaining an electron from other atoms, making them negatively-charged ions. When an atom gains an electron to become a negatively-charged ion this is indicated by a minus sign after the element symbol; for example, F-. Thus, the columns of the periodic table represent the potential shared state of these elements' outer electron shells that is responsible for their similar chemical characteristics.

Key Points

- In the Bohr model of the atom, the nucleus contains the majority of the mass of the atom in its protons and neutrons.
- Orbiting the positively-charged core are the negatively charged electrons, which contribute little in terms of mass, but are electrically equivalent to the protons in the nucleus.
- In most cases, electrons fill the lower- energy orbitals first, followed by the next higher energy orbital until it is full, and so on until all electrons have been placed.
- Atoms tend to be most stable with a full outer shell (one which, after the first, contains 8 electrons), leading to what is commonly called the " octet rule ".
- The properties of an element are determined by its outermost electrons, or those in the highest energy orbital.
- Atoms that do not have full outer shells will tend to gain or lose electrons, resulting in a full outer shell and, therefore, stability.

Key Terms

- **octet rule**: A rule stating that atoms lose, gain, or share electrons in order to have a full valence shell of 8 electrons. (Hydrogen is excluded because it can hold a maximum of 2 electrons in its valence shell.)
- **electron shell**: The collective states of all electrons in an atom having the same principal quantum number (visualized as an orbit in which the electrons move).

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2.6: Atoms, Isotopes, Ions, and Molecules - Electron Orbitals

Learning Objectives

- Distinguish between electron orbitals in the Bohr model versus the quantum mechanical orbitals

Although useful to explain the reactivity and chemical bonding of certain elements, the Bohr model of the atom does not accurately reflect how electrons are spatially distributed surrounding the nucleus. They do not circle the nucleus like the earth orbits the sun, but are rather found in electron orbitals. These relatively complex shapes result from the fact that electrons behave not just like particles, but also like waves. Mathematical equations from quantum mechanics known as wave functions can predict within a certain level of probability where an electron might be at any given time. The area where an electron is most likely to be found is called its orbital.

First Electron Shell

The closest orbital to the nucleus, called the 1s orbital, can hold up to two electrons. This orbital is equivalent to the innermost electron shell of the Bohr model of the atom. It is called the 1s orbital because it is spherical around the nucleus. The 1s orbital is always filled before any other orbital. Hydrogen has one electron; therefore, it has only one spot within the 1s orbital occupied. This is designated as $1s^1$, where the superscripted 1 refers to the one electron within the 1s orbital. Helium has two electrons; therefore, it can completely fill the 1s orbital with its two electrons. This is designated as $1s^2$, referring to the two electrons of helium in the 1s orbital. On the periodic table, hydrogen and helium are the only two elements in the first row (period); this is because they are the sole elements to have electrons only in their first shell, the 1s orbital.

Second Electron Shell

The second electron shell may contain eight electrons. This shell contains another spherical s orbital and three “dumbbell” shaped p orbitals, each of which can hold two electrons. After the 1s orbital is filled, the second electron shell is filled, first filling its 2s orbital and then its three p orbitals. When filling the p orbitals, each takes a single electron; once each p orbital has an electron, a second may be added. Lithium (Li) contains three electrons that occupy the first and second shells. Two electrons fill the 1s orbital, and the third electron then fills the 2s orbital. Its electron configuration is $1s^2 2s^1$. Neon (Ne), on the other hand, has a total of ten electrons: two are in its innermost 1s orbital, and eight fill its second shell (two each in the 2s and three p orbitals). Thus, it is an inert gas and energetically stable: it rarely forms a chemical bond with other atoms.

Third Electron Shell

Larger elements have additional orbitals, making up the third electron shell. Subshells d and f have more complex shapes and contain five and seven orbitals, respectively. Principal shell 3n has s, p, and d subshells and can hold 18 electrons. Principal shell 4n has s, p, d, and f orbitals and can hold 32 electrons. Moving away from the nucleus, the number of electrons and orbitals found in the energy levels increases. Progressing from one atom to the next in the periodic table, the electron structure can be worked out by fitting an extra electron into the next available orbital. While the concepts of electron shells and orbitals are closely related, orbitals provide a more accurate depiction of the electron configuration of an atom because the orbital model specifies the different shapes and special orientations of all the places that electrons may occupy.

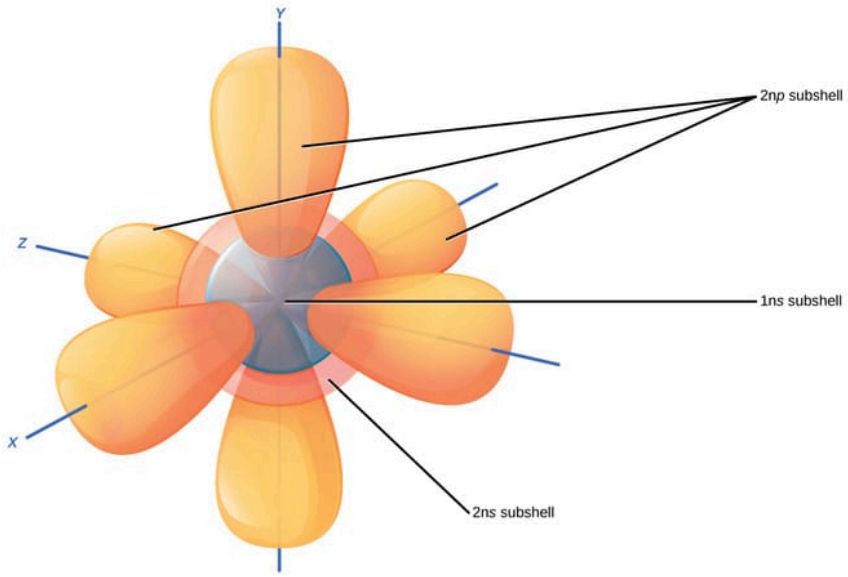


Figure 2.6.1: Diagram of the S and P orbitals: The s subshells are shaped like spheres. Both the 1n and 2n principal shells have an s orbital, but the size of the sphere is larger in the 2n orbital. Each sphere is a single orbital. p subshells are made up of three dumbbell-shaped orbitals. Principal shell 2n has a p subshell, but shell 1 does not.

Key Points

- The Bohr model of the atom does not accurately reflect how electrons are spatially distributed around the nucleus as they do not circle the nucleus like the earth orbits the sun.
- The electron orbitals are the result of mathematical equations from quantum mechanics known as wave functions and can predict within a certain level of probability where an electron might be at any given time.
- The number and type of orbitals increases with increasing atomic number, filling in various electron shells.
- The area where an electron is most likely to be found is called its orbital.

Key Terms

- **electron shell**: The collective states of all electrons in an atom having the same principal quantum number (visualized as an orbit in which the electrons move).
- **orbital**: A specification of the energy and probability density of an electron at any point in an atom or molecule.

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2.7: Atoms, Isotopes, Ions, and Molecules - Chemical Reactions and Molecules

Learning Objectives

- Describe the properties of chemical reactions and compounds

According to the octet rule, elements are most stable when their outermost shell is filled with electrons. This is because it is energetically favorable for atoms to be in that configuration. However, since not all elements have enough electrons to fill their outermost shells, atoms form chemical bonds with other atoms, which helps them obtain the electrons they need to attain a stable electron configuration. When two or more atoms chemically bond with each other, the resultant chemical structure is a molecule. The familiar water molecule, H_2O, consists of two hydrogen atoms and one oxygen atom, which bond together to form water. Atoms can form molecules by donating, accepting, or sharing electrons to fill their outer shells.

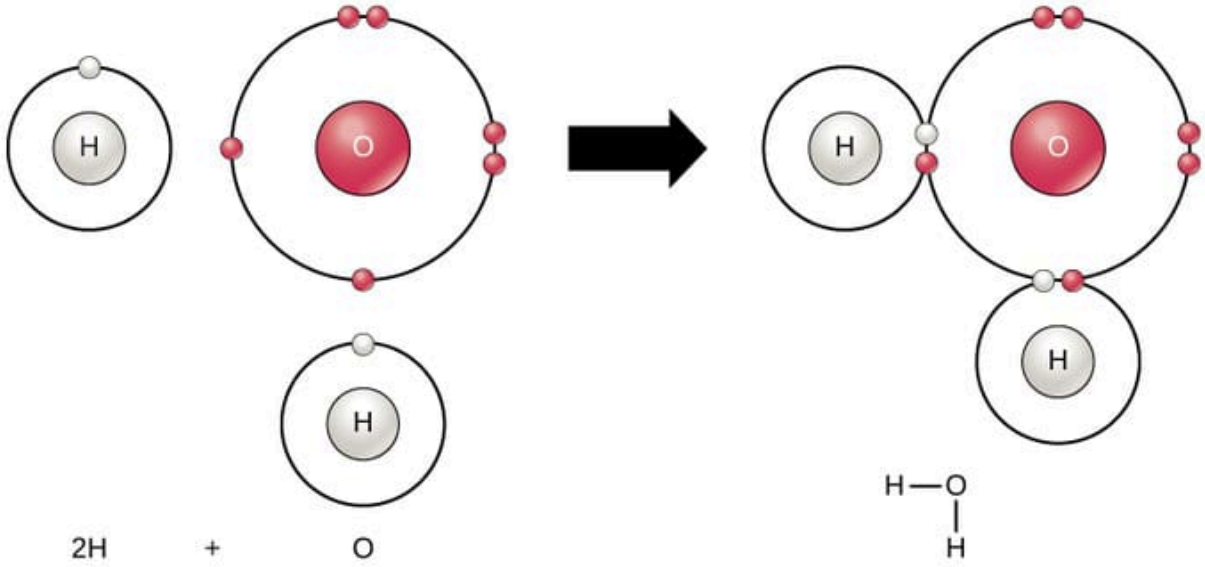


Figure 2.7.1: Atoms bond to form molecules: Two or more atoms may bond with each other to form a molecule. When two hydrogens and an oxygen share electrons via covalent bonds, a water molecule is formed.

Chemical reactions occur when two or more atoms bond together to form molecules or when bonded atoms are broken apart. The substances used in the beginning of a chemical reaction are called the reactants (usually found on the left side of a chemical equation), and the substances found at the end of the reaction are known as the products (usually found on the right side of a chemical equation). An arrow is typically drawn between the reactants and products to indicate the direction of the chemical reaction. For the creation of the water molecule shown above, the chemical equation would be:

$$2\,H_2{}^+O_2 \longrightarrow 2\,H_2O \tag{2.7.1}$$

An example of a simple chemical reaction is the breaking down of hydrogen peroxide molecules, each of which consists of two hydrogen atoms bonded to two oxygen atoms (H_2O_2). The reactant hydrogen peroxide is broken down into water (H_2O), and oxygen, which consists of two bonded oxygen atoms (O_2). In the equation below, the reaction includes two hydrogen peroxide molecules and two water molecules. This is an example of a balanced chemical equation, wherein the number of atoms of each element is the same on each side of the equation. According to the law of conservation of matter, the number of atoms before and after a chemical reaction should be equal, such that no atoms are, under normal circumstances, created or destroyed.

$$2\,H_2O_2 \longrightarrow 2\,H_2O^+O_2 \tag{2.7.2}$$

Even though all of the reactants and products of this reaction are molecules (each atom remains bonded to at least one other

atom), in this reaction only hydrogen peroxide and water are representative of a subclass of molecules known as compounds: they contain atoms of more than one type of element. Molecular oxygen, on the other hand, consists of two doubly bonded oxygen atoms and is not classified as a compound but as an element.

Irreversible and Reversible Reactions

Some chemical reactions, such as the one shown above, can proceed in one direction until the reactants are all used up. The equations that describe these reactions contain a unidirectional arrow and are irreversible. Reversible reactions are those that can go in either direction. In reversible reactions, reactants are turned into products, but when the concentration of product goes beyond a certain threshold, some of these products will be converted back into reactants; at this point, the designations of products and reactants are reversed. This back and forth continues until a certain relative balance between reactants and products occurs: a state called equilibrium. These situations of reversible reactions are often denoted by a chemical equation with a double headed arrow pointing towards both the reactants and products.

For example, in human blood, excess hydrogen ions (H^+) bind to bicarbonate ions (HCO_3^-) forming an equilibrium state with carbonic acid (H_2CO_3). If carbonic acid were added to this system, some of it would be converted to bicarbonate and hydrogen ions.

In biological reactions, however, equilibrium is rarely obtained because the concentrations of the reactants or products or both are constantly changing, often with a product of one reaction being a reactant for another. To return to the example of excess hydrogen ions in the blood, the formation of carbonic acid will be the major direction of the reaction. However, the carbonic acid can also leave the body as carbon dioxide gas (via exhalation) instead of being converted back to bicarbonate ion, thus driving the reaction to the right by the chemical law known as law of mass action. These reactions are important for maintaining the homeostasis of our blood.

Interactive Element

Interactive: What is a Chemical Reaction?: Explore reactions in which chemical bonds are formed and broken with this model. Press run, then try heating and cooling the atoms to see how temperature affects the balance between bond formation and breaking.

Key Points

- Atoms form chemical bonds with other atoms thereby obtaining the electrons they need to attain a stable electron configuration.
- The substances used in the beginning of a chemical reaction are called the reactants and the substances found at the end of the reaction are known as the products.
- Some reactions are reversible and will reach a relative balance between reactants and products: a state called equilibrium.
- An arrow is typically drawn between the reactants and products to indicate the direction of the chemical reaction.

Key Terms

- **reactant**: Any of the participants present at the start of a chemical reaction.
- **molecule**: The smallest particle of a specific compound that retains the chemical properties of that compound; two or more atoms held together by chemical bonds.
- **reaction**: A transformation in which one or more substances is converted into another by combination or decomposition

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2.8: Atoms, Isotopes, Ions, and Molecules - Ions and Ionic Bonds

Learning Objectives

- Predict whether a given element will more likely form a cation or an anion

Ions and Ionic Bonds

Some atoms are more stable when they gain or lose an electron (or possibly two) and form ions. This results in a full outermost electron shell and makes them energetically more stable. Now, because the number of electrons does not equal the number of protons, each ion has a net charge. Cations are positive ions that are formed by losing electrons (as the number of protons is now greater than the number of electrons). Negative ions are formed by gaining electrons and are called anions (wherein there are more electrons than protons in a molecule). Anions are designated by their elemental name being altered to end in “-ide”. For example, the anion of chlorine is called chloride, and the anion of sulfur is called sulfide.

This movement of electrons from one element to another is referred to as electron transfer. As illustrated, sodium (Na) only has one electron in its outer electron shell. It takes less energy for sodium to donate that one electron than it does to accept seven more electrons to fill the outer shell. When sodium loses an electron, it will have 11 protons, 11 neutrons, and only 10 electrons. This leaves it with an overall charge of +1 since there are now more protons than electrons. It is now referred to as a sodium ion. Chlorine (Cl) in its lowest energy state (called the ground state) has seven electrons in its outer shell. Again, it is more energy efficient for chlorine to gain one electron than to lose seven. Therefore, it tends to gain an electron to create an ion with 17 protons, 17 neutrons, and 18 electrons. This gives it a net charge of -1 since there are now more electrons than protons. It is now referred to as a chloride ion. In this example, sodium will donate its one electron to empty its shell, and chlorine will accept that electron to fill its shell. Both ions now satisfy the octet rule and have complete outer shells. These transactions can normally only take place simultaneously; in order for a sodium atom to lose an electron, it must be in the presence of a suitable recipient like a chlorine atom.

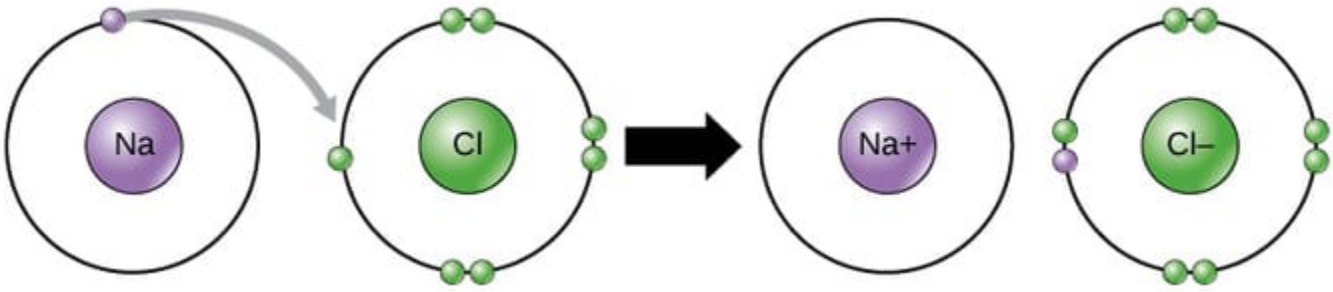


Figure 2.8.1: Electron Transfer Between Na and Cl: In the formation of an ionic compound, metals lose electrons and nonmetals gain electrons to achieve an octet. In this example, sodium loses one electron to empty its shell and chlorine accepts that electron to fill its shell.

Ionic bonds are formed between ions with opposite charges. For instance, positively charged sodium ions and negatively charged chloride ions bond together to form sodium chloride, or table salt, a crystalline molecule with zero net charge. The attractive force holding the two atoms together is called the electromagnetic force and is responsible for the attraction between oppositely charged ions.

Certain salts are referred to in physiology as electrolytes (including sodium, potassium, and calcium). Electrolytes are ions necessary for nerve impulse conduction, muscle contractions, and water balance. Many sports drinks and dietary supplements provide these ions to replace those lost from the body via sweating during exercise.

Key Points

- Ions form from elements when they gain or lose an electron causing the number of protons to be unequal to the number of electrons, resulting in a net charge.
- If there are more electrons than protons (from an element gaining one or more electrons), the ion is negatively charged and called an anion.
- If there are more protons than electrons (via loss of electrons), the ion is positively charged and is called a cation.
- Ionic bonds result from the interaction between a positively charged cation and a negatively charged anion.

Key Terms

- **ion**: An atom, or group of atoms, bearing an electrical charge, such as the sodium and chlorine atoms in a salt solution.
- **ionic bond**: A strong chemical bond caused by the electrostatic attraction between two oppositely charged ions.

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2.9: Atoms, Isotopes, Ions, and Molecules - Covalent Bonds and Other Bonds and Interactions

Learning Objectives

- Compare the relative strength of different types of bonding interactions

The octet rule can be satisfied by the sharing of electrons between atoms to form covalent bonds. These bonds are stronger and much more common than are ionic bonds in the molecules of living organisms. Covalent bonds are commonly found in carbon-based organic molecules, such as DNA and proteins. Covalent bonds are also found in inorganic molecules such as H_2O, CO_2, and O_2. One, two, or three pairs of electrons may be shared between two atoms, making single, double, and triple bonds, respectively. The more covalent bonds between two atoms, the stronger their connection. Thus, triple bonds are the strongest.

The strength of different levels of covalent bonding is one of the main reasons living organisms have a difficult time in acquiring nitrogen for use in constructing nitrogenous molecules, even though molecular nitrogen, N_2, is the most abundant gas in the atmosphere. Molecular nitrogen consists of two nitrogen atoms triple bonded to each other. The resulting strong triple bond makes it difficult for living systems to break apart this nitrogen in order to use it as constituents of biomolecules, such as proteins, DNA, and RNA.

The formation of water molecules is an example of covalent bonding. The hydrogen and oxygen atoms that combine to form water molecules are bound together by covalent bonds. The electron from the hydrogen splits its time between the incomplete outer shell of the hydrogen atom and the incomplete outer shell of the oxygen atom. In return, the oxygen atom shares one of its electrons with the hydrogen atom, creating a two-electron single covalent bond. To completely fill the outer shell of oxygen, which has six electrons in its outer shell, two electrons (one from each hydrogen atom) are needed. Each hydrogen atom needs only a single electron to fill its outer shell, hence the well-known formula H_2O. The electrons that are shared between the two elements fill the outer shell of each, making both elements more stable.

Polar Covalent Bonds

There are two types of covalent bonds: polar and nonpolar. In a polar covalent bond, the electrons are unequally shared by the atoms because they are more attracted to one nucleus than the other. The relative attraction of an atom to an electron is known as its electronegativity: atoms that are more attracted to an electron are considered to be more electronegative. Because of the unequal distribution of electrons between the atoms of different elements, a slightly positive (δ+) or slightly negative (δ-) charge develops. This partial charge is known as a dipole; this is an important property of water and accounts for many of its characteristics. The dipole in water occurs because oxygen has a higher electronegativity than hydrogen, which means that the shared electrons spend more time in the vicinity of the oxygen nucleus than they do near the nucleus of the hydrogen atoms.

	Bond type	Molecular shape	Molecular type
Water	δ− O H δ+ Polar covalent	δ+ H H O δ− Bent	Polar
Methane	C H Nonpolar covalent	H H C H H Tetrahedral	Nonpolar
Carbon dioxide	δ− O = C δ+ Polar covalent	O = C = O Linear	Nonpolar

Figure 2.9.1: Polar and Nonpolar Covalent Bonds: Whether a molecule is polar or nonpolar depends both on bond type and molecular shape. Both water and carbon dioxide have polar covalent bonds, but carbon dioxide is linear, so the partial charges on the molecule cancel each other out.

Nonpolar Covalent Bonds

Nonpolar covalent bonds form between two atoms of the same element or between different elements that share electrons equally. For example, molecular oxygen (O_2) is nonpolar because the electrons will be equally distributed between the two oxygen atoms. The four bonds of methane are also considered to be nonpolar because the electronegativies of carbon and hydrogen are nearly identical.

Hydrogen Bonds and Van Der Waals Interactions

Not all bonds are ionic or covalent; weaker bonds can also form between molecules. Two types of weak bonds that frequently occur are hydrogen bonds and van der Waals interactions. Without these two types of bonds, life as we know it would not exist.

Hydrogen bonds provide many of the critical, life-sustaining properties of water and also stabilize the structures of proteins and DNA, the building block of cells. When polar covalent bonds containing hydrogen are formed, the hydrogen atom in that bond has a slightly positive charge (δ+) because the shared electrons are pulled more strongly toward the other element and away from the hydrogen atom. Because the hydrogen has a slightly positive charge, it's attracted to neighboring negative charges. The weak interaction between the δ+ charge of a hydrogen atom from one molecule and the δ- charge of a more electronegative atom is called a hydrogen bond. Individual hydrogen bonds are weak and easily broken; however, they occur in very large numbers in water and in organic polymers, and the additive force can be very strong. For example, hydrogen bonds are responsible for zipping together the DNA double helix.

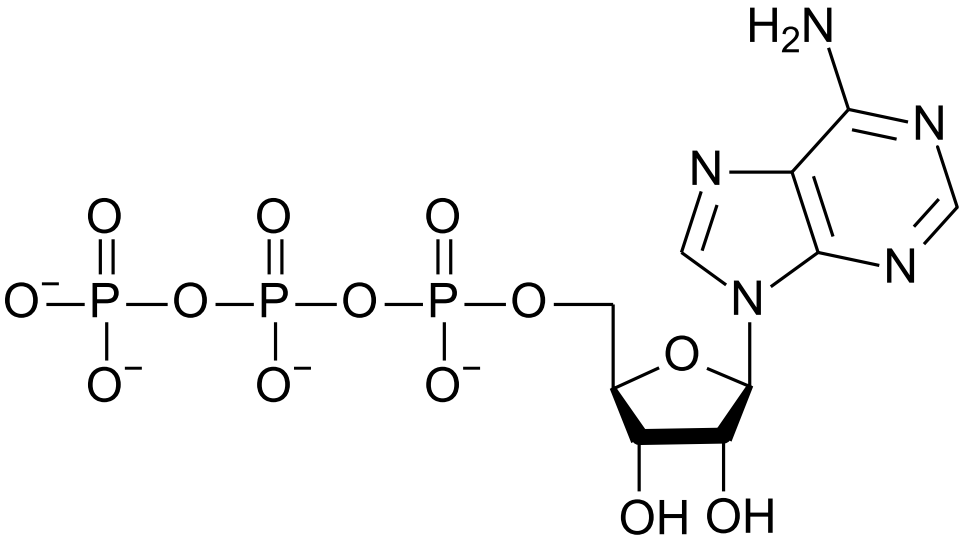


Figure 2.9.1: Adenosine Triphosphate, ATP: Adenosine Triphosphate, or ATP, is the most commonly used cofactor in nature. Its biosynthesis involves the fixation of nitrogen to provide feedstocks that eventually produce the carbon-nitrogen bonds it contains.

Like hydrogen bonds, van der Waals interactions are weak interactions between molecules. Van der Waals attractions can occur between any two or more molecules and are dependent on slight fluctuations of the electron densities, which can lead to slight temporary dipoles around a molecule. For these attractions to happen, the molecules need to be very close to one another. These bonds, along with hydrogen bonds, help form the three-dimensional structures of the proteins in our cells that are required for their proper function.

Interactive Element

Interactions between different types of molecules: In this interactive, you can explore how different types of molecules interact with each other based on their bonds.

Key Points

- A polar covalent bond arises when two atoms of different electronegativity share two electrons unequally.
- A non-polar covalent bond is one in which the electrons are shared equally between two atoms.
- Hydrogen bonds and Van Der Waals are responsible for the folding of proteins, the binding of ligands to proteins, and many other processes between molecules.

Key Terms

- **hydrogen bond**: A weak bond in which a hydrogen atom in one molecule is attracted to an electronegative atom (usually nitrogen or oxygen) in the same or different molecule.
- **covalent bond**: A type of chemical bond where two atoms are connected to each other by the sharing of two or more electrons.
- **dipole**: Any object (such as a magnet, polar molecule or antenna), that is oppositely charged at two points (or poles).

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2.10: Atoms, Isotopes, Ions, and Molecules - Hydrogen Bonding and Van der Waals Forces

Learning Objectives

- Describe how hydrogen bonds and van der Waals interactions occur

Ionic and covalent bonds between elements require energy to break. Ionic bonds are not as strong as covalent, which determines their behavior in biological systems. However, not all bonds are ionic or covalent bonds. Weaker bonds can also form between molecules. Two weak bonds that occur frequently are hydrogen bonds and van der Waals interactions.

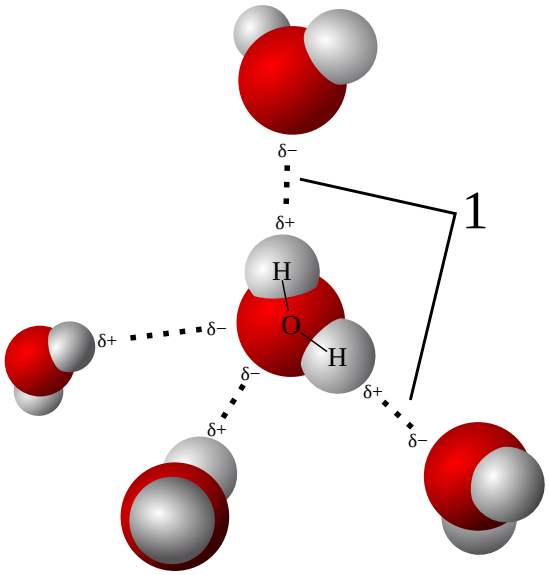


Figure 2.10.1: Hydrogen bonds between water molecules: The slightly negative oxygen side of the water molecule and the slightly positive hydrogen side of the water molecule are attracted to each other and form a hydrogen bond. (Public Domain; Magasjukur2 via Wikipedia)

Hydrogen Bonding

Hydrogen bonds provide many of the critical, life-sustaining properties of water and also stabilize the structures of proteins and DNA, the building block of cells. When polar covalent bonds containing hydrogen form, the hydrogen in that bond has a slightly positive charge because hydrogen's one electron is pulled more strongly toward the other element and away from the hydrogen. Because the hydrogen is slightly positive, it will be attracted to neighboring negative charges. When this happens, an interaction occurs between the $\delta^+$of the hydrogen from one molecule and the δ– charge on the more electronegative atoms of another molecule, usually oxygen or nitrogen, or within the same molecule. This interaction is called a hydrogen bond. This type of bond is common and occurs regularly between water molecules. Individual hydrogen bonds are weak and easily broken; however, they occur in very large numbers in water and in organic polymers, creating a major force in combination. Hydrogen bonds are also responsible for zipping together the DNA double helix.

Applications for Hydrogen Bonds

Hydrogen bonds occur in inorganic molecules, such as water, and organic molecules, such as DNA and proteins. The two complementary strands of DNA are held together by hydrogen bonds between complementary nucleotides (A&T, C&G). Hydrogen bonding in water contributes to its unique properties, including its high boiling point (100 °C) and surface tension.



Figure 2.10.1: Water droplets on a leaf: The hydrogen bonds formed between water molecules in water droplets are stronger than the other intermolecular forces between the water molecules and the leaf, contributing to high surface tension and distinct water droplets.

In biology, intramolecular hydrogen bonding is partly responsible for the secondary, tertiary, and quaternary structures of proteins and nucleic acids. The hydrogen bonds help the proteins and nucleic acids form and maintain specific shapes.

Van der Waals Interactions

Like hydrogen bonds, van der Waals interactions are weak attractions or interactions between molecules. Van der Waals attractions can occur between any two or more molecules and are dependent on slight fluctuations of the electron densities, which are not always symmetrical around an atom. For these attractions to happen, the molecules need to be very close to one another. These bonds—along with ionic, covalent, and hydrogen bonds—contribute to the three-dimensional structure of proteins that is necessary for their proper function.

Interactive Element

Van der Waals attraction: Explore how Van der Waals attractions and temperature affect intermolecular interactions.

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Key Points

- Hydrogen bonds provide many of the critical, life-sustaining properties of water and also stabilize the structures of proteins and DNA, the building block of cells.
- Hydrogen bonds occur in inorganic molecules, such as water, and organic molecules, such as DNA and proteins.
- Van der Waals attractions can occur between any two or more molecules and are dependent on slight fluctuations of the electron densities.
- While hydrogen bonds and van der Waals interactions are weak individually, they are strong combined in vast numbers.

Key Terms

- **van der Waals interactions**: A weak force of attraction between electrically neutral molecules that collide with or pass very close to each other. The van der Waals force is caused by temporary attractions between electron-rich regions of one molecule and electron-poor regions of another.
- **electronegativity**: The tendency of an atom or molecule to draw electrons towards itself, form dipoles, and thus form bonds.
- **hydrogen bond**: The attraction between a partially positively-charged hydrogen atom attached to a highly electronegative atom (such as nitrogen, oxygen, or fluorine) and another nearby electronegative atom.

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2.11: Water - Water's Polarity

Learning Objectives

- Describe the actions that occur due to water's polarity

One of water's important properties is that it is composed of polar molecules. The two hydrogen atoms and one oxygen atom within water molecules (H_2O) form polar covalent bonds. While there is no net charge to a water molecule, the polarity of water creates a slightly positive charge on hydrogen and a slightly negative charge on oxygen, contributing to water's properties of attraction. Water's charges are generated because oxygen is more electronegative, or electron loving, than hydrogen. Thus, it is more likely that a shared electron would be found near the oxygen nucleus than the hydrogen nucleus. Since water is a nonlinear, or bent, molecule, the difference in electronegativities between the oxygen and hydrogen atoms generates the partial negative charge near the oxygen and partial positive charges near both hydrogens.



Figure 2.11.1: Nonpolar Molecules: Oil and water do not mix. As this macro image of oil and water shows, oil does not dissolve in water but forms droplets instead. This is due to it being a nonpolar compound.

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

Interactive Element

Hydrogen bonds: This interactive shows the interaction of the hydrogen bonds among water molecules.

Key Points

- The difference in electronegativities between oxygen and hydrogen atoms creates partial negative and positive charges, respectively, on the atoms.
- Water molecules attract or are attracted to other polar molecules.

- Molecules that do not dissolve in water are known as hydrophobic (water fearing) molecules.

Key Terms

- **hydrophilic**: having an affinity for water; able to absorb, or be wetted by water
- **hydrophobic**: lacking an affinity for water; unable to absorb, or be wetted by water
- **polarity**: The intermolecular forces between the slightly positively-charged end of one molecule to the negative end of another or the same molecule.

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2.12: Water - Gas, Liquid, and Solid Water

Learning Objectives

- Explain the biological significance of ice's ability to float on water

Water's States: Gas, Liquid, and Solid

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

Interactive Element

***Phases of matter**: See what happens to intermolecular bonds during phase changes in this interactive.*

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

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

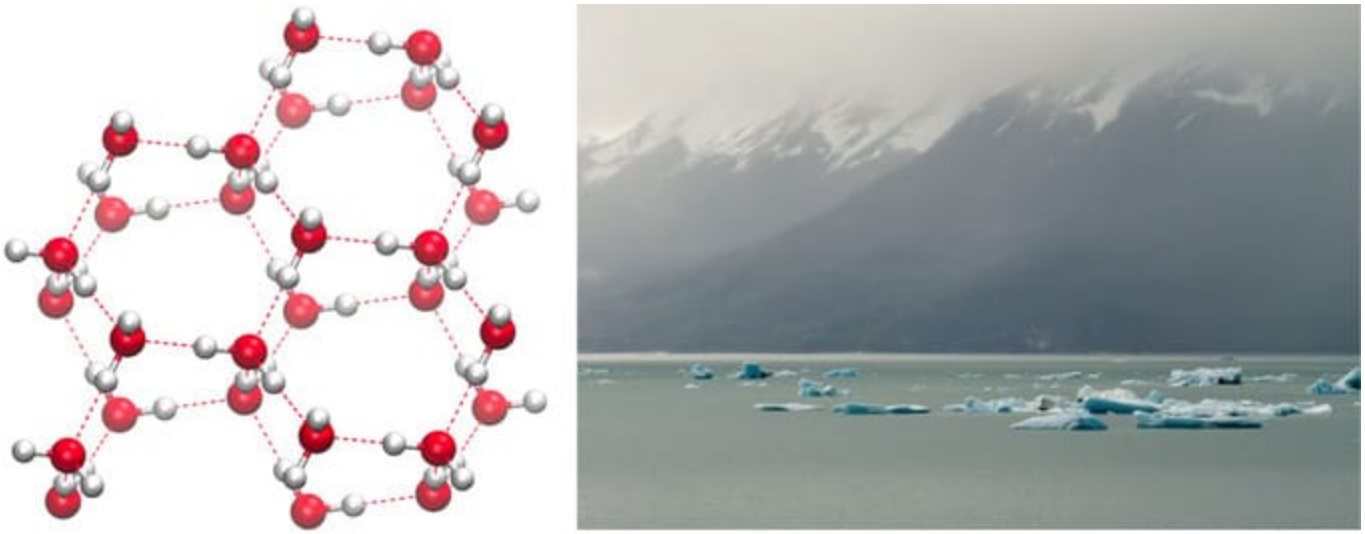


Figure 2.12.1: Ice Density: Hydrogen bonding makes ice less dense than liquid water. The (a) lattice structure of ice makes it less dense than the freely flowing molecules of liquid water, enabling it to (b) float on water.

Key Points

- As water is boiled, kinetic energy causes the hydrogen bonds to break completely and allows water molecules to escape into the air as gas (steam or water vapor).
- When water freezes, water molecules form a crystalline structure maintained by hydrogen bonding.
- Solid water, or ice, is less dense than liquid water.
- Ice is less dense than water because the orientation of hydrogen bonds causes molecules to push farther apart, which lowers the density.
- For other liquids, solidification when the temperature drops includes the lowering of kinetic energy, which allows molecules to pack more tightly and makes the solid denser than its liquid form.
- Because ice is less dense than water, it is able to float at the surface of water.

Key Terms

- **density**: A measure of the amount of matter contained by a given volume.

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2.13: Water - Heat of Vaporization

Learning Objectives

- Explain how heat of vaporization is related to the boiling point of water

Water in its liquid form has an unusually high boiling point temperature, a value close to 100°C. As a result of the network of hydrogen bonding present between water molecules, a high input of energy is required to transform one gram of liquid water into water vapor, an energy requirement called the heat of vaporization. Water has a heat of vaporization value of 40.65 kJ/mol. A considerable amount of heat energy (586 calories) is required to accomplish this change in water. This process occurs on the surface of water. As liquid water heats up, hydrogen bonding makes it difficult to separate the water molecules from each other, which is required for it to enter its gaseous phase (steam). As a result, water acts as a heat sink, or heat reservoir, and requires much more heat to boil than does a liquid such as ethanol (grain alcohol), whose hydrogen bonding with other ethanol molecules is weaker than water's hydrogen bonding. Eventually, as water reaches its boiling point of 100° Celsius (212° Fahrenheit), the heat is able to break the hydrogen bonds between the water molecules, and the kinetic energy (motion) between the water molecules allows them to escape from the liquid as a gas. Even when below its boiling point, water's individual molecules acquire enough energy from each other such that some surface water molecules can escape and vaporize; this process is known as evaporation.

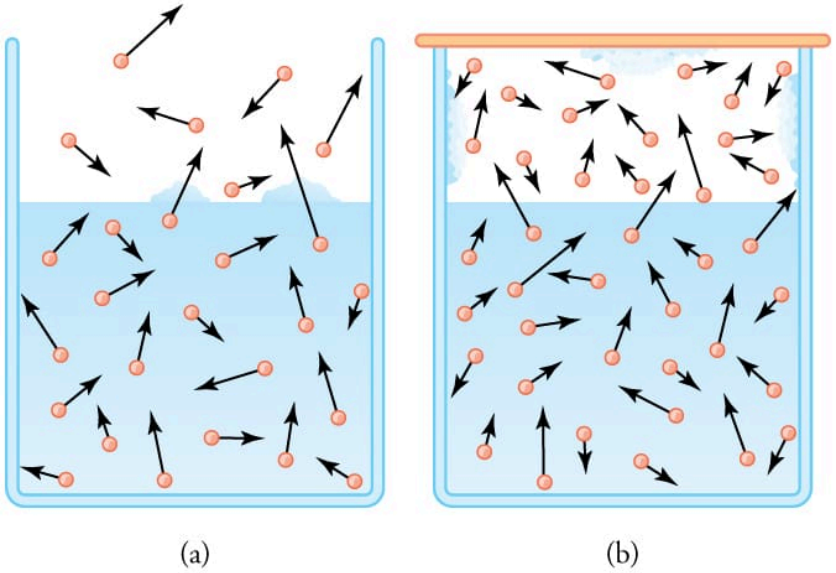


Figure 2.13.1: Humidity, Evaporation, and Boiling: (a) Because of the distribution of speeds and kinetic energies, some water molecules can break away to the vapor phase even at temperatures below the ordinary boiling point. (b) If the container is sealed, evaporation will continue until there is enough vapor density for the condensation rate to equal the evaporation rate. This vapor density and the partial pressure it creates are the saturation values. They increase with temperature and are independent of the presence of other gases, such as air. They depend only on the vapor pressure of water.

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

Key Points

- The dissociation of liquid water molecules, which changes the substance to a gas, requires a lot of energy.
- The boiling point of water is the temperature in which there is enough energy to break the hydrogen bonds between water molecules.
- Water is converted from its liquid form to its gaseous form (steam) when the heat of vaporization is reached.

- Evaporation of sweat (mostly water) removes heat from the surface of skin, cooling the body.

Key Terms

- **heat of vaporization**: The energy required to transform a given quantity of a substance from a liquid into a gas at a given pressure (often atmospheric pressure).

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2.14: Water - High Heat Capacity

Learning Objectives

- Explain the biological significance of water's high specific heat

Water's High Heat Capacity

The capability for a molecule to absorb heat energy is called heat capacity, which can be calculated by the equation shown in the figure. Water's high heat capacity is a property caused by hydrogen bonding among water molecules. When heat is absorbed, hydrogen bonds are broken and water molecules can move freely. When the temperature of water decreases, the hydrogen bonds are formed and release a considerable amount of energy. Water has the highest specific heat capacity of any liquid. Specific heat is defined as the amount of heat one gram of a substance must absorb or lose to change its temperature by one degree Celsius. For water, this amount is one calorie, or 4.184 Joules. As a result, it takes water a long time to heat and a long time to cool. In fact, the specific heat capacity of water is about five times more than that of sand. This explains why the land cools faster than the sea.

C=QΔT.C=QΔT.

The resistance to sudden temperature changes makes water an excellent habitat, allowing organisms to survive without experiencing wide temperature fluctuation. Furthermore, because many organisms are mainly composed of water, the property of high heat capacity allows highly regulated internal body temperatures. For example, the temperature of your body does not drastically drop to the same temperature as the outside temperature while you are skiing or playing in the snow. Due to its high heat capacity, water is used by warm blooded animals to more evenly disperse heat in their bodies; it acts in a similar manner to a car's cooling system, transporting heat from warm places to cool places, causing the body to maintain a more even temperature.

Key Points

- Water has the highest heat capacity of all liquids.
- Oceans cool slower than the land due to the high heat capacity of water.
- To change the temperature of 1 gram of water by 1 degree Celsius, it takes 1.00 calorie.

Key Terms

- **heat capacity**: The capability of a substance to absorb heat energy
- **specific heat**: the amount of heat, in calories, needed to raise the temperature of 1 gram of water by 1 degree Celsius

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2.15: Water - Water's Solvent Properties

Learning Objectives

- Explain why some molecules do not dissolve in water.

Water's Solvent Properties

Water, which not only dissolves many compounds but also dissolves more substances than any other liquid, is considered the universal solvent. A polar molecule with partially-positive and negative charges, it readily dissolves ions and polar molecules. Water is therefore referred to as a solvent: a substance capable of dissolving other polar molecules and ionic compounds. The charges associated with these molecules form hydrogen bonds with water, surrounding the particle with water molecules. This is referred to as a sphere of hydration, or a hydration shell, and serves to keep the particles separated or dispersed in the water.

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

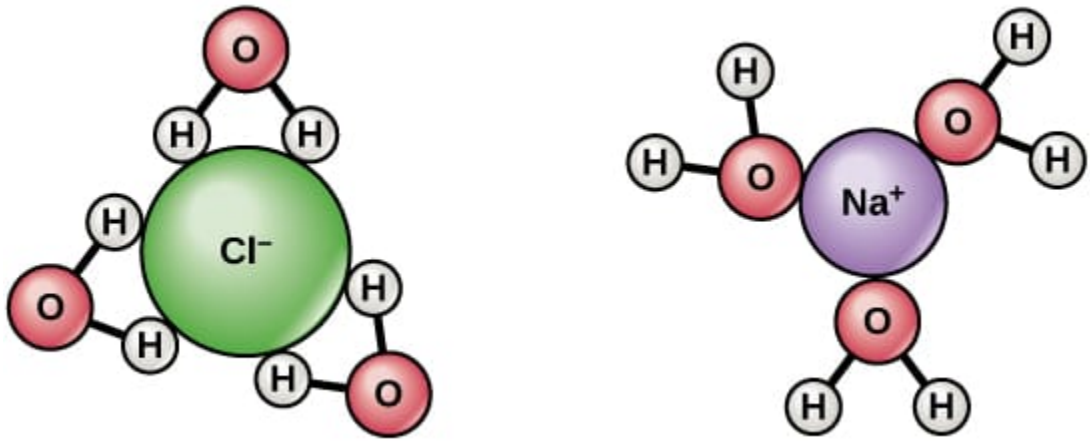


Figure 2.15.1: Dissociation of NaCl in water: When table salt (NaCl) is mixed in water, spheres of hydration form around the ions.

Since many biomolecules are either polar or charged, water readily dissolves these hydrophilic compounds. Water is a poor solvent, however, for hydrophobic molecules such as lipids. Nonpolar molecules experience hydrophobic interactions in water: the water changes its hydrogen bonding patterns around the hydrophobic molecules to produce a cage-like structure called a clathrate. This change in the hydrogen-bonding pattern of the water solvent causes the system's overall entropy to greatly decrease, as the molecules become more ordered than in liquid water. Thermodynamically, such a large decrease in entropy is not spontaneous, and the hydrophobic molecule will not dissolve.

Key Points

- Water dissociates salts by separating the cations and anions and forming new interactions between the water and ions.
- Water dissolves many biomolecules, because they are polar and therefore hydrophilic.

Key Terms

- **dissociation**: The process by which a compound or complex body breaks up into simpler constituents such as atoms or ions, usually reversibly.
- **hydration shell**: The term given to a solvation shell (a structure composed of a chemical that acts as a solvent and surrounds a solute species) with a water solvent; also referred to as a hydration sphere.

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2.16: Water - Cohesive and Adhesive Properties

Learning Objectives

- Describe the cohesive and adhesive properties of water.

Water's Cohesive and Adhesive Properties

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

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

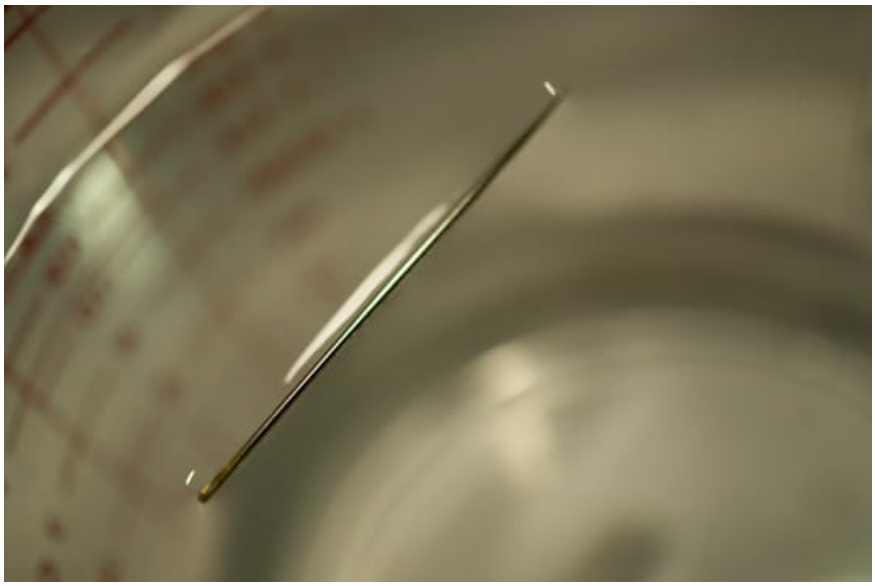


Figure 2.16.1: Surface Tension: The weight of the needle is pulling the surface downward; at the same time, the surface tension is pulling it up, suspending it on the surface of the water and keeping it from sinking. Notice the indentation in the water around the needle.

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

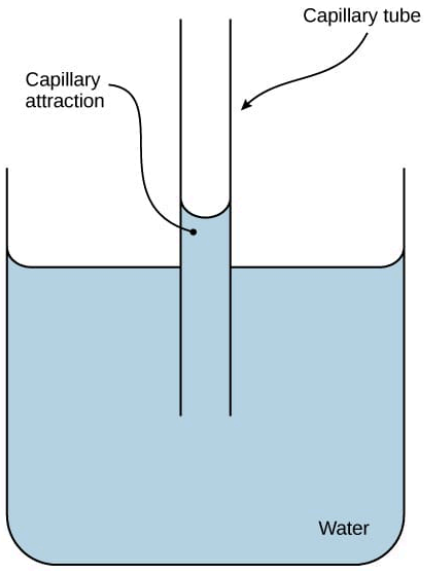


Figure 2.16.1: Adhesion: Capillary action in a glass tube is caused by the adhesive forces exerted by the internal surface of the glass exceeding the cohesive forces between the water molecules themselves.

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

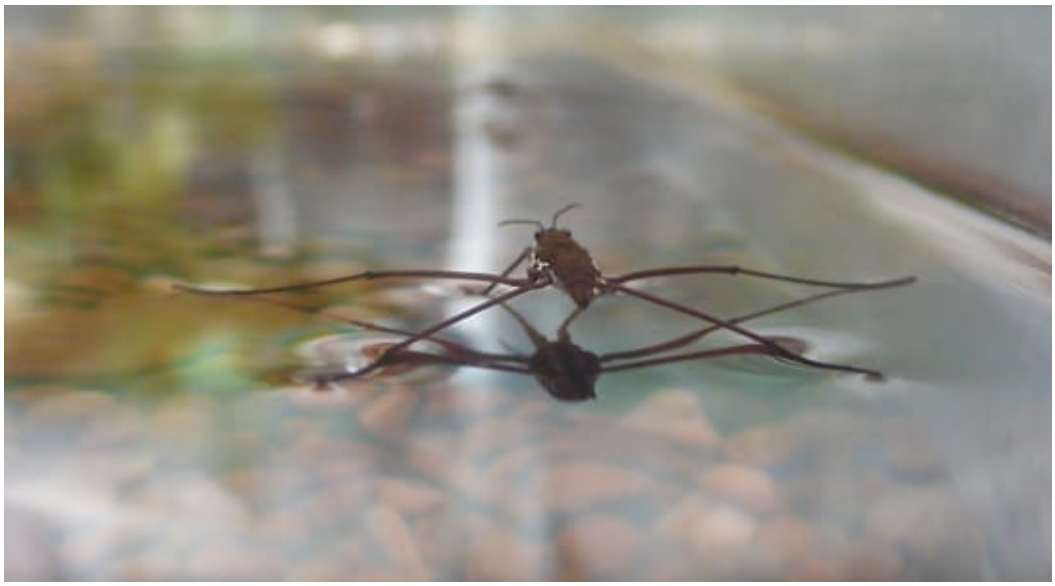


Figure 2.16.1: Cohesion & Adhesion: Water’s cohesive and adhesive properties allow this water strider (Gerris sp.) to stay afloat.

Key Points

- Cohesion holds hydrogen bonds together to create surface tension on water.
- Since water is attracted to other molecules, adhesive forces pull the water toward other molecules.
- Water is transported in plants through both cohesive and adhesive forces; these forces pull water and the dissolved minerals from the roots to the leaves and other parts of the plant.

Key Terms

- **adhesion**: The ability of a substance to stick to an unlike substance; attraction between unlike molecules
- **cohesion**: Various intermolecular forces that hold solids and liquids together; attraction between like molecules

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2.17: Water - pH, Buffers, Acids, and Bases

Learning Objectives

- Explain the composition of buffer solutions and how they maintain a steady pH

Self-Ionization of Water

Hydrogen ions are spontaneously generated in pure water by the dissociation (ionization) of a small percentage of water molecules into equal numbers of hydrogen (H^+) ions and hydroxide (OH^-) ions. The hydroxide ions remain in solution because of their hydrogen bonds with other water molecules; the hydrogen ions, consisting of naked protons, are immediately attracted to un-ionized water molecules and form hydronium ions (H_3O^+). By convention, scientists refer to hydrogen ions and their concentration as if they were free in this state in liquid water.

$$2\,H_2O \leftrightharpoons H_3O^+ + OH^- \tag{2.17.1}$$

The concentration of hydrogen ions dissociating from pure water is 1×10^{-7} moles H^+ ions per liter of water. The pH is calculated as the negative of the base 10 logarithm of this concentration:

$$pH = -\log_{10}[H^+] \tag{2.17.2}$$

The negative log of 1×10^{-7} is equal to 7.0, which is also known as neutral pH. Human cells and blood each maintain near-neutral pH.

pH Scale

The pH of a solution indicates its acidity or basicity (alkalinity). The pH scale is an inverse logarithm that ranges from 0 to 14: anything below 7.0 (ranging from 0.0 to 6.9) is acidic, and anything above 7.0 (from 7.1 to 14.0) is basic (or alkaline). Extremes in pH in either direction from 7.0 are usually considered inhospitable to life. The pH in cells (6.8) and the blood (7.4) are both very close to neutral, whereas the environment in the stomach is highly acidic, with a pH of 1 to 2.

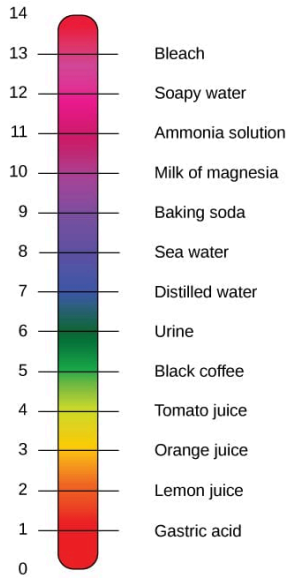


Figure 2.17.1: The pH scale: The pH scale measures the concentration of hydrogen ions (H^+) in a solution.

Non-neutral pH readings result from dissolving acids or bases in water. Using the negative logarithm to generate positive integers, high concentrations of hydrogen ions yield a low pH, and low concentrations a high pH.

An acid is a substance that increases the concentration of hydrogen ions (H^+) in a solution, usually by dissociating one of its hydrogen atoms. A base provides either hydroxide ions (OH^-) or other negatively-charged ions that react with hydrogen ions in solution, thereby reducing the concentration of H^+ and raising the pH.

Strong Acids and Strong Bases

The stronger the acid, the more readily it donates H^+. For example, hydrochloric acid (HCl) is highly acidic and completely dissociates into hydrogen and chloride ions, whereas the acids in tomato juice or vinegar do not completely dissociate and are considered weak acids; conversely, strong bases readily donate OH^- and/or react with hydrogen ions. Sodium hydroxide (NaOH) and many household cleaners are highly basic and give up OH^- rapidly when placed in water; the OH^- ions react with H^+ in solution, creating new water molecules and lowering the amount of free H^+ in the system, thereby raising the overall pH. An example of a weak basic solution is seawater, which has a pH near 8.0, close enough to neutral that well-adapted marine organisms thrive in this alkaline environment.

Buffers

How can organisms whose bodies require a near-neutral pH ingest acidic and basic substances (a human drinking orange juice, for example) and survive? Buffers are the key. Buffers usually consist of a weak acid and its conjugate base; this enables them to readily absorb excess H^+ or OH^-, keeping the system's pH within a narrow range.

Maintaining a constant blood pH is critical to a person's well-being. The buffer that maintains the pH of human blood involves carbonic acid (H_2CO_3), bicarbonate ion (HCO_3^-), and carbon dioxide (CO_2). When bicarbonate ions combine with free hydrogen ions and become carbonic acid, hydrogen ions are removed, moderating pH changes. Similarly, excess carbonic acid can be converted into carbon dioxide gas and exhaled through the lungs; this prevents too many free hydrogen ions from building up in the blood and dangerously reducing its pH; likewise, if too much OH^- is introduced into the system, carbonic acid will combine with it to create bicarbonate, lowering the pH. Without this buffer system, the body's pH would fluctuate enough to jeopardize survival.

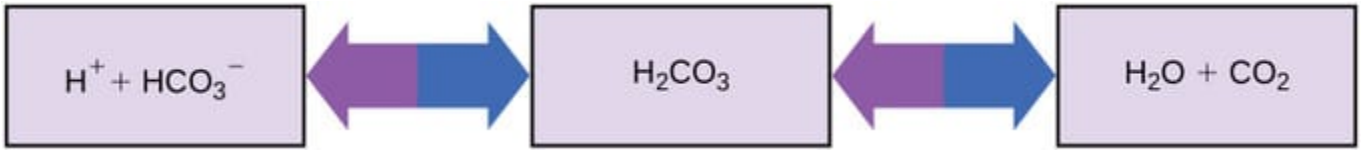


Figure 2.17.1: Buffers in the body: This diagram shows the body's buffering of blood pH levels: the blue arrows show the process of raising pH as more CO2 is made; the purple arrows indicate the reverse process, lowering pH as more bicarbonate is created.

Antacids, which combat excess stomach acid, are another example of buffers. Many over-the-counter medications work similarly to blood buffers, often with at least one ion (usually carbonate) capable of absorbing hydrogen and moderating pH, bringing relief to those that suffer "heartburn" from stomach acid after eating.

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Key Points

- A basic solution will have a pH above 7.0, while an acidic solution will have a pH below 7.0.
- Buffers are solutions that contain a weak acid and its a conjugate base; as such, they can absorb excess H^+ ions or OH^- ions, thereby maintaining an overall steady pH in the solution.
- pH is equal to the negative logarithm of the concentration of H^+ ions in solution: $pH = -\log[H^+]$.

Key Terms

- **alkaline**: having a pH greater than 7; basic
- **acidic**: having a pH less than 7
- **buffer**: a solution composed of a weak acid and its conjugate base that can be used to stabilize the pH of a solution

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2.18: Carbon - The Chemical Basis for Life

Learning Objectives

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

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



Figure 2.18.1: Carbon is present in all life: All living things contain carbon in some form, and carbon is the primary component of macromolecules, including proteins, lipids, nucleic acids, and carbohydrates. Carbon exists in many forms in this leaf, including in the cellulose to form the leaf's structure and in chlorophyll, the pigment which makes the leaf green.

Carbon is Important to Life

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

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

Structure of Carbon

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

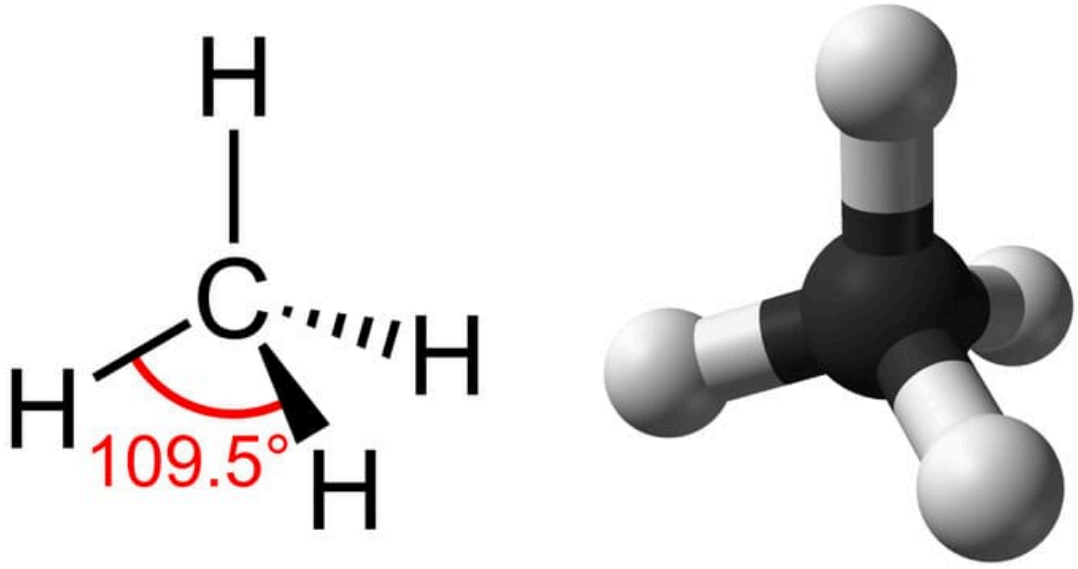


Figure 2.18.1: Structure of Methane: Methane has a tetrahedral geometry, with each of the four hydrogen atoms spaced 109.5° apart.

Key Points

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

Key Terms

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

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2.19: Carbon - Hydrocarbons

Learning Objectives

- Discuss the role of hydrocarbons in biomacromolecules

Hydrocarbons

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

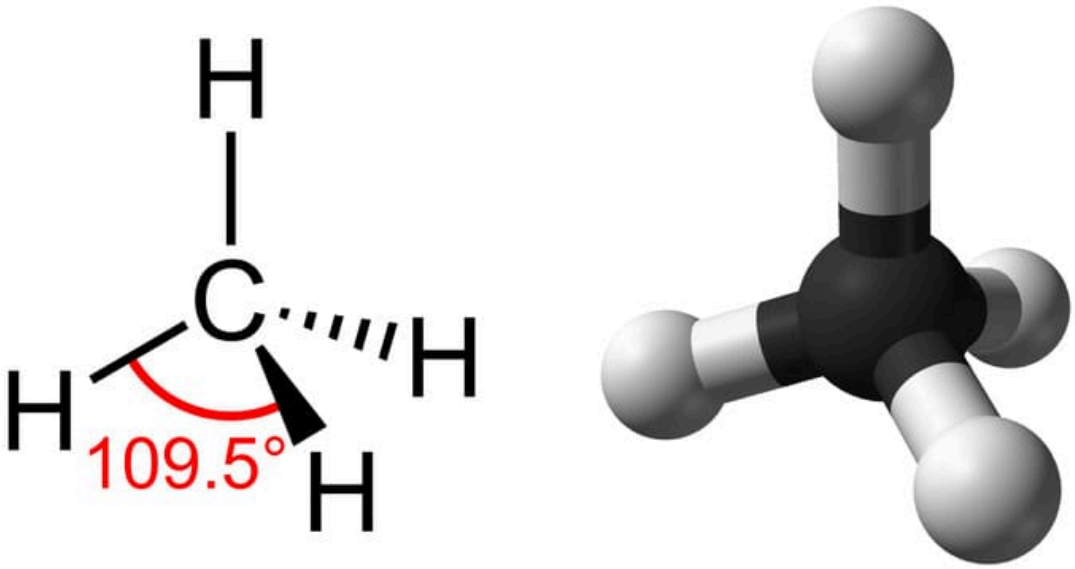


Figure 2.19.1: Methane: Methane has a tetrahedral geometry, with each of the four hydrogen atoms spaced 109.5° apart.

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

Hydrocarbon Chains

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

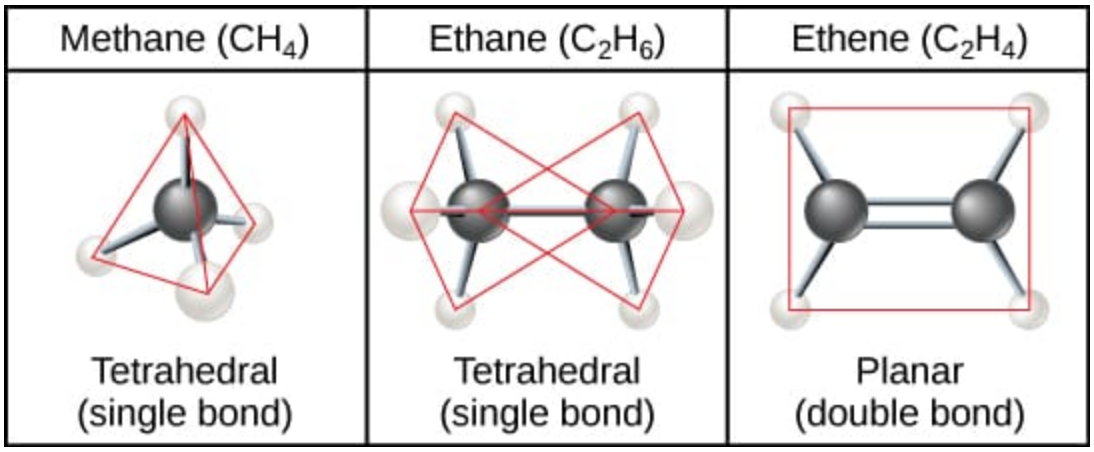


Figure 2.19.1: Hydrocarbon Chains: When carbon forms single bonds with other atoms, the shape is tetrahedral. When two carbon atoms form a double bond, the shape is planar, or flat. Single bonds, like those found in ethane, are able to rotate. Double bonds, like those found in ethene cannot rotate, so the atoms on either side are locked in place.

Hydrocarbon Rings

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

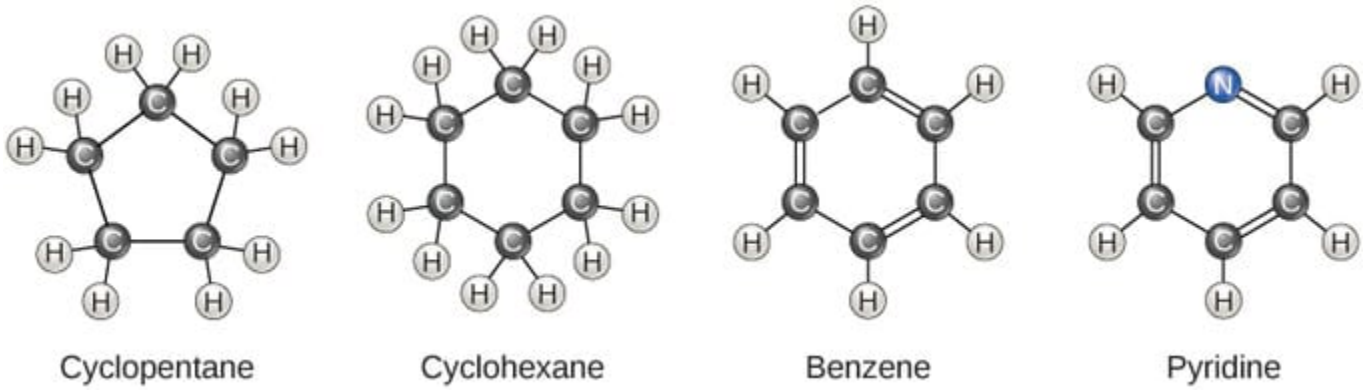


Figure 2.19.1: Hydrocarbon Rings: Carbon can form five-and six membered rings. Single or double bonds may connect the carbons in the ring, and nitrogen may be substituted for carbon.

Key Points

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

Key Terms

- **covalent bond**: A type of chemical bond where two atoms are connected to each other by the sharing of two or more electrons.

- **aliphatic**: Of a class of organic compounds in which the carbon atoms are arranged in an open chain.
- **aromatic**: Having a closed ring of alternate single and double bonds with delocalized electrons.

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2.20: Carbon - Organic Isomers

Learning Objectives

- Give examples of isomers

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

Structural Isomers

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

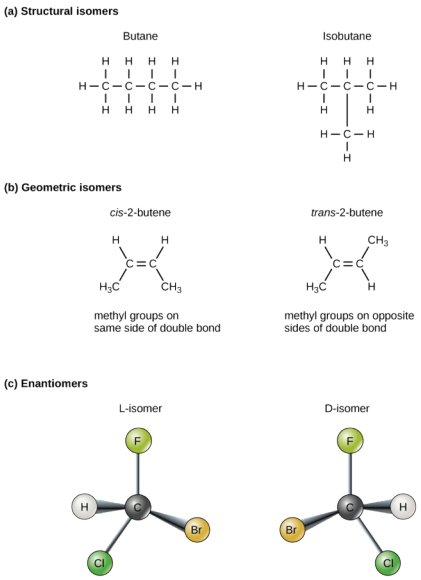


Figure 2.20.1: Isomers: Molecules that have the same number and type of atoms arranged differently are called isomers. (a) Structural isomers have a different covalent arrangement of atoms. (b) Geometric isomers have a different arrangement of atoms around a double bond. (c) Enantiomers are mirror images of each other.

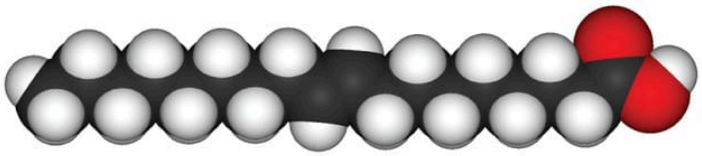
Geometric Isomers

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

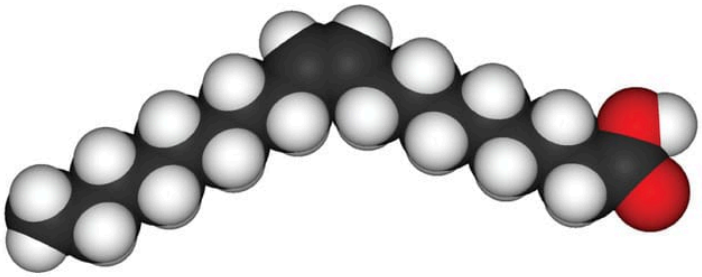
Cis or Trans Configurations

In triglycerides (fats and oils), long carbon chains known as fatty acids may contain double bonds, which can be in either the cis

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



Eliadic acid



Oleic acid

Figure 2.20.1: Cis and Trans Fatty Acids: These space-filling models show a cis (oleic acid) and a trans (eliadic acid) fatty acid. Notice the bend in the molecule cause by the cis configuration.

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

Key Points

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

Key Terms

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

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2.21: Carbon - Organic Enantiomers

Learning Objectives

- Give examples of enantiomers

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

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

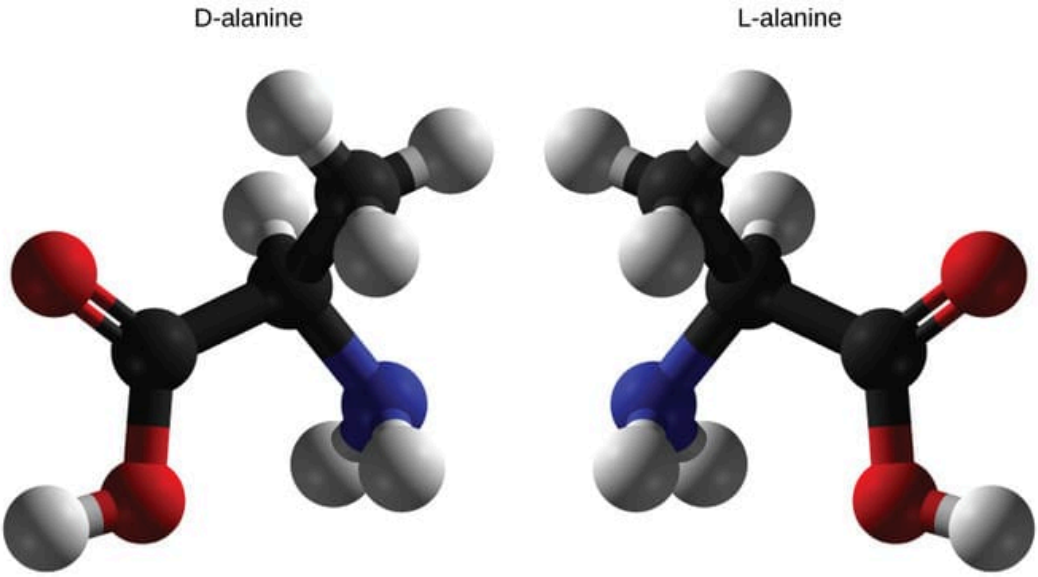


Figure 2.21.1: Enantiomers: D-alanine and L-alanine are examples of enantiomers or mirror images. Only the L-forms of amino acids are used to make proteins.

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

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

Key Points

- Enantiomers are stereoisomers, a type of isomer where the order of the atoms in the two molecules is the same but their arrangement in space is different.
- Many molecules in the bodies of living beings are enantiomers; there is sometimes a large difference in the effects of two enantiomers on organisms.
- Enantiopure compounds refer to samples having, within the limits of detection, molecules of only one chirality.
- Compounds that are enantiomers of each other have the same physical properties except for the direction in which they rotate polarized light and how they interact with different optical isomers of other compounds.

Key Terms

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

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2.22: Carbon - Organic Molecules and Functional Groups

Learning Objectives

- Describe the importance of functional groups to organic molecules

Location of Functional Groups

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

Properties of Functional Groups

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

Classifying Functional Groups

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

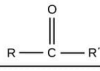
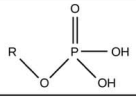
Functional Group	Structure	Properties
Hydroxyl		Polar
Methyl		Nonpolar
Carbonyl		Polar
Carboxyl		Charged, ionizes to release H^+. Since carboxyl groups can release H^+ ions into solution, they are considered acidic.
Amino		Charged, accepts H^+ to form NH_3^+. Since amino groups can remove H^+ from solution,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

Figure 2.22.1: Examples of functional groups: The functional groups shown here are found in many different biological molecules, where “R” is the organic molecule.

Hydrogen Bonds between Functional Groups

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

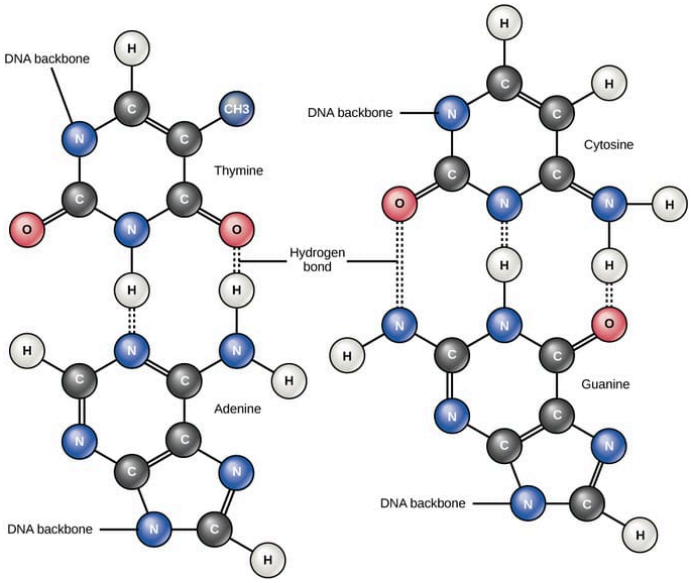


Figure 2.22.1: Hydrogen bonds in DNA: Hydrogen bonds connect two strands of DNA together to create the double-helix structure.

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Key Points

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

Key Terms

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

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2.23: Synthesis of Biological Macromolecules - Types of Biological Macromolecules

Learning Objectives

- Identify the four major classes of biological macromolecules

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



Figure 2.23.1: Sources of biological macromolecules: Foods such as bread, fruit, and cheese are rich sources of biological macromolecules.

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

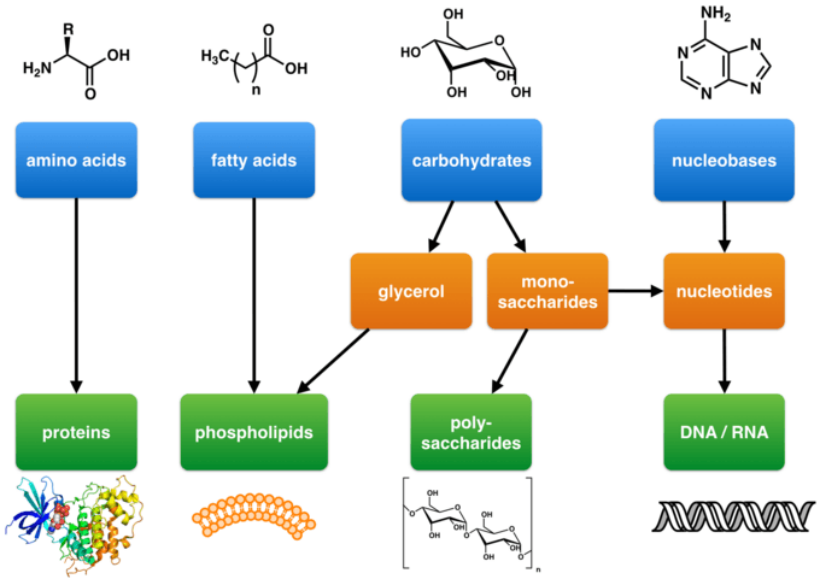
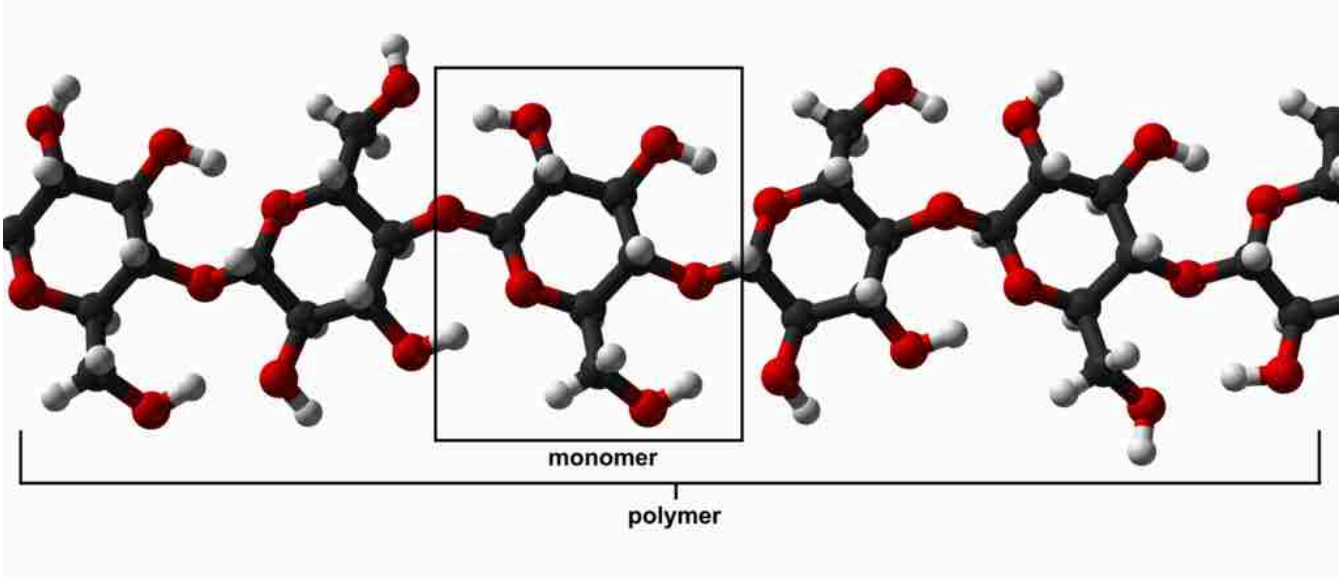


Figure 2.23.2: Living organisms are made up of chemical building blocks: All organisms are composed of a variety of these biological macromolecules.

Monomers and Polymers

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



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

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

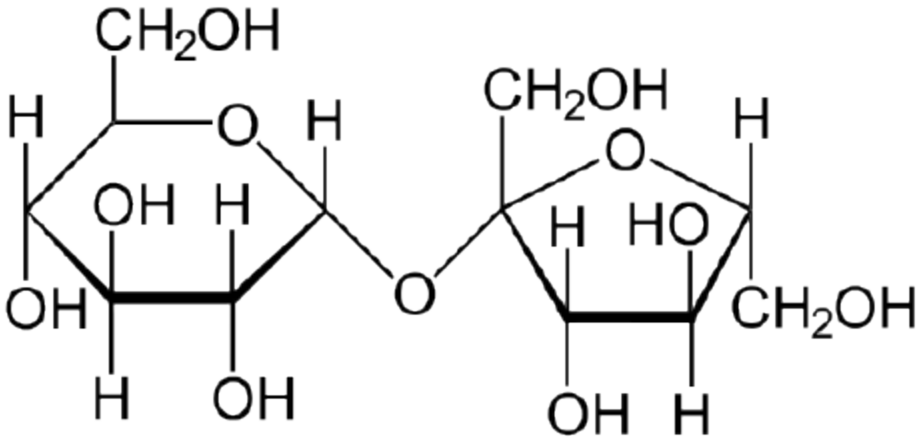


Figure 2.23.3: The molecule sucrose (common table sugar): The carbohydrate monosaccharides (fructose and glucose) are joined to make the disaccharide sucrose.

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

Four Classes of Biological Macromolecules

There are four major classes of biological macromolecules:

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

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

Interactive: Monomers and Polymers

Carbohydrates, proteins, and nucleic acids are built from small molecular units that are connected to each other by strong covalent bonds. The small molecular units are called monomers (mono means one, or single), and they are linked together into long chains called polymers (poly means many, or multiple). Each different type of macromolecule, except lipids, is built from a different set of monomers that resemble each other in composition and size. Lipids are not polymers, because they are not built from monomers (units with similar composition).

Key Points

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

Key Terms

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

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2.24: Synthesis of Biological Macromolecules - Dehydration Synthesis

Learning Objectives

- Explain dehydration (or condensation) reactions

Dehydration Synthesis

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

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

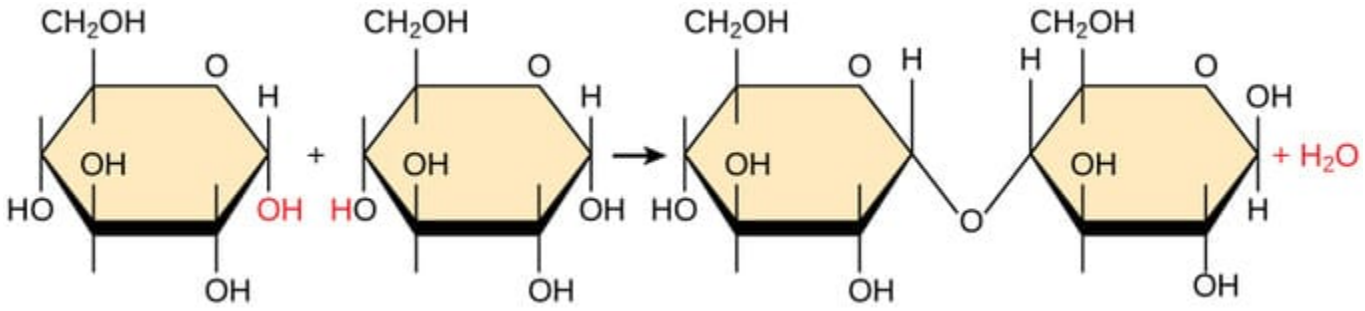


Figure 2.24.1: A dehydration synthesis reaction involving un-ionized moners..: In the dehydration synthesis reaction between two molecules of glucose, a hydroxyl group from the first glucose is combined with a hydrogen from the second glucose, creating a covalent bond that links the two monomeric sugars (monosaccharides) together to form the dissacharide maltose. In the process, a water molecule is formed.

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

image

Figure 2.24.1: A dehydration synthesis reaction involving ionized monomers.: In the dehydration synthesis reaction between two amino acids, with are ionized in aqueous environments like the cell, an oxygen from the first amino acid is combined with two hydrogens from the second amino acid, creating a covalent bond that links the two monomers together to form a dipeptide. In the process a water molecule is formed.

As additional monomers join via multiple dehydration synthesis reactions, the chain of repeating monomers begins to form a polymer. Different types of monomers can combine in many configurations, giving rise to a diverse group of macromolecules. Three of the four major classes of biological macromolecules (complex carbohydrates, nucleic acids, and proteins), are composed of monomers that join together via dehydration synthesis reactions. Complex carbohydrates are formed from monosaccharides, nucleic acids are formed from mononucleotides, and proteins are formed from amino acids.

There is great diversity in the manner by which monomers can combine to form polymers. For example, glucose monomers are the constituents of starch, glycogen, and cellulose. These three are polysaccharides, classified as carbohydrates, that have formed as a result of multiple dehydration synthesis reactions between glucose monomers. However, the manner by which

glucose monomers join together, specifically locations of the covalent bonds between connected monomers and the orientation (stereochemistry) of the covalent bonds, results in these three different polysaccharides with varying properties and functions. In nucleic acids and proteins, the location and stereochemistry of the covalent linkages connecting the monomers do not vary from molecule to molecule, but instead the multiple kinds of monomers (five different monomers in nucleic acids, A, G, C, T, and U mononucleotides; 21 different amino acids monomers in proteins) are combined in a huge variety of sequences. Each protein or nucleic acid with a different sequence is a different molecule with different properties.

Key Points

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

Key Terms

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

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2.25: Synthesis of Biological Macromolecules - Hydrolysis

Learning Objectives

- Explain hydrolysis reactions

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

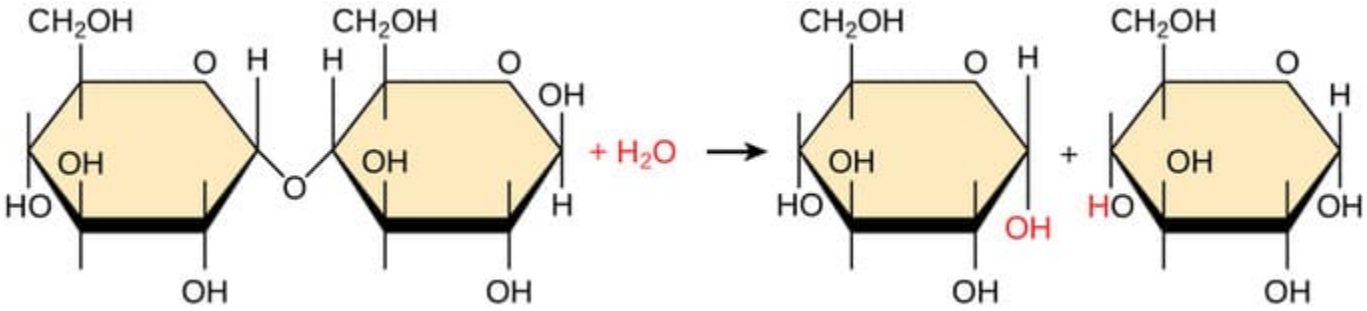


Figure 2.25.1: Hydrolysis reaction generating un-ionized products.: In the hydrolysis reaction shown here, the disaccharide maltose is broken down to form two glucose monomers with the addition of a water molecule. One glucose gets a hydroxyl group at the site of the former covalent bond, the other glucose gets a hydrogen atom. This is the reverse of the dehydration synthesis reaction joining these two monomers.

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

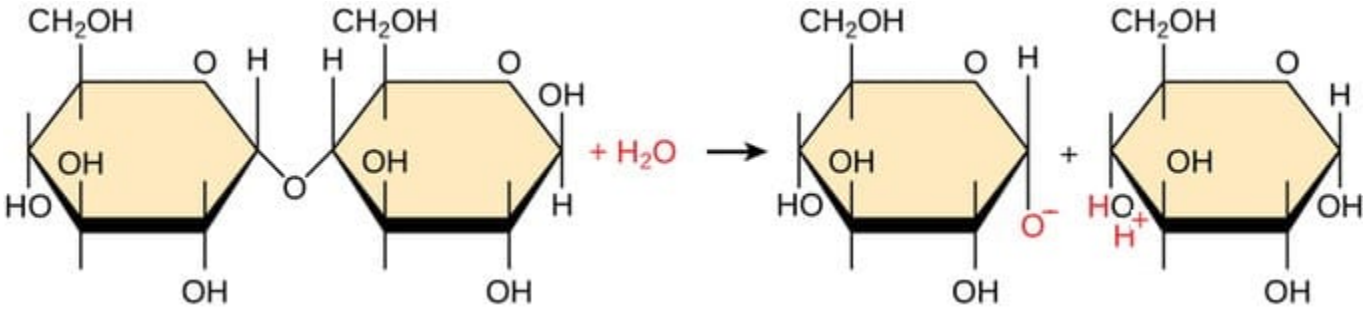


Figure 2.25.1: Hydrolysis reaction generating ionized products.: In the hydrolysis reaction shown here, the dipeptide is broken down to form two ionized amino acids with the addition of a water molecule. One amino acid gets an oxygen atom and a negative charge, the other amino acid gets two hydrogen atoms and a positive charge. This is the reverse of the dehydration synthesis reaction joining these two monomers.

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

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

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

macromolecules is an overall energy-releasing process and provides energy for cellular activities.

Exercise 2.25.1

1. What are biological macromolecules? Name the four major classes.
2. Biological macromolecules are organic. What does that mean?
3. What are monomers? What are polymer?
4. Explain the process “dehydration synthesis.” Is there another name for this process? Explain.
5. Explain Figure 1 in your own words.
6. Give an example of how condensation can form different carbohydrates.
7. Explain the process of Hydrolysis.
8. Explain Figure 2 in your own words.
9. What role do enzymes play in hydrolysis and condensation? Explain.
10. In our bodies, food is hydrolyzed, or broken down into smaller molecules. Explain why.
11. The breakdown of macromolecules provides...
12. Create a comparison chart to indicate the enzymes that break down carbohydrates, proteins, and lipids.

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Key Points

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

Key Terms

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

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3: BIOLOGICAL MACROMOLECULES

3.1: Carbohydrates - Carbohydrate Molecules

3.2: Carbohydrates - Importance of Carbohydrates

3.3: Lipid Molecules - Introduction

3.4: Lipid Molecules - Waxes

3.5: Lipid Molecules - Phospholipids

3.6: Lipid Molecules - Steroids

3.7: Proteins - Types and Functions of Proteins

3.8: Proteins - Amino Acids

3.9: Proteins - Protein Structure

3.10: Proteins - Denaturation and Protein Folding

3.11: Nucleic Acids - DNA and RNA

3.12: Nucleic Acids - The DNA Double Helix

3.13: Nucleic Acids - DNA Packaging

3.14: Nucleic Acids - Types of RNA

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3.1: Carbohydrates - Carbohydrate Molecules

Learning Objectives

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

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

Monosaccharides

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

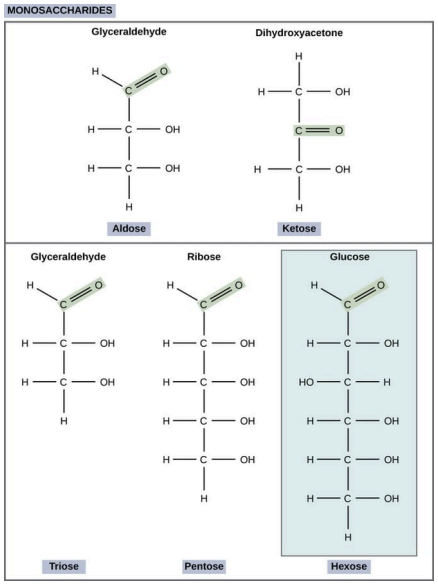


Figure 3.1.1: Monosaccharides: Monosaccharides are classified based on the position of their carbonyl group and the number of carbons in the backbone. Aldoses have a carbonyl group (indicated in green) at the end of the carbon chain, and ketoses have a carbonyl group in the middle of the carbon chain. Trioses, pentoses, and hexoses have three, five, and six carbon backbones, respectively.

Common Monosaccharides

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

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

Disaccharides

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

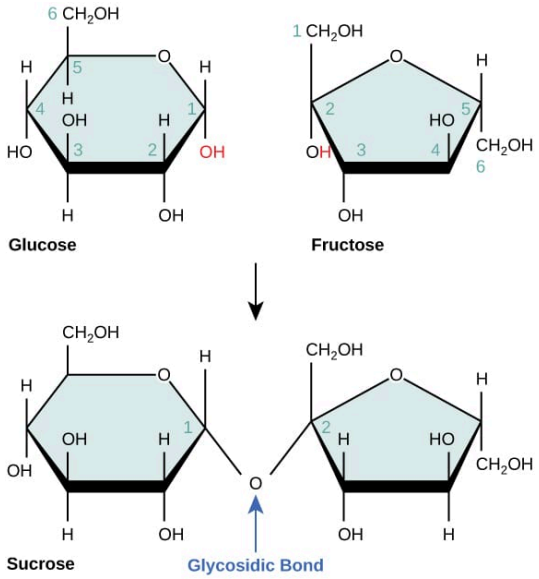


Figure 3.1.1: Disaccharides: Sucrose is formed when a monomer of glucose and a monomer of fructose are joined in a dehydration reaction to form a glycosidic bond. In the process, a water molecule is lost. By convention, the carbon atoms in a monosaccharide are numbered from the terminal carbon closest to the carbonyl group. In sucrose, a glycosidic linkage is formed between carbon 1 in glucose and carbon 2 in fructose.

Common Disaccharides

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

Polysaccharides

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

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

Common Polysaccharides

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

Cellulose is the most abundant natural biopolymer. The cell wall of plants is mostly made of cellulose and provides structural

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

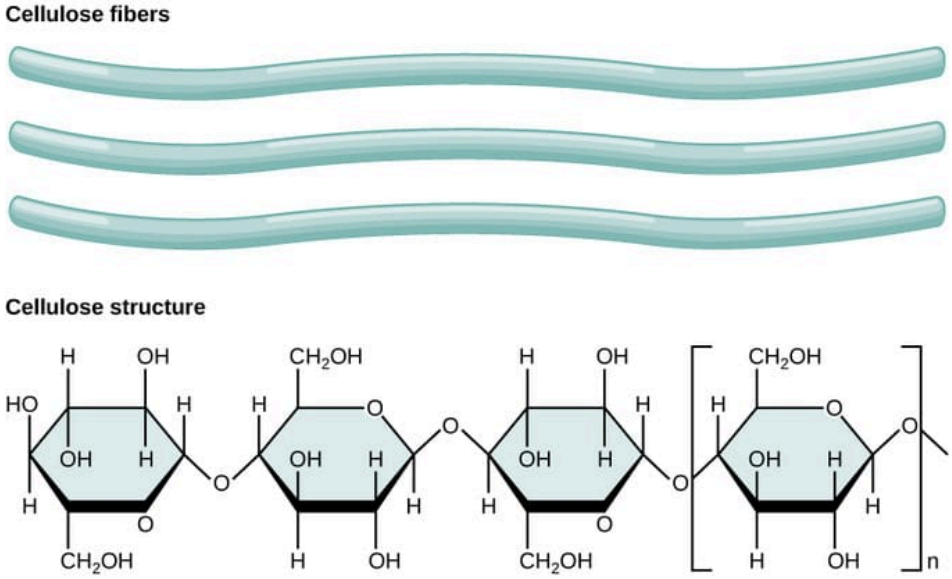


Figure 3.1.1: Polysaccharides: In cellulose, glucose monomers are linked in unbranched chains by β 1-4 glycosidic linkages. Because of the way the glucose subunits are joined, every glucose monomer is flipped relative to the next one resulting in a linear, fibrous structure.

Carbohydrate Function

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

Key Points

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

Key Terms

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

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3.2: Carbohydrates - Importance of Carbohydrates

Learning Objectives

- Describe the benefits provided to organisms by carbohydrates

Benefits of Carbohydrates

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

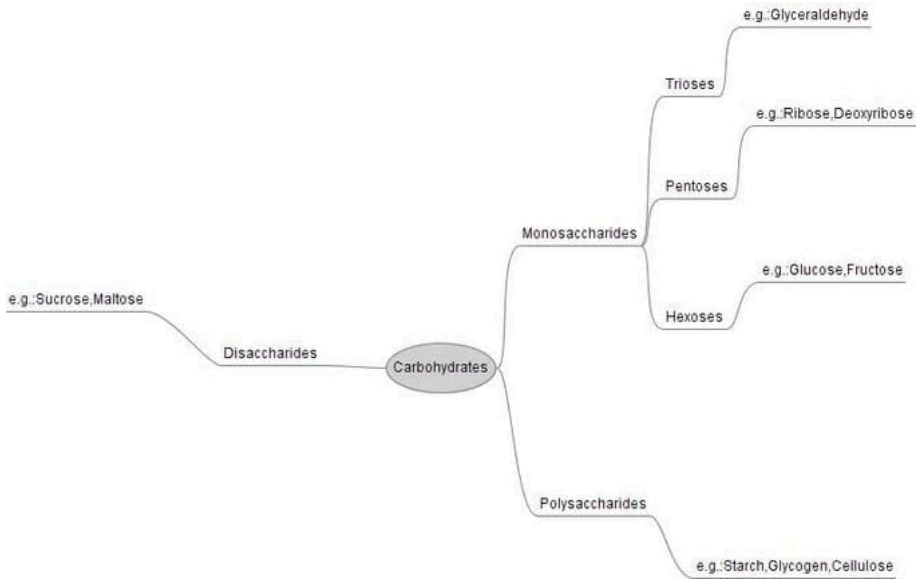


Figure 3.2.1: Carbohydrates: Carbohydrates are biological macromolecules that are further divided into three subtypes: monosaccharides, disaccharides, and polysaccharides. Like all macromolecules, carbohydrates are necessary for life and are built from smaller organic molecules.

Carbohydrates in Nutrition

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

Carbohydrates should be supplemented with proteins, vitamins, and fats to be parts of a well-balanced diet. Calorie-wise, a gram of carbohydrate provides 4.3 Kcal. In comparison, fats provide 9 Kcal/g, a less desirable ratio. Carbohydrates contain soluble and insoluble elements; the insoluble part is known as fiber, which is mostly cellulose. Fiber has many uses; it promotes regular bowel movement by adding bulk, and it regulates the rate of consumption of blood glucose. Fiber also helps to remove excess cholesterol from the body. Fiber binds and attaches to the cholesterol in the small intestine and prevents the cholesterol particles from entering the bloodstream. Then cholesterol exits the body via the feces. Fiber-rich diets also have a protective role in reducing the occurrence of colon cancer. In addition, a meal containing whole grains and vegetables gives a feeling of fullness. As an immediate source of energy, glucose is broken down during the process of cellular respiration, which produces adenosine triphosphate (ATP), the energy currency of the cell. Without the consumption of carbohydrates, the availability of "instant energy"

would be reduced. Eliminating carbohydrates from the diet is not the best way to lose weight. A low-calorie diet that is rich in whole grains, fruits, vegetables, and lean meat, together with plenty of exercise and plenty of water, is the more sensible way to lose weight.

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Key Points

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

Key Terms

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

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3.3: Lipid Molecules - Introduction

Learning Objectives

- Differentiate between saturated and unsaturated fatty acids

Glycerol and Fatty Acids

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

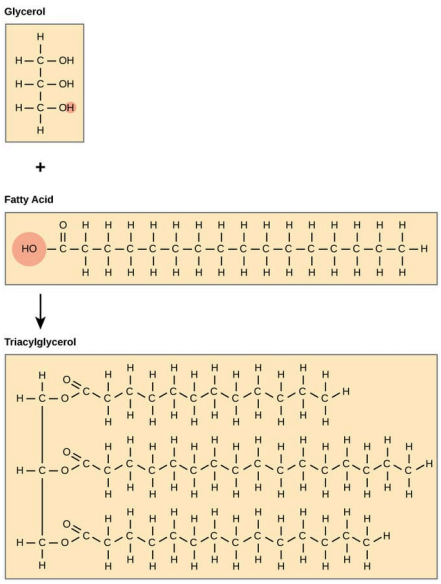


Figure 3.3.1: Triacylglycerols: Triacylglycerol is formed by the joining of three fatty acids to a glycerol backbone in a dehydration reaction. Three molecules of water are released in the process.

Saturated vs. Unsaturated Fatty Acids

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

When the hydrocarbon chain contains a double bond, the fatty acid is said to be unsaturated. Oleic acid is an example of an unsaturated fatty acid. Most unsaturated fats are liquid at room temperature and are called oils. If there is only one double bond in the molecule, then it is known as a monounsaturated fat; e.g. olive oil. If there is more than one double bond, then it is known as a polyunsaturated fat; e.g. canola oil. Unsaturated fats help to lower blood cholesterol levels whereas saturated fats contribute to plaque formation in the arteries.

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

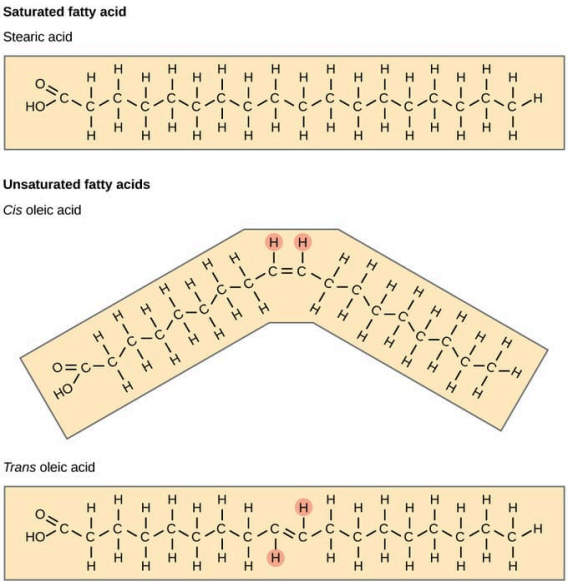


Figure 3.3.1: Fatty Acids: Saturated fatty acids have hydrocarbon chains connected by single bonds only. Unsaturated fatty acids have one or more double bonds. Each double bond may be in a cis or trans configuration. In the cis configuration, both hydrogens are on the same side of the hydrocarbon chain. In the trans configuration, the hydrogens are on opposite sides. A cis double bond causes a kink in the chain.

Trans Fats

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

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

Essential Fatty Acids

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

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

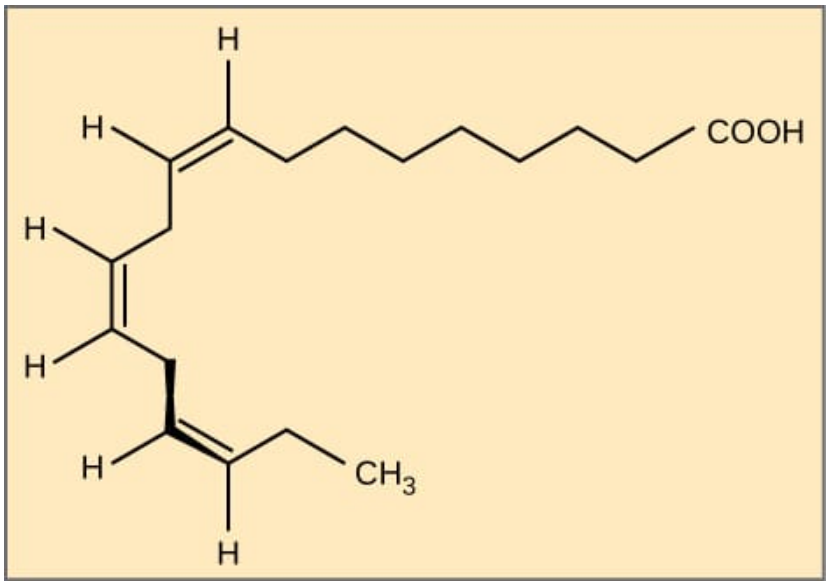


Figure 3.3.1: Omega Fatty Acids: Alpha-linolenic acid is an example of an omega-3 fatty acid. It has three cis double bonds and, as a result, a curved shape. For clarity, the carbons are not shown. Each singly bonded carbon has two hydrogens associated with it, also not shown.

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

Key Points

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

Key Terms

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

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3.4: Lipid Molecules - Waxes

Learning Objectives

- Describe the roles played by waxes

Waxes

Waxes are a type of long chain nonpolar lipid. Natural waxes are typically esters of fatty acids and long chain alcohols. Waxes are synthesized by many animals and plants. Animal wax esters are typically derived from a variety of carboxylic acids and fatty alcohols. The composition of a wax depends not only on the species, but also on the geographic location of the organism. The best known animal wax is beeswax, but other insects secrete waxes as well. A major component of beeswax is the ester myricyl palmitate, which bees use for constructing honeycombs. Spermaceti is also a wax that occurs in large amounts in the oil of a sperm whale's head. One of its main constituents is cetyl palmitate, an ester of a fatty acid and fatty alcohol. Plant waxes are derived from mixtures of long-chain hydrocarbons containing functional groups such as alkanes, fatty acids, alcohols, diols, ketones, and aldehydes. Plants also use waxes as a protective coating to control evaporation and hydration and to prevent them from drying out. Waxes are valuable to both plants and animals because of their hydrophobic nature. This makes them water resistant, which prevents water from sticking on surfaces.



Figure 3.4.1: Plant Waxes: Waxy coverings on some leaves are used as protective coatings.

Unlike most natural waxes, which are esters, synthetic waxes consist of long-chain hydrocarbons lacking functional groups. Paraffin wax is a type of synthetic wax derived from petroleum and refined by vacuum distillation. Synthetic waxes may also be obtained from polyethylene. Millions of of these waxes are produced annually, and they are used in adhesives, cosmetics, sealants and lubricants, insecticides, and UV protection. They are also used in foods like chewing gum.

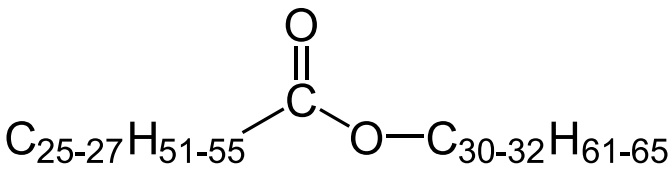


Figure 3.4.1: Generic structure formula of bee waxes: Ester myricyl palmitate is a major component of beeswax.

Key Points

- Natural waxes are typically esters of fatty acids and long chain alcohols.
- Animal wax esters are derived from a variety of carboxylic acids and fatty alcohols.
- Plant waxes are derived from mixtures of long-chain hydrocarbons containing functional groups.
- Because of their hydrophobic nature, waxes prevent water from sticking on plants and animals.
- Synthetic waxes are derived from petroleum or polyethylene and consist of long-chain hydrocarbons that lack functional groups.
- Synthetic and waxes are used in adhesives, cosmetics, food, and many other commercial products.

Key Terms

- **paraffin wax**: A waxy white solid hydrocarbon mixture used to make candles, wax paper, lubricants, and sealing materials.
- **polyethylene**: A polymer consisting of many ethylene monomers bonded together; used for kitchenware, containers etc.

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3.5: Lipid Molecules - Phospholipids

Learning Objectives

- Describe phospholipids and their role in cells

Defining Characteristics of Phospholipids

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

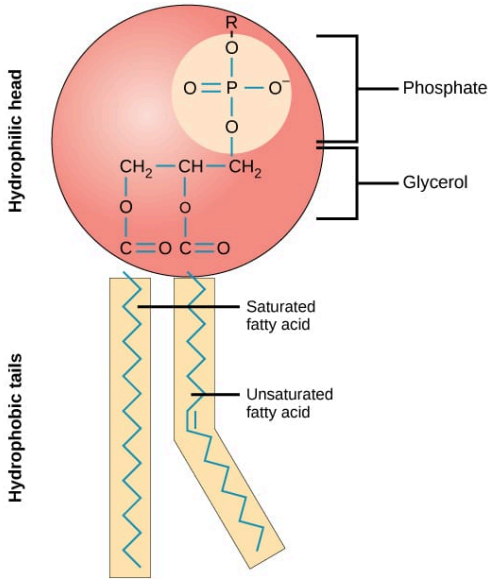


Figure 3.5.1: Phospholipid Molecule: A phospholipid is a molecule with two fatty acids and a modified phosphate group attached to a glycerol backbone. The phosphate may be modified by the addition of charged or polar chemical groups. Two chemical groups that may modify the phosphate, choline and serine, are shown here. Both choline and serine attach to the phosphate group at the position labeled R via the hydroxyl group indicated in green.

Structure of a Phospholipid Molecule

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

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

Phospholipids and Biological Membranes

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

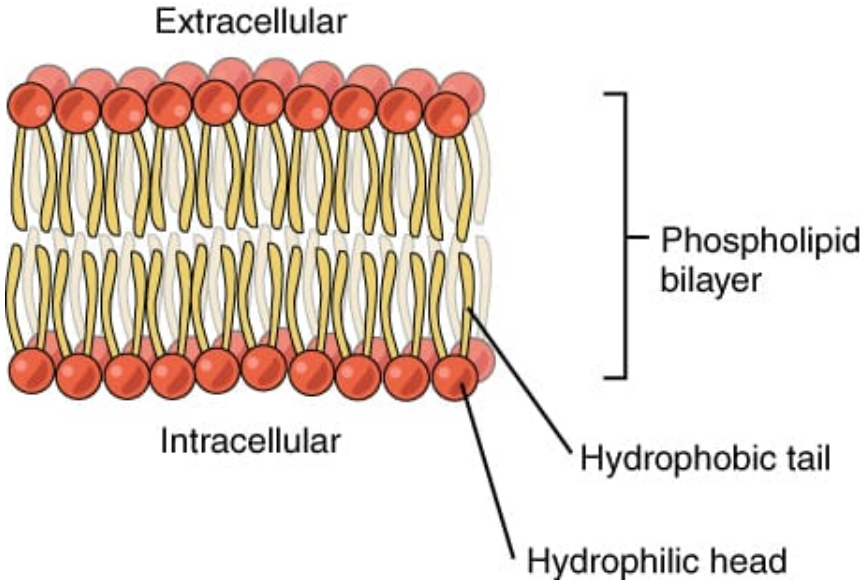


Figure 3.5.1: Phospholipid Bilayer: The phospholipid bilayer consists of two adjacent sheets of phospholipids, arranged tail to tail. The hydrophobic tails associate with one another, forming the interior of the membrane. The polar heads contact the fluid inside and outside of the cell.

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

Membrane Fluidity

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

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

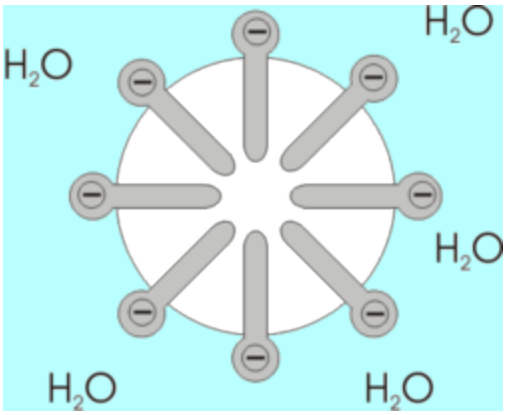


Figure 3.5.1: Micelles: An example of micelles in water.

Key Points

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

Key Terms

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

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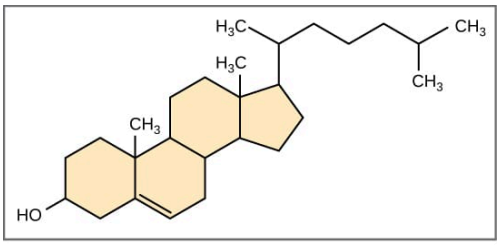
3.6: Lipid Molecules - Steroids

Learning Objectives

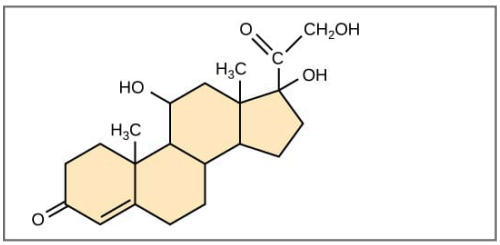
- Describe some functions of steroids

Structure of Steroid Molecules

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



Cholesterol



Cortisol

Figure 3.6.1: Steroid Structures: Steroids, such as cholesterol and cortisol, are composed of four fused hydrocarbon rings.

Cholesterol

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

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

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

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Key Points

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

Key Terms

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

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3.7: Proteins - Types and Functions of Proteins

Learning Objectives

- Differentiate among the types and functions of proteins

Types and Functions of Proteins

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

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

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

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

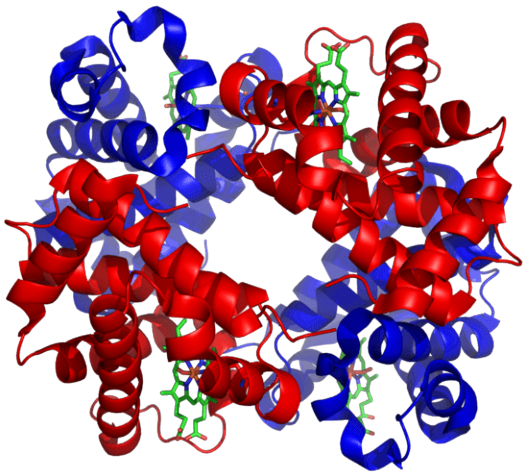


Figure 3.7.1: Human Hemoglobin: Structure of human hemoglobin. The proteins' α and β subunits are in red and blue, and the iron-containing heme groups in green. From the protein data base.

Because form determines function, any slight change to a protein's shape may cause the protein to become dysfunctional. Small

changes in the amino acid sequence of a protein can cause devastating genetic diseases such as Huntington's disease or sickle cell anemia.

Enzymes

Enzymes are proteins that catalyze biochemical reactions, which otherwise would not take place. These enzymes are essential for chemical processes like digestion and cellular metabolism. Without enzymes, most physiological processes would proceed so slowly (or not at all) that life could not exist.

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

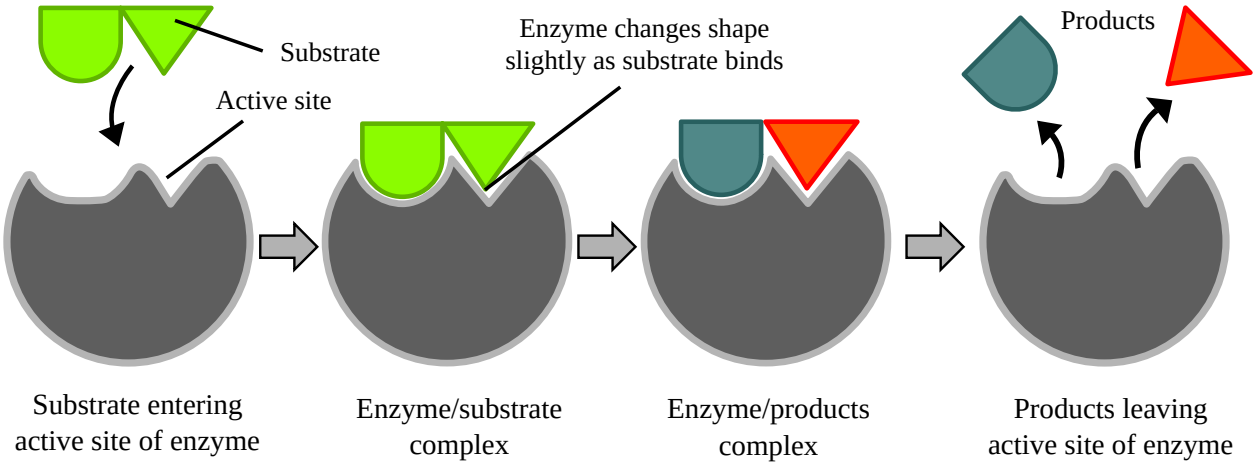


Figure 3.7.1: Enzyme reaction: A catabolic enzyme reaction showing the substrate matching the exact shape of the active site.

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

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

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

Hormones

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

Other Protein Functions

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

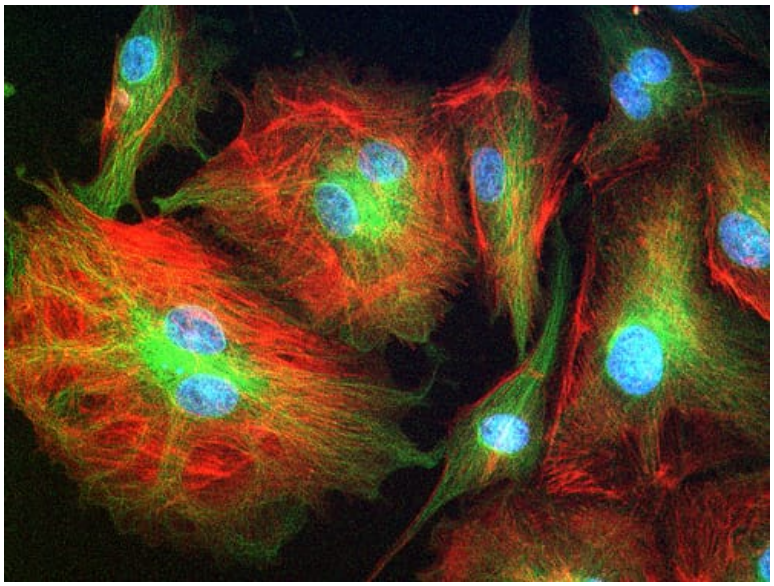


Figure 3.7.1: Tubulin: The structural protein tubulin stained red in mouse cells.

Key Points

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

Key Terms

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

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3.8: Proteins - Amino Acids

Learning Objectives

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

Structure of an Amino Acid

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

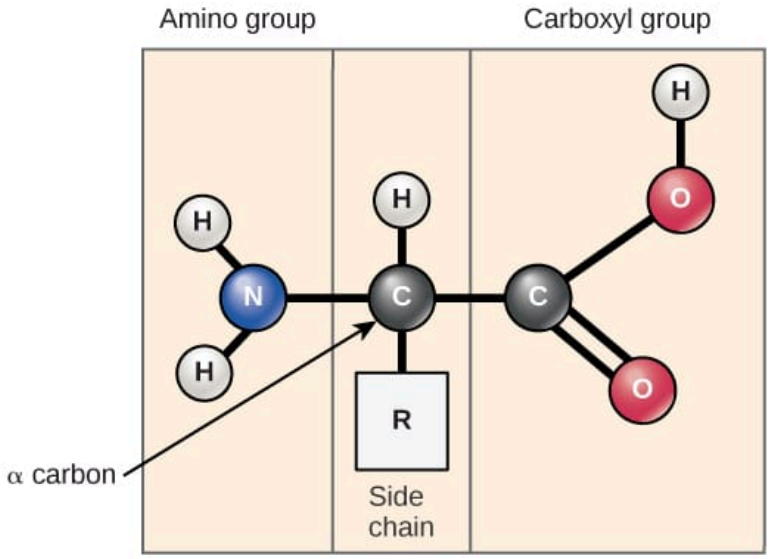


Figure 3.8.1: Amino acid structure: Amino acids have a central asymmetric carbon to which an amino group, a carboxyl group, a hydrogen atom, and a side chain (R group) are attached. This amino acid is unionized, but if it were placed in water at pH 7, its amino group would pick up another hydrogen and a positive charge, and the hydroxyl in its carboxyl group would lose and a hydrogen and gain a negative charge.

Types of Amino Acids

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

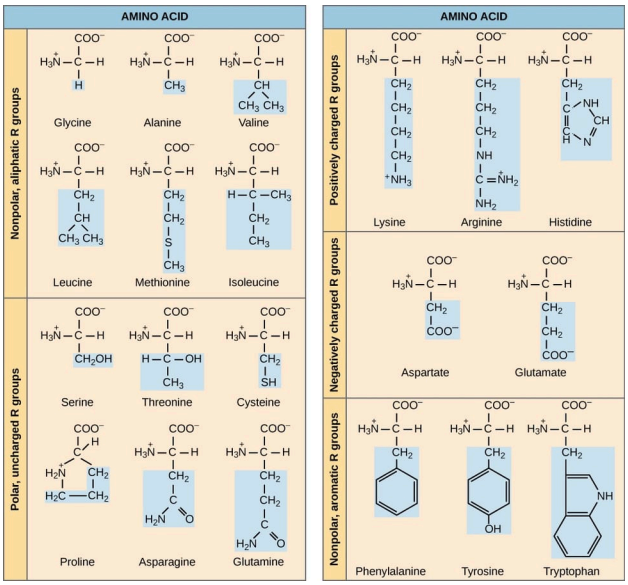


Figure 3.8.1: Types of amino acids: There are 21 common amino acids commonly found in proteins, each with a different R group (variant group) that determines its chemical nature. The 21st amino acid, not shown here, is selenocysteine, with an R group of -CH_2-SeH.

Characteristics of Amino Acids

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

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

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

Peptide Bonds

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

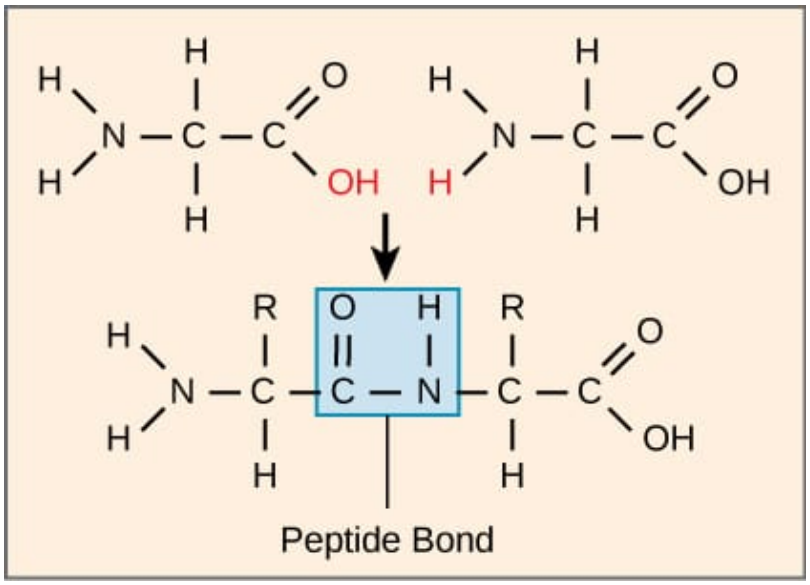


Figure 3.8.1: Peptide bond formation: Peptide bond formation is a dehydration synthesis reaction. The carboxyl group of one amino acid is linked to the amino group of the incoming amino acid. In the process, a molecule of water is released.

Polypeptide Chains

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

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

Key Points

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

Key Terms

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

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3.9: Proteins - Protein Structure

Learning Objectives

- Summarize the four levels of protein structure

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

Primary Structure

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

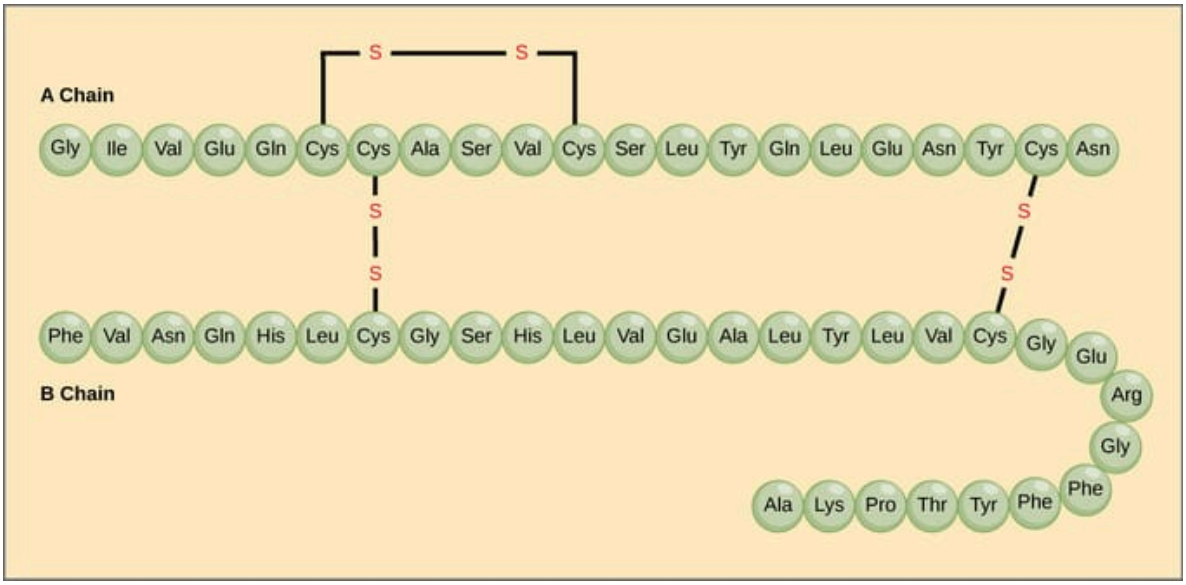


Figure 3.9.1: Primary structure: The A chain of insulin is 21 amino acids long and the B chain is 30 amino acids long, and each sequence is unique to the insulin protein.

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

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

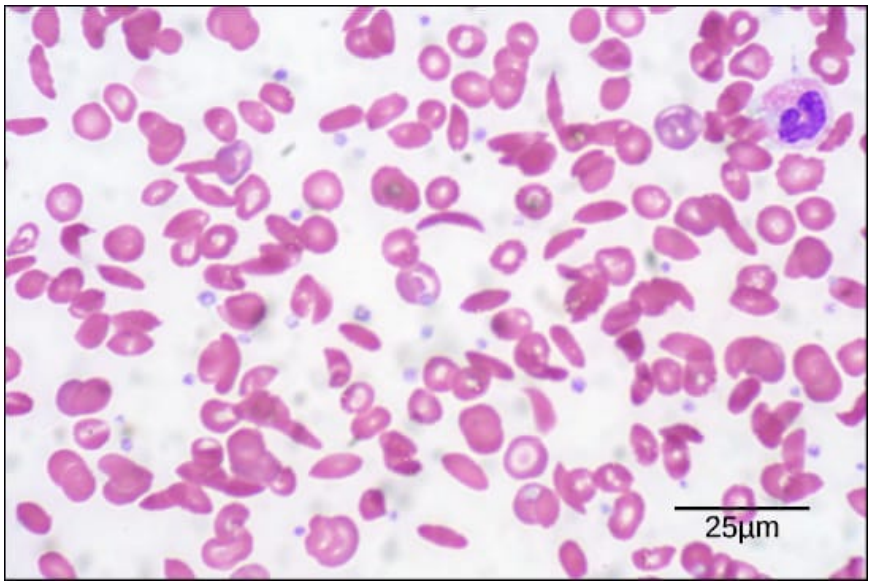


Figure 3.9.1: Sickle cell disease: Sickle cells are crescent shaped, while normal cells are disc-shaped.

Secondary Structure

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

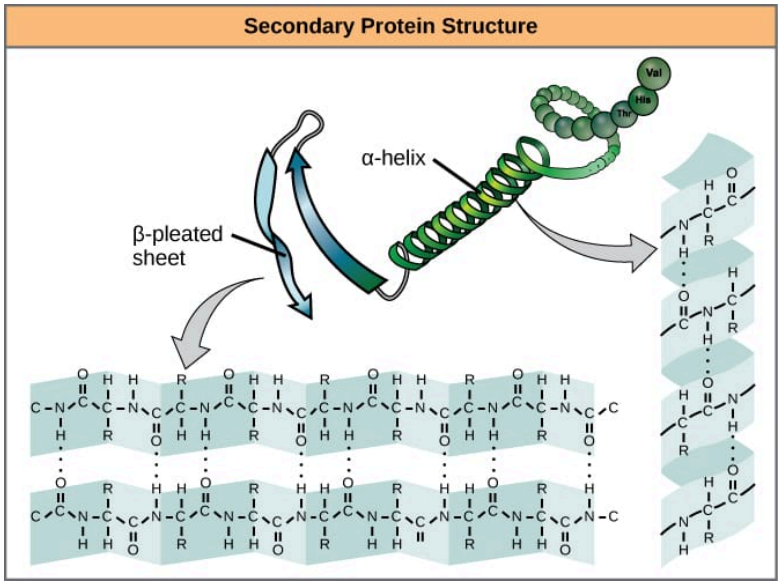


Figure 3.9.1: Secondary structure: The α-helix and β-pleated sheet form because of hydrogen bonding between carbonyl and amino groups in the peptide backbone. Certain amino acids have a propensity to form an α-helix, while others have a propensity to form a β-pleated sheet.

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

In β-pleated sheets, stretches of amino acids are held in an almost fully-extended conformation that "pleats" or zig-zags due

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

Tertiary Structure

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

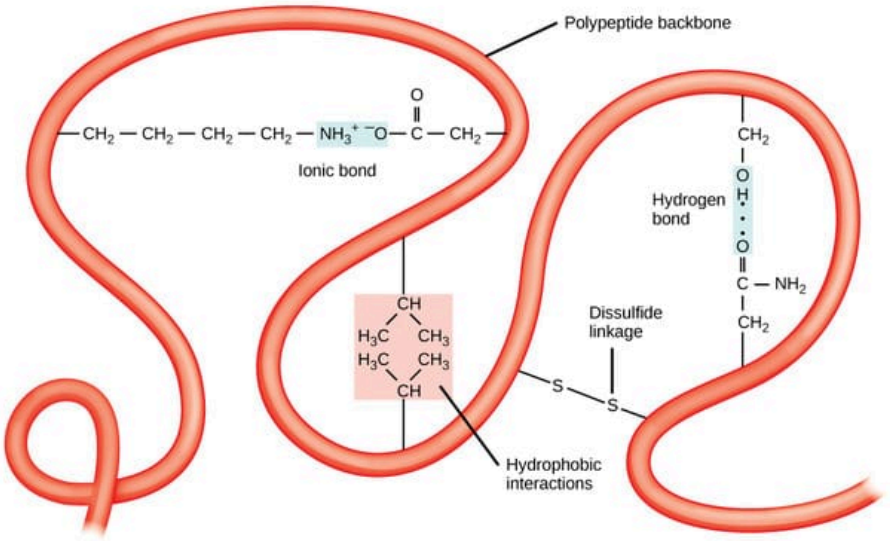


Figure 3.9.1: Tertiary structure: The tertiary structure of proteins is determined by hydrophobic interactions, ionic bonding, hydrogen bonding, and disulfide linkages.

Quaternary Structure

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

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

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

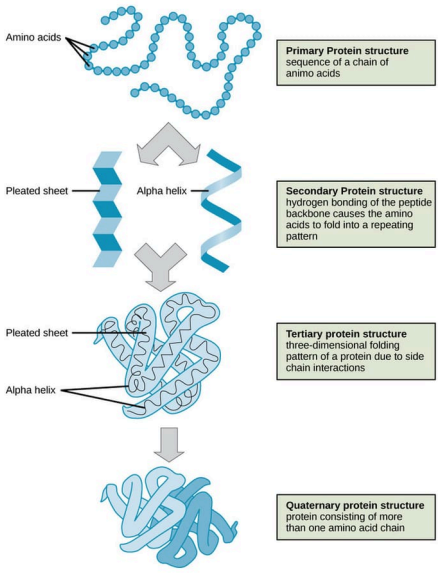


Figure 3.9.1: Four levels of protein structure: The four levels of protein structure can be observed in these illustrations.

Key Points

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

Key Terms

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

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3.10: Proteins - Denaturation and Protein Folding

Learning Objectives

- Discuss the process of protein denaturation

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

Changing the Shape of a Protein

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

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

Reversing Denaturation

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

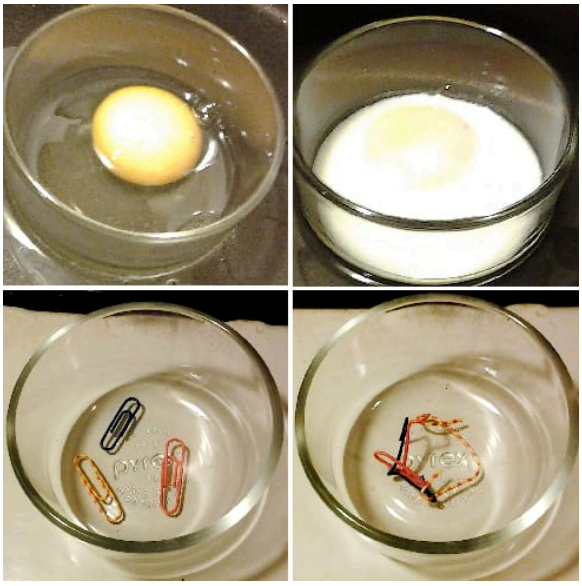


Figure 3.10.1: Denaturing a protein is occasionally irreversible: (Top) The protein albumin in raw and cooked egg white. (Bottom) A paperclip analogy visualizes the process: when cross-linked, paperclips ('amino acids') no longer move freely; their structure is rearranged and 'denatured'.

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

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Key Points

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

Key Terms

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

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3.11: Nucleic Acids - DNA and RNA

Learning Objectives

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

Types of Nucleic Acids

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

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

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

Nucleotides

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

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

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

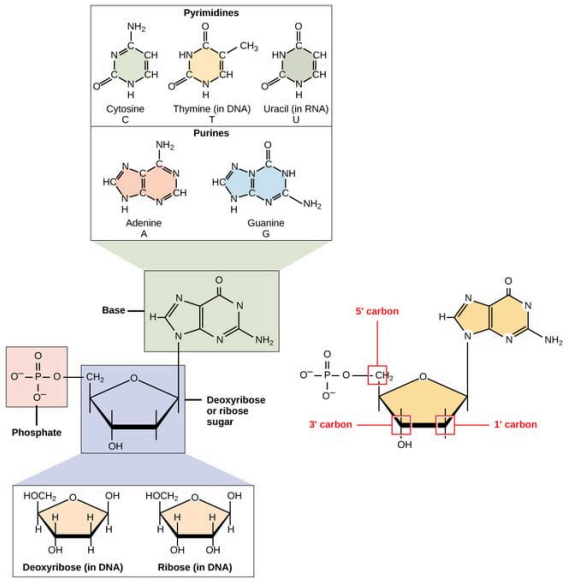


Figure 3.11.1: DNA and RNA: A nucleotide is made up of three components: a nitrogenous base, a pentose sugar, and one or more phosphate groups. Carbon residues in the pentose are numbered 1′ through 5′ (the prime distinguishes these residues from those in the base, which are numbered without using a prime notation). The base is attached to the 1′ position of the ribose, and the phosphate is attached to the 5′ position. When a polynucleotide is formed, the 5′ phosphate of the incoming nucleotide attaches to the 3′ hydroxyl group at the end of the growing chain. Two types of pentose are found in nucleotides, deoxyribose (found in DNA) and ribose (found in RNA). Deoxyribose is similar in structure to ribose, but it has an H instead of an OH at the 2′ position. Bases can be divided into two categories: purines and pyrimidines. Purines have a double ring structure, and pyrimidines have a single ring.

Nitrogenous Base

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

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

Five-Carbon Sugar

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

Phosphate Group

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

Key Points

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

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

Key Terms

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

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3.12: Nucleic Acids - The DNA Double Helix

Learning Objectives

- Describe the structure of DNA

A Double-Helix Structure

DNA has a double-helix structure, with sugar and phosphate on the outside of the helix, forming the sugar-phosphate backbone of the DNA. The nitrogenous bases are stacked in the interior in pairs, like the steps of a staircase; the pairs are bound to each other by hydrogen bonds. The two strands of the helix run in opposite directions. This *antiparallel* orientation is important to DNA replication and in many nucleic acid interactions.

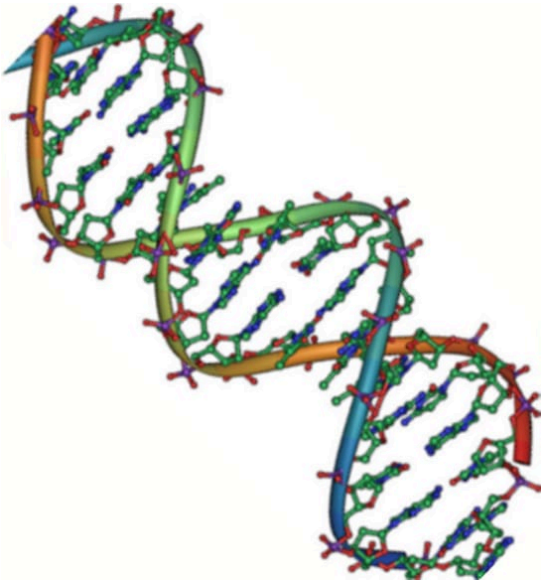


Figure 3.12.1: DNA is a Double Helix: Native DNA is an antiparallel double helix. The phosphate backbone (indicated by the curvy lines) is on the outside, and the bases are on the inside. Each base from one strand interacts via hydrogen bonding with a base from the opposing strand.

Base Pairs

Only certain types of base pairing are allowed. This means Adenine pairs with Thymine, and Guanine pairs with Cytosine. This is known as the base complementary rule because the DNA strands are complementary to each other. If the sequence of one strand is AATTGGCC, the complementary strand would have the sequence TTAACCGG.

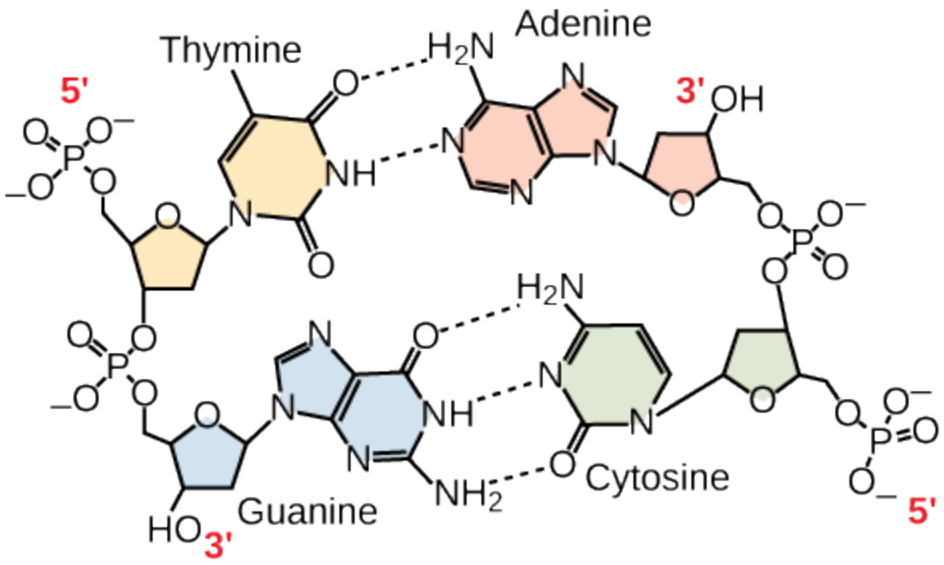


Figure 3.12.1: Antiparallel Strands: In a double stranded DNA molecule, the two strands run antiparallel to one another so one is upside down compared to the other. The phosphate backbone is located on the outside, and the bases are in the middle. Adenine forms hydrogen bonds (or base pairs) with thymine, and guanine base pairs with cytosine.

DNA Replication

During DNA replication, each strand is copied, resulting in a daughter DNA double helix containing one parental DNA strand and a newly synthesized strand. At this time it is possible a mutation may occur. A mutation is a change in the sequence of the nitrogen bases. For example, in the sequence AATTGGCC, a mutation may cause the second T to change to a G. Most of the time when this happens the DNA is able to fix itself and return the original base to the sequence. However, sometimes the repair is unsuccessful, resulting in different proteins being created.

Key Points

- The structure of DNA is called a double helix, which looks like a twisted staircase.
- The sugar and phosphate make up the backbone, while the nitrogen bases are found in the center and hold the two strands together.
- The nitrogen bases can only pair in a certain way: A pairing with T and C pairing with G. This is called *base pairing*.
- Due to the *base pairing*, the DNA strands are *complementary* to each other, run in opposite directions, and are called antiparallel strands.

Key Terms

- **mutation**: any error in base pairing during the replication of DNA
- **sugar-phosphate backbone**: The outer support of the ladder, forming strong covalent bonds between monomers of DNA.
- **base pairing**: The specific way in which bases of DNA line up and bond to one another; A always with T and G always with C.

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3.13: Nucleic Acids - DNA Packaging

Learning Objectives

- Describe how DNA is packaged differently in prokaryotes and eukaryotes

A eukaryote contains a well-defined nucleus, whereas in prokaryotes the chromosome lies in the cytoplasm in an area called the nucleoid. In eukaryotic cells, DNA and RNA synthesis occur in a separate compartment from protein synthesis. In prokaryotic cells, both processes occur together. What advantages might there be to separating the processes? What advantages might there be to having them occur together?

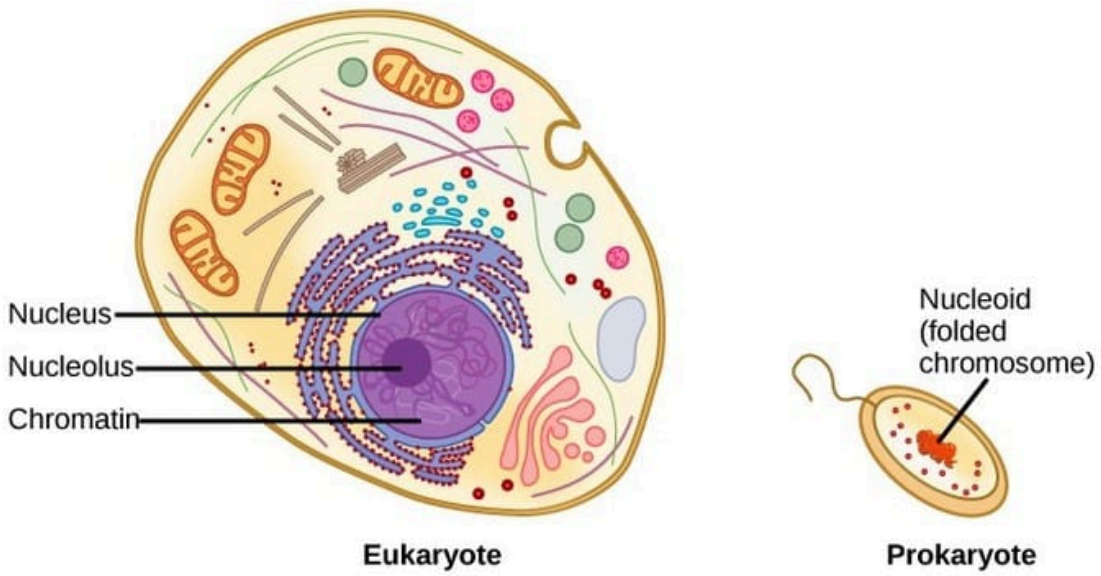


Figure 3.13.1: Eukaryotic and prokaryotic cells: A eukaryote contains a well-defined nucleus, whereas in prokaryotes, the chromosome lies in the cytoplasm in an area called the nucleoid.

The size of the genome in one of the most well-studied prokaryotes, *E.coli,* is 4.6 million base pairs (approximately 1.1 mm, if cut and stretched out). So how does this fit inside a small bacterial cell? The DNA is twisted by what is known as supercoiling. Supercoiling means that DNA is either under-wound (less than one turn of the helix per 10 base pairs) or over-wound (more than 1 turn per 10 base pairs) from its normal relaxed state. Some proteins are known to be involved in the supercoiling; other proteins and enzymes such as DNA gyrase help in maintaining the supercoiled structure.

Eukaryotes, whose chromosomes each consist of a linear DNA molecule, employ a different type of packing strategy to fit their DNA inside the nucleus. At the most basic level, DNA is wrapped around proteins known as histones to form structures called nucleosomes. The histones are evolutionarily conserved proteins that are rich in basic amino acids and form an octamer. The DNA (which is negatively charged because of the phosphate groups) is wrapped tightly around the histone core. This nucleosome is linked to the next one with the help of a linker DNA. This is also known as the “beads on a string” structure. This is further compacted into a 30 nm fiber, which is the diameter of the structure. At the metaphase stage the chromosomes are at their most compact, approximately 700 nm in width, and are found in association with scaffold proteins.

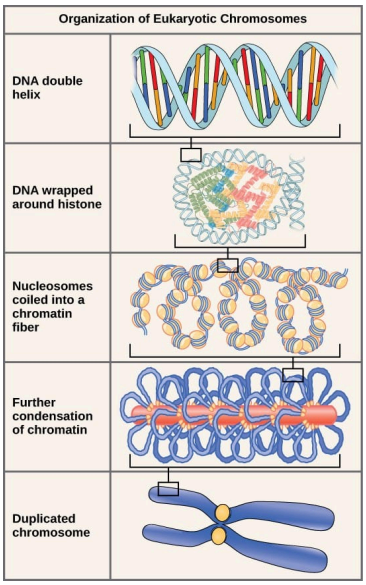


Figure 3.13.1: Eukaryotic chromosomes: These figures illustrate the compaction of the eukaryotic chromosome.

In interphase, eukaryotic chromosomes have two distinct regions that can be distinguished by staining. The tightly packaged region is known as heterochromatin, and the less dense region is known as euchromatin.

Heterochromatin usually contains genes that are not expressed, and is found in the regions of the centromere and telomeres. The euchromatin usually contains genes that are transcribed, with DNA packaged around nucleosomes but not further compacted.

Key Points

- In eukaryotic cells, DNA and RNA synthesis occur in a different location than protein synthesis; in prokaryotic cells, both these processes occur together.
- DNA is “supercoiled” in prokaryotic cells, meaning that the DNA is either under-wound or over-wound from its normal relaxed state.
- In eukaryotic cells, DNA is wrapped around proteins known as histones to form structures called nucleosomes.

Key Terms

- **nucleosomes**: The fundamental subunit of chromatin, composed of a little less than two turns of DNA wrapped around a set of eight proteins called histones.
- **histones**: The chief protein components of chromatin, which act as spools around which DNA winds.

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3.14: Nucleic Acids - Types of RNA

Learning Objectives

- Describe the structure and function of RNA

RNA Structure and Function

The two main types of nucleic acids are deoxyribonucleic acid (DNA) and ribonucleic acid (RNA). DNA is the genetic material found in all living organisms and is found in the nucleus of eukaryotes and in the chloroplasts and mitochondria. In prokaryotes, the DNA is not enclosed in a membranous envelope.

The other type of nucleic acid, RNA, is mostly involved in protein synthesis. Just like in DNA, RNA is made of monomers called nucleotides. Each nucleotide is made up of three components: a nitrogenous base, a pentose (five-carbon) sugar called ribose, and a phosphate group. Each nitrogenous base in a nucleotide is attached to a sugar molecule, which is attached to one or more phosphate groups.

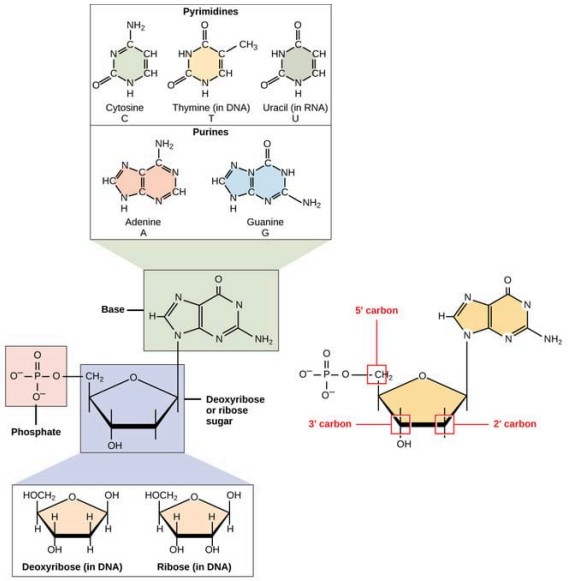


Figure 3.14.1: RNA Structure: A nucleotide is made up of three components: a nitrogenous base, a pentose sugar, and one or more phosphate groups. Carbon residues in the pentose are numbered 1′ through 5′ (the prime distinguishes these residues from those in the base, which are numbered without using a prime notation). The base is attached to the 1′ position of the ribose, and the phosphate is attached to the 5′ position. When a polynucleotide is formed, the 5′ phosphate of the incoming nucleotide attaches to the 3′ hydroxyl group at the end of the growing chain. Two types of pentose are found in nucleotides, deoxyribose (found in DNA) and ribose (found in RNA). Deoxyribose is similar in structure to ribose, but it has an H instead of an OH at the 2′ position. Bases can be divided into two categories: purines and pyrimidines. Purines have a double ring structure, and pyrimidines have a single ring.

In RNA, the nitrogenous bases vary slightly from those of DNA. Adenine (A), guanine (G), and cytosine (C) are present, but instead of thymine (T), a pyrimidine called uracil (U) pairs with adenine. RNA is a single stranded molecule, compared to the double helix of DNA.

The DNA molecules never leave the nucleus but instead use an intermediary to communicate with the rest of the cell. This intermediary is the messenger RNA (mRNA). When proteins need to be made, the mRNA enters the nucleus and attaches itself to one of the DNA strands. Being complementary, the sequence of nitrogen bases of the RNA is opposite that of the DNA. This is called transcription. For example, if the DNA strand reads TCCAAGTC, then the mRNA strand would read AGGUUCAG. The mRNA then carries the code out of the nucleus to organelles called ribosomes for the assembly of proteins.

Once the mRNA has reached the ribosomes, they do not read the instructions directly. Instead, another type of RNA called transfer RNA (tRNA) needs to translate the information from the mRNA into a usable form. The tRNA attaches to the mRNA, but with the opposite base pairings. It then reads the sequence in sets of three bases called codons. Each possible three letter arrangement of A,C,U,G (e.g., AAA, AAU, GGC, etc) is a specific instruction, and the correspondence of these instructions and the amino acids is known as the "genetic code." Though exceptions to or variations on the code exist, the standard genetic code holds true in most organisms.

The ribosome acts like a giant clamp, holding all of the players in position, and facilitating both the pairing of bases between the messenger and transfer RNAs, and the chemical bonding between the amino acids. The ribosome has special subunits known as ribosomal RNAs (rRNA) because they function in the ribosome. These subunits do not carry instructions for making a specific proteins (i.e., they are not messenger RNAs) but instead are an integral part of the ribosome machinery that is used to make proteins from mRNAs. The making of proteins by reading instructions in mRNA is generally known as " translation."

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Key Points

- The nitrogen bases in RNA include adenine (A), guanine (G), cytosine (C), and uracil (U).
- Messenger RNA (mRNA) carries the code from the DNA to the ribosomes, while transfer RNA (tRNA) converts that code into a usable form.
- Ribosomes are the sites where tRNA and rRNA assemble proteins.
- RNA differs from DNA in that it is single stranded, has uracil instead of thymine, carries the code for making proteins instead of directing all of the cell 's functions, and has ribose as its five-carbon sugar instead of deoxyribose.

Key Terms

- **codon**: a sequence of three adjacent nucleotides, which encode for a specific amino acid during protein synthesis or translation
- **transcription**: the synthesis of RNA under the direction of DNA

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4: CELL STRUCTURE

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4.1: Studying Cells - Cells as the Basic Unit of Life

Learning Objectives

- State the general characteristics of a cell

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

Cells as Building Blocks

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

Types of Specialized Cells

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

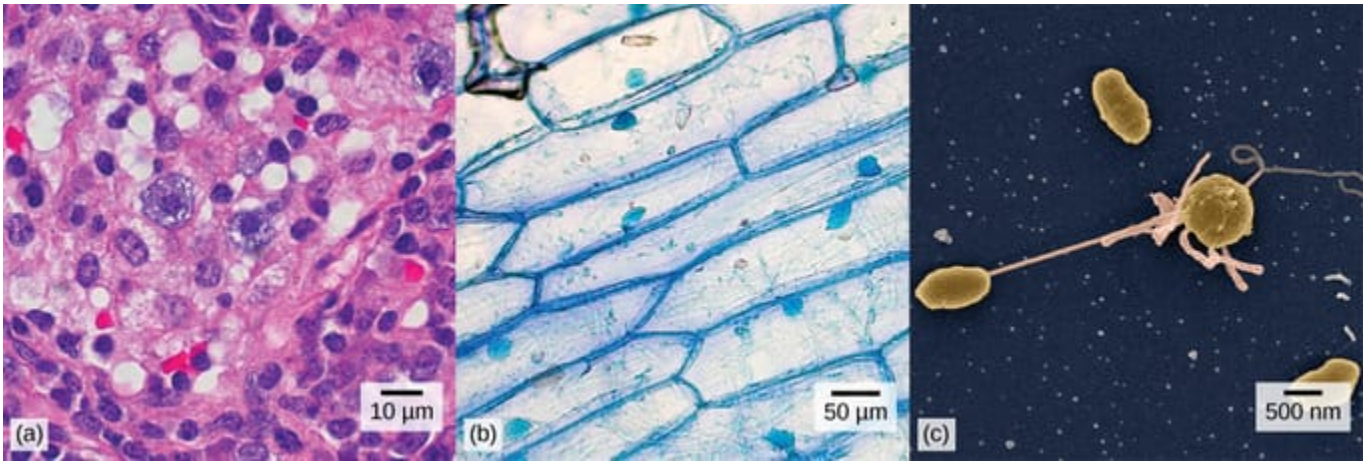


Figure 4.1.1: Various Cell Types: (a) Nasal sinus cells (viewed with a light microscope), (b) onion cells (viewed with a light microscope), and (c) Vibrio tasmaniensis bacterial cells (seen through a scanning electron microscope) are from very different organisms, yet all share certain characteristics of basic cell structure.

Key Points

- A living thing can be composed of either one cell or many cells.
- There are two broad categories of cells: prokaryotic and eukaryotic cells.

- Cells can be highly specialized with specific functions and characteristics.

Key Terms

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

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4.2: Studying Cells - Microscopy

Learning Objectives

- Compare and contrast light and electron microscopy.

Microscopy

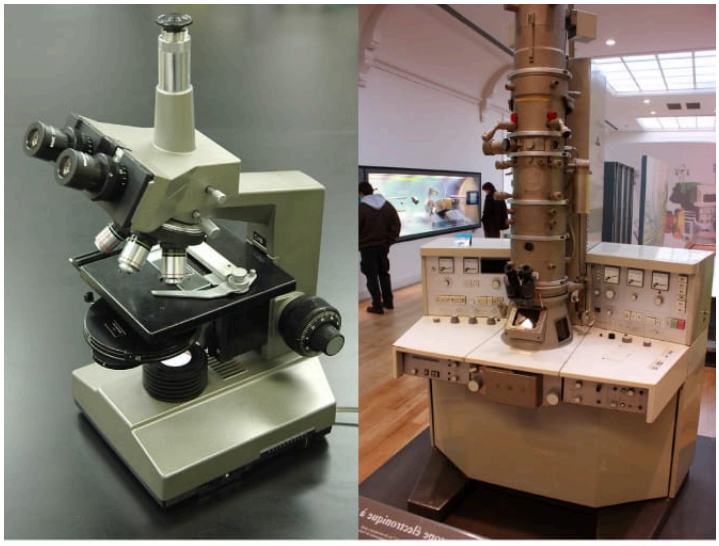
Cells vary in size. With few exceptions, individual cells cannot be seen with the naked eye, so scientists use microscopes (micro- = “small”; -scope = “to look at”) to study them. A microscope is an instrument that magnifies an object. Most photographs of cells are taken with a microscope; these images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

The optics of a microscope’s lenses change the orientation of the image that the user sees. 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. Because of the manner by which light travels through the lenses, this system of two lenses produces an inverted image (binocular, or dissecting microscopes, work in a similar manner, but they include an additional magnification system that makes the final image appear to be upright).

Light Microscopes

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

Most student microscopes are classified as light microscopes. Visible light passes and is bent through 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.



(a) (b)

Figure 4.2.1: Light and Electron Microscopes: (a) Most light microscopes used in a college biology lab can magnify cells up to approximately 400 times and have a resolution of about 200 nanometers. (b) Electron microscopes provide a much higher magnification, 100,000x, and a have a resolution of 50 picometers.

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

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, it also provides higher resolving power. The method used to prepare the specimen for viewing with an electron microscope kills the specimen. Electrons have short wavelengths (shorter than photons) that move best in a vacuum, so living cells cannot be viewed with an electron microscope.

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

Key Points

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

Key Terms

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

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4.3: Studying Cells - Cell Theory

Learning Objectives

- Identify the components of cell theory

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 protista (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" 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, microscope construction, and staining techniques enabled other scientists to see some components inside cells.

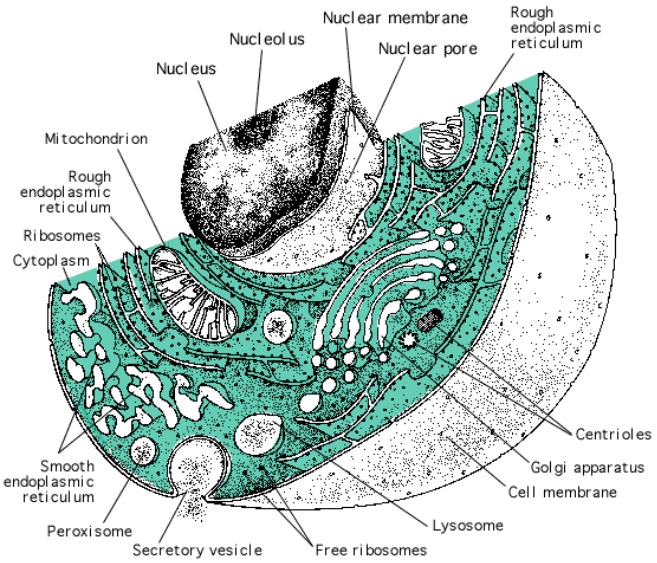


Figure 4.3.1: Structure of an Animal Cell: The cell is the basic unit of life and the study of the cell led to the development of the cell theory.

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

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

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

The expanded version of the cell theory can also include:

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

Key Points

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

Key Terms

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

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4.4: Studying Cells - Cell Size

Learning Objectives

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

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

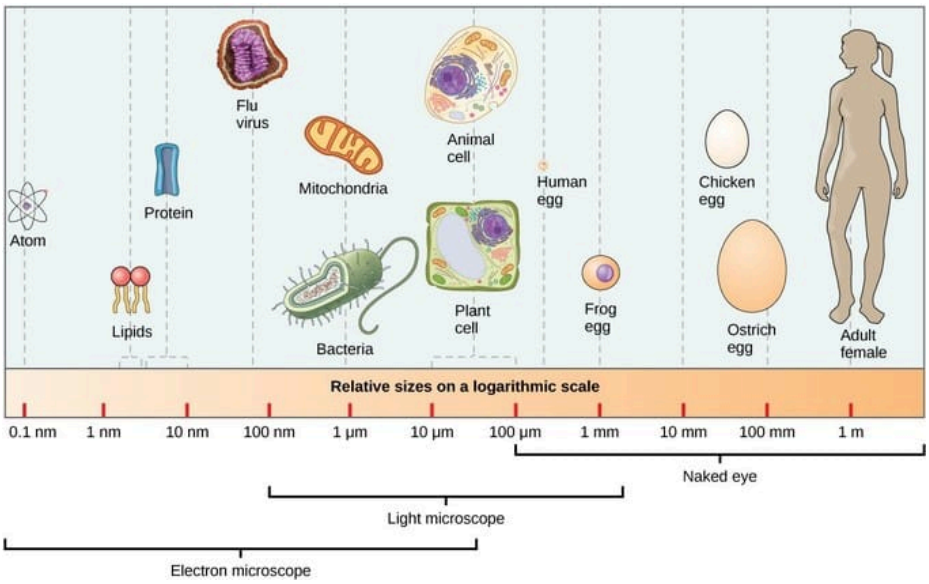


Figure 4.4.1: Relative Size of Atoms to Humans: This figure shows relative sizes on a logarithmic scale (recall that each unit of increase in a logarithmic scale represents a 10-fold increase in the quantity being measured).

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

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

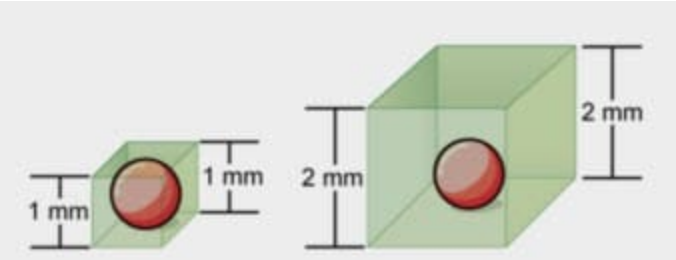


Figure 4.4.1: Surface Area to Volume Ratios: Notice that as a cell increases in size, its surface area-to-volume ratio decreases. When there is insufficient surface area to support a cell's increasing volume, a cell will either divide or die. The cell on the left has a volume of 1 mm3 and a surface area of 6 mm2, with a surface area-to-volume ratio of 6 to 1, whereas the cell on the right has a volume of 8 mm3 and a surface area of 24 mm2, with a surface area-to-volume ratio of 3 to 1.

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

Increased volume can lead to biological problems. King Kong, the fictional giant gorilla, would have insufficient lung surface area to meet his oxygen needs, and could not survive. For small organisms with their high surface area to volume ratio, friction and fluid dynamics (wind, water flow) are relatively much more important, and gravity much less important, than for large animals.

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

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Key Points

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

Key Terms

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

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4.5: Prokaryotic Cells - Characteristics of Prokaryotic Cells

Learning Objectives

- Describe the structure of prokaryotic cells

Components of Prokaryotic Cells

All cells share four common components:

1. a plasma membrane: an outer covering that separates the cell's interior from its surrounding environment.
2. cytoplasm: a jelly-like cytosol within the cell in which other cellular components are found
3. DNA: the genetic material of the cell
4. ribosomes: where protein synthesis occurs

However, prokaryotes differ from eukaryotic cells in several ways.

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

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

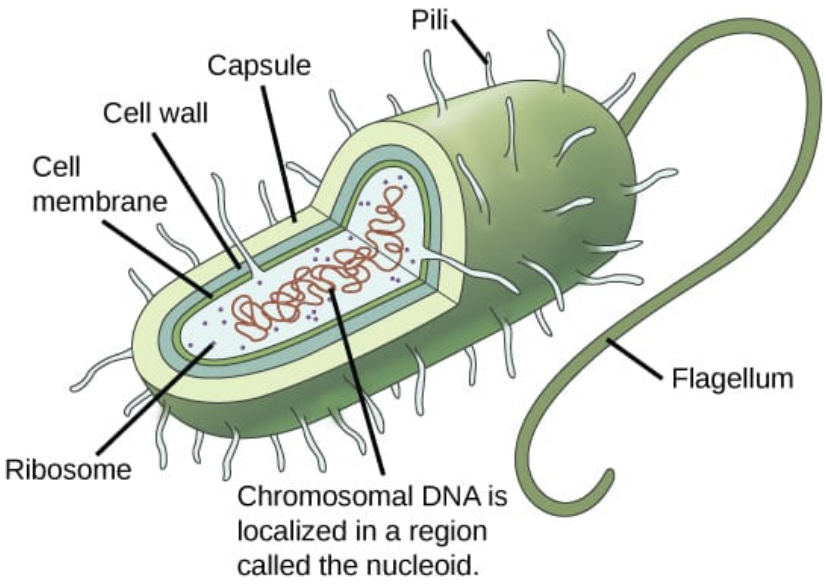


Figure 4.5.1: General Structure of a Prokaryotic Cell: This figure shows the generalized structure of a prokaryotic cell.All prokaryotes have chromosomal DNA localized in a nucleoid, ribosomes, a cell membrane, and a cell wall.The other structures shown are present in some, but not all, bacteria.

Cell Size

At 0.1 to 5.0 µm in diameter, prokaryotic cells are significantly smaller than eukaryotic cells, which have diameters ranging from 10 to 100 µm. The small size of prokaryotes allows ions and organic molecules that enter them to quickly diffuse to other parts

of the cell. Similarly, any wastes produced within a prokaryotic cell can quickly diffuse out. This is not the case in eukaryotic cells, which have developed different structural adaptations to enhance intracellular transport.

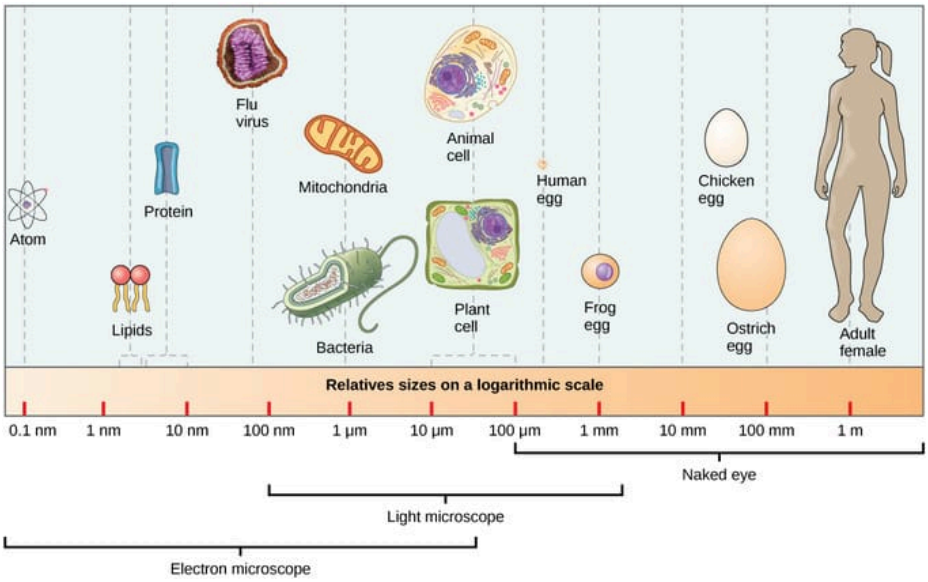


Figure 4.5.1: Microbial Size: This figure shows relative sizes of microbes on a logarithmic scale (recall that each unit of increase in a logarithmic scale represents a 10-fold increase in the quantity being measured).

Small size, in general, is necessary for all cells, whether prokaryotic or eukaryotic. Let's examine why that is so. First, we'll consider the area and volume of a typical cell. Not all cells are spherical in shape, but most tend to approximate a sphere. You may remember from your high school geometry course that the formula for the surface area of a sphere is $4\pi r^2$, while the formula for its volume is $4/3\pi r^3$. Thus, as the radius of a cell increases, its surface area increases as the square of its radius, but its volume increases as the cube of its radius (much more rapidly). Therefore, as a cell increases in size, its surface area-to-volume ratio decreases. This same principle would apply if the cell had the shape of a cube. If the cell grows too large, the plasma membrane will not have sufficient surface area to support the rate of diffusion required for the increased volume. In other words, as a cell grows, it becomes less efficient. One way to become more efficient is to divide; another way is to develop organelles that perform specific tasks. These adaptations led to the development of more sophisticated cells called eukaryotic cells.

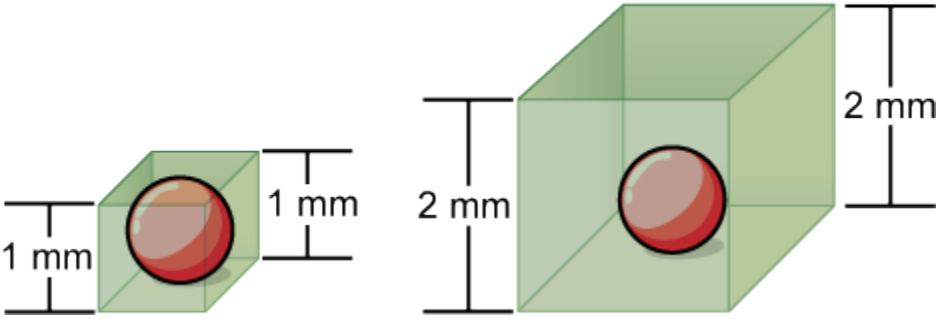


Figure 4.5.1: Cell Surface Size: Notice that as a cell increases in size, its surface area-to-volume ratio decreases.When there is insufficient surface area to support a cell's increasing volume, a cell will either divide or die.The cell on the left has a volume of 1 mm3 and a surface area of 6 mm2, with a surface area-to-volume ratio of 6 to 1, whereas the cell on the right has a volume of 8 mm3 and a surface area of 24 mm2, with a surface area-to-volume ratio of 3 to 1.

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Key Points

- Prokaryotes lack an organized nucleus and other membrane-bound organelles.
- Prokaryotic DNA is found in a central part of the cell called the nucleoid.
- The cell wall of a prokaryote acts as an extra layer of protection, helps maintain cell shape, and prevents dehydration.
- Prokaryotic cell size ranges from 0.1 to 5.0 μm in diameter.
- The small size of prokaryotes allows quick entry and diffusion of ions and molecules to other parts of the cell while also allowing fast removal of waste products out of the cell.

Key Terms

- **eukaryotic**: Having complex cells in which the genetic material is organized into membrane-bound nuclei.
- **prokaryotic**: Of cells, lacking a nucleus.
- **nucleoid**: the irregularly-shaped region within a prokaryote cell where the genetic material is localized

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4.6: Eukaryotic Cells - Characteristics of Eukaryotic Cells

Learning Objectives

- Describe the structure of eukaryotic cells

Eukaryotic Cell Structure

Like a prokaryotic cell, a eukaryotic cell has a plasma membrane, cytoplasm, and ribosomes. However, unlike prokaryotic cells, eukaryotic cells have:

1. a membrane-bound nucleus
2. numerous membrane-bound organelles (including the endoplasmic reticulum, Golgi apparatus, chloroplasts, and mitochondria)
3. several rod-shaped chromosomes

Because a eukaryotic cell's nucleus is surrounded by a membrane, it is often said to have a "true nucleus. " Organelles (meaning "little organ") have specialized cellular roles, just as the organs of your body have specialized roles. They allow different functions to be compartmentalized in different areas of the cell.

The Nucleus & Its Structures

Typically, the nucleus is the most prominent organelle in a cell. Eukaryotic cells have a true nucleus, which means the cell's DNA is surrounded by a membrane. Therefore, the nucleus houses the cell's DNA and directs the synthesis of proteins and ribosomes, the cellular organelles responsible for protein synthesis. The nuclear envelope is a double-membrane structure that constitutes the outermost portion of the nucleus. 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 cytoplasm. The nucleoplasm is the semi-solid fluid inside the nucleus where we find the chromatin and the nucleolus. Furthermore, chromosomes are structures within the nucleus that are made up of DNA, the genetic material. In prokaryotes, DNA is organized into a single circular chromosome. In eukaryotes, chromosomes are linear structures.

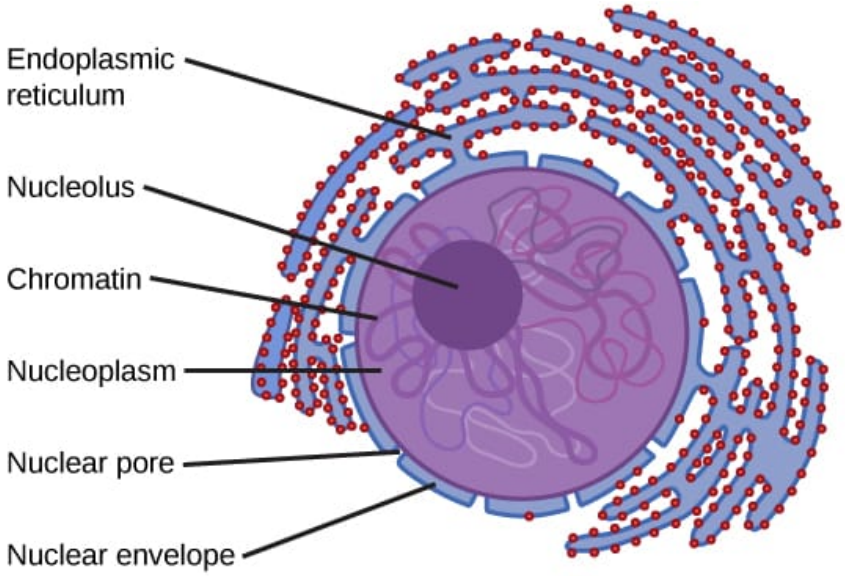


Figure 4.6.1: Eukaryotic Nucleus: The nucleus stores chromatin (DNA plus proteins) in a gel-like substance called the nucleoplasm.The nucleolus is a condensed region of chromatin where ribosome synthesis occurs.The boundary of the nucleus is called the nuclear envelope.It consists of two phospholipid bilayers: an outer membrane and an inner membrane.The nuclear membrane is continuous with the endoplasmic reticulum.Nuclear pores allow substances to enter and exit the nucleus.

Other Membrane-Bound Organelles

Mitochondria are oval-shaped, double membrane organelles that have their own ribosomes and DNA. These organelles are often called the “energy factories” of a cell because they are responsible for making adenosine triphosphate (ATP), the cell’s main energy-carrying molecule, by conducting cellular respiration. The endoplasmic reticulum modifies proteins and synthesizes lipids, while the golgi apparatus is where the sorting, tagging, packaging, and distribution of lipids and proteins takes place. Peroxisomes are small, round organelles enclosed by single membranes; they carry out oxidation reactions that break down fatty acids and amino acids. Peroxisomes also detoxify many poisons that may enter the body. Vesicles and vacuoles are membrane-bound sacs that function in storage and transport. Other than the fact that vacuoles are somewhat larger than vesicles, there is a very subtle distinction between them: the membranes of vesicles can fuse with either the plasma membrane or other membrane systems within the cell. All of these organelles are found in each and every eukaryotic cell.

Animal Cells Versus Plant Cells

While all eukaryotic cells contain the aforementioned organelles and structures, there are some striking differences between animal and plant cells. Animal cells have a centrosome and lysosomes, whereas plant cells do not. The centrosome is a microtubule-organizing center found near the nuclei of animal cells while lysosomes take care of the cell’s digestive process.

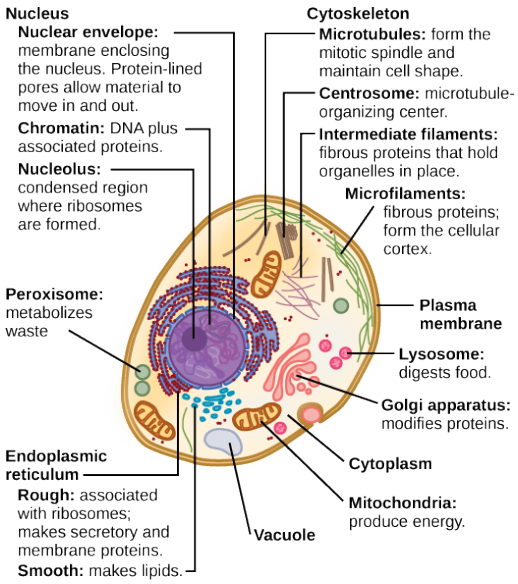


Figure 4.6.1: Animal Cells: Despite their fundamental similarities, there are some striking differences between animal and plant cells.Animal cells have centrioles, centrosomes, and lysosomes, whereas plant cells do not.

In addition, plant cells have a cell wall, a large central vacuole, chloroplasts, and other specialized plastids, whereas animal cells do not. The cell wall protects the cell, provides structural support, and gives shape to the cell while the central vacuole plays a key role in regulating the cell's concentration of water in changing environmental conditions. Chloroplasts are the organelles that carry out photosynthesis.

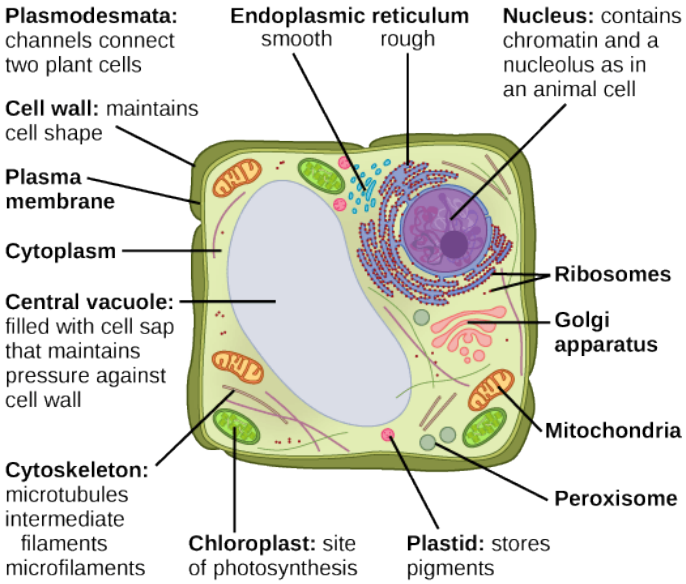


Figure 4.6.1: Plant Cells: Plant cells have a cell wall, chloroplasts, plasmodesmata, and plastids used for storage, and a large central vacuole, whereas animal cells do not.

Key Points

- Eukaryotic cells are larger than prokaryotic cells and have a "true" nucleus, membrane-bound organelles, and rod-shaped chromosomes.
- The nucleus houses the cell's DNA and directs the synthesis of proteins and ribosomes.
- Mitochondria are responsible for ATP production; the endoplasmic reticulum modifies proteins and synthesizes lipids; and the golgi apparatus is where the sorting of lipids and proteins takes place.
- Peroxisomes carry out oxidation reactions that break down fatty acids and amino acids and detoxify poisons; vesicles and vacuoles function in storage and transport.

- Animal cells have a centrosome and lysosomes while plant cells do not.
- Plant cells have a cell wall, a large central vacuole, chloroplasts, and other specialized plastids, whereas animal cells do not.

Key Terms

- **eukaryotic**: Having complex cells in which the genetic material is organized into membrane-bound nuclei.
- **organelle**: A specialized structure found inside cells that carries out a specific life process (e.g. ribosomes, vacuoles).
- **photosynthesis**: the process by which plants and other photoautotrophs generate carbohydrates and oxygen from carbon dioxide, water, and light energy in chloroplasts

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4.7: Eukaryotic Cells - The Plasma Membrane and the Cytoplasm

Learning Objectives

- Explain the structure and purpose of the plasma membrane of a cell

The Plasma Membrane

Despite differences in structure and function, all living cells in multicellular organisms have a surrounding plasma membrane (also known as the cell membrane). As the outer layer of your skin separates your body from its environment, the plasma membrane separates the inner contents of a cell from its exterior environment. The plasma membrane can be described as a phospholipid bilayer with embedded proteins that controls the passage of organic molecules, ions, water, and oxygen into and out of the cell. Wastes (such as carbon dioxide and ammonia) also leave the cell by passing through the membrane.

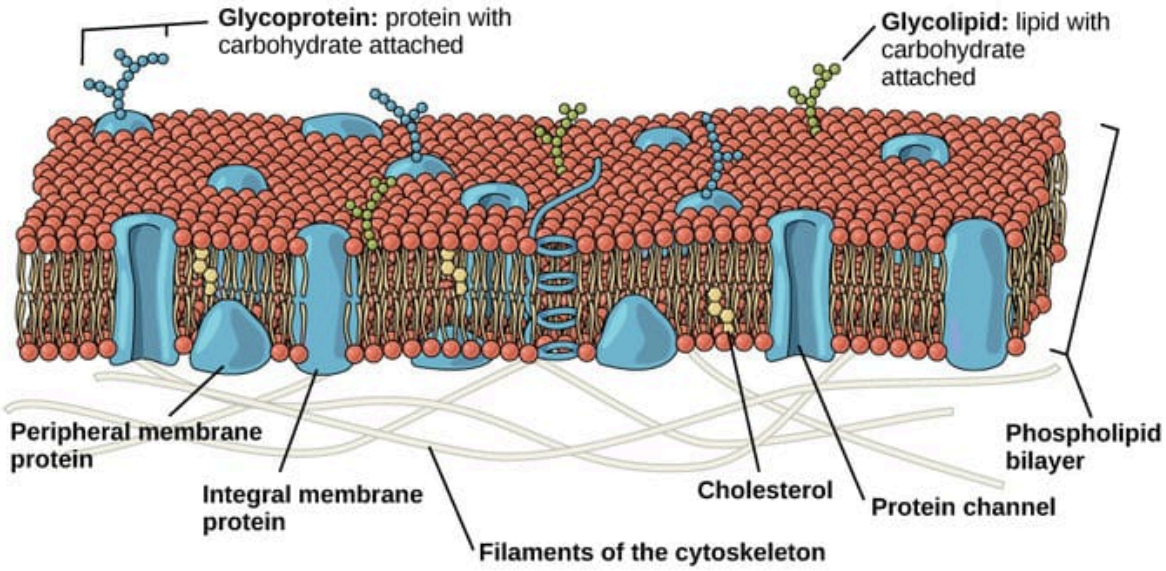


Figure 4.7.1: Eukaryotic Plasma Membrane: The eukaryotic plasma membrane is a phospholipid bilayer with proteins and cholesterol embedded in it.

The cell membrane is an extremely pliable structure composed primarily of two adjacent sheets of phospholipids. Cholesterol, also present, contributes to the fluidity of the membrane. A single phospholipid molecule consists of a polar phosphate “head,” which is hydrophilic, and a non-polar lipid “tail,” which is hydrophobic. Unsaturated fatty acids result in kinks in the hydrophobic tails. The phospholipid bilayer consists of two phospholipids arranged tail to tail. The hydrophobic tails associate with one another, forming the interior of the membrane. The polar heads contact the fluid inside and outside of the cell.

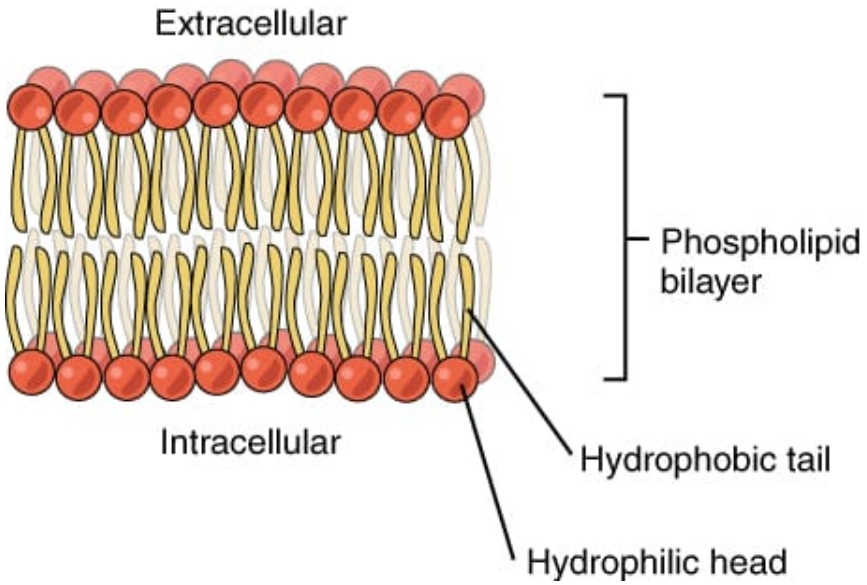


Figure 4.7.1: Phospholipid Bilayer: The phospholipid bilayer consists of two adjacent sheets of phospholipids, arranged tail to tail. The hydrophobic tails associate with one another, forming the interior of the membrane. The polar heads contact the fluid inside and outside of the cell.

The plasma membrane's main function is to regulate the concentration of substances inside the cell. These substances include ions such as Ca^{++}, Na^{+}, K^{+}, and Cl^{-}; nutrients including sugars, fatty acids, and amino acids; and waste products, particularly carbon dioxide (CO_2), which must leave the cell.

The membrane's lipid bilayer structure provides the cell with access control through permeability. The phospholipids are tightly packed together, while the membrane has a hydrophobic interior. This structure causes the membrane to be selectively permeable. A membrane that has selective permeability allows only substances meeting certain criteria to pass through it unaided. In the case of the plasma membrane, only relatively small, non-polar materials can move through the lipid bilayer (remember, the lipid tails of the membrane are nonpolar). Some examples of these materials are other lipids, oxygen and carbon dioxide gases, and alcohol. However, water-soluble materials—such as glucose, amino acids, and electrolytes—need some assistance to cross the membrane because they are repelled by the hydrophobic tails of the phospholipid bilayer.

Transport Across the Membrane

All substances that move through the membrane do so by one of two general methods, which are categorized based on whether or not energy is required. Passive (non-energy requiring) transport is the movement of substances across the membrane without the expenditure of cellular energy. During this type of transport, materials move by simple diffusion or by facilitated diffusion through the membrane, down their concentration gradient. Water passes through the membrane in a diffusion process called osmosis. Osmosis is the diffusion of water through a semi-permeable membrane down its concentration gradient. It occurs when there is an imbalance of solutes outside of a cell versus inside the cell. The solution that has the higher concentration of solutes is said to be hypertonic and the solution that has the lower concentration of solutes is said to be hypotonic. Water molecules will diffuse out of the hypotonic solution and into the hypertonic solution (unless acted upon by hydrostatic forces).

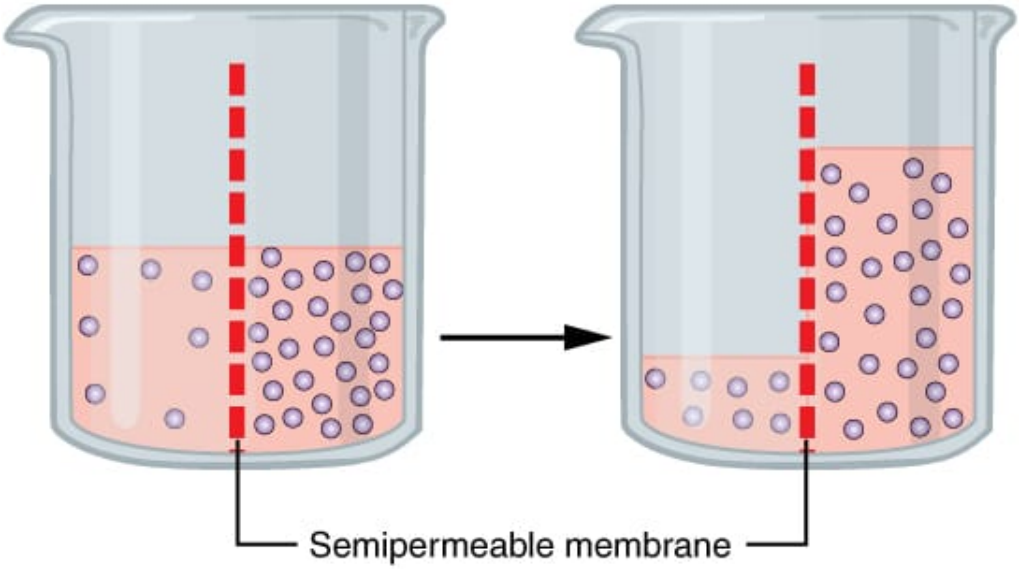


Figure 4.7.1: Osmosis: Osmosis is the diffusion of water through a semipermeable membrane down its concentration gradient. If a membrane is permeable to water, though not to a solute, water will equalize its own concentration by diffusing to the side of lower water concentration (and thus the side of higher solute concentration). In the beaker on the left, the solution on the right side of the membrane is hypertonic.

In contrast to passive transport, active (energy-requiring) transport is the movement of substances across the membrane using energy from adenosine triphosphate (ATP). The energy is expended to assist material movement across the membrane in a direction against their concentration gradient. Active transport may take place with the help of protein pumps or through the use of vesicles. Another form of this type of transport is endocytosis, where a cell envelopes extracellular materials using its cell membrane. The opposite process is known as exocytosis. This is where a cell exports material using vesicular transport.

Cytoplasm

The cell's plasma membrane also helps contain the cell's cytoplasm, which provides a gel-like environment for the cell's organelles. The cytoplasm is the location for most cellular processes, including metabolism, protein folding, and internal transportation.

Key Points

- All eukaryotic cells have a surrounding plasma membrane, which is also known as the cell membrane.
- The plasma membrane is made up by a phospholipid bilayer with embedded proteins that separates the internal contents of the cell from its surrounding environment.
- Only relatively small, non- polar materials can easily move through the lipid bilayer of the plasma membrane.
- Passive transport is the movement of substances across the membrane that does not require the use of energy while active transport is the movement of substances across the membrane using energy.
- Osmosis is the diffusion of water through a semi- permeable membrane down its concentration gradient; this occurs when there is an imbalance of solutes outside of a cell compared to the inside the cell.

Key Terms

- **phospholipid**: Any lipid consisting of a diglyceride combined with a phosphate group and a simple organic molecule such as choline or ethanolamine; they are important constituents of biological membranes
- **hypertonic**: having a greater osmotic pressure than another
- **hypotonic**: Having a lower osmotic pressure than another; a cell in this environment causes water to enter the cell, causing it to swell.

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4.8: Eukaryotic Cells - The Nucleus and Ribosomes

Learning Objectives

- Explain the purpose of the nucleus in eukaryotic cells

The Nucleus

One of the main differences between prokaryotic and eukaryotic cells is the nucleus. As previously discussed, prokaryotic cells lack an organized nucleus while eukaryotic cells contain membrane-bound nuclei (and organelles) that house the cell's DNA and direct the synthesis of ribosomes and proteins.

The nucleus stores chromatin (DNA plus proteins) in a gel-like substance called the nucleoplasm. To understand chromatin, it is helpful to first consider chromosomes. Chromatin describes the material that makes up chromosomes, which are structures within the nucleus that are made up of DNA, the hereditary material. You may remember that in prokaryotes, DNA is organized into a single circular chromosome. In eukaryotes, chromosomes are linear structures. Every eukaryotic species has a specific number of chromosomes in the nuclei of its body's cells. For example, in humans, the chromosome number is 46, while in fruit flies, it is eight. Chromosomes are only visible and distinguishable from one another when the cell is getting ready to divide. In order to organize the large amount of DNA within the nucleus, proteins called histones are attached to chromosomes; the DNA is wrapped around these histones to form a structure resembling beads on a string. These protein-chromosome complexes are called chromatin.

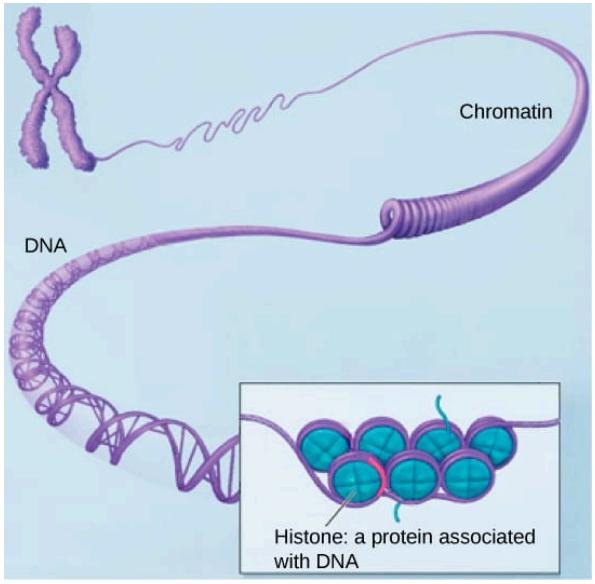


Figure 4.8.1: DNA is highly organized: This image shows various levels of the organization of chromatin (DNA and protein). Along the chromatin threads, unwound protein-chromosome complexes, we find DNA wrapped around a set of histone proteins.

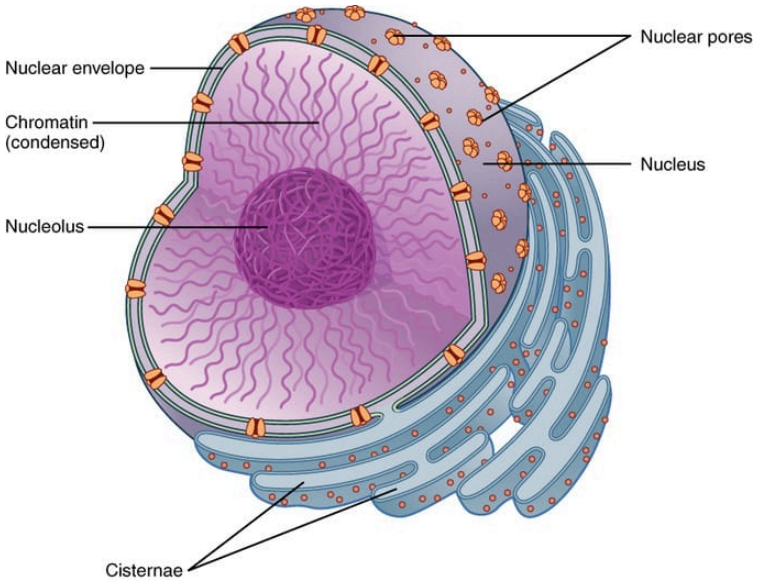


Figure 4.8.1: The nucleus stores the hereditary material of the cell: The nucleus is the control center of the cell. The nucleus of living cells contains the genetic material that determines the entire structure and function of that cell.

The nucleoplasm is also where we find the nucleolus. The nucleolus is a condensed region of chromatin where ribosome synthesis occurs. Ribosomes, large complexes of protein and ribonucleic acid (RNA), are the cellular organelles responsible for protein synthesis. They receive their “orders” for protein synthesis from the nucleus where the DNA is transcribed into messenger RNA (mRNA). This mRNA travels to the ribosomes, which translate the code provided by the sequence of the nitrogenous bases in the mRNA into a specific order of amino acids in a protein.

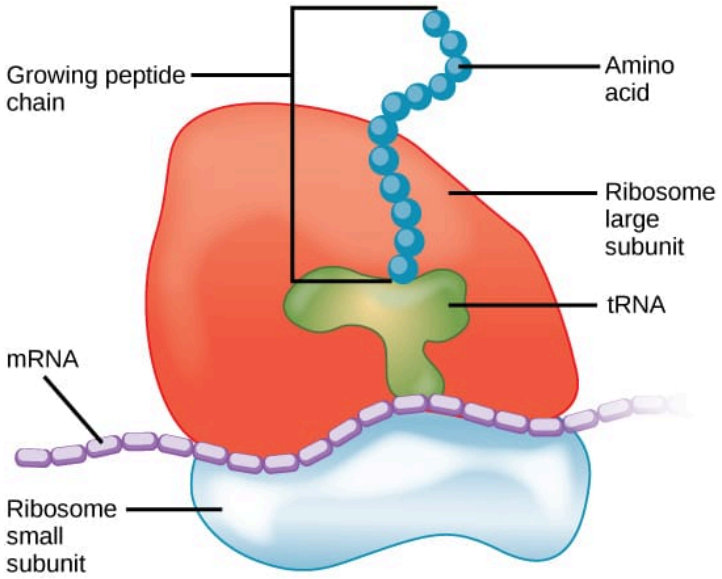


Figure 4.8.1: Ribosomes are responsible for protein synthesis: Ribosomes are made up of a large subunit (top) and a small subunit (bottom). During protein synthesis, ribosomes assemble amino acids into proteins.

Lastly, the boundary of the nucleus is called the nuclear envelope. It consists of two phospholipid bilayers: an outer membrane and an inner membrane. The nuclear membrane is continuous with the endoplasmic reticulum, while nuclear pores allow substances to enter and exit the nucleus.

Key Points

- The nucleus contains the cell ‘s DNA and directs the synthesis of ribosomes and proteins.
- Found within the nucleoplasm, the nucleolus is a condensed region of chromatin where ribosome synthesis occurs.

- Chromatin consists of DNA wrapped around histone proteins and is stored within the nucleoplasm.
- Ribosomes are large complexes of protein and ribonucleic acid (RNA) responsible for protein synthesis when DNA from the nucleus is transcribed.

Key Terms

- **histone**: any of various simple water-soluble proteins that are rich in the basic amino acids lysine and arginine and are complexed with DNA in the nucleosomes of eukaryotic chromatin
- **nucleolus**: a conspicuous, rounded, non-membrane bound body within the nucleus of a cell
- **chromatin**: a complex of DNA, RNA, and proteins within the cell nucleus out of which chromosomes condense during cell division

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4.9: Eukaryotic Cells - Mitochondria

Learning Objectives

- Explain the role of the mitochondria.

One of the major features distinguishing prokaryotes from eukaryotes is the presence of mitochondria. Mitochondria are double-membraned organelles that contain their own ribosomes and DNA. Each membrane is a phospholipid bilayer embedded with proteins. Eukaryotic cells may contain anywhere from one to several thousand mitochondria, depending on the cell's level of energy consumption. Each mitochondrion measures 1 to 10 micrometers (or greater) in length and exists in the cell as an organelle that can be ovoid to worm-shaped to intricately branched.

Mitochondria Structure

Most mitochondria are surrounded by two membranes, which would result when one membrane-bound organism was engulfed into a vacuole by another membrane-bound organism. The mitochondrial inner membrane is extensive and involves substantial infoldings called cristae that resemble the textured, outer surface of alpha-proteobacteria. The matrix and inner membrane are rich with the enzymes necessary for aerobic respiration.

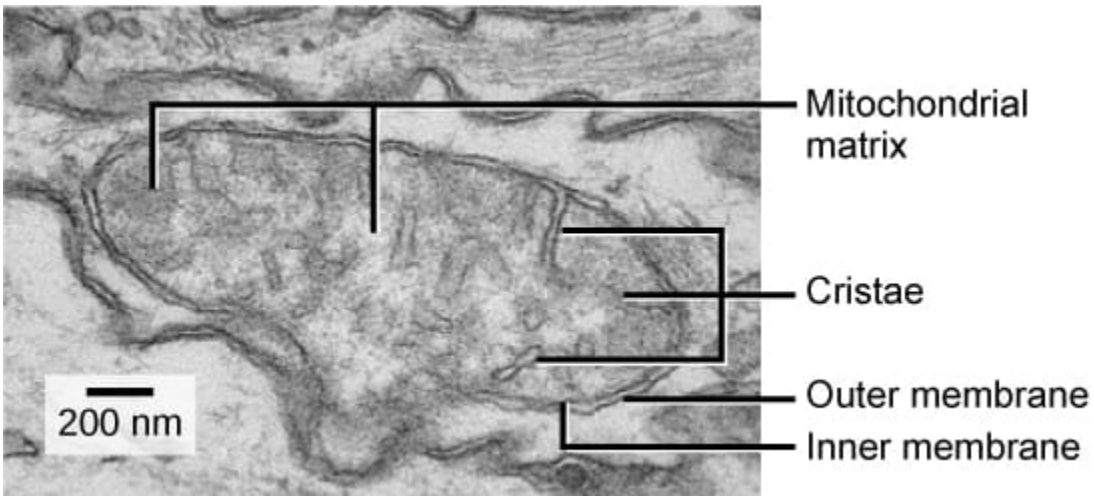


Figure 4.9.1: Mitochondrial structure: This electron micrograph shows a mitochondrion as viewed with a transmission electron microscope. This organelle has an outer membrane and an inner membrane. The inner membrane contains folds, called cristae, which increase its surface area. The space between the two membranes is called the intermembrane space, and the space inside the inner membrane is called the mitochondrial matrix. ATP synthesis takes place on the inner membrane.

Mitochondria have their own (usually) circular DNA chromosome that is stabilized by attachments to the inner membrane and carries genes similar to genes expressed by alpha-proteobacteria. Mitochondria also have special ribosomes and transfer RNAs that resemble these components in prokaryotes. These features all support the hypothesis that mitochondria were once free-living prokaryotes.

Mitochondria Function

Mitochondria 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. ATP represents the short-term stored energy of the cell. Cellular respiration is the process of making ATP using the chemical energy found in glucose and other nutrients. In mitochondria, this process uses oxygen and produces carbon dioxide as a waste product. In fact, the carbon dioxide that you exhale with every breath comes from the cellular reactions that produce carbon dioxide as a by-product.

It is important to point out that muscle cells have a very high concentration of mitochondria that produce ATP. Your muscle cells need a lot of energy to keep your body moving. When your cells don't get enough oxygen, they do not make a lot of ATP. Instead, the small amount of ATP they make in the absence of oxygen is accompanied by the production of lactic acid.

In addition to the aerobic generation of ATP, mitochondria have several other metabolic functions. One of these functions is to generate clusters of iron and sulfur that are important cofactors of many enzymes. Such functions are often associated with the reduced mitochondrion-derived organelles of anaerobic eukaryotes.

Origins of Mitochondria

There are two hypotheses about the origin of mitochondria: endosymbiotic and autogenous, but the most accredited theory at present is endosymbiosis. The endosymbiotic hypothesis suggests mitochondria were originally prokaryotic cells, capable of implementing oxidative mechanisms. These prokaryotic cells may have been engulfed by a eukaryote and became endosymbionts living inside the eukaryote.

Key Points

- Mitochondria contain their own ribosomes and DNA; combined with their double membrane, these features suggest that they might have once been free-living prokaryotes that were engulfed by a larger cell.
- Mitochondria have an important role in cellular respiration through the production of ATP, using chemical energy found in glucose and other nutrients.
- Mitochondria are also responsible for generating clusters of iron and sulfur, which are important cofactors of many enzymes.

Key Terms

- **alpha-proteobacteria**: A taxonomic class within the phylum Proteobacteria — the phototropic proteobacteria.
- **adenosine triphosphate**: a multifunctional nucleoside triphosphate used in cells as a coenzyme, often called the "molecular unit of energy currency" in intracellular energy transfer
- **cofactor**: an inorganic molecule that is necessary for an enzyme to function

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4.10: Eukaryotic Cells - Comparing Plant and Animal Cells

Learning Objectives

- Differentiate between the structures found in animal and plant cells

Animal Cells versus Plant Cells

Each eukaryotic cell has a plasma membrane, cytoplasm, a nucleus, ribosomes, mitochondria, peroxisomes, and in some, vacuoles; however, there are some striking differences between animal and plant cells. While both animal and plant cells have microtubule organizing centers (MTOCs), animal cells also have centrioles associated with the MTOC: a complex called the centrosome. Animal cells each have a centrosome and lysosomes, whereas plant cells do not. Plant cells have a cell wall, chloroplasts and other specialized plastids, and a large central vacuole, whereas animal cells do not.

The Centrosome

The centrosome is a microtubule-organizing center found near the nuclei of animal cells. 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 (the organelle where all microtubules originate) replicates itself before a cell divides, and the centrioles appear to have some role in pulling the duplicated chromosomes to opposite ends of the dividing cell. However, the exact function of the centrioles in cell division isn't clear, because cells that have had the centrosome removed can still divide; and plant cells, which lack centrosomes, are capable of cell division.

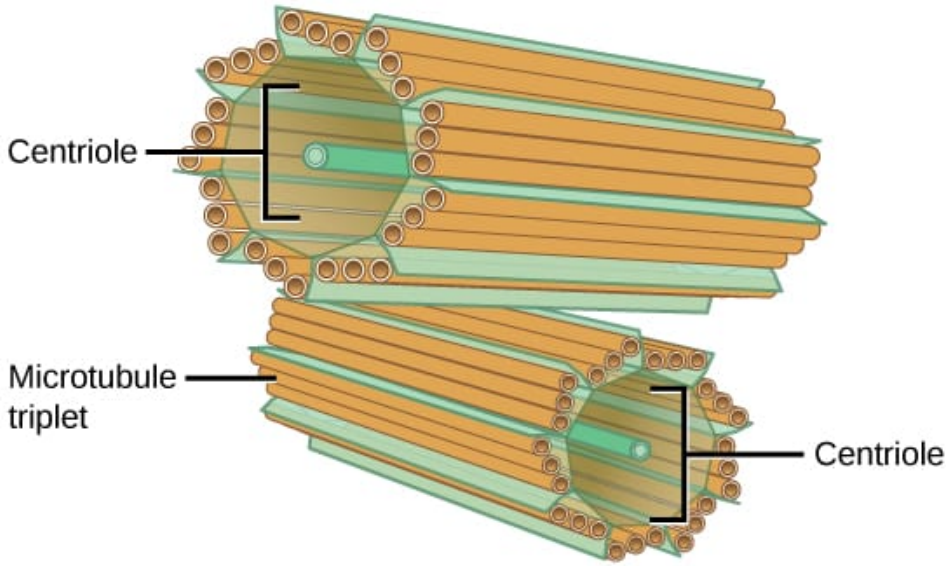


Figure 4.10.1: The Centrosome Structure: The centrosome consists of two centrioles that lie at right angles to each other. Each centriole is a cylinder made up of nine triplets of microtubules. Nontubulin proteins (indicated by the green lines) hold the microtubule triplets together.

Lysosomes

Animal cells have another set of organelles not found in plant cells: lysosomes. The lysosomes are the cell's "garbage disposal." In plant cells, the digestive processes take place in vacuoles. Enzymes within the lysosomes aid the breakdown of proteins, polysaccharides, lipids, nucleic acids, and even worn-out organelles. These enzymes are active at a much lower pH than that of the cytoplasm. Therefore, the pH within lysosomes is more acidic than the pH of the cytoplasm. Many reactions that take place in the cytoplasm could not occur at a low pH, so the advantage of compartmentalizing the eukaryotic cell into organelles is apparent.

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 protistan 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 comprised of glucose units. When you bite into a raw vegetable, like celery, it crunches. That's because you are tearing the rigid cell walls of the celery cells with your teeth.

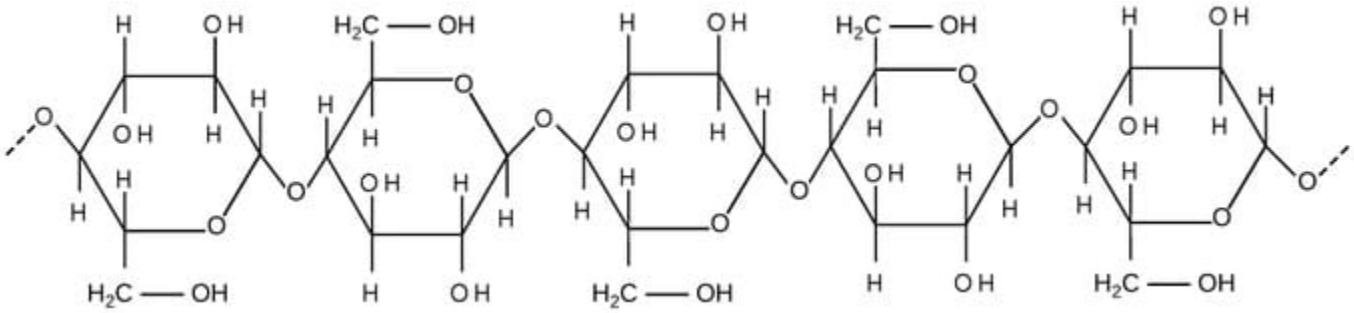


Figure 4.10.1: Cellulose: Cellulose is a long chain of β-glucose molecules connected by a 1-4 linkage. The dashed lines at each end of the figure indicate a series of many more glucose units. The size of the page makes it impossible to portray an entire cellulose molecule.

Chloroplasts

Like mitochondria, chloroplasts have their own DNA and ribosomes, but chloroplasts have an entirely different function. Chloroplasts are plant cell organelles that carry out photosynthesis. Photosynthesis is the series of reactions that use carbon dioxide, water, and light energy to make glucose and oxygen. This is a major difference between plants and animals; plants (autotrophs) are able to make their own food, like sugars, while animals (heterotrophs) must ingest their food.

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. Each stack of thylakoids is called a granum (plural = grana). The fluid enclosed by the inner membrane that surrounds the grana is called the stroma.

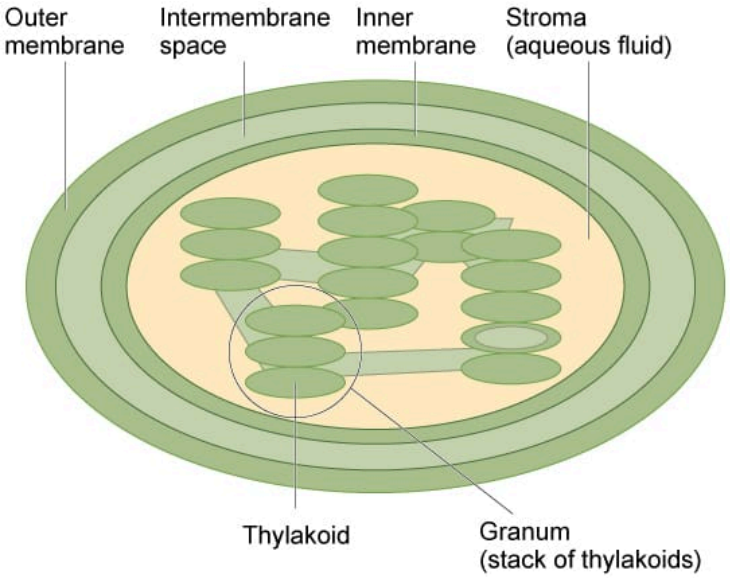


Figure 4.10.1: The Chloroplast Structure: The chloroplast has an outer membrane, an inner membrane, and membrane structures called thylakoids that are stacked into grana. The space inside the thylakoid membranes is called the thylakoid space. The light harvesting reactions take place in the thylakoid membranes, and the synthesis of sugar takes place in the fluid inside the inner membrane, which is called the stroma.

The chloroplasts contain a green pigment called chlorophyll, which captures the light energy that drives the reactions of photosynthesis. Like plant cells, photosynthetic protists also have chloroplasts. Some bacteria perform photosynthesis, but their

chlorophyll is not relegated to an organelle.

The Central Vacuole

The central vacuole plays a key role in regulating the cell's concentration of water in changing environmental conditions. When you forget to water a plant for a few days, it wilts. That's 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. As the central vacuole shrinks, it leaves the cell wall unsupported. This loss of support to the cell walls of plant cells results in the wilted appearance of the plant. The central vacuole also supports the expansion of the cell. When the central vacuole holds more water, the cell gets larger without having to invest a lot of energy in synthesizing new cytoplasm.

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Key Points

- Centrosomes and lysosomes are found in animal cells, but do not exist within plant cells.
- The lysosomes are the animal cell's "garbage disposal", while in plant cells the same function takes place in vacuoles.
- Plant cells have a cell wall, chloroplasts and other specialized plastids, and a large central vacuole, which are not found within animal cells.
- The cell wall is a rigid covering that protects the cell, provides structural support, and gives shape to the cell.
- The chloroplasts, found in plant cells, contain a green pigment called chlorophyll, which captures the light energy that drives the reactions of plant photosynthesis.
- The central vacuole plays a key role in regulating a plant cell's concentration of water in changing environmental conditions.

Key Terms

- **protist**: Any of the eukaryotic unicellular organisms including protozoans, slime molds and some algae; historically grouped into the kingdom Protoctista.
- **autotroph**: Any organism that can synthesize its food from inorganic substances, using heat or light as a source of energy
- **heterotroph**: an organism that requires an external supply of energy in the form of food, as it cannot synthesize its own

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4.11: The Endomembrane System and Proteins - Vesicles and Vacuoles

Learning Objectives

- Summarize the functions of vesicles and vacuoles in cells

Vesicles and vacuoles are membrane-bound sacs that function in storage and transport. Other than the fact that vacuoles are somewhat larger than vesicles, there is a very subtle distinction between them: the membranes of vesicles can fuse with either the plasma membrane or other membrane systems within the cell. The membrane of a vacuole does not fuse with the membranes of other cellular components. Additionally, some agents within plant vacuoles, such as enzymes, break down macromolecules.

Vesicles

A vesicle is a small structure within a cell, consisting of fluid enclosed by a lipid bilayer. Vesicles form naturally during the processes of secretion (exocytosis), uptake (phagocytosis) and transport of materials within the cytoplasm. Alternatively, they may be prepared artificially, in which case they are called liposomes. Vesicles can fuse with the plasma membrane to release their contents outside the cell. Vesicles can also fuse with other organelles within the cell.

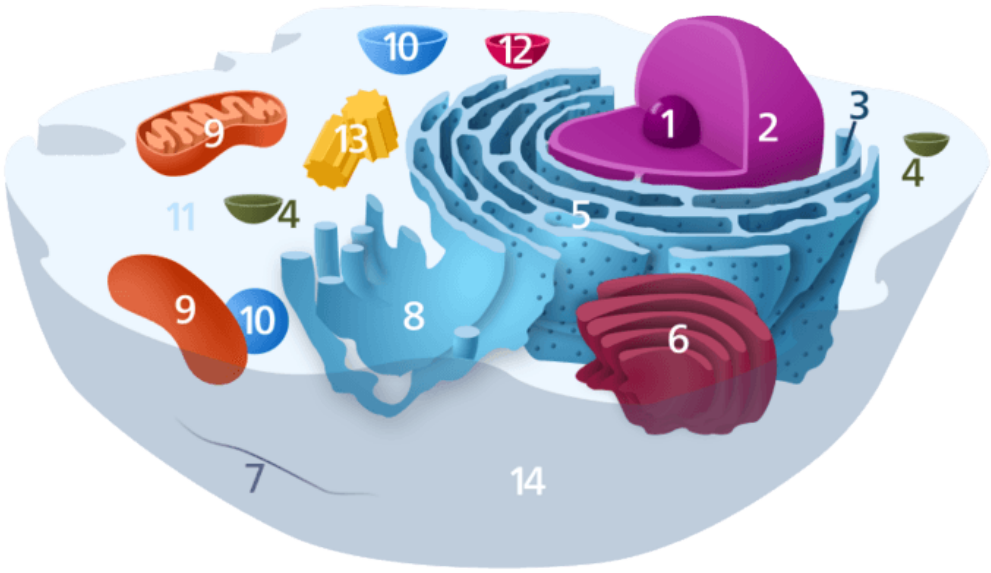


Figure 4.11.1: Animal Cell: In this animal cell illustration #4 denotes a vacuole.

Vesicles perform a variety of functions. Because they are separated from the cytosol, the inside of a vesicle can be different from the cytosolic environment. For this reason, vesicles are a basic tool used by the cell for organizing cellular substances. Vesicles are involved in metabolism, transport, buoyancy control, and enzyme storage. They can also act as chemical reaction chambers.

Lysosomes

Animal cells have a set of organelles not found in plant cells: lysosomes. Lysosomes are a cell's "garbage disposal." Enzymes within the lysosomes aid the breakdown of proteins, polysaccharides, lipids, nucleic acids, and worn-out organelles. These enzymes are active at a much lower pH than that of the cytoplasm. Therefore, the pH within lysosomes is more acidic than the pH of the cytoplasm. Many reactions that take place in the cytoplasm could not occur at a low pH, so again, the advantage of compartmentalizing the eukaryotic cell into organelles is apparent.

Vacuoles

Vacuoles are an essential component of plant cells. If you look at the figure below, you will see that plant cells each have a large central vacuole that occupies most of the area of the cell. The central vacuole plays a key role in regulating the cell's concentration of water in changing environmental conditions, and houses the digestive processes.

Have you ever noticed that if you forget to water a plant for a few days, it wilts? That's 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. As the central vacuole shrinks, it leaves the cell wall unsupported. This loss of support to the cell walls of plant cells results in the wilted appearance of the plant.

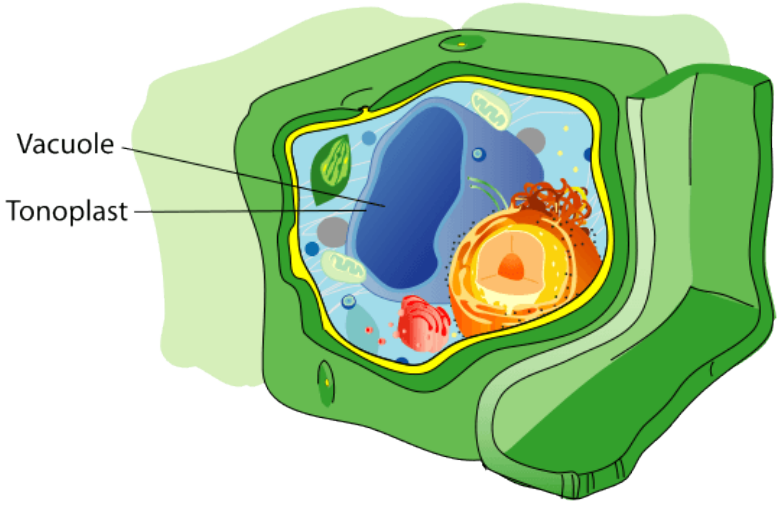


Figure 4.11.1: Plant Cell Structure: The Central Vacuole in a typical plant cell is quite large and is surrounded by the tonoplast or vacuolar membrane.

The central vacuole also supports the expansion of the cell. When the central vacuole holds more water, the cell gets larger without having to invest a lot of energy in synthesizing new cytoplasm.

Contractile vacuoles are found in certain protists, especially those in Phylum *Ciliophora*. These vacuoles take water from the cytoplasm and excrete it from the cell to avoid bursting due to osmotic pressure.

Key Points

- Vesicles are small structures within a cell, consisting of fluid enclosed by a lipid bilayer involved in transport, buoyancy control, and enzyme storage.
- Lysosomes, which are found in animal cells, are the cell's "garbage disposal." The digestive processes take place in these, and enzymes within them aid in the breakdown of proteins, polysaccharides, lipids, nucleic acids, and worn-out organelles.
- Central vacuoles, which are found in plants, play a key role in regulating the cell's concentration of water in changing environmental conditions.

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4.12: The Endomembrane System and Proteins - The Endoplasmic Reticulum

Learning Objectives

- Describe the structure of the endoplasmic reticulum and its role in synthesis and metabolism

The Endoplasmic Reticulum

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

Rough ER

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. Ribosomes transfer their newly synthesized proteins into the lumen of the RER where they undergo structural modifications, such as folding or the acquisition of side chains. These modified proteins will be incorporated into cellular membranes—the membrane of the ER or those of other organelles —or secreted from the cell (such as protein hormones, enzymes). The RER also makes phospholipids for cellular membranes. If the phospholipids or modified proteins are not destined to stay in the RER, they will reach their destinations via transport vesicles that bud from the RER's membrane. Since the RER is engaged in modifying proteins (such as enzymes, for example) that will be secreted from the cell, the RER is abundant in cells that secrete proteins. This is the case with cells of the liver, for example.

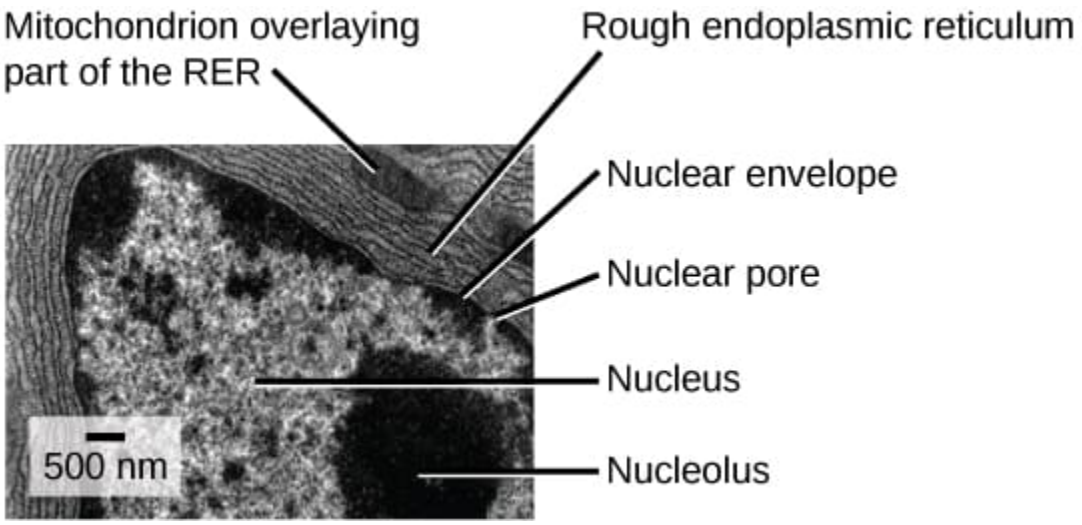


Figure 4.12.1: Rough Endoplasmic Reticulum: This transmission electron micrograph shows the rough endoplasmic reticulum and other organelles in a pancreatic cell.

Smooth ER

The smooth endoplasmic reticulum (SER) is continuous with the RER but has few or no ribosomes on its cytoplasmic surface. Functions of the SER include synthesis of carbohydrates, lipids, and steroid hormones; detoxification of medications and poisons; and storage of calcium ions. In muscle cells, a specialized SER called the sarcoplasmic reticulum is responsible for storage of the calcium ions that are needed to trigger the coordinated contractions of the muscle cells.

Key Points

- If the endoplasmic reticulum (ER) has ribosomes attached to it, it is called rough ER; if it does not, then it is called smooth ER.
- The proteins made by the rough endoplasmic reticulum are for use outside of the cell.
- Functions of the smooth endoplasmic reticulum include synthesis of carbohydrates, lipids, and steroid hormones; detoxification of medications and poisons; and storage of calcium ions.

Key Terms

- **lumen**: The cavity or channel within a tube or tubular organ.
- **reticulum**: A network

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4.13: The Endomembrane System and Proteins - The Golgi Apparatus

Learning Objectives

- Describe the structure of the Golgi apparatus and its role in protein modification and secretion

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

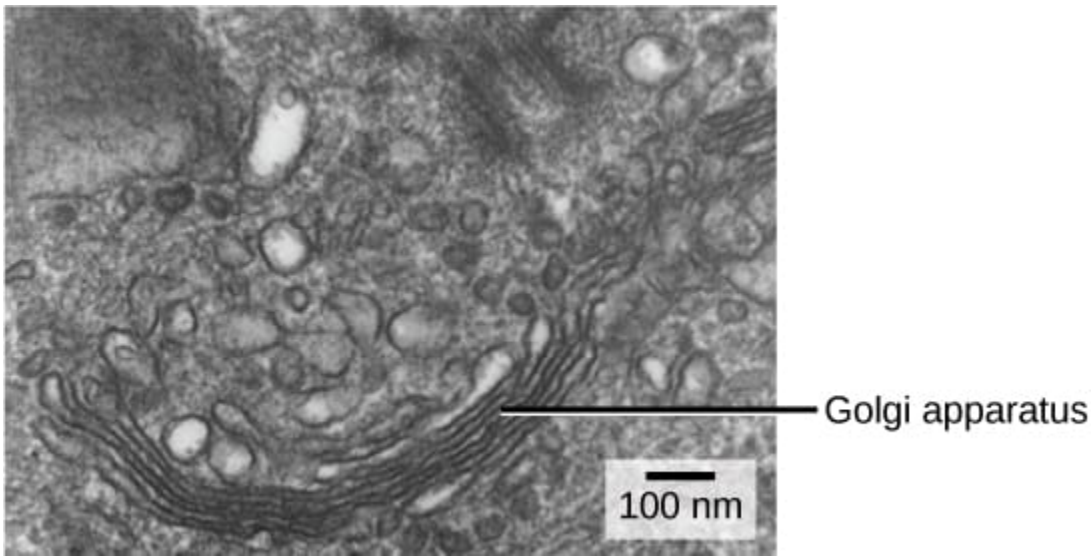


Figure 4.13.1: The Golgi apparatus sorts and packages cellular products: The Golgi apparatus in this white blood cell is visible as a stack of semicircular, flattened rings in the lower portion of the image. Several vesicles can be seen near the Golgi apparatus.

The receiving side of the Golgi apparatus is called the cis face. The opposite side is called the trans face. The transport vesicles that formed from the ER travel to the cis 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 that allow them to be sorted. The most frequent modification is the addition of short chains of sugar molecules. These newly-modified proteins and lipids are then tagged with phosphate groups or other small molecules so that they can be routed to their proper destinations.

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

In another example of form following function, 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 abundance of Golgi. In plant cells, the Golgi apparatus has the 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.

Key Points

- The Golgi apparatus is a series of flattened sacs that sort and package cellular materials.
- The Golgi apparatus has a cis face on the ER side and a trans face opposite of the ER.
- The *trans* face secretes the materials into vesicles, which then fuse with the cell membrane for release from the cell.

Key Terms

- **vesicle**: A membrane-bound compartment found in a cell.

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4.14: The Endomembrane System and Proteins - Lysosomes

Learning Objectives

- Describe how lysosomes function as the cell's waste disposal system

A lysosome has three main functions: the breakdown/digestion of macromolecules (carbohydrates, lipids, proteins, and nucleic acids), cell membrane repairs, and responses against foreign substances such as bacteria, viruses and other antigens. When food is eaten or absorbed by the cell, the lysosome releases its enzymes to break down complex molecules including sugars and proteins into usable energy needed by the cell to survive. If no food is provided, the lysosome's enzymes digest other organelles within the cell in order to obtain the necessary nutrients.

In addition to their role as the digestive component and organelle-recycling facility of animal cells, lysosomes are considered to be parts of the endomembrane system. Lysosomes also use their hydrolytic enzymes to destroy pathogens (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 or endocytosis, 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.

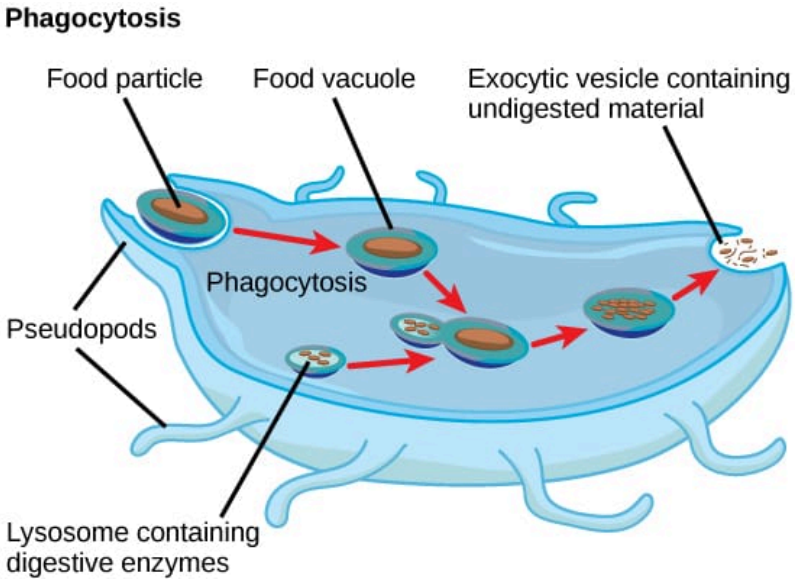


Figure 4.14.1: Lysosomes digest foreign substances that might harm the cell: A macrophage has engulfed (phagocytized) a potentially pathogenic bacterium and then fuses with a lysosomes within the cell to destroy the pathogen. Other organelles are present in the cell but for simplicity are not shown.

A lysosome is composed of lipids, which make up the membrane, and proteins, which make up the enzymes within the membrane. Usually, lysosomes are between 0.1 to 1.2µm, but the size varies based on the cell type. The general structure of a lysosome consists of a collection of enzymes surrounded by a single-layer membrane. The membrane is a crucial aspect of its structure because without it the enzymes within the lysosome that are used to breakdown foreign substances would leak out and digest the entire cell, causing it to die.

Lysosomes are found in nearly every animal-like eukaryotic cell. They are so common in animal cells because, when animal cells take in or absorb food, they need the enzymes found in lysosomes in order to digest and use the food for energy. On the other hand, lysosomes are not commonly-found in plant cells. Lysosomes are not needed in plant cells because they have cell walls that are tough enough to keep the large/foreign substances that lysosomes would usually digest out of the cell.

Key Points

- Lysosomes breakdown/digest macromolecules (carbohydrates, lipids, proteins, and nucleic acids), repair cell membranes, and respond against foreign substances such as bacteria, viruses and other antigens.
- Lysosomes contain enzymes that break down the macromolecules and foreign invaders.
- Lysosomes are composed of lipids and proteins, with a single membrane covering the internal enzymes to prevent the lysosome from digesting the cell itself.
- Lysosomes are found in all animal cells, but are rarely found within plant cells due to the tough cell wall surrounding a plant cell that keeps out foreign substances.

Key Terms

- **enzyme**: a globular protein that catalyses a biological chemical reaction
- **lysosome**: An organelle found in all types of animal cells which contains a large range of digestive enzymes capable of splitting most biological macromolecules.

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4.15: The Endomembrane System and Proteins - Peroxisomes

Learning Objectives

- Name the various functions that peroxisomes perform inside the cell

Peroxisomes

A type of organelle found in both animal cells and plant cells, a peroxisome is a membrane-bound cellular organelle that contains mostly enzymes. Peroxisomes perform important functions, including lipid metabolism and chemical detoxification. They also carry out oxidation reactions that break down fatty acids and amino acids.

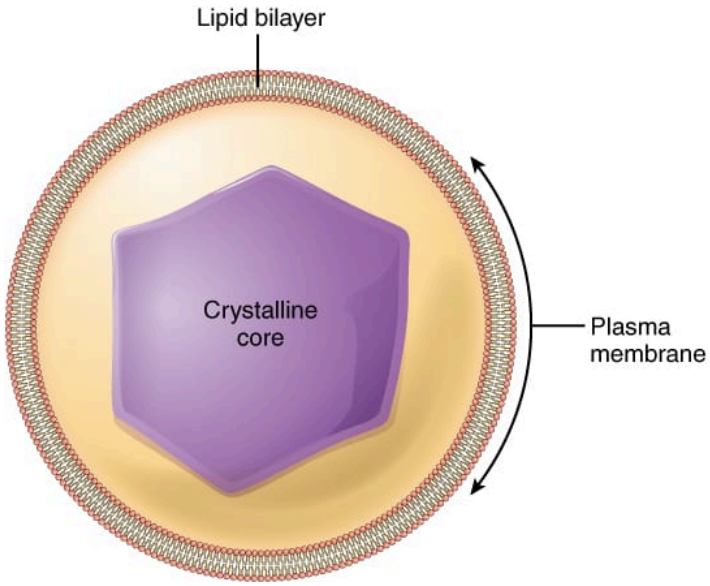


Figure 4.15.1: Peroxisomes: Peroxisomes are membrane-bound organelles that contain an abundance of enzymes for detoxifying harmful substances and lipid metabolism.

In contrast to the digestive enzymes found in lysosomes, the enzymes within peroxisomes serve to transfer hydrogen atoms from various molecules to oxygen, producing hydrogen peroxide (H_2O_2). In this way, peroxisomes neutralize poisons, such as alcohol, that enter the body. In order to appreciate the importance of peroxisomes, it is necessary to understand the concept of reactive oxygen species.

Reactive oxygen species (ROS), such as peroxides and free radicals, are the highly-reactive products of many normal cellular processes, including the mitochondrial reactions that produce ATP and oxygen metabolism. Examples of ROS include the hydroxyl radical OH, H_2O_2, and superoxide (O_{-2}). Some ROS are important for certain cellular functions, such as cell signaling processes and immune responses against foreign substances. Many ROS, however, are harmful to the body. Free radicals are reactive because they contain free unpaired electrons; they can easily oxidize other molecules throughout the cell, causing cellular damage and even cell death. Free radicals are thought to play a role in many destructive processes in the body, from cancer to coronary artery disease.

Peroxisomes oversee reactions that neutralize free radicals. They produce large amounts of the toxic H_2O_2 in the process, but contain enzymes that convert H_2O_2 into water and oxygen. These by-products are then safely released into the cytoplasm. Like miniature sewage treatment plants, peroxisomes neutralize harmful toxins so that they do not cause damage in the cells. The liver is the organ primarily responsible for detoxifying the blood before it travels throughout the body; liver cells contain an exceptionally high number of peroxisomes.

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Key Points

- Lipid metabolism and chemical detoxification are important functions of peroxisomes.
- Peroxisomes are responsible for oxidation reactions that break down fatty acids and amino acids.
- Peroxisomes oversee reactions that neutralize free radicals, which cause cellular damage and cell death.
- Peroxisomes chemically neutralize poisons through a process that produces large amounts of toxic H_2O_2, which is then converted into water and oxygen.
- The liver is the organ primarily responsible for detoxifying the blood before it travels throughout the body; as a result, liver cells contain large amounts of peroxisomes.

Key Terms

- **enzyme**: a globular protein that catalyses a biological chemical reaction
- **free radical**: Any molecule, ion or atom that has one or more unpaired electrons; they are generally highly reactive and often only occur as transient species.

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4.16: The Cytoskeleton - Microfilaments

Learning Objectives

- Describe the structure and function of microfilaments

Microfilaments

If all the organelles were removed from a cell, the plasma membrane and the cytoplasm would not be the only components left. Within the cytoplasm there would still be ions and organic molecules, plus a network of protein fibers that help maintain the shape of the cell, secure some organelles in specific positions, allow cytoplasm and vesicles to move within the cell, and enable unicellular organisms to move independently. This network of protein fibers is known as the cytoskeleton. There are three types of fibers within the cytoskeleton: microfilaments, intermediate filaments, and microtubules. Of the three types of protein fibers in the cytoskeleton, microfilaments are the narrowest. They function in cellular movement, have a diameter of about 7 nm, and are made of two intertwined strands of a globular protein called actin. For this reason, microfilaments are also known as actin filaments.

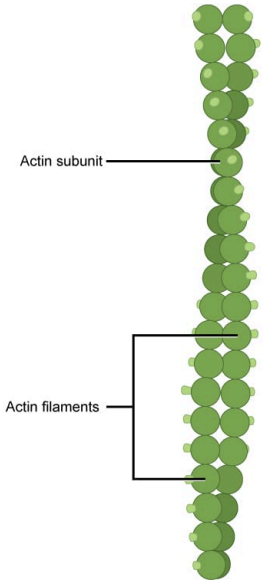


Figure 4.16.1: Microfilaments are the thinnest component of the cytoskeleton.: Microfilaments are made of two intertwined strands of actin.

Actin is powered by ATP to assemble its filamentous form, which serves as a track for the movement of a motor protein called myosin. This enables actin to engage in cellular events requiring motion such as cell division in animal cells and cytoplasmic streaming, which is the circular movement of the cell cytoplasm in plant cells. Actin and myosin are plentiful in muscle cells. When your actin and myosin filaments slide past each other, your muscles contract.

Microfilaments also provide some rigidity and shape to the cell. They can depolymerize (disassemble) and reform quickly, thus enabling a cell to change its shape and move. White blood cells (your body's infection-fighting cells) make good use of this ability. They can move to the site of an infection and engulf the pathogen.

Key Points

- Microfilaments assist with cell movement and are made of a protein called actin.
- Actin works with another protein called myosin to produce muscle movements, cell division, and cytoplasmic streaming.
- Microfilaments keep organelles in place within the cell.

Key Terms

- **actin**: A globular structural protein that polymerizes in a helical fashion to form an actin filament (or microfilament).
- **filamentous**: Having the form of threads or filaments
- **myosin**: a large family of motor proteins found in eukaryotic tissues, allowing mobility in muscles

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4.17: The Cytoskeleton - Intermediate Filaments and Microtubules

Learning Objectives

- Describe the roles of microtubules as part of the cell's cytoskeleton

Microtubules

As their name implies, microtubules are small hollow tubes. Microtubules, along with microfilaments and intermediate filaments, come under the class of organelles known as the cytoskeleton. The cytoskeleton is the framework of the cell which forms the structural supporting component. Microtubules are the largest element of the cytoskeleton. The walls of the microtubule are made of polymerized dimers of α-tubulin and β-tubulin, two globular proteins. With a diameter of about 25 nm, microtubules are the widest components of the cytoskeleton. They help the cell resist compression, provide a track along which vesicles move through the cell, and pull replicated chromosomes to opposite ends of a dividing cell. Like microfilaments, microtubules can dissolve and reform quickly.

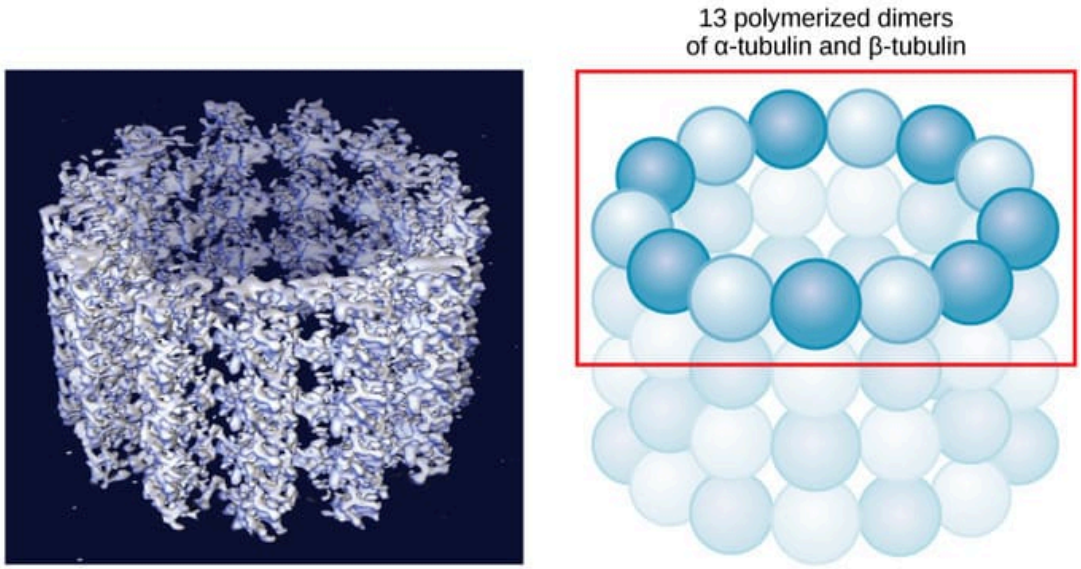


Figure 4.17.1: Micrtubule Structure: Microtubules are hollow, with walls consisting of 13 polymerized dimers of α-tubulin and β-tubulin (right image). The left image shows the molecular structure of the tube.

Microtubules are also the structural elements of flagella, cilia, and centrioles (the latter are the two perpendicular bodies of the centrosome). In animal cells, the centrosome is the microtubule-organizing center. In eukaryotic cells, flagella and cilia are quite different structurally from their counterparts in prokaryotes.

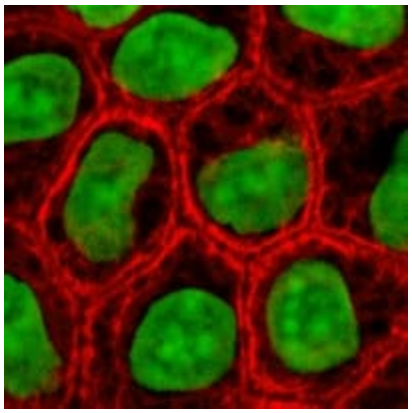


Figure 4.17.1: Stained Keratin Intermediate filaments: Keratin cytoskeletal intermediate filaments are concentrated around the edge of the cells and merge into the surface membrane. This network of intermediate filaments from cell to cell holds together tissues like skin.

Intermediate Filaments

Intermediate filaments (IFs) are cytoskeletal components found in animal cells. They are composed of a family of related proteins sharing common structural and sequence features. Intermediate filaments have an average diameter of 10 nanometers, which is between that of 7 nm actin (microfilaments), and that of 25 nm microtubules, although they were initially designated 'intermediate' because their average diameter is between those of narrower microfilaments (actin) and wider myosin filaments found in muscle cells. Intermediate filaments contribute to cellular structural elements and are often crucial in holding together tissues like skin.

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, many of them extend along the entire surface of the plasma membrane. They are short, hair-like structures that are used to move entire cells (such as paramecia) or 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 trap particulate matter and move it toward your nostrils).

Despite their differences in length and number, flagella and cilia share a common structural arrangement of microtubules called a "9 + 2 array." This is an appropriate name because a single flagellum or cilium is made of a ring of nine microtubule doublets surrounding a single microtubule doublet in the center.

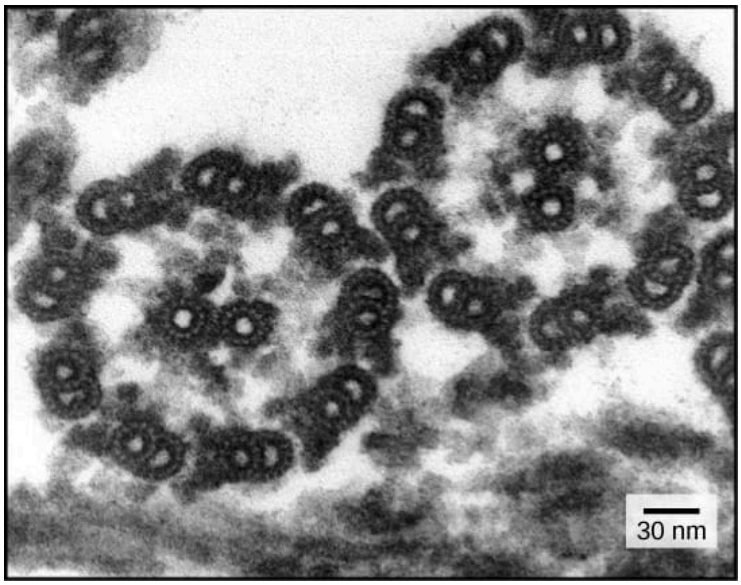


Figure 4.17.1: Microtubules are the structural component of flagella: This transmission electron micrograph of two flagella shows the 9 + 2 array of microtubules: nine microtubule doublets surround a single microtubule doublet.

Key Points

- Microtubules help the cell resist compression, provide a track along which vesicles can move throughout the cell, and are the components of cilia and flagella.
- Cilia and flagella are hair-like structures that assist with locomotion in some cells, as well as line various structures to trap particles.
- The structures of cilia and flagella are a “9+2 array,” meaning that a ring of nine microtubules is surrounded by two more microtubules.
- Microtubules attach to replicated chromosomes during cell division and pull them apart to opposite ends of the pole, allowing the cell to divide with a complete set of chromosomes in each daughter cell.

Key Terms

- **microtubule**: Small tubes made of protein and found in cells; part of the cytoskeleton
- **flagellum**: a flagellum is a lash-like appendage that protrudes from the cell body of certain prokaryotic and eukaryotic cells
- **cytoskeleton**: A cellular structure like a skeleton, contained within the cytoplasm.

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4.18: Connections between Cells and Cellular Activities - Extracellular Matrix of Animal Cells

Learning Objectives

- Explain the role of the extracellular matrix in animal cells

Extracellular Matrix of Animal Cells

Most animal cells release materials into the extracellular space. The primary components of these materials are proteins. Collagen is the most abundant of the proteins. Its fibers are interwoven with carbohydrate-containing protein molecules called proteoglycans. Collectively, these materials are called the extracellular matrix. 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.

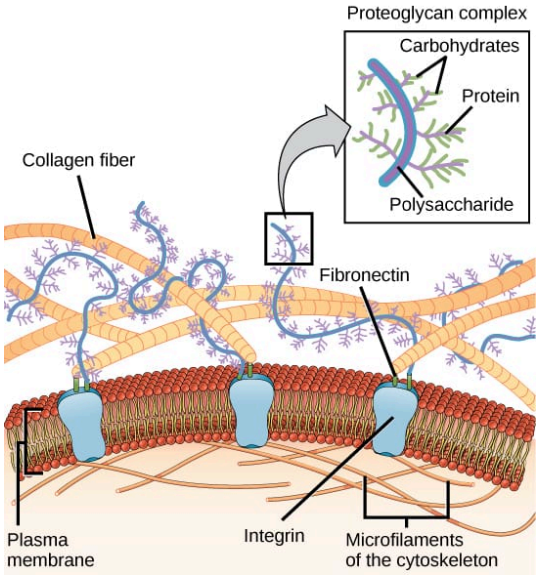


Figure 4.18.1: The Extracellular Matrix: The extracellular matrix consists of a network of proteins and carbohydrates.

How does this cell communication occur? Cells have protein receptors on the extracellular surfaces of their plasma membranes. When a molecule within the matrix binds to the receptor, it changes the molecular structure of the receptor. The receptor, in turn, changes the conformation of the microfilaments positioned just inside the plasma membrane. These conformational changes induce chemical signals inside the cell that reach the nucleus and turn “on” or “off” the transcription of specific sections of DNA. This affects the production of associated proteins, thus changing the activities within the cell.

An example of the role of the extracellular matrix in cell communication can be seen in blood clotting. When the cells lining a blood vessel are damaged, they display a protein receptor called tissue factor. When a tissue factor binds with another factor in the extracellular matrix, it causes platelets to adhere to the wall of the damaged blood vessel and stimulates the adjacent smooth muscle cells in the blood vessel to contract (thus constricting the blood vessel). Subsequently, a series of steps are initiated which then prompt the platelets to produce clotting factors.

Key Points

- The extracellular matrix of animal cells is made up of proteins and carbohydrates.
- Cell communication within tissue and tissue formation are main functions of the extracellular matrix of animal cells.
- Tissue communication is kick-started when a molecule within the matrix binds a receptor; the end results are conformational

changes that induce chemical signals that ultimately change activities within the cell.

Key Terms

- **collagen**: Any of more than 28 types of glycoprotein that forms elongated fibers, usually found in the extracellular matrix of connective tissue.
- **proteoglycan**: Any of many glycoproteins that have heteropolysaccharide side chains
- **extracellular matrix**: All the connective tissues and fibres that are not part of a cell, but rather provide support.

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4.19: Connections between Cells and Cellular Activities - Intercellular Junctions

Learning Objectives

- Describe the purpose of intercellular junctions in the structure of cells

Intercellular Junctions

The extracellular matrix allows cellular communication within tissues through conformational changes that induce chemical signals, which ultimately transform activities within the cell. However, cells are also capable of communicating with each other via direct contact through intercellular junctions.

There are some differences in the ways that plant and animal cells communicate directly. Plasmodesmata are junctions between plant cells, whereas animal cell contacts are carried out through tight junctions, gap junctions, and desmosomes.

Junctions in Plant Cells

In general, long stretches of the plasma membranes of neighboring plant cells cannot touch one another because they are separated by the cell wall that surrounds each cell. How then can a plant transfer water and other soil nutrients from its roots, through its stems, and to its leaves? This transport primarily uses the vascular tissues (xylem and phloem); however, there are also structural modifications called plasmodesmata (singular: plasmodesma) that facilitate direct communication in plant cells. Plasmodesmata are numerous channels that pass between cell walls of adjacent plant cells and connect their cytoplasm; thereby, enabling materials to be transported from cell to cell, and thus throughout the plant.

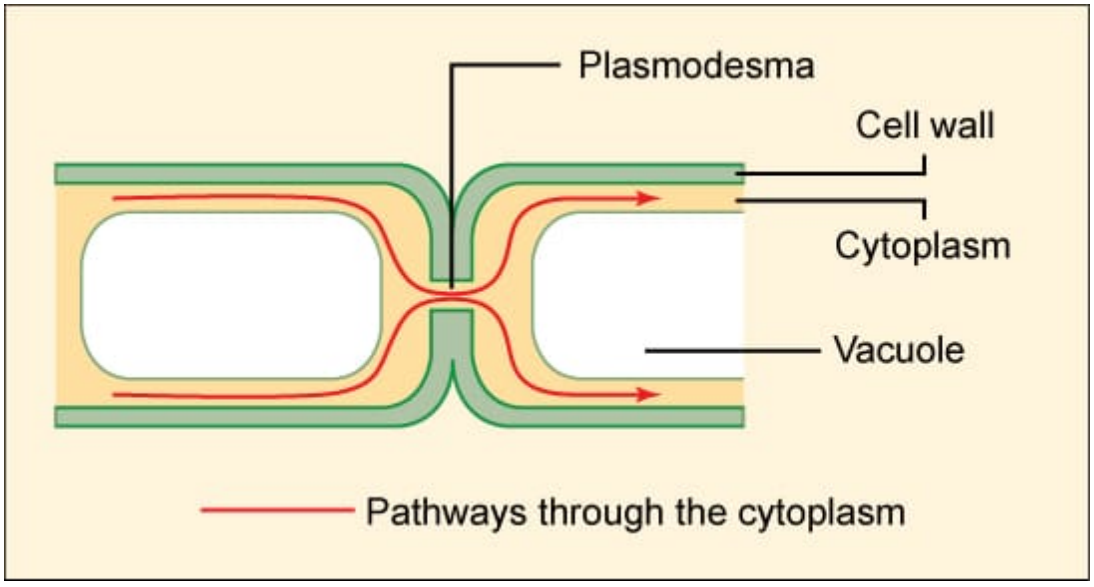


Figure 4.19.1: Plasmodesmata: A plasmodesma is a channel between the cell walls of two adjacent plant cells. Plasmodesmata allow materials to pass from the cytoplasm of one plant cell to the cytoplasm of an adjacent cell.

Junctions in Animal Cells

Communication between animal cells can be carried out through three types of junctions. The first, a tight junction, is a watertight seal between two adjacent animal cells. The cells are held tightly against each other by proteins (predominantly two proteins

called claudins and occludins). This tight adherence prevents materials from leaking between the cells. These junctions are typically found in epithelial tissues that line internal organs and cavities and comprise most of the skin. For example, the tight junctions of the epithelial cells lining your urinary bladder prevent urine from leaking out into the extracellular space.

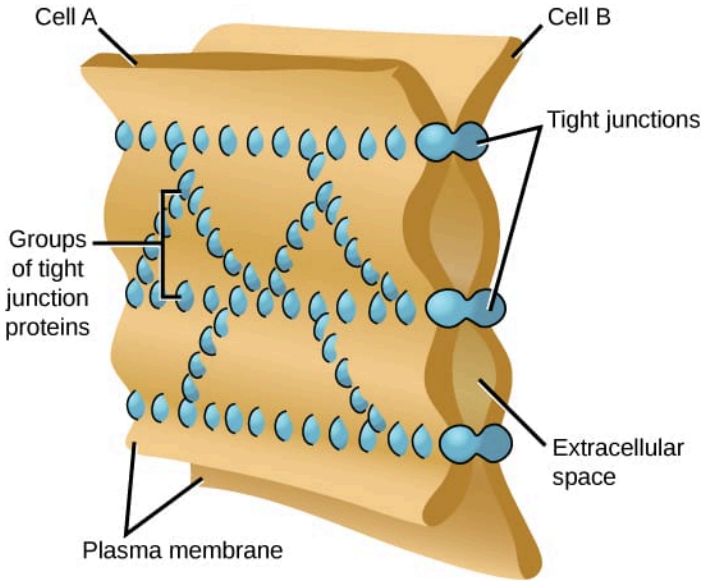


Figure 4.19.1: Tight Junctions: Tight junctions form watertight connections between adjacent animal cells. Proteins create tight junction adherence.

Also found only in animal cells are desmosomes, the second type of intercellular junctions in these cell types. Desmosomes act like spot welds between adjacent epithelial cells, connecting them. Short proteins called cadherins in the plasma membrane connect to intermediate filaments to create desmosomes. The cadherins join two adjacent cells together and maintain the cells in a sheet-like formation in organs and tissues that stretch, such as the skin, heart, and muscles.

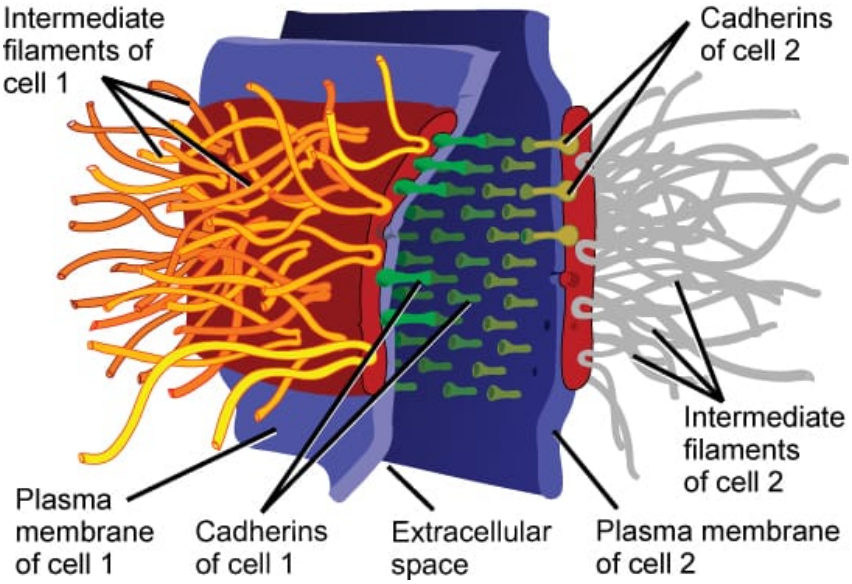


Figure 4.19.1: Desmosomes: A desmosome forms a very strong spot weld between cells. It is created by the linkage of cadherins and intermediate filaments.

Lastly, similar to plasmodesmata in plant cells, gap junctions are the third type of direct junction found within animal cells. These junctions are channels between adjacent cells that allow for the transport of ions, nutrients, and other substances that enable cells to communicate. Structurally, however, gap junctions and plasmodesmata differ. Gap junctions develop when a set of six proteins (called connexins) in the plasma membrane arrange themselves in an elongated doughnut-like configuration called a connexon. When the pores (“doughnut holes”) of connexons in adjacent animal cells align, a channel between the two cells forms. Gap junctions are particularly important in cardiac muscle. The electrical signal for the muscle to contract is passed efficiently

through gap junctions, which allows the heart muscle cells to contract in tandem.

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Key Points

- Plasmodesmata are intercellular junctions between plant cells that enable the transportation of materials between cells.
- A tight junction is a watertight seal between two adjacent animal cells, which prevents materials from leaking out of cells.
- Desmosomes connect adjacent cells when cadherins in the plasma membrane connect to intermediate filaments.
- Similar to plasmodesmata, gap junctions are channels between adjacent cells that allow for the transport of ions, nutrients, and other substances.

Key Terms

- **plasmodesma**: A microscopic channel traversing the cell walls of plant cells and some algal cells, enabling transport and communication between them.
- **connexon**: An assembly of six connexins forming a bridge called a gap junction between the cytoplasms of two adjacent cells.
- **occludin**: Together with the claudin group of proteins, it is the main component of the tight junctions.

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5: STRUCTURE AND FUNCTION OF PLASMA MEMBRANES

5.1: Components and Structure - Components of Plasma Membranes

5.2: Components and Structure - Fluid Mosaic Model

5.3: Components and Structure - Membrane Fluidity

5.4: Passive Transport - The Role of Passive Transport

5.5: Passive Transport - Selective Permeability

5.6: Passive Transport - Diffusion

5.7: Passive Transport - Facilitated Transport

5.8: Passive Transport - Osmosis

5.9: Passive Transport - Tonicity

5.10: Active Transport - Electrochemical Gradient

5.11: Active Transport - Primary Active Transport

5.12: Active Transport - Secondary Active Transport

5.13: Bulk Transport - Endocytosis

5.14: Bulk Transport - Exocytosis

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5.1: Components and Structure - Components of Plasma Membranes

Learning Objectives

- Describe the function and components of the plasma membrane

Structure of Plasma Membranes

The plasma membrane (also known as the cell membrane or cytoplasmic membrane) is a biological membrane that separates the interior of a cell from its outside environment.

The primary function of the plasma membrane is to protect the cell from its surroundings. Composed of a phospholipid bilayer with embedded proteins, the plasma membrane is selectively permeable to ions and organic molecules and regulates the movement of substances in and out of cells. Plasma membranes must be very flexible in order to allow certain cells, such as red blood cells and white blood cells, to change shape as they pass through narrow capillaries.

The plasma membrane also plays a role in anchoring the cytoskeleton to provide shape to the cell, and in attaching to the extracellular matrix and other cells to help group cells together to form tissues. The membrane also maintains the cell potential.

In short, if the cell is represented by a castle, the plasma membrane is the wall that provides structure for the buildings inside the wall, regulates which people leave and enter the castle, and conveys messages to and from neighboring castles. Just as a hole in the wall can be a disaster for the castle, a rupture in the plasma membrane causes the cell to lyse and die.

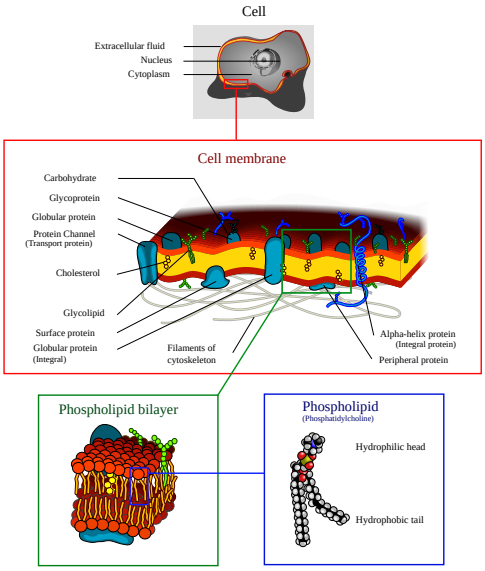


Figure 5.1.1: The plasma membrane: The plasma membrane is composed of phospholipids and proteins that provide a barrier between the external environment and the cell, regulate the transportation of molecules across the membrane, and communicate with other cells via protein receptors.

The Plasma Membrane and Cellular Transport

The movement of a substance across the selectively permeable plasma membrane can be either “passive”—i.e., occurring without the input of cellular energy —or “active”—i.e., its transport requires the cell to expend energy.

The cell employs a number of transport mechanisms that involve biological membranes:

1. Passive osmosis and diffusion: transports gases (such as O_2 and CO_2) and other small molecules and ions
2. Transmembrane protein channels and transporters: transports small organic molecules such as sugars or amino acids
3. Endocytosis: transports large molecules (or even whole cells) by engulfing them
4. Exocytosis: removes or secretes substances such as hormones or enzymes

The Plasma Membrane and Cellular Signaling

Among the most sophisticated functions of the plasma membrane is its ability to transmit signals via complex proteins. These proteins can be receptors, which work as receivers of extracellular inputs and as activators of intracellular processes, or markers, which allow cells to recognize each other.

Membrane receptors provide extracellular attachment sites for effectors like hormones and growth factors, which then trigger intracellular responses. Some viruses, such as Human Immunodeficiency Virus (HIV), can hijack these receptors to gain entry into the cells, causing infections.

Membrane markers allow cells to recognize one another, which is vital for cellular signaling processes that influence tissue and organ formation during early development. This marking function also plays a later role in the “self”-versus-“non-self” distinction of the immune response. Marker proteins on human red blood cells, for example, determine blood type (A, B, AB, or O).

Key Points

- The principal components of the plasma membrane are lipids (phospholipids and cholesterol), proteins, and carbohydrates.
- The plasma membrane protects intracellular components from the extracellular environment.
- The plasma membrane mediates cellular processes by regulating the materials that enter and exit the cell.
- The plasma membrane carries markers that allow cells to recognize one another and can transmit signals to other cells via receptors.

Key Terms

- **plasma membrane**: The semipermeable barrier that surrounds the cytoplasm of a cell.
- **receptor**: A protein on a cell wall that binds with specific molecules so that they can be absorbed into the cell.

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5.2: Components and Structure - Fluid Mosaic Model

Learning Objectives

- Describe the fluid mosaic model of cell membranes

The fluid mosaic model was first proposed by S.J. Singer and Garth L. Nicolson in 1972 to explain the structure of the plasma membrane. The model has evolved somewhat over time, but it 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—that gives the membrane a fluid character. Plasma membranes range from 5 to 10 nm in thickness. For comparison, human red blood cells, visible via light microscopy, are approximately 8 µm wide, or approximately 1,000 times wider than a plasma membrane. The proportions of proteins, lipids, and carbohydrates in the plasma membrane vary with cell type. For example, myelin contains 18% protein and 76% lipid. The mitochondrial inner membrane contains 76% protein and 24% lipid.

The Components and Functions of the Plasma Membrane	
Component	**Location**
Phospholipid	Main fabric of the membrane
Cholesterol	Attached between phospholipids and between the two phospholipid layers
Integral proteins (for example, integrins)	Embedded within the phospholipid layer(s). May or may not penetrate through both layers
Peripheral proteins	On the inner or outer surface of the phospholipid bilayer; not embedded within the phospholipids
Carbohydrates (components of glycoproteins and glycolipids)	Generally attached to proteins on the outside membrane layer

Figure 5.2.1: The Components and functions of the Plasma Membrane: The principal components of a plasma membrane are lipids (phospholipids and cholesterol), proteins, and carbohydrates attached to some of the lipids and some of the proteins.

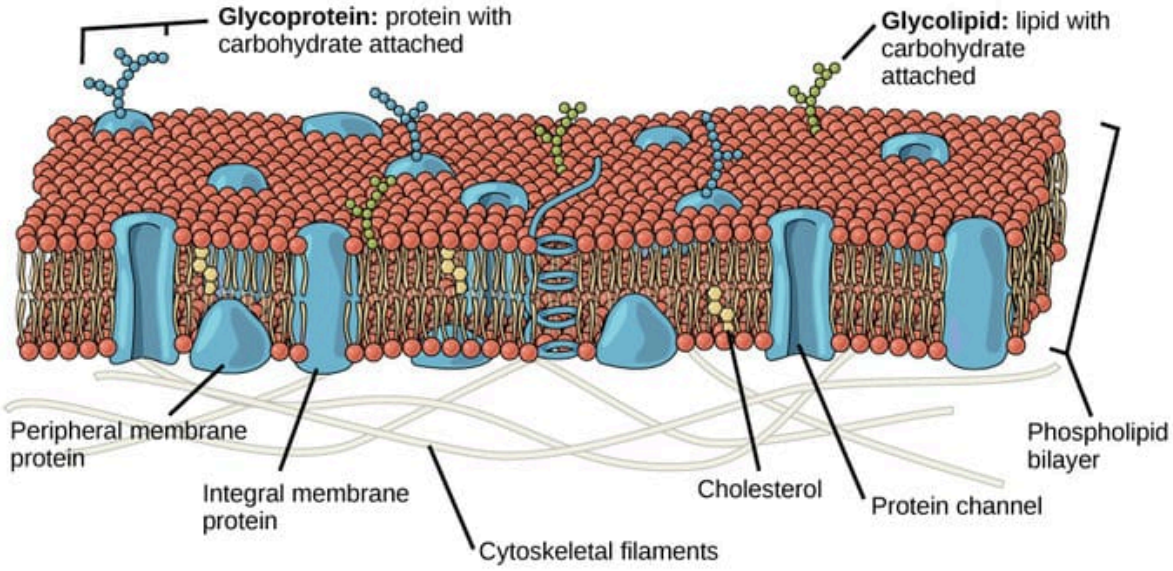


Figure 5.2.1: The fluid mosaic model of the plasma membrane: The fluid mosaic model of the plasma membrane describes the plasma membrane as a fluid combination of phospholipids, cholesterol, and proteins. Carbohydrates attached to lipids (glycolipids) and to proteins (glycoproteins) extend from the outward-facing surface of the membrane.

The main fabric of the membrane is composed of amphiphilic or dual-loving, phospholipid molecules. The hydrophilic or water-loving areas of these molecules are in contact with the aqueous fluid both inside and outside the cell. Hydrophobic, or water-hating molecules, tend to be non- polar. A phospholipid molecule consists of a three-carbon glycerol backbone with two fatty acid molecules attached to carbons 1 and 2, and a phosphate-containing group attached to the third carbon. This arrangement gives the overall molecule an area described as its head (the phosphate-containing group), which has a polar character or negative

charge, and an area called the tail (the fatty acids), which has no charge. They interact with other non-polar molecules in chemical reactions, but generally do not interact with polar molecules. When placed in water, hydrophobic molecules tend to form a ball or cluster. The hydrophilic regions of the phospholipids tend to form hydrogen bonds with water and other polar molecules on both the exterior and interior of the cell. Thus, the membrane surfaces that face the interior and exterior of the cell are hydrophilic. In contrast, the middle of the cell membrane is hydrophobic and will not interact with water. Therefore, phospholipids form an excellent lipid bilayer cell membrane that separates fluid within the cell from the fluid outside of the cell.

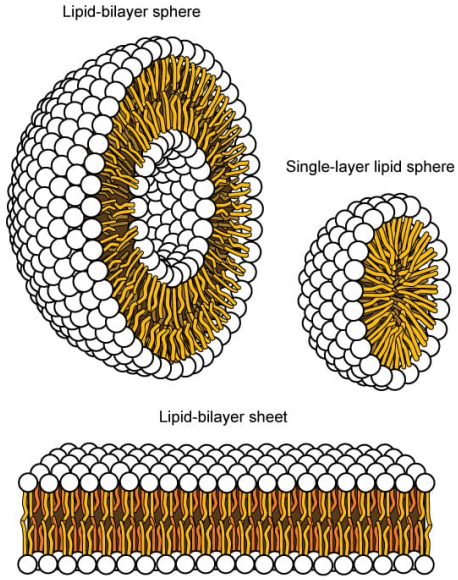


Figure 5.2.1: Phospholipid aggregation: In an aqueous solution, phospholipids tend to arrange themselves with their polar heads facing outward and their hydrophobic tails facing inward.

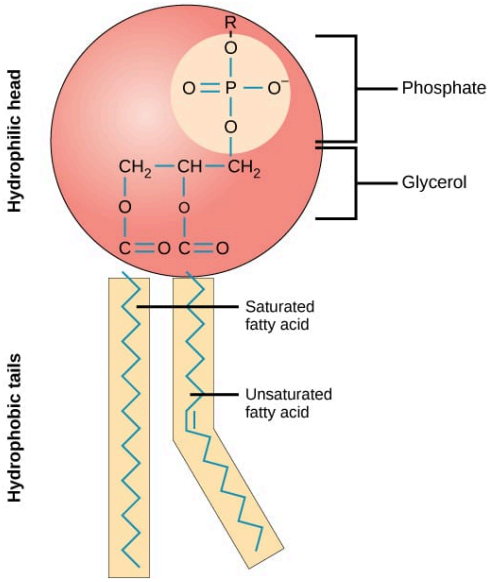


Figure 5.2.1: The structure of a phospholipid molecule: This phospholipid molecule is composed of a hydrophilic head and two hydrophobic tails. The hydrophilic head group consists of a phosphate-containing group attached to a glycerol molecule. The hydrophobic tails, each containing either a saturated or an unsaturated fatty acid, are long hydrocarbon chains.

Proteins make up the second major component of plasma membranes. Integral proteins (some specialized types are called integrins) are, as their name suggests, integrated completely into the membrane structure, and their hydrophobic membrane-spanning regions interact with the hydrophobic region of the the phospholipid bilayer. Single-pass integral membrane proteins usually have a hydrophobic transmembrane segment that consists of 20–25 amino acids. Some span only part of the membrane—associating with a single layer—while others stretch from one side of the membrane to the other, and are exposed on either side. Some complex proteins are composed of up to 12 segments of a single protein, which are extensively folded and embedded in the membrane. This type of protein has a hydrophilic region or regions, and one or several mildly hydrophobic regions. This arrangement of regions of the protein tends to orient the protein alongside the phospholipids, with the hydrophobic

region of the protein adjacent to the tails of the phospholipids and the hydrophilic region or regions of the protein protruding from the membrane and in contact with the cytosol or extracellular fluid.

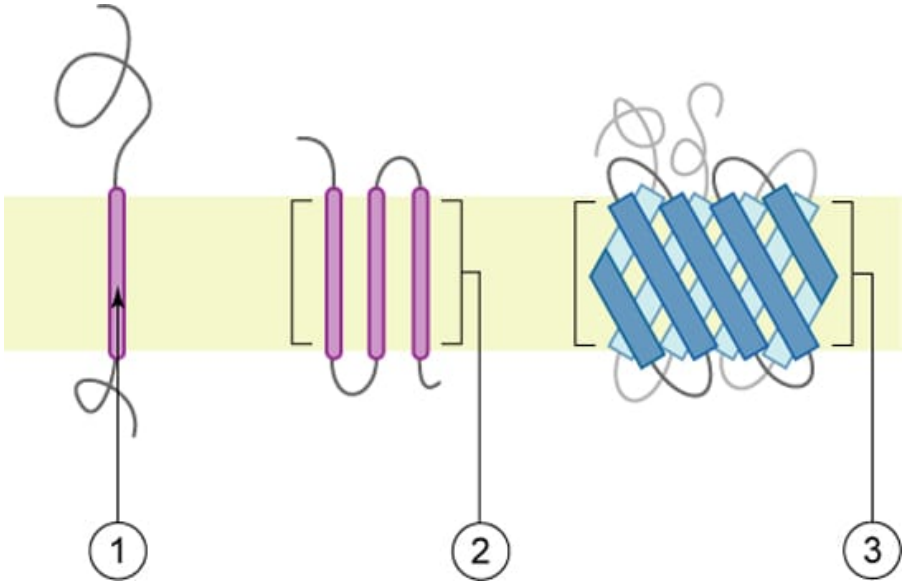


Figure 5.2.1: Structure of integral membrane proteins: Integral membrane proteins may have one or more alpha-helices that span the membrane (examples 1 and 2), or they may have beta-sheets that span the membrane (example 3).

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 can be either straight or branched. Along with peripheral proteins, carbohydrates form specialized sites on the cell surface that allow cells to recognize each other. This recognition function is very important to cells, as it allows the immune system to differentiate between body cells (called “self”) and foreign cells or tissues (called “non-self”). Similar types of glycoproteins and glycolipids are found on the surfaces of viruses and may change frequently, preventing immune cells from recognizing and attacking them. These carbohydrates on the exterior surface of the cell—the carbohydrate components of both glycoproteins and glycolipids—are collectively referred to as the glycocalyx (meaning “sugar coating”). The glycocalyx is highly hydrophilic and attracts large amounts of water to the surface of the cell. This aids in the interaction of the cell with its watery environment and in the cell’s ability to obtain substances dissolved in the water.

Key Points

- The main fabric of the membrane is composed of amphiphilic or dual-loving, phospholipid molecules.
- Integral proteins, the second major component of plasma membranes, are integrated completely into the membrane structure with their hydrophobic membrane-spanning regions interacting with the hydrophobic region of the phospholipid bilayer.
- Carbohydrates, the third major component of plasma membranes, are always found on the exterior surface of cells where they are bound either to proteins (forming glycoproteins) or to lipids (forming glycolipids).

Key Terms

- **amphiphilic**: Having one surface consisting of hydrophilic amino acids and the opposite surface consisting of hydrophobic (or lipophilic) ones.
- **hydrophilic**: Having an affinity for water; able to absorb, or be wetted by water, “water-loving.”
- **hydrophobic**: Lacking an affinity for water; unable to absorb, or be wetted by water, “water-fearing.”

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5.3: Components and Structure - Membrane Fluidity

Learning Objectives

- Explain the function of membrane fluidity in the structure of cells

Membrane Fluidity

There are multiple factors that lead to membrane fluidity. First, the mosaic characteristic of the membrane helps the plasma membrane remain fluid. The integral proteins and lipids exist in the membrane as separate but loosely-attached molecules. The membrane is not like a balloon that can expand and contract; rather, it is fairly rigid and can burst if penetrated or if a cell takes in too much water. However, because of its mosaic nature, a very fine needle can easily penetrate a plasma membrane without causing it to burst; the membrane will flow and self-seal when the needle is extracted.

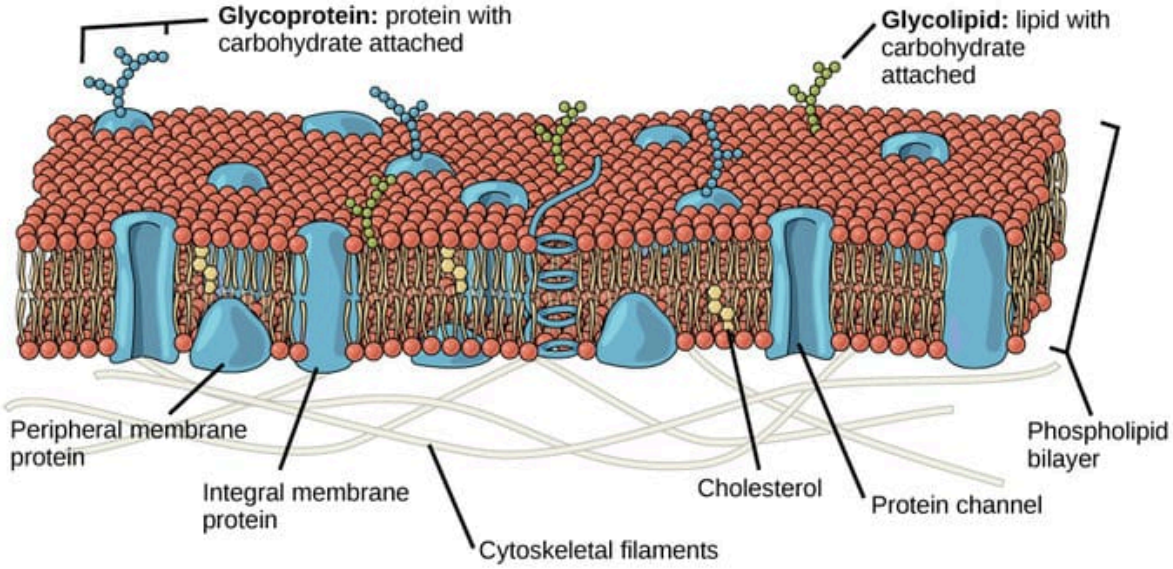


Figure 5.3.1: Membrane Fluidity: The plasma membrane is a fluid combination of phospholipids, cholesterol, and proteins. Carbohydrates attached to lipids (glycolipids) and to proteins (glycoproteins) extend from the outward-facing surface of the membrane.

The second factor that leads to fluidity is the nature of the phospholipids themselves. In their saturated form, the fatty acids in phospholipid tails are saturated with bound hydrogen atoms; there are no double bonds between adjacent carbon atoms. This results in tails that are relatively straight. In contrast, unsaturated fatty acids do not contain a maximal number of hydrogen atoms, although they do contain some double bonds between adjacent carbon atoms; a double bond results in a bend of approximately 30 degrees in the string of carbons. Thus, if saturated fatty acids, with their straight tails, are compressed by decreasing temperatures, they press in on each other, making a dense and fairly rigid membrane. If unsaturated fatty acids are compressed, the “kinks” in their tails elbow adjacent phospholipid molecules away, maintaining some space between the phospholipid molecules. This “elbow room” helps to maintain fluidity in the membrane at temperatures at which membranes with saturated fatty acid tails in their phospholipids would “freeze” or solidify. The relative fluidity of the membrane is particularly important in a cold environment. A cold environment tends to compress membranes composed largely of saturated fatty acids, making them less fluid and more susceptible to rupturing. Many organisms (fish are one example) are capable of adapting to cold environments by changing the proportion of unsaturated fatty acids in their membranes in response to the lowering of the temperature.

In animals, the third factor that keeps the membrane fluid is cholesterol. It lies alongside the phospholipids in the membrane and tends to dampen the effects of temperature on the membrane. Thus, cholesterol functions as a buffer, preventing lower temperatures from inhibiting fluidity and preventing higher temperatures from increasing fluidity too much. Cholesterol extends in both directions the range of temperature in which the membrane is appropriately fluid and, consequently, functional. Cholesterol

also serves other functions, such as organizing clusters of transmembrane proteins into lipid rafts.

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Key Points

- The membrane is fluid but also fairly rigid and can burst if penetrated or if a cell takes in too much water.
- The mosaic nature of the plasma membrane allows a very fine needle to easily penetrate it without causing it to burst and allows it to self-seal when the needle is extracted.
- If saturated fatty acids are compressed by decreasing temperatures, they press in on each other, making a dense and fairly rigid membrane.
- If unsaturated fatty acids are compressed, the “kinks” in their tails push adjacent phospholipid molecules away, which helps maintain fluidity in the membrane.
- The ratio of saturated and unsaturated fatty acids determines the fluidity in the membrane at cold temperatures.
- Cholesterol functions as a buffer, preventing lower temperatures from inhibiting fluidity and preventing higher temperatures from increasing fluidity.

Key Terms

- **phospholipid**: Any lipid consisting of a diglyceride combined with a phosphate group and a simple organic molecule such as choline or ethanolamine; they are important constituents of biological membranes
- **fluidity**: A measure of the extent to which something is fluid. The reciprocal of its viscosity.

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5.4: Passive Transport - The Role of Passive Transport

Learning Objectives

- Indicate the manner in which various materials cross the cell membrane

Plasma membranes must allow or prevent certain substances from entering or leaving a cell. In other words, plasma membranes are selectively permeable; they allow some substances to pass 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 other cells; they must have a way of obtaining these materials from extracellular fluids. This may happen passively, as certain materials move back and forth, or the cell may have special mechanisms that facilitate transport. Some materials are so important to a cell that it spends some of its energy (hydrolyzing adenosine triphosphate (ATP)) to obtain these materials. Red blood cells use some of their energy to do this. All cells spend the majority of their energy to maintain an imbalance of sodium and potassium ions between the interior and exterior of the cell.

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

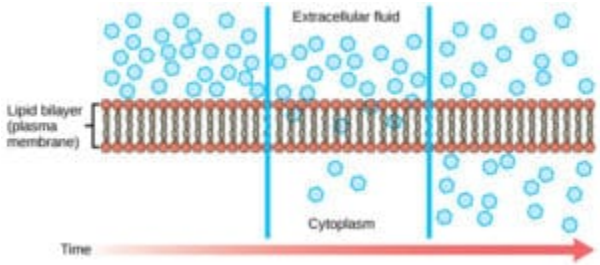


Figure 5.4.1: Passive Transport: Diffusion is a type of passive transport. Diffusion through a permeable membrane moves a substance from an area of high concentration (extracellular fluid, in this case) down its concentration gradient (into the cytoplasm).

The passive forms of transport, diffusion and osmosis, move materials of small molecular weight across membranes. Substances diffuse from areas of high concentration to areas of lower concentration; this process continues until the substance is evenly distributed in a system. In solutions containing more than one substance, each type of molecule diffuses according to its own concentration gradient, independent of the diffusion of other substances. Many factors can affect the rate of diffusion, including, but not limited to, concentration gradient, size of the particles that are diffusing, and temperature of the system.

In living systems, diffusion of substances in and out of cells is mediated by the plasma membrane. Some materials diffuse readily through the membrane, but others are hindered; their passage is made possible by specialized proteins, such as channels and transporters. The chemistry of living things occurs in aqueous solutions; 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 that facilitate transport.

Key Points

- Plasma membranes are selectively permeable; if they were to lose this selectivity, the cell would no longer be able to sustain itself.
- In passive transport, substances simply move from an area of higher concentration to an area of lower concentration, which does not require the input of energy.
- Concentration gradient, size of the particles that are diffusing, and temperature of the system affect the rate of diffusion.
- Some materials diffuse readily through the membrane, but others require specialized proteins, such as channels and transporters, to carry them into or out of the cell.

Key Terms

- **concentration gradient**: A concentration gradient is present when a membrane separates two different concentrations of molecules.
- **passive transport**: A movement of biochemicals and other atomic or molecular substances across membranes that does not require an input of chemical energy.
- **permeable**: Of or relating to substance, substrate, membrane or material that absorbs or allows the passage of fluids.

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5.5: Passive Transport - Selective Permeability

Learning Objectives

- Describe how membrane permeability, concentration gradient, and molecular properties affect biological diffusion rates.

Selective Permeability

Plasma membranes are asymmetric: the interior of the membrane is not identical to the exterior of the membrane. In fact, there is a considerable difference between the array of phospholipids and proteins between the two leaflets that form a membrane. On the interior of the membrane, some proteins serve to anchor the membrane to fibers of the cytoskeleton. There are peripheral proteins on the exterior of the membrane that bind elements of the extracellular matrix. 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.

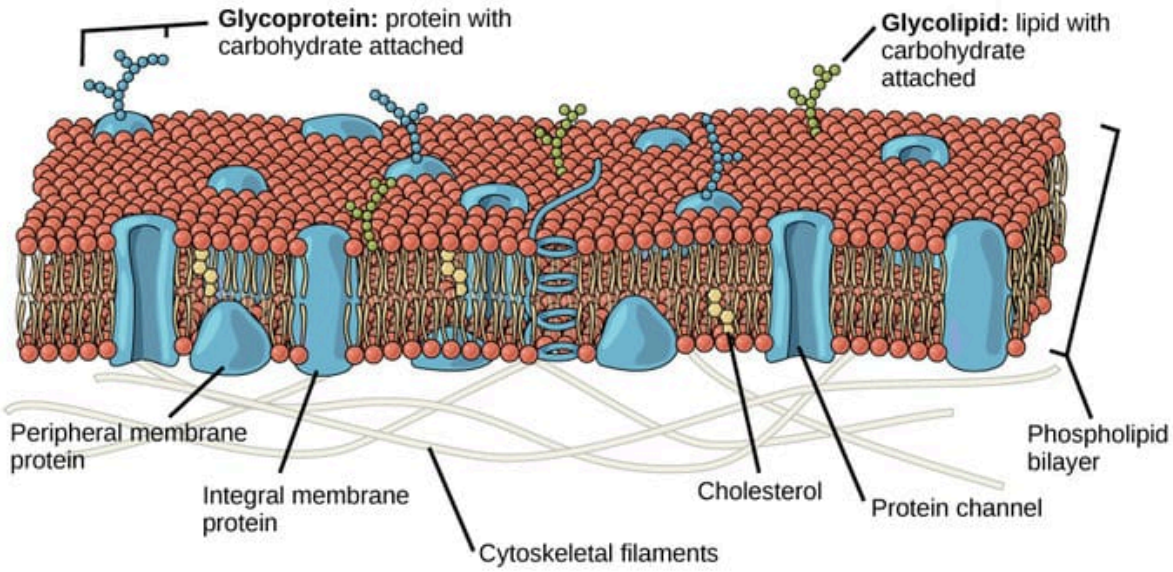


Figure 5.5.1: Asymmetry in Plasma Membranes: The exterior surface of the plasma membrane is not identical to the interior surface of the same membrane.

Recall that plasma membranes are amphiphilic; that is, they have hydrophilic and hydrophobic regions. This characteristic helps the movement of some materials through the membrane and hinders the movement of others. Lipid-soluble material with a low molecular weight 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 and hormones 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 so pass through membranes by simple diffusion.

Polar substances 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, while 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 special means of penetrating plasma membranes. Simple sugars and amino acids also need help with transport across plasma membranes, achieved by various transmembrane proteins (channels).

Diffusion across a semipermeable membrane: This interactive shows that smaller molecules have an easier time making it across a semipermeable membrane. Adjust the pore size so the larger molecules can make it through!

Key Points

- The interior and exterior surfaces of the plasma membrane are not identical, which adds to the selective permeability of the membrane.
- Fat soluble substances are able to pass easily to the hydrophobic interior of the plasma membrane and diffuse into the cell.
- Polar molecules and charged molecules do not diffuse easily through the lipid core of the plasma membrane and must be transported across by proteins, sugars, or amino acids.

Key Terms

- **polar**: a separation of electric charge leading to a molecule or its chemical groups having an electric dipole
- **amphiphilic**: Having one surface consisting of hydrophilic amino acids and the opposite surface consisting of hydrophobic (or lipophilic) ones.

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5.6: Passive Transport - Diffusion

Learning Objectives

- Describe diffusion and the factors that affect how materials move across the cell membrane.

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 a space. You are familiar with diffusion of substances through the air. For example, think about someone opening a bottle of ammonia in a room filled with people. The ammonia gas is at its highest concentration in the bottle; its lowest concentration is at the edges of the room. The ammonia vapor will diffuse, or spread away, from the bottle; gradually, more and more people will smell the ammonia as it spreads. Materials move within the cell 's cytosol by diffusion, and certain materials move through the plasma membrane by diffusion. Diffusion expends no energy. On the contrary, concentration gradients are a form of potential energy, dissipated as the gradient is eliminated.

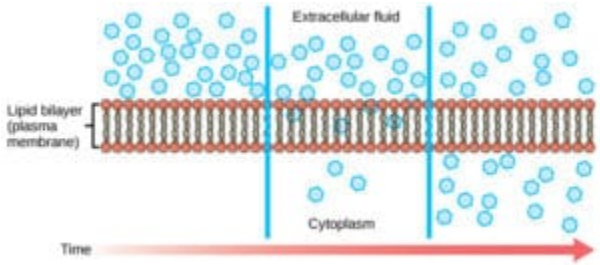


Figure 5.6.1: Diffusion: Diffusion through a permeable membrane moves a substance from an area of high concentration (extracellular fluid, in this case) down its concentration gradient (into the cytoplasm).

Each separate substance in a medium, such as the extracellular fluid, has its own concentration gradient independent of the concentration gradients of other materials. In addition, each substance will diffuse according to that gradient. Within a system, there will be different rates of diffusion of the different substances in the medium.

Factors That Affect Diffusion

Molecules move constantly in a random manner at a rate that depends on their mass, their environment, and the amount of thermal energy they possess, which in turn is a function of temperature. This movement accounts for the diffusion of molecules through whatever medium in which they are localized. A substance will tend to move into any space available to it until it is evenly distributed throughout it. After a substance has diffused completely through a space removing its concentration gradient, molecules will still move around in the space, but there will be no net movement of the number of molecules from one area to another. This lack of a concentration gradient in which there is no net movement of a substance is known as dynamic equilibrium. While diffusion will go forward in the presence of a concentration gradient of a substance, 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: Heavier molecules move more slowly; therefore, they diffuse more slowly. The reverse is true for lighter molecules.
- Temperature: Higher temperatures increase the energy and therefore the movement of the molecules, increasing the rate of diffusion. Lower temperatures decrease the energy of the molecules, thus decreasing the rate of diffusion.
- Solvent density: As the density of a solvent increases, the rate of diffusion decreases. The molecules slow down because they have a more difficult time getting through the denser medium. If the medium is less dense, diffusion increases. Because cells primarily use diffusion to move materials within the cytoplasm, any increase in the cytoplasm's density will inhibit the movement of the materials. An example of this is a person experiencing dehydration. As the body's cells lose water, the rate

of diffusion decreases in the cytoplasm, and the cells' functions deteriorate. Neurons tend to be very sensitive to this effect. Dehydration frequently leads to unconsciousness and possibly coma because of the decrease in diffusion rate within the cells.
- Solubility: As discussed earlier, nonpolar or lipid-soluble materials pass through plasma membranes more easily than polar materials, allowing a faster rate of diffusion.
- Surface area and thickness of the plasma membrane: Increased surface area increases the rate of diffusion, whereas a thicker membrane reduces it.
- Distance travelled: The greater the distance that a substance must travel, the slower the rate of diffusion. This places an upper limitation on cell size. A large, spherical cell will die because nutrients or waste cannot reach or leave the center of the cell. Therefore, cells must either be small in size, as in the case of many prokaryotes, or be flattened, as with many single-celled eukaryotes.

A variation of diffusion is the process of filtration. In filtration, material moves according to its concentration gradient through a membrane; sometimes the rate of diffusion is enhanced by pressure, causing the substances to filter more rapidly. This occurs in the kidney where blood pressure forces large amounts of water and accompanying dissolved substances, or solutes, out of the blood and into the renal tubules. The rate of diffusion in this instance is almost totally dependent on pressure. One of the effects of high blood pressure is the appearance of protein in the urine, which is "squeezed through" by the abnormally high pressure.

Key Points

- Substances diffuse according to their concentration gradient; within a system, different substances in the medium will each diffuse at different rates according to their individual gradients.
- After a substance has diffused completely through a space, removing its concentration gradient, molecules will still move around in the space, but there will be no net movement of the number of molecules from one area to another, a state known as dynamic equilibrium.
- Several factors affect the rate of diffusion of a solute including the mass of the solute, the temperature of the environment, the solvent density, and the distance traveled.

Key Terms

- **diffusion**: The passive movement of a solute across a permeable membrane
- **concentration gradient**: A concentration gradient is present when a membrane separates two different concentrations of molecules.

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5.7: Passive Transport - Facilitated Transport

Learning Objectives

- Explain why and how passive transport occurs

Facilitated transport is a type of passive transport. Unlike simple diffusion where materials pass through a membrane without the help of proteins, in facilitated transport, also called facilitated diffusion, materials diffuse across the plasma membrane with the help of membrane proteins. A concentration gradient exists that would allow these materials to diffuse into the cell without expending cellular energy. However, these materials are ions or polar molecules that are repelled by the hydrophobic parts of the cell membrane. Facilitated transport proteins shield these materials from the repulsive force of the membrane, allowing them to diffuse into the cell.

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. Some of these integral proteins are collections of beta-pleated sheets that form a channel through the phospholipid bilayer. Others are carrier proteins which bind with the substance and aid its diffusion through the membrane.

Channels

The integral proteins involved in facilitated transport are collectively referred to as transport proteins; they function as either channels for the material or carriers. In both cases, they are transmembrane proteins. Channels are specific for the substance that is being transported. Channel proteins have hydrophilic domains exposed to the intracellular and extracellular fluids; they additionally have a hydrophilic channel through their core that provides a hydrated opening through the membrane layers. Passage through the channel allows polar compounds to avoid the nonpolar central layer of the plasma membrane that would otherwise slow or prevent their entry into the cell. Aquaporins are channel proteins that allow water to pass through the membrane at a very high rate.

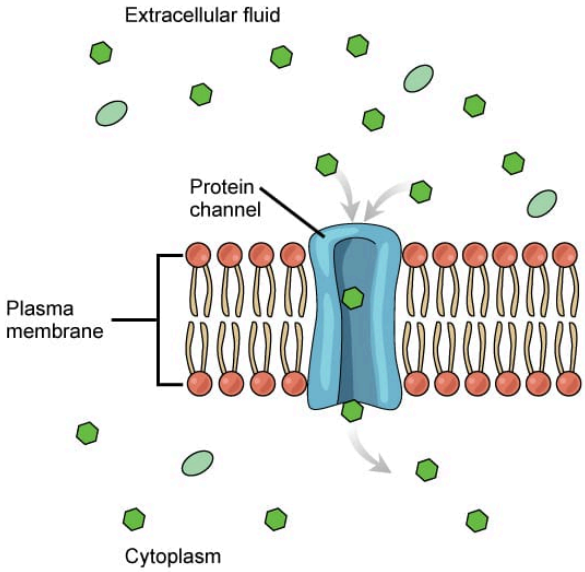


Figure 5.7.1: Channel Proteins in Facilitated Transport: Facilitated transport moves substances down their concentration gradients. They may cross the plasma membrane with the aid of channel proteins.

Channel proteins are either open at all times or they are “gated,” which controls the opening of the channel. The attachment of a particular ion to the channel protein may control the opening or other mechanisms or substances may be involved. In some tissues, sodium and chloride ions pass freely through open channels, whereas in other tissues, a gate must be opened

to allow passage. An example of this occurs in the kidney, where both forms of channels are found in different parts of the renal tubules. Cells involved in the transmission of electrical impulses, such as nerve and muscle cells, have gated channels for sodium, potassium, and calcium in their membranes. Opening and closing of these channels changes the relative concentrations on opposing sides of the membrane of these ions, resulting in the facilitation of electrical transmission along membranes (in the case of nerve cells) or in muscle contraction (in the case of muscle cells).

Carrier Proteins

Another type of protein embedded in the plasma membrane is a carrier protein. This protein binds a substance and, in doing so, triggers a change of its own shape, moving the bound molecule from the outside of the cell to its interior; depending on the gradient, the material may move in the opposite direction. Carrier proteins are typically specific for a single substance. This adds to the overall selectivity of the plasma membrane. The exact mechanism for the change of shape is poorly understood. Proteins can change shape when their hydrogen bonds are affected, but this may not fully explain this mechanism. Each carrier protein is specific to one substance, and there are a finite number of these proteins in any membrane. This can cause problems in transporting enough of the material for the cell to function properly.

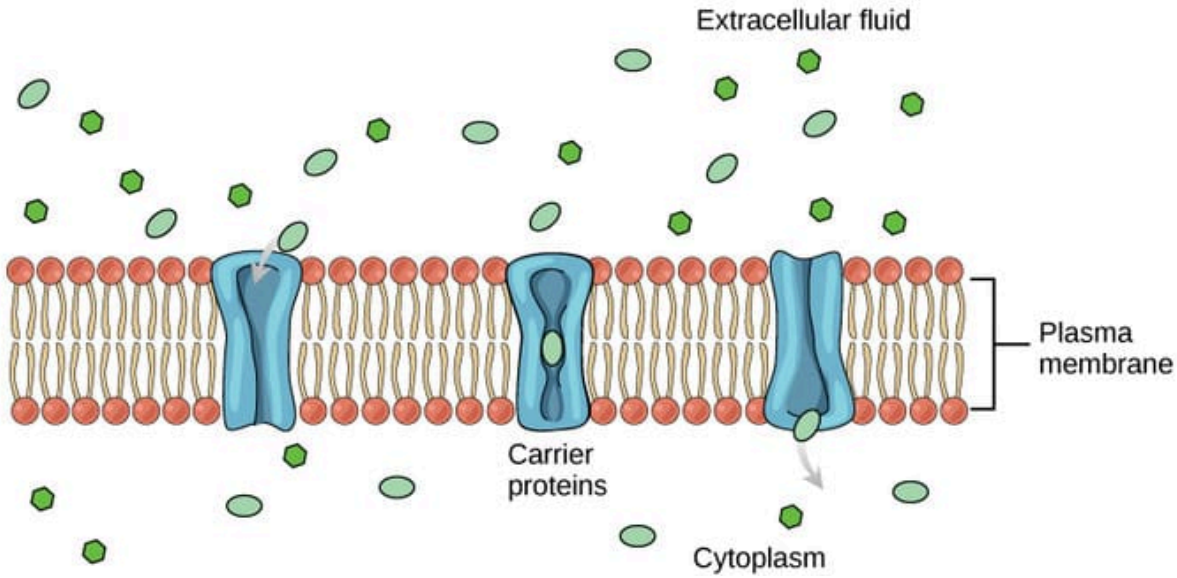


Figure 5.7.1: Carrier Proteins: Some substances are able to move down their concentration gradient across the plasma membrane with the aid of carrier proteins. Carrier proteins change shape as they move molecules across the membrane.

An example of this process occurs in the kidney. Glucose, water, salts, ions, and amino acids needed by the body are filtered in one part of the kidney. This filtrate, which includes glucose, is then reabsorbed in another part of the kidney. Because there are only a finite number of carrier proteins for glucose, if more glucose is present than the proteins can handle, the excess is not transported; it is excreted from the body in the urine. In a diabetic individual, this is described as “spilling glucose into the urine.” A different group of carrier proteins called glucose transport proteins, or GLUTs, are involved in transporting glucose and other hexose sugars through plasma membranes within the body.

Channel and carrier proteins transport material at different rates. Channel proteins transport much more quickly than do carrier proteins. Channel proteins facilitate diffusion at a rate of tens of millions of molecules per second, whereas carrier proteins work at a rate of a thousand to a million molecules per second.

Key Points

- A concentration gradient exists that would allow ions and polar molecules to diffuse into the cell, but these materials are repelled by the hydrophobic parts of the cell membrane.
- Facilitated diffusion uses integral membrane proteins to move polar or charged substances across the hydrophobic regions of the membrane.
- Channel proteins can aid in the facilitated diffusion of substances by forming a hydrophilic passage through the plasma membrane through which polar and charged substances can pass.

- Channel proteins can be open at all times, constantly allowing a particular substance into or out of the cell, depending on the concentration gradient; or they can be gated and can only be opened by a particular biological signal.
- Carrier proteins aid in facilitated diffusion by binding a particular substance, then altering their shape to bring that substance into or out of the cell.

Key Terms

- **facilitated diffusion**: The spontaneous passage of molecules or ions across a biological membrane passing through specific transmembrane integral proteins.
- **membrane protein**: Proteins that are attached to, or associated with the membrane of a cell or an organelle.

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5.8: Passive Transport - Osmosis

Learning Objectives

- Describe the process of osmosis and explain how concentration gradient affects osmosis

Osmosis and Semipermeable Membranes

Osmosis is the movement of water through a semipermeable membrane according to the concentration gradient of water across the membrane, which is inversely proportional to the concentration of solutes. Semipermeable membranes, also termed selectively permeable membranes or partially permeable membranes, allow certain molecules or ions to pass through by diffusion.

While diffusion transports materials across membranes and within cells, osmosis transports only water across a membrane. The semipermeable membrane limits the diffusion of solutes in the water. Not surprisingly, the aquaporin proteins that facilitate water movement play a large role in osmosis, most prominently in red blood cells and the membranes of kidney tubules.

Mechanism of Osmosis

Osmosis is a special case of diffusion. Water, like other substances, moves from an area of high concentration to one of low concentration. An obvious question is what makes water move at all? Imagine a beaker with a semipermeable membrane separating the two sides or halves. On both sides of the membrane the water level is the same, but there are different concentrations of a dissolved substance, or solute, that cannot cross the membrane (otherwise the concentrations on each side would be balanced by the solute crossing the membrane). If the volume of the solution on both sides of the membrane is the same but the concentrations of solute are different, then there are different amounts of water, the solvent, on either side of the membrane. If there is more solute in one area, then there is less water; if there is less solute in one area, then there must be more water.

To illustrate this, imagine two full glasses of water. One has a single teaspoon of sugar in it, whereas the second one contains one-quarter cup of sugar. If the total volume of the solutions in both cups is the same, which cup contains more water? Because the large amount of sugar in the second cup takes up much more space than the teaspoon of sugar in the first cup, the first cup has more water in it.

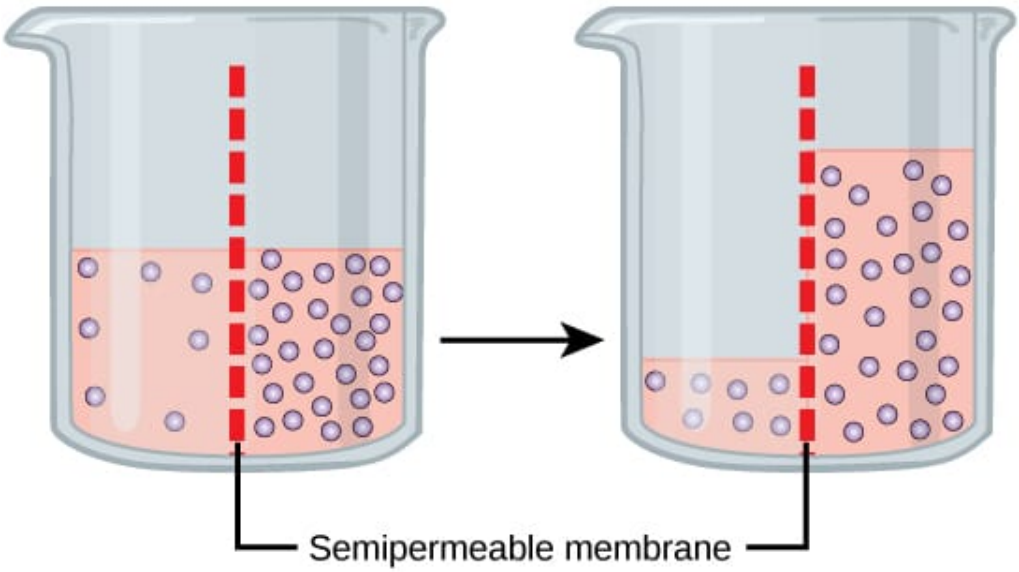


Figure 5.8.1: Osmosis: In osmosis, water always moves from an area of higher water concentration to one of lower concentration. In the diagram shown, the solute cannot pass through the selectively permeable membrane, but the water can.

Returning to the beaker example, recall that it has a mixture of solutes on either side of the 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 passing 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. Thus, 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 or until the hydrostatic pressure of the water balances the osmotic pressure. In the beaker example, this means that the level of fluid in the side with a higher solute concentration will go up.

Key Points

- Osmosis occurs according to the concentration gradient of water across the membrane, which is inversely proportional to the concentration of solutes.
- Osmosis occurs until the concentration gradient of water goes to zero or until the hydrostatic pressure of the water balances the osmotic pressure.
- Osmosis occurs when there is a concentration gradient of a solute within a solution, but the membrane does not allow diffusion of the solute.

Key Terms

- **solute**: Any substance that is dissolved in a liquid solvent to create a solution
- **osmosis**: The net movement of solvent molecules from a region of high solvent potential to a region of lower solvent potential through a partially permeable membrane
- **semipermeable membrane**: A type of biological membrane that will allow certain molecules or ions to pass through it by diffusion and occasionally by specialized facilitated diffusion

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5.9: Passive Transport - Tonicity

Learning Objectives

- Define tonicity and describe its relevance to osmosis

Tonicity describes how an extracellular solution can change the volume of a cell by affecting osmosis. A solution's tonicity often directly correlates with the osmolarity of the solution. Osmolarity describes the total solute concentration of the solution. A solution with low osmolarity has a greater number of water molecules relative to the number of solute particles; a solution with high osmolarity has fewer water molecules with respect to solute particles. In a situation in which solutions of two different osmolarities are separated by a membrane permeable to water, though not to the solute, water will move from the side of the membrane with lower osmolarity (and more water) to the side with higher osmolarity (and less water). This effect makes sense if you remember that the solute cannot move across the membrane, and thus the only component in the system that can move—the water—moves along its own concentration gradient. An important distinction that concerns living systems is that osmolarity measures the number of particles (which may be molecules) in a solution. Therefore, a solution that is cloudy with cells may have a lower osmolarity than a solution that is clear if the second solution contains more dissolved molecules than there are cells.

Hypotonic Solutions

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 situation, the extracellular fluid has lower osmolarity 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 in the solution than does the cell. In this situation, water will follow its concentration gradient and enter the cell, causing the cell to expand.

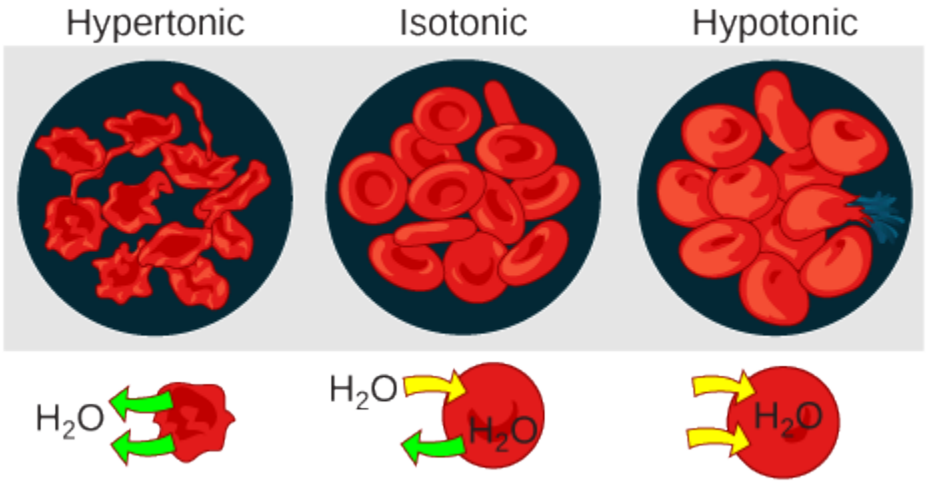


Figure 5.9.1: Changes in Cell Shape Due to Dissolved Solutes: Osmotic pressure changes the shape of red blood cells in hypertonic, isotonic, and hypotonic solutions.

Hypertonic Solutions

As for a hypertonic solution, the prefix hyper- refers to the extracellular fluid having a higher osmolarity than the cell's cytoplasm; therefore, the fluid contains less water than the cell does. Because the cell has a relatively higher concentration of water, water will leave the cell, and the cell will shrink.

Isotonic Solutions

In an isotonic solution, the extracellular fluid has the same osmolarity as the cell. If the osmolarity of the cell matches that of the extracellular fluid, there will be no net movement of water into or out of the cell, although water will still move in and out.

Blood cells and plant cells in hypertonic, isotonic, and hypotonic solutions take on characteristic appearances. Cells in an isotonic solution retain their shape. Cells in a hypotonic solution swell as water enters the cell, and may burst if the concentration gradient is large enough between the inside and outside of the cell. Cells in a hypertonic solution shrink as water exits the cell, becoming shriveled.

Key Points

- Osmolarity describes the total solute concentration of a solution; solutions with a low solute concentration have a low osmolarity, while those with a high osmolarity have a high solute concentration.
- Water moves from the side of the membrane with lower osmolarity (and more water) to the side with higher osmolarity (and less water).
- In a hypotonic solution, the extracellular fluid has a lower osmolarity than the fluid inside the cell; water enters the cell.
- In a hypertonic solution, the extracellular fluid has a higher osmolarity than the fluid inside the cell; water leaves the cell.
- In an isotonic solution, the extracellular fluid has the same osmolarity as the cell; there will be no net movement of water into or out of the cell.

Key Terms

- **osmolarity**: The osmotic concentration of a solution, normally expressed as osmoles of solute per litre of solution.
- **hypotonic**: Having a lower osmotic pressure than another; a cell in this environment causes water to enter the cell, causing it to swell.
- **hypertonic**: having a greater osmotic pressure than another
- **isotonic**: having the same osmotic pressure

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5.10: Active Transport - Electrochemical Gradient

Learning Objectives

- Define an electrochemical gradient and describe how a cell moves substances against this gradient

Electrochemical Gradients

Simple concentration gradients are differential concentrations of a substance across a space or a membrane, but in living systems, gradients are more complex. Because ions move into and out of cells and because cells contain proteins that do not move across the membrane and are mostly negatively charged, there is also 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. In a living cell, the concentration gradient of Na^+ tends to drive it into the cell, and the electrical gradient of Na^+ (a positive ion) also 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^+, a positive ion, also tends to drive it into the cell, but the concentration gradient of K^+ tends to drive K^+ out of the cell. The combined gradient of concentration and electrical charge that affects an ion is called its electrochemical gradient.

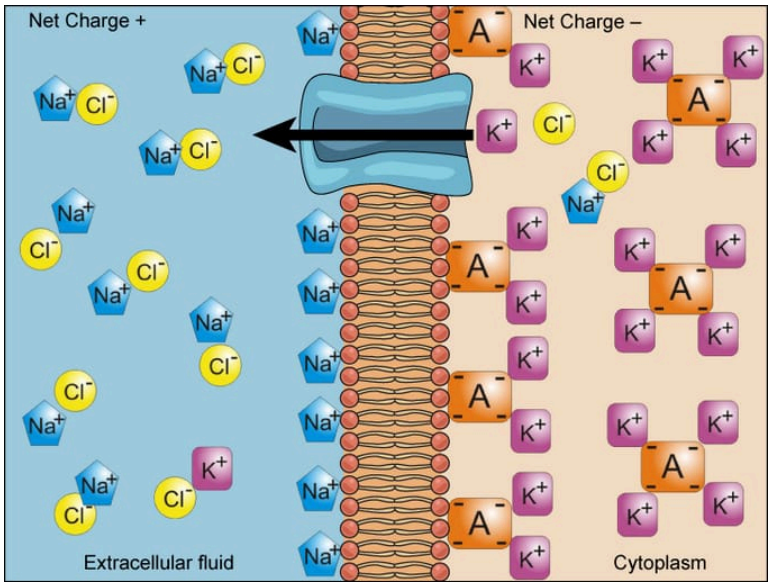


Figure 5.10.1: Electrochemical Gradient: Electrochemical gradients arise from the combined effects of concentration gradients and electrical gradients.

Moving Against a Gradient

To move substances against a concentration or electrochemical gradient, the cell must use energy. This energy is harvested from adenosine triphosphate (ATP) generated through the cell's metabolism. Active transport mechanisms, collectively called pumps, work against electrochemical gradients. 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 movements. Much of a cell's supply of metabolic energy may be spent maintaining these processes. For example, most of a red blood cell's metabolic energy is used to maintain the imbalance between exterior and interior sodium and potassium levels required by the cell. Because active transport mechanisms depend on a cell's 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 small molecules. Primary active transport moves ions across a membrane and creates a difference in charge across that membrane, which is directly dependent on ATP. Secondary active transport describes the movement of material that is due to the electrochemical gradient established by primary active transport that does not directly require ATP.

Carrier Proteins for Active Transport

An important membrane adaption for active transport is the presence of specific carrier proteins or pumps to facilitate movement. There are three types of these proteins or transporters: uniporters, symporters, and antiporters. A uniporter carries one specific ion or molecule. A symporter carries two different ions or molecules, both in the same direction. An antiporter also carries two different ions or molecules, but in different directions. All of these transporters can also transport small, uncharged organic molecules like glucose. These three types of carrier proteins are also found in facilitated diffusion, but they do not require ATP to work in that process. Some examples of pumps for active transport are Na^+-K^+ ATPase, which carries sodium and potassium ions, and H^+-K^+ ATPase, which carries hydrogen and potassium ions. Both of these are antiporter carrier proteins. Two other carrier protein pumps are Ca^{2+} ATPase and H^+ATPase, which carry only calcium and only hydrogen ions, respectively.

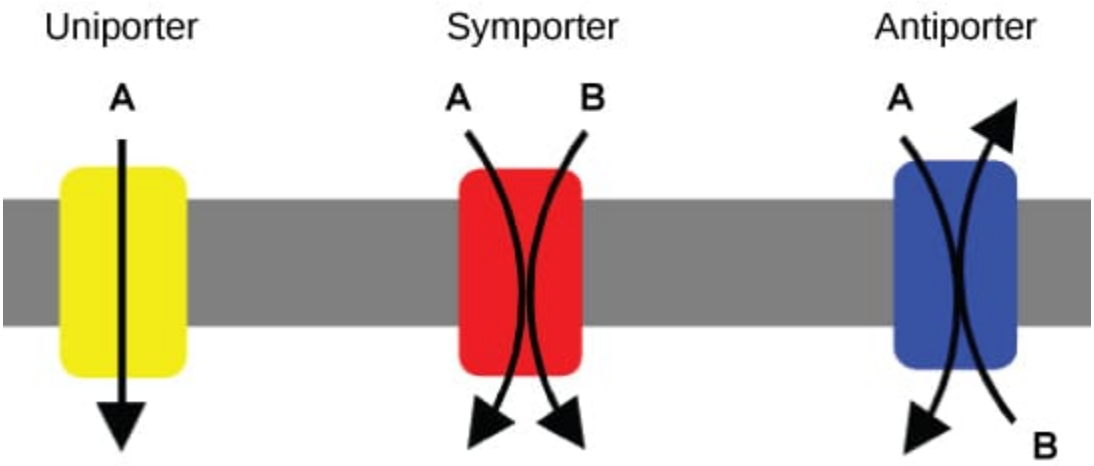


Figure 5.10.1: Uniporters, Symporters, and Antiporters: A uniporter carries one molecule or ion. A symporter carries two different molecules or ions, both in the same direction. An antiporter also carries two different molecules or ions, but in different directions.

Key Points

- The electrical and concentration gradients of a membrane tend to drive sodium into and potassium out of the cell, and active transport works against these gradients.
- To move substances against a concentration or electrochemical gradient, the cell must utilize energy in the form of ATP during active transport.
- Primary active transport, which is directly dependent on ATP, moves ions across a membrane and creates a difference in charge across that membrane.
- Secondary active transport, created by primary active transport, is the transport of a solute in the direction of its electrochemical gradient and does not directly require ATP.
- Carrier proteins such as uniporters, symporters, and antiporters perform primary active transport and facilitate the movement of solutes across the cell's membrane.

Key Terms

- **adenosine triphosphate**: a multifunctional nucleoside triphosphate used in cells as a coenzyme, often called the "molecular unit of energy currency" in intracellular energy transfer
- **active transport**: movement of a substance across a cell membrane against its concentration gradient (from low to high concentration) facilitated by ATP conversion
- **electrochemical gradient**: The difference in charge and chemical concentration across a membrane.

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5.11: Active Transport - Primary Active Transport

Learning Objectives

- Describe how a cell moves sodium and potassium out of and into the cell against its electrochemical gradient

Primary Active Transport

The primary active transport that functions with the active transport of sodium and potassium allows secondary active transport to occur. The secondary transport method is still considered active because it depends on the use of energy as does primary transport.

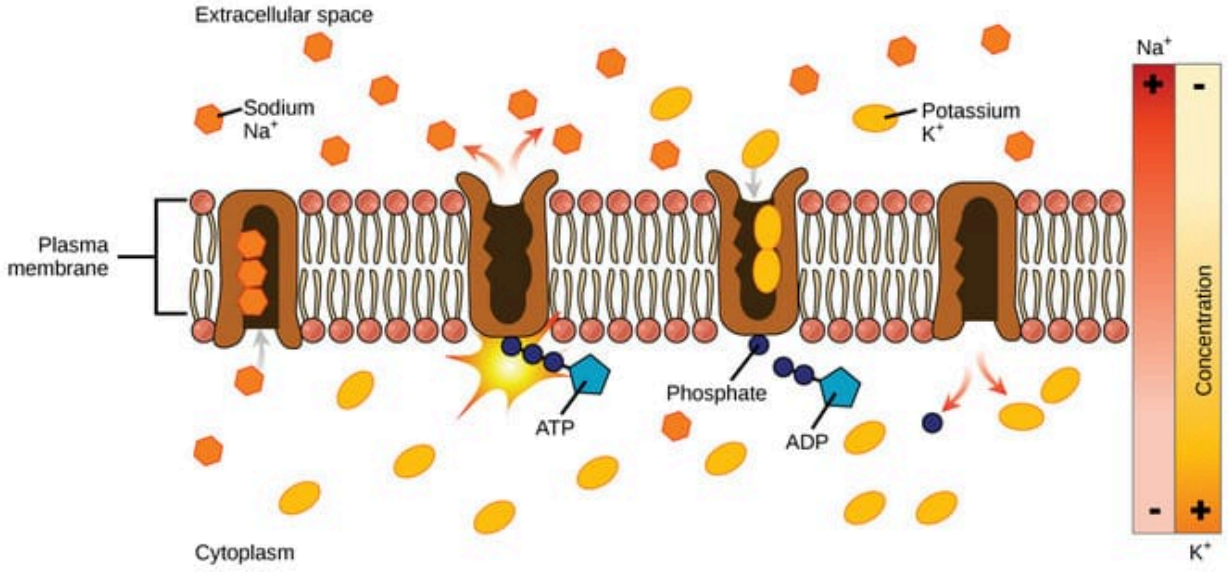


Figure 5.11.1: Active Transport of Sodium and Potassium: Primary active transport moves ions across a membrane, creating an electrochemical gradient (electrogenic transport).

One of the most important pumps in animals cells is the sodium-potassium pump (Na^+-K^+ ATPase), which maintains the electrochemical gradient (and the correct concentrations of Na^+ and K^+) in living cells. The sodium-potassium pump moves two K^+ into the cell while moving three Na^+ out of the cell. The Na+-K+ ATPase exists in two forms, depending on its orientation to the interior or exterior of the cell and its affinity for either sodium or potassium ions. The process consists of the following six steps:

- With the enzyme oriented towards the interior of the cell, the carrier has a high affinity for sodium ions. Three sodium ions bind to the protein.
- ATP is hydrolyzed by the protein carrier, and a low-energy phosphate group attaches to it.
- As a result, the carrier changes shape and re-orients itself towards the exterior of the membrane. The protein's affinity for sodium decreases, and the three sodium ions leave the carrier.
- The shape change increases the carrier's affinity for potassium ions, and two such ions attach to the protein. Subsequently, the low-energy phosphate group detaches from the carrier.
- With the phosphate group removed and potassium ions attached, the carrier protein repositions itself towards the interior of the cell.
- The carrier protein, in its new configuration, has a decreased affinity for potassium, and the two ions are released into the cytoplasm. The protein now has a higher affinity for sodium ions, and the process starts again.

Several things have happened as a result of this process. At this point, there are more sodium ions outside of the cell than inside

and more potassium ions inside than out. For every three ions of sodium that move out, two ions of potassium move in. This results in the interior being slightly more negative relative to the exterior. This difference in charge is important in creating the conditions necessary for the secondary process. The sodium-potassium pump is, therefore, an electrogenic pump (a pump that creates a charge imbalance), creating an electrical imbalance across the membrane and contributing to the membrane potential.

Key Points

- The sodium-potassium pump moves K+ into the cell while moving Na+ at a ratio of three Na+ for every two K+ ions.
- When the sodium-potassium- ATPase enzyme points into the cell, it has a high affinity for sodium ions and binds three of them, hydrolyzing ATP and changing shape.
- As the enzyme changes shape, it reorients itself towards the outside of the cell, and the three sodium ions are released.
- The enzyme's new shape allows two potassium to bind and the phosphate group to detach, and the carrier protein repositions itself towards the interior of the cell.
- The enzyme changes shape again, releasing the potassium ions into the cell.
- After potassium is released into the cell, the enzyme binds three sodium ions, which starts the process over again.

Key Terms

- **electrogenic pump**: An ion pump that generates a net charge flow as a result of its activity.
- **Na+-K+ ATPase**: An enzyme located in the plasma membrane of all animal cells that pumps sodium out of cells while pumping potassium into cells.

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5.12: Active Transport - Secondary Active Transport

Learning Objectives

- Differentiate between primary and secondary active transport

Secondary Active Transport (Co-transport)

Unlike in primary active transport, in secondary active transport, ATP is not directly coupled to the molecule of interest. Instead, another molecule is moved up its concentration gradient, which generates an electrochemical gradient. The molecule of interest is then transported down the electrochemical gradient. While this process still consumes ATP to generate that gradient, the energy is not directly used to move the molecule across the membrane, hence it is known as secondary active transport. Both antiporters and symporters are used in secondary active transport. Co-transporters can be classified as symporters and antiporters depending on whether the substances move in the same or opposite directions across the cell membrane.

Secondary active transport brings sodium ions, and possibly other compounds, into the cell. As sodium ion concentrations build outside the plasma membrane because of the action of the primary active transport process, an electrochemical gradient is created. If a channel protein exists and is open, the sodium ions will be pulled through the membrane. This movement is used to transport other substances that can attach themselves to the transport protein through the membrane. Many amino acids, as well as glucose, enter a cell this way. This secondary process is also used to store high-energy hydrogen ions in the mitochondria of plant and animal cells for the production of ATP. The potential energy that accumulates in the stored hydrogen ions is translated into kinetic energy as the ions surge through the channel protein ATP synthase, and that energy is used to convert ADP into ATP.

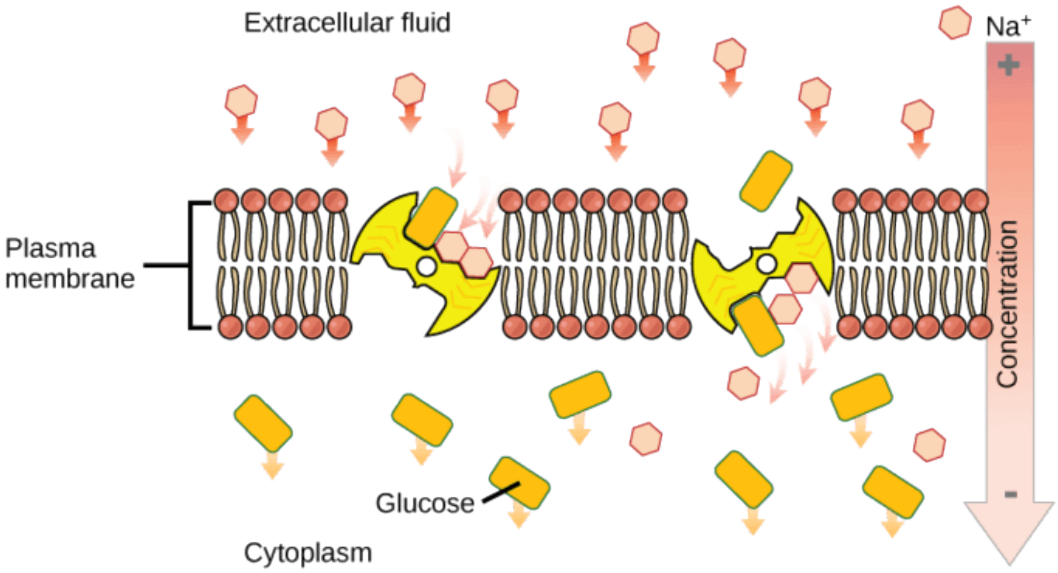


Figure 5.12.1: Secondary Active Transport: An electrochemical gradient, created by primary active transport, can move other substances against their concentration gradients, a process called co-transport or secondary active transport.

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Key Points

- While secondary active transport consumes ATP to generate the gradient down which a molecule is moved, the energy is not directly used to move the molecule across the membrane.
- Both antiporters and symporters are used in secondary active transport.
- Secondary active transport brings sodium ions into the cell, and as sodium ion concentrations build outside the plasma membrane, an electrochemical gradient is created.
- If a channel protein is open via primary active transport, the ions will be pulled through the membrane along with other substances that can attach themselves to the transport protein through the membrane.
- Secondary active transport is used to store high-energy hydrogen ions in the mitochondria of plant and animal cells for the production of ATP.
- The potential energy in the hydrogen ions is translated into kinetic energy as the ions surge through the channel protein ATP synthase, and that energy is used to convert ADP into ATP.

Key Terms

- **secondary active transport**: A method of transport in which the electrochemical potential difference created by pumping ions out of the cell is used to transport molecules across a membrane.

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5.13: Bulk Transport - Endocytosis

Learning Objectives

- Describe endocytosis, including phagocytosis, pinocytosis, and receptor-mediated 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 intracellular vesicle formed from the plasma membrane.

Phagocytosis

Phagocytosis (the condition of "cell eating") is the process by which large particles, such as cells or relatively large particles, are taken in by a cell. For example, when microorganisms invade the human body, a type of white blood cell called a neutrophil will remove the invaders through this process, surrounding and engulfing the microorganism, which is then destroyed by the neutrophil.

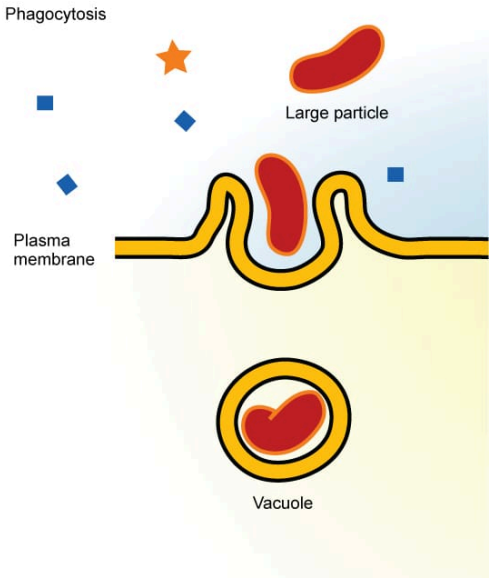


Figure 5.13.1: Phagocytosis: In phagocytosis, the cell membrane surrounds the particle and engulfs it.

In preparation for phagocytosis, a portion of the inward-facing surface of the plasma membrane becomes coated with a protein called clathrin, which stabilizes this section of the membrane. The coated portion of the membrane then extends from the body of the cell and surrounds the particle, eventually enclosing it. Once the vesicle containing the particle is enclosed within the cell, the clathrin disengages from the membrane and the vesicle merges with a lysosome for the breakdown of the material in the newly-formed compartment (endosome). When accessible nutrients from the degradation of the vesicular contents have been extracted, the newly-formed endosome merges with the plasma membrane and releases its contents into the extracellular fluid. The endosomal membrane again becomes part of the plasma membrane.

Pinocytosis

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 is a process that takes in molecules, including water, which the cell needs from the extracellular fluid. Pinocytosis results in a much smaller vesicle than does phagocytosis, and the vesicle does not need to merge with a lysosome.

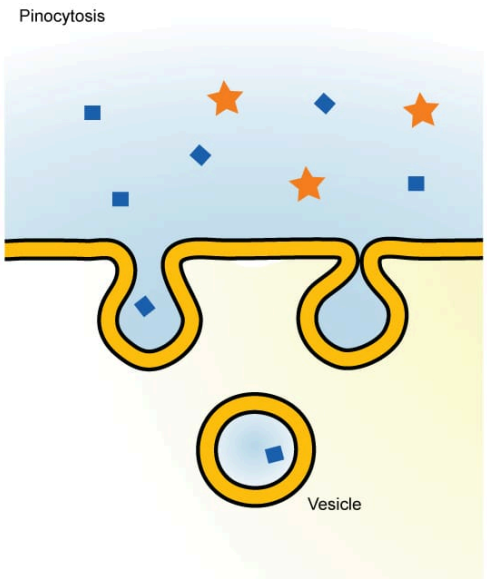


Figure 5.13.1: Pinocytosis: In pinocytosis, the cell membrane invaginates, surrounds a small volume of fluid, and pinches off.

Potocytosis, a variant of pinocytosis, is a process that uses a coating protein, called caveolin, on the cytoplasmic side of the plasma membrane, which performs a similar function to clathrin. The cavities in the plasma membrane that form the vacuoles have membrane receptors and lipid rafts in addition to caveolin. The vacuoles or vesicles formed in caveolae (singular caveola) are smaller than those in pinocytosis. Potocytosis is used to bring small molecules into the cell and to transport these molecules through the cell for their release on the other side of the cell, a process called transcytosis.

Receptor-mediated Endocytosis

A targeted variation of endocytosis, known as receptor-mediated endocytosis, employs receptor proteins in the plasma membrane that have a specific binding affinity for certain substances. In receptor-mediated endocytosis, as in phagocytosis, clathrin is attached to the cytoplasmic side of the plasma membrane. If uptake of a compound is dependent on receptor-mediated endocytosis and the process is ineffective, the material 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 the 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 LDL particles from their blood.

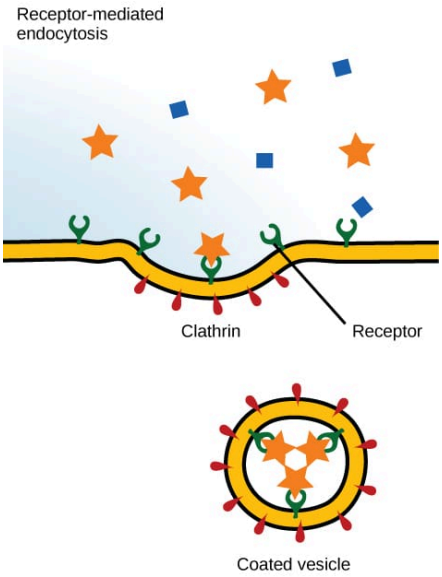


Figure 5.13.1: Receptor-Mediated Endocytosis: In receptor-mediated endocytosis, uptake of substances by the cell is targeted to a single type of substance that binds to the receptor on the external surface of the cell membrane.

Although receptor-mediated endocytosis is designed to bring specific substances that are normally found in the extracellular fluid into the cell, other substances may gain entry into the cell at the same site. Flu viruses, diphtheria, and cholera toxin all have sites that cross-react with normal receptor-binding sites and gain entry into cells.

Key Points

- Endocytosis consists of phagocytosis, pinocytosis, and receptor -mediated endocytosis.
- Endocytosis takes particles into the cell that are too large to passively cross the cell membrane.
- Phagocytosis is the taking in of large food particles, while pinocytosis takes in liquid particles.
- Receptor-mediated endocytosis uses special receptor proteins to help carry large particles across the cell membrane.

Key Terms

- **endosome**: An endocytic vacuole through which molecules internalized during endocytosis pass en route to lysosomes
- **neutrophil**: A cell, especially a white blood cell that consumes foreign invaders in the blood.

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5.14: Bulk Transport - Exocytosis

Learning Objectives

- Describe exocytosis and the processes used to release materials from the cell.

Exocytosis' main purpose is to expel material from the cell into the extracellular fluid; this is the opposite of what occurs in endocytosis. In exocytosis, waste material is enveloped in a membrane and fuses with the interior of the plasma membrane. This fusion opens the membranous envelope on the exterior of the cell and the waste material is expelled into the extracellular space. Exocytosis is used continuously by plant and animal cells to excrete waste from the cells.

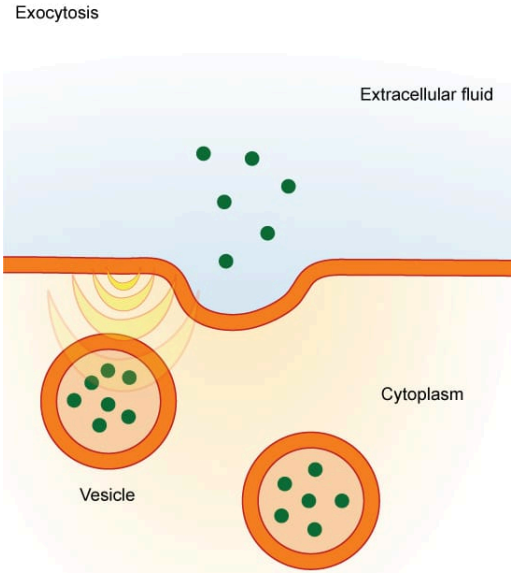


Figure 5.14.1: Exocytosis: In exocytosis, vesicles containing substances fuse with the plasma membrane. The contents are then released to the exterior of the cell.

Exocytosis is composed of five main stages. The first stage is called vesicle trafficking. This involves the steps required to move, over a significant distance, the vesicle containing the material that is to be disposed. The next stage that occurs is vesicle tethering, which links the vesicle to the cell membrane by biological material at half the diameter of a vesicle. Next, the vesicle's membrane and the cell membrane connect and are held together in the vesicle docking step. This stage of exocytosis is then followed by vesicle priming, which includes all of the molecular rearrangements and protein and lipid modifications that take place after initial docking. In some cells, there is no priming. The final stage, vesicle fusion, involves the merging of the vesicle membrane with the target membrane. This results in the release of the unwanted materials into the space outside the cell.

Some examples of cells releasing molecules via exocytosis include the secretion of proteins of the extracellular matrix and secretion of neurotransmitters into the synaptic cleft by synaptic vesicles. Some examples of cells using exocytosis include: the secretion of proteins like enzymes, peptide hormones and antibodies from different cells, the flipping of the plasma membrane, the placement of integral membrane proteins(IMPs) or proteins that are attached biologically to the cell, and the recycling of plasma membrane bound receptors (molecules on the cell membrane that intercept signals).

membrane that intercept signals).

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Key Points

- Exocytosis is the opposite of endocytosis as it involves releasing materials from the cell.
- Exocytosis has five stages, each leading up to the vesicle binding with the cell membrane.
- Many bodily functions include the use of exocytosis, such as the release of neurotransmitters into the synaptic cleft and the release of enzymes into the blood.

Key Terms

- **secretion**: The act of secreting (producing and discharging) a substance, especially from a gland.
- **vesicle**: A membrane-bound compartment found in a cell.

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6: METABOLISM

6.1: Energy and Metabolism - The Role of Energy and Metabolism

6.2: Energy and Metabolism - Types of Energy

6.3: Energy and Metabolism - Metabolic Pathways

6.4: Energy and Metabolism - Metabolism of Carbohydrates

6.5: Potential, Kinetic, Free, and Activation Energy - Free Energy

6.6: Potential, Kinetic, Free, and Activation Energy - The First Law of Thermodynamics

6.7: Potential, Kinetic, Free, and Activation Energy - The Second Law of Thermodynamics

6.8: Potential, Kinetic, Free, and Activation Energy - Activation Energy

6.9: ATP - Adenosine Triphosphate

6.10: Enzymes - Active Site and Substrate Specificity

6.11: Enzymes - Control of Metabolism Through Enzyme Regulation

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6.1: Energy and Metabolism - The Role of Energy and Metabolism

Learning Objectives

- Explain the importance of metabolism

Energy and Metabolism

All living organisms need energy to grow and reproduce, maintain their structures, and respond to their environments. Metabolism is the set of life-sustaining chemical processes that enables organisms transform the chemical energy stored in molecules into energy that can be used for cellular processes. Animals consume food to replenish energy; their metabolism breaks down the carbohydrates, lipids, proteins, and nucleic acids to provide chemical energy for these processes. Plants convert light energy from the sun into chemical energy stored in molecules during the process of photosynthesis.

Bioenergetics and Chemical Reactions

Scientists use the term bioenergetics to discuss the concept of energy flow through living systems such as cells. Cellular processes such as the building and breaking down of complex molecules occur through step-by-step chemical reactions. Some of these chemical reactions are spontaneous and release energy, whereas others require energy to proceed. All of the chemical reactions that take place inside cells, including those that use energy and those that release energy, are the cell's metabolism.

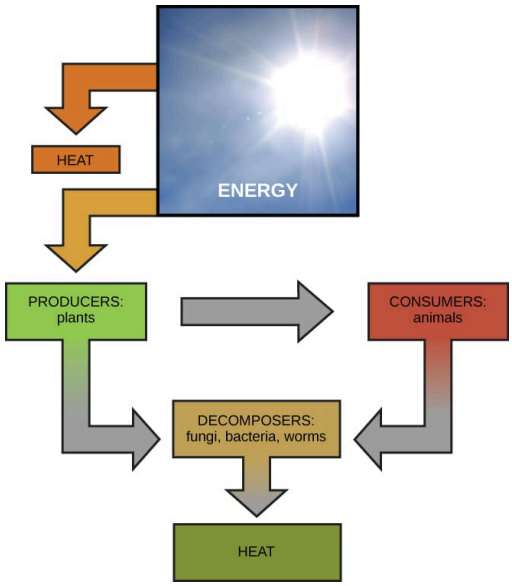


Figure 6.1.1: Most energy comes from the sun, either directly or indirectly: Most life forms on earth get their energy from the sun. Plants use photosynthesis to capture sunlight, and herbivores eat those plants to obtain energy. Carnivores eat the herbivores, and decomposers digest plant and animal matter.

Cellular Metabolism

Every task performed by living organisms requires energy. Energy is needed to perform heavy labor and exercise, but humans also use a great deal of energy while thinking and even while sleeping. For every action that requires energy, many chemical reactions take place to provide chemical energy to the systems of the body, including muscles, nerves, heart, lungs, and brain.

The living cells of every organism constantly use energy to survive and grow. Cells break down complex carbohydrates into simple sugars that the cell can use for energy. Muscle cells may consumer energy to build long muscle proteins from small amino acid molecules. Molecules can be modified and transported around the cell or may be distributed to the entire organism. Just as energy is required to both build and demolish a building, energy is required for both the synthesis and breakdown of molecules.

Many cellular process require a steady supply of energy provided by the cell's metabolism. Signaling molecules such as hormones and neurotransmitters must be synthesized and then transported between cells. Pathogenic bacteria and viruses are ingested and broken down by cells. Cells must also export waste and toxins to stay healthy, and many cells must swim or move surrounding materials via the beating motion of cellular appendages like cilia and flagella.



Figure 6.1.1: Eating provides energy for activities like flight: A hummingbird needs energy to maintain prolonged periods of flight. The hummingbird obtains its energy from taking in food and transforming the nutrients into energy through a series of biochemical reactions. The flight muscles in birds are extremely efficient in energy production.

Key Points

- All living organisms need energy to grow and reproduce, maintain their structures, and respond to their environments; metabolism is the set of the processes that makes energy available for cellular processes.
- Metabolism is a combination of chemical reactions that are spontaneous and release energy and chemical reactions that are non-spontaneous and require energy in order to proceed.
- Living organisms must take in energy via food, nutrients, or sunlight in order to carry out cellular processes.
- The transport, synthesis, and breakdown of nutrients and molecules in a cell require the use of energy.

Key Terms

- **metabolism**: the complete set of chemical reactions that occur in living cells
- **bioenergetics**: the study of the energy transformations that take place in living organisms
- **energy**: the capacity to do work

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6.2: Energy and Metabolism - Types of Energy

Learning Objectives

- Differentiate between types of energy

Energy is a property of objects which can be transferred to other objects or converted into different forms, but cannot be created or destroyed. Organisms use energy to survive, grow, respond to stimuli, reproduce, and for every type of biological process. The potential energy stored in molecules can be converted to chemical energy, which can ultimately be converted to kinetic energy, enabling an organism to move. Eventually, most of energy used by organisms is transformed into heat and dissipated.

Kinetic Energy

Energy associated with objects in motion is called kinetic energy. For example, when an airplane is in flight, the airplane is moving through air very quickly—doing work to enact change on its surroundings. The jet engines are converting potential energy in fuel to the kinetic energy of movement. A wrecking ball can perform a large amount of damage, even when moving slowly. However, a still wrecking ball cannot perform any work and therefore has no kinetic energy. A speeding bullet, a walking person, the rapid movement of molecules in the air that produces heat, and electromagnetic radiation, such as sunlight, all have kinetic energy.

Potential Energy

What if that same motionless wrecking ball is lifted two stories above a car with a crane? If the suspended wrecking ball is not moving, is there energy associated with it? Yes, the wrecking ball has energy because the wrecking ball has the potential to do work. This form of energy is called potential energy because it is possible for that object to do work in a given state.

Objects transfer their energy between potential and kinetic states. As the wrecking ball hangs motionlessly, it has 0%0% kinetic and 100%100%potential energy. Once the ball is released, its kinetic energy increases as the ball picks up speed. At the same time, the ball loses potential energy as it nears the ground. 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 6.2.1: Potential energy vs. kinetic energy: Water behind a dam has potential energy. Moving water, such as in a waterfall or a rapidly flowing river, has kinetic energy.

Chemical Energy

Potential energy is not only associated with the location of matter, but also with the structure of matter. A spring on the ground has potential energy if it is compressed, as does a rubber band that is pulled taut. The same principle applies to molecules. On a chemical level, the bonds that hold the atoms of molecules together have potential energy. This type of potential energy is called chemical energy, and like all potential energy, it can be used to do work.

For example, chemical energy is contained in the gasoline molecules that are used to power cars. When gas ignites in the engine, the bonds within its molecules are broken, and the energy released is used to drive the pistons. The potential energy stored within chemical bonds can be harnessed to perform work for biological processes. Different metabolic processes break down organic molecules to release the energy for an organism to grow and survive.

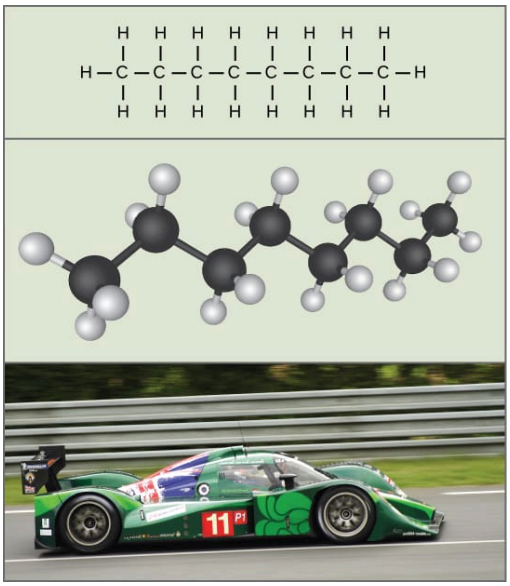


Figure 6.2.1: Chemical energy: The molecules in gasoline (octane, the chemical formula shown) contain chemical energy. This energy is transformed into kinetic energy that allows a car to race on a racetrack.

Key Points

- All organisms use different forms of energy to power the biological processes that allow them to grow and survive.
- Kinetic energy is the energy associated with objects in motion.
- Potential energy is the type of energy associated with an object's potential to do work.
- Chemical energy is the type of energy released from the breakdown of chemical bonds and can be harnessed for metabolic processes.

Key Terms

- **chemical energy**: The net potential energy liberated or absorbed during the course of a chemical reaction.
- **potential energy**: Energy possessed by an object because of its position (in a gravitational or electric field), or its condition (as a stretched or compressed spring, as a chemical reactant, or by having rest mass).
- **kinetic energy**: The energy possessed by an object because of its motion, equal to one half the mass of the body times the square of its velocity.

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6.3: Energy and Metabolism - Metabolic Pathways

Learning Objectives

- Describe the two major types of metabolic pathways

Metabolic Pathways

The processes of making and breaking down carbohydrate molecules illustrate two types of metabolic pathways. A metabolic pathway is a step-by-step series of interconnected biochemical reactions that convert a substrate molecule or molecules through a series of metabolic intermediates, eventually yielding a final product or products. For example, one metabolic pathway for carbohydrates breaks large molecules down into glucose. Another metabolic pathway might build glucose into large carbohydrate molecules for storage. The first of these processes requires energy and is referred to as anabolic. The second process produces energy and is referred to as catabolic. Consequently, metabolism is composed of these two opposite pathways:

1. Anabolism (building molecules)
2. Catabolism (breaking down molecules)

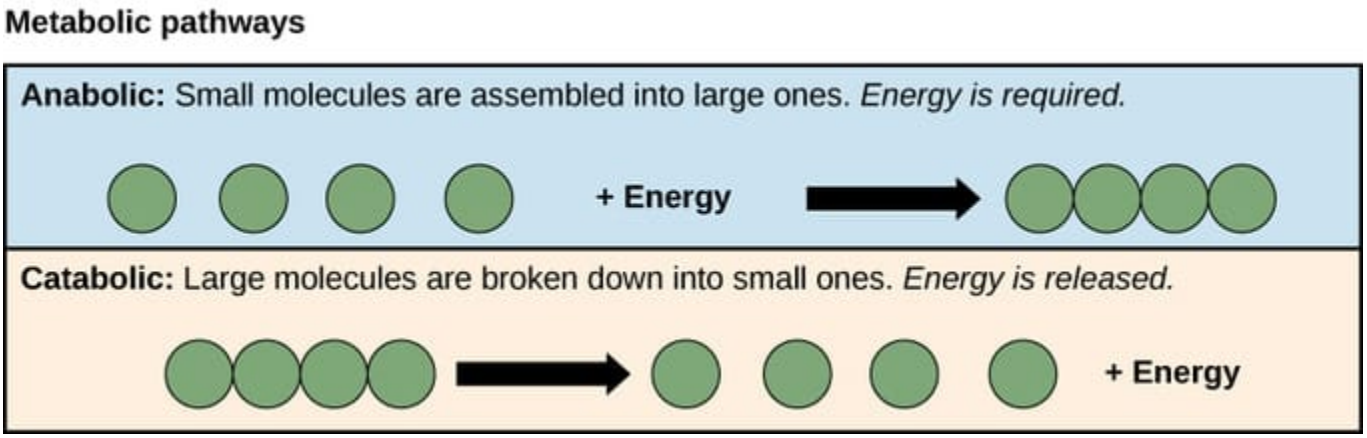


Figure 6.3.1: Anabolic and catabolic pathways: Anabolic pathways are those that require energy to synthesize larger molecules. Catabolic pathways are those that generate energy by breaking down larger molecules. Both types of pathways are required for maintaining the cell's energy balance.

Anabolic Pathways

Anabolic pathways require an input of energy to synthesize complex molecules from simpler ones. One example of an anabolic pathway is the synthesis of sugar from CO_2. Other examples include the synthesis of large proteins from amino acid building blocks and the synthesis of new DNA strands from nucleic acid building blocks. These processes are critical to the life of the cell, take place constantly, and demand energy provided by ATP and other high-energy molecules like NADH (nicotinamide adenine dinucleotide) and NADPH.

Catabolic Pathways

Catabolic pathways involve the degradation of complex molecules into simpler ones, releasing the chemical energy stored in the bonds of those molecules. Some catabolic pathways can capture that energy to produce ATP, the molecule used to power all cellular processes. Other energy-storing molecules, such as lipids, are also broken down through similar catabolic reactions to release energy and make ATP.

Importance of Enzymes

Chemical reactions in metabolic pathways rarely take place spontaneously. 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.

Key Points

- A metabolic pathway is a series of chemical reactions in a cell that build and breakdown molecules for cellular processes.
- Anabolic pathways synthesize molecules and require energy.
- Catabolic pathways break down molecules and produce energy.
- Because almost all metabolic reactions take place non-spontaneously, proteins called enzymes help facilitate those chemical reactions.

Key Terms

- **catabolism**: destructive metabolism, usually including the release of energy and breakdown of materials
- **enzyme**: a globular protein that catalyses a biological chemical reaction
- **anabolism**: the constructive metabolism of the body, as distinguished from catabolism

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6.4: Energy and Metabolism - Metabolism of Carbohydrates

Learning Objectives

- Analyze the importance of carbohydrate metabolism to energy production

Metabolism of Carbohydrates

Carbohydrates are one of the major forms of energy for animals and plants. Plants build carbohydrates using light energy from the sun (during the process of photosynthesis), while animals eat plants or other animals to obtain carbohydrates. Plants store carbohydrates in long polysaccharides chains called starch, while animals store carbohydrates as the molecule glycogen. These large polysaccharides contain many chemical bonds and therefore store a lot of chemical energy. When these molecules are broken down during metabolism, the energy in the chemical bonds is released and can be harnessed for cellular processes.



Figure 6.4.1: All living things use carbohydrates as a form of energy.: Plants, like this oak tree and acorn, use energy from sunlight to make sugar and other organic molecules. Both plants and animals (like this squirrel) use cellular respiration to derive energy from the organic molecules originally produced by plants

Energy Production from Carbohydrates (Cellular Respiration)

The metabolism of any monosaccharide (simple sugar) can produce energy for the cell to use. Excess carbohydrates are stored as starch in plants and as glycogen in animals, ready for metabolism if the energy demands of the organism suddenly increase. When those energy demands increase, carbohydrates are broken down into constituent monosaccharides, which are then distributed to all the living cells of an organism. Glucose ($C_6H_{12}O_6$) is a common example of the monosaccharides used for energy production.

Inside the cell, each sugar molecule is broken down through a complex series of chemical reactions. As chemical energy is released from the bonds in the monosaccharide, it is harnessed to synthesize high-energy adenosine triphosphate (ATP) molecules. ATP is the primary energy currency of all cells. Just as the dollar is used as currency to buy goods, cells use molecules of ATP to perform immediate work and power chemical reactions.

The breakdown of glucose during metabolism is call cellular respiration can be described by the equation:

$$C_6H_{12}O_6+6O_2 \rightarrow 6CO_2+6H_2O+\text{energy}$$

Producing Carbohydrates (Photosynthesis)

Plants and some other types of organisms produce carbohydrates through the process called photosynthesis. During photosynthesis, plants convert light energy into chemical energy by building carbon dioxide gas molecules (CO_2) into sugar molecules like glucose. Because this process involves building bonds to synthesize a large molecule, it requires an input of energy (light) to proceed. The synthesis of glucose by photosynthesis is described by this equation (notice that it is the reverse of the previous equation):

$$6CO_2 + 6H_2O + \text{energy} \rightarrow C_6H_{12}O_6 + 6O_2$$

As part of plants' chemical processes, glucose molecules can be combined with and converted into other types of sugars. In plants, glucose is stored in the form of starch, which can be broken down back into glucose via cellular respiration in order to supply ATP.

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Key Points

- The breakdown of glucose living organisms utilize to produce energy is described by the equation: $C_6H_{12}O_6+6O_2 \rightarrow 6CO_2+6H_2O+\text{energy}$.
- The photosynthetic process plants utilize to synthesize glucose is described by the equation:$6CO_2+6H_2O+\text{energy} \rightarrow C_6H_{12}O_6+6O_2$
- Glucose that is consumed is used to make energy in the form of ATP, which is used to perform work and power chemical reactions in the cell.
- During photosynthesis, plants convert light energy into chemical energy that is used to build molecules of glucose.

Key Terms

- **adenosine triphosphate**: a multifunctional nucleoside triphosphate used in cells as a coenzyme, often called the “molecular unit of energy currency” in intracellular energy transfer
- **glucose**: a simple monosaccharide (sugar) with a molecular formula of C6H12O6; it is a principal source of energy for cellular metabolism

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6.5: Potential, Kinetic, Free, and Activation Energy - Free Energy

Learning Objectives

- Discuss the concept of free energy.

Free Energy

Since chemical reactions release energy when energy-storing bonds are broken, how is the energy associated with 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 quantitate these energy transfers. Free energy is called Gibbs free energy (G) after Josiah Willard Gibbs, the scientist who developed the measurement. 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, resulting in entropy. Gibbs free energy specifically refers to the energy associated with a chemical reaction that is available after accounting for entropy. In other words, Gibbs free energy is usable energy or energy that is available to do work.

Calculating ΔG

Every chemical reaction involves a change in free energy, called delta G (ΔG). The change in free energy can be calculated for any system that undergoes a change, such as a chemical reaction. To calculate ΔG, subtract the amount of energy lost to entropy (denoted as ΔS) from the total energy change of the system. This total energy change in the system is called enthalpy and is denoted as ΔH. The formula for calculating ΔG is as follows, where the symbol T refers to absolute temperature in Kelvin (degrees Celsius + 273): $G=\Delta H-T\Delta S$.

The standard free energy change of a chemical reaction is expressed as an amount of energy per mole of the reaction product (either in kilojoules or kilocalories, kJ/mol or kcal/mol; 1 kJ = 0.239 kcal) under standard pH, temperature, and pressure conditions. Standard pH, temperature, and pressure conditions are generally calculated at pH 7.0 in biological systems, 25 degrees Celsius, and 100 kilopascals (1 atm pressure), respectively. It is important to note that cellular conditions vary considerably from these standard conditions; therefore, standard calculated ΔG values for biological reactions will be different inside the cell.

Endergonic and Exergonic Reactions

If energy is released during a chemical reaction, then the resulting value from the above equation will be a negative number. In other words, reactions that release energy have a $\Delta G < 0$. A negative ΔG also means that the products of the reaction have less free energy than the reactants because they gave off some free energy during the reaction. Reactions that have a negative ΔG and, consequently, release free energy, are called exergonic reactions. Exergonic means energy is exiting the system. These reactions are also referred to as spontaneous reactions because they can occur without the addition of energy into the system. Understanding which chemical reactions are spontaneous and release free energy is extremely useful for biologists because these reactions can be harnessed to perform work inside the cell. An important distinction must be drawn between the term spontaneous and the idea of a chemical reaction that occurs 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 requires an input of energy rather than releasing energy, 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; they are non-spontaneous. An endergonic reaction will not take place on its own without the addition of free energy.

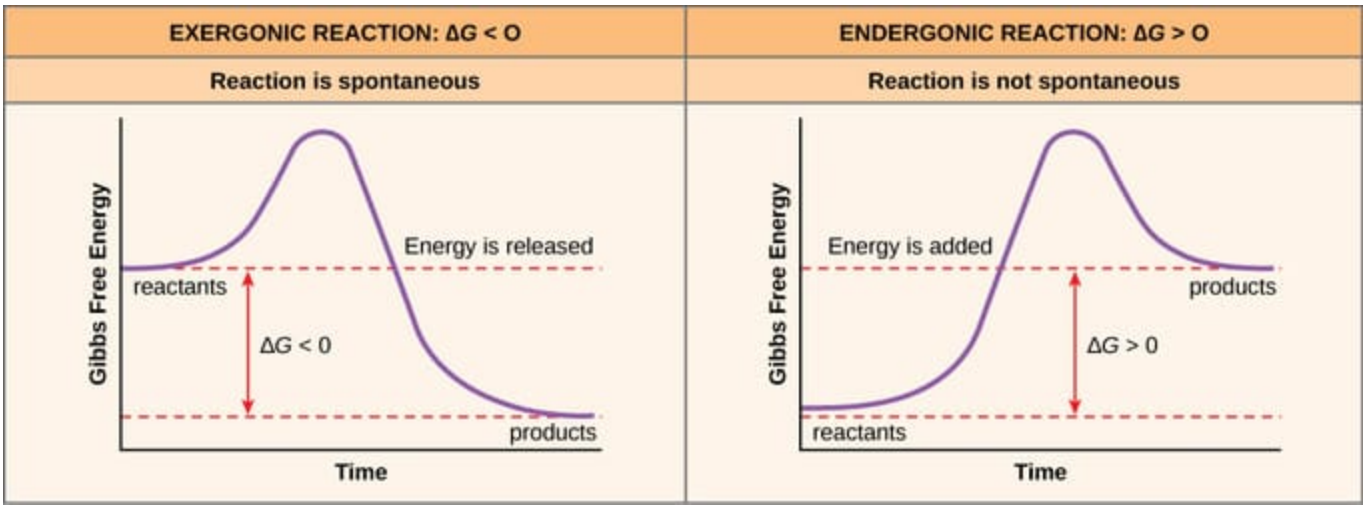


Figure 6.5.1: Exergonic and Endergonic Reactions: Exergonic and endergonic reactions result in changes in Gibbs free energy. Exergonic reactions release energy; endergonic reactions require energy to proceed.

Free Energy and Biological Processes

In a living cell, chemical reactions are constantly moving towards equilibrium, but never reach it. A living cell is an open system: materials pass in and out, the cell recycles the products of certain chemical reactions into other reactions, and chemical equilibrium is never reached. In this way, living organisms are in a constant energy-requiring, uphill battle against equilibrium and entropy.

When complex molecules, such as starches, are built from simpler molecules, such as sugars, the anabolic process requires energy. Therefore, the chemical reactions involved in anabolic processes are endergonic reactions. On the other hand, the catabolic process of breaking sugar down into simpler molecules releases energy in a series of exergonic reactions. As in the example of rust above, the breakdown of sugar involves spontaneous reactions, but these reactions don't occur instantaneously. An important concept in the study of metabolism and energy is that of chemical equilibrium. Most chemical reactions are reversible. They can proceed in both directions, releasing energy into their environment in one direction, and absorbing it from the environment in the other direction.



Figure 6.5.1: Endergonic and Exergonic Processes: Shown are some examples of endergonic processes (ones that require energy) and exergonic processes (ones that release energy). These include (a) a compost pile decomposing, (b) a chick hatching from a fertilized egg, (c) sand art being destroyed, and (d) a ball rolling down a hill.

Key Points

- Every chemical reaction involves a change in free energy, called delta G (ΔG).
- To calculate ΔG, subtract the amount of energy lost to entropy (ΔS) from the total energy change of the system; this total energy change in the system is called enthalpy (ΔH): $\Delta G = \Delta H - T\Delta S$.
- Endergonic reactions require an input of energy; the ΔG for that reaction will be a positive value.
- Exergonic reactions release free energy; the ΔG for that reaction will be a negative value.

Key Terms

- **exergonic reaction**: A chemical reaction where the change in the Gibbs free energy is negative, indicating a spontaneous reaction
- **endergonic reaction**: A chemical reaction in which the standard change in free energy is positive, and energy is absorbed
- **Gibbs free energy**: The difference between the enthalpy of a system and the product of its entropy and absolute temperature

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6.6: Potential, Kinetic, Free, and Activation Energy - The First Law of Thermodynamics

Learning Objectives

- Describe the first law of thermodynamics

Thermodynamics is the study of heat energy and other types of energy, such as work, and the various ways energy is transferred within chemical systems. “Thermo-” refers to heat, while “dynamics” refers to motion.

The First Law of Thermodynamics

The first law of thermodynamics deals with the total amount of energy in the universe. The law states that this total amount of energy is constant. 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 can be transferred from place to place or changed between different forms, but it cannot be created or destroyed. The transfers and transformations of energy take place around us all the time. For instance, light bulbs transform electrical energy into light energy, and gas stoves transform chemical energy from natural gas into heat energy. Plants perform one of the most biologically useful transformations of energy on Earth: they convert the energy of sunlight into the chemical energy stored within organic molecules.

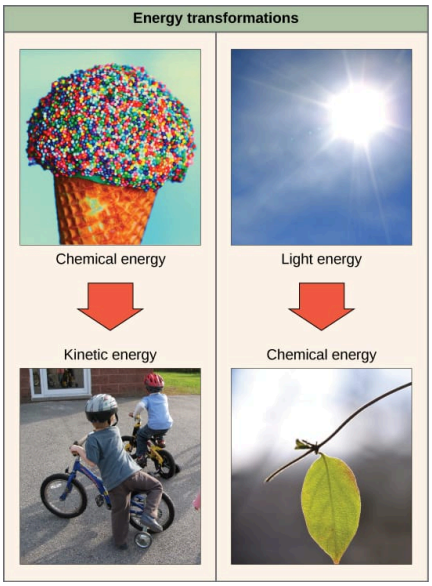


Figure 6.6.1: The first law of thermodynamics: Shown are two examples of energy being transferred from one system to another and transformed from one form to another. Humans can convert the chemical energy in food, like this ice cream cone, into kinetic energy by riding a bicycle. Plants can convert electromagnetic radiation (light energy) from the sun into chemical energy.

The System and Surroundings

Thermodynamics often divides the universe into two categories: the system and its surroundings. In chemistry, the system almost always refers to a given chemical reaction and the container in which it takes place. The first law of thermodynamics tells us that energy can neither be created nor destroyed, so we know that the energy that is absorbed in an endothermic chemical reaction must have been lost from the surroundings. Conversely, in an exothermic reaction, the heat that is released in the reaction is given off and absorbed by the surroundings. Stated mathematically, we have:

$\Delta E = \Delta E_{sys} + \Delta E_{surr} = 0$

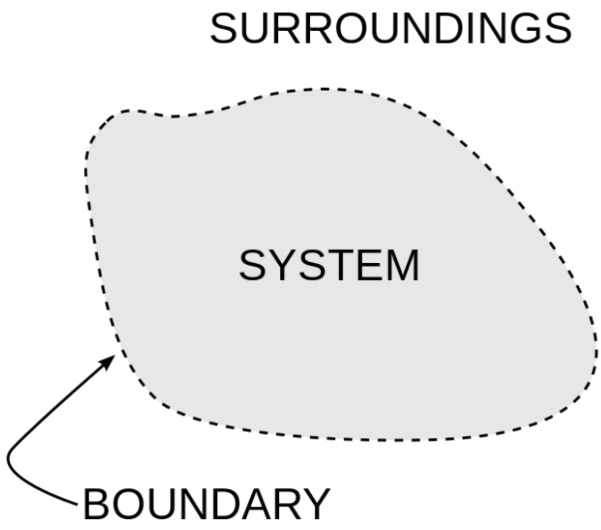


Figure 6.6.1: The system and surroundings: A basic diagram showing the fundamental distinction between the system and its surroundings in thermodynamics.

Heat and Work

We know that chemical systems can either absorb heat from their surroundings, if the reaction is endothermic, or release heat to their surroundings, if the reaction is exothermic. However, chemical reactions are often used to do work instead of just exchanging heat. For instance, when rocket fuel burns and causes a space shuttle to lift off from the ground, the chemical reaction, by propelling the rocket, is doing work by applying a force over a distance.

If you've ever witnessed a video of a space shuttle lifting off, the chemical reaction that occurs also releases tremendous amounts of heat and light. Another useful form of the first law of thermodynamics relates heat and work for the change in energy of the internal system:

$$\Delta E_{sys} = Q + W$$

While this formulation is more commonly used in physics, it is still important to know for chemistry.



Figure 6.6.1: Rocket launch: The powerful chemical reaction propelling the rocket lets off tremendous heat to the surroundings and does work on the surroundings (the rocket) as well.

Key Points

- According to the first law of thermodynamics, the total amount of energy in the universe is constant.
- Energy can be transferred from place to place or transformed into different forms, but it cannot be created or destroyed.
- Living organisms have evolved to obtain energy from their surroundings in forms that they can transfer or transform into usable energy to do work.

Key Terms

- **first law of thermodynamics**: A version of the law of conservation of energy, specialized for thermodynamical systems, that states that the energy of an isolated system is constant and can neither be created nor destroyed.
- **work**: A measure of energy expended by moving an object, usually considered to be force times distance. No work is done if the object does not move.

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6.7: Potential, Kinetic, Free, and Activation Energy - The Second Law of Thermodynamics

Learning Objectives

- Explain how living organisms can increase their order despite the second law of thermodynamics

The Second Law of Thermodynamics

A living cell ‘s primary tasks of obtaining, transforming, and using energy to do work may seem simple enough, but they are more problematic than they appear. The second law of thermodynamics explains why: No energy transfers or transformations in the universe are completely efficient. In every energy transfer, some amount of energy is lost in a form that is unusable. In most cases, this energy is in the form of heat. Thermodynamically, heat energy is defined as the energy transferred from one system to another that is not doing work. For example, when an airplane flies through the air, some of the energy of the flying plane is lost as heat energy due to friction with the surrounding air. This friction heats the air by temporarily increasing the speed of air molecules. Likewise, some energy is lost in the form of heat during cellular metabolic reactions. This is good for warm-blooded creatures like us because heat energy helps to maintain our body temperature. Strictly speaking, no energy transfer is completely efficient because some energy is lost in an unusable form.

Entropy

An important concept in physical systems is disorder (also known as randomness). The more energy that is lost by a system to its surroundings, the less ordered and more random the system is. Scientists define the measure of randomness or disorder within a system as entropy. High entropy means high disorder and low energy. To better understand entropy, remember that it requires energy to maintain structure. For example, think about an ice cube. It is made of water molecules bound together in an orderly lattice. This arrangement takes energy to maintain. When the ice cube melts and becomes water, its molecules are more disordered, in a random arrangement as opposed to a structure. Overall, there is less energy in the system inside the molecular bonds. Therefore, water can be said to have greater entropy than ice.

This holds true for solids, liquids, and gases in general. Solids have the highest internal energy holding them together and therefore the lowest entropy. Liquids are more disordered and it takes less energy to hold them together. Therefore they are higher in entropy than solids, but lower than gases, which are so disordered that they have the highest entropy and lowest amount of energy spent holding them together.

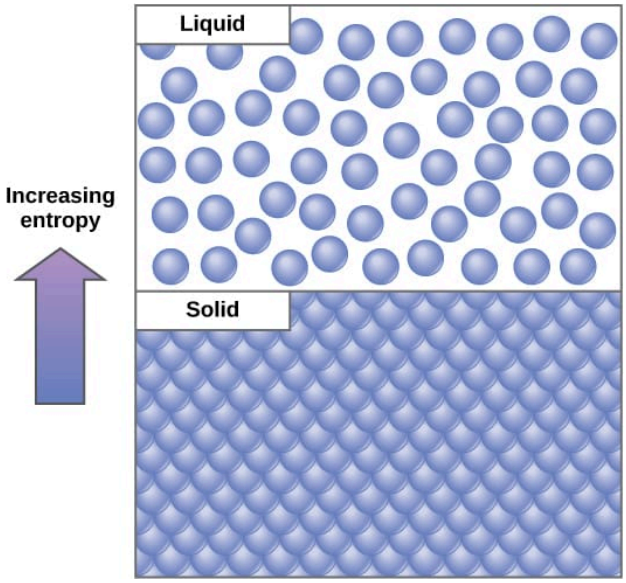


Figure 6.7.1: Entropy: Entropy is a measure of randomness or disorder in a system. Gases have higher entropy than liquids, and liquids have higher entropy than solids.

Entropy changes also occur in chemical reactions. In an exergonic chemical reaction where energy is released, entropy increases because the final products have less energy inside them holding their chemical bonds together. That energy has been lost to the environment, usually in the form of heat.

All physical systems can be thought of in this way. Living things are highly ordered, requiring constant energy input to be maintained in a state of low entropy. As living systems take in energy-storing molecules and transform them through chemical reactions, they lose some amount of usable energy in the process because no reaction is completely efficient. They also produce waste and by-products that are not useful energy sources. This process increases the entropy of the system's surroundings. Since all energy transfers result in the loss of some usable energy, the second law of thermodynamics states that every energy transfer or transformation increases the entropy of the universe. Even though living things are highly ordered and maintain a state of low entropy, the entropy of the universe in total is constantly increasing due to the loss of usable energy with each energy transfer that occurs. Essentially, living things are in a continuous uphill battle against this constant increase in universal entropy.

Key Points

- During energy transfer, some amount of energy is lost in the form of unusable heat energy.
- Because energy is lost in an unusable form, no energy transfer is completely efficient.
- The more energy that is lost by a system to its surroundings, the less ordered and more random the system is.
- Entropy is a measure of randomness and disorder; high entropy means high disorder and low energy.
- As chemical reactions reach a state of equilibrium, entropy increases; and as molecules at a high concentration in one place diffuse and spread out, entropy also increases.

Key Terms

- **second law of thermodynamics**: Every energy transfer or transformation increases the entropy of the universe since all energy transfers result in the loss of some usable energy.
- **entropy**: A measure of randomness and disorder in a system.

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6.8: Potential, Kinetic, Free, and Activation Energy - Activation Energy

Learning Objectives

- Discuss the concept of activation energy

Many chemical reactions, and almost all biochemical reactions do not occur spontaneously and must have an initial input of energy (called the activation energy) to get started. Activation energy must be considered when analyzing both endergonic and exergonic reactions. Exergonic reactions have a net release of energy, but they still require a small amount of energy input before they can proceed with their energy-releasing steps. This small amount of energy input necessary for all chemical reactions to occur is called the activation energy (or free energy of activation) and is abbreviated E_A.

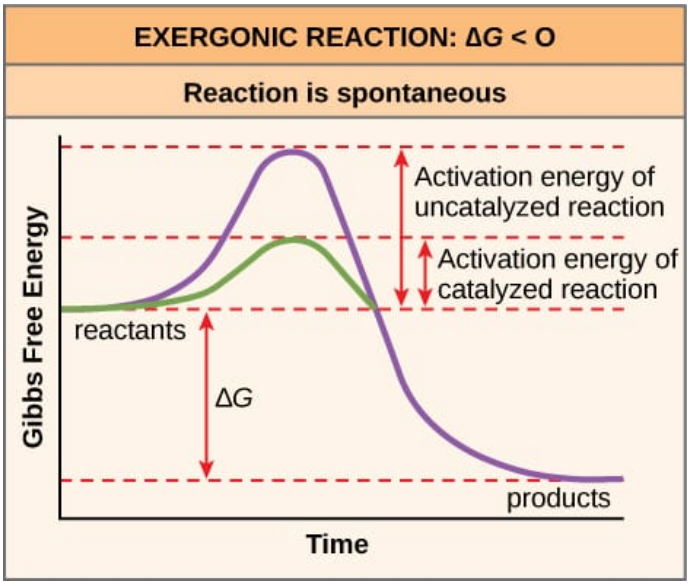


Figure 6.8.1: Activation energy: Activation energy is the energy required for a reaction to proceed; it is lower if the reaction is catalyzed. The horizontal axis of this diagram describes the sequence of events in time.

Activation Energy in Chemical Reactions

Why would an energy-releasing, negative ΔG reaction actually require some energy to proceed? The reason lies in the steps that take place during a chemical reaction. During chemical reactions, certain chemical bonds are broken and new ones are formed. For example, when a glucose molecule is broken down, bonds between the carbon atoms of the molecule are broken. Since these are energy-storing bonds, they release energy when broken. However, to get them into a state that allows the bonds to break, the molecule must be somewhat contorted. A small energy input is required to achieve this contorted state, which is called the *transition state*: it is a high-energy, unstable state. For this reason, reactant molecules don't last long in their transition state, but very quickly proceed to the next steps of the chemical reaction.

Cells will at times couple an exergonic reaction ($\Delta G<0$) with endergonic reactions ($\Delta G>0$), allowing them to proceed. This spontaneous shift from one reaction to another is called energy coupling. The free energy released from the exergonic reaction is absorbed by the
endergonic reaction. One example of energy coupling using ATP involves a transmembrane ion pump that is extremely important for cellular function.

Free Energy Diagrams

Free energy diagrams illustrate the energy profiles for a given reaction. Whether the reaction is exergonic ($\Delta G<0$) or endergonic ($\Delta G>0$) determines whether the products in the diagram will exist at a lower or higher energy state than the reactants. However, the measure of the activation energy is *independent* of the reaction's ΔG. In other words, at a given temperature, the activation energy depends on the nature of the chemical transformation that takes place, but not on the relative energy state of the reactants and products.

Although the image above discusses the concept of activation energy within the context of the exergonic forward reaction, the same principles apply to the reverse reaction, which must be endergonic. Notice that the activation energy for the reverse reaction is larger than for the forward reaction.

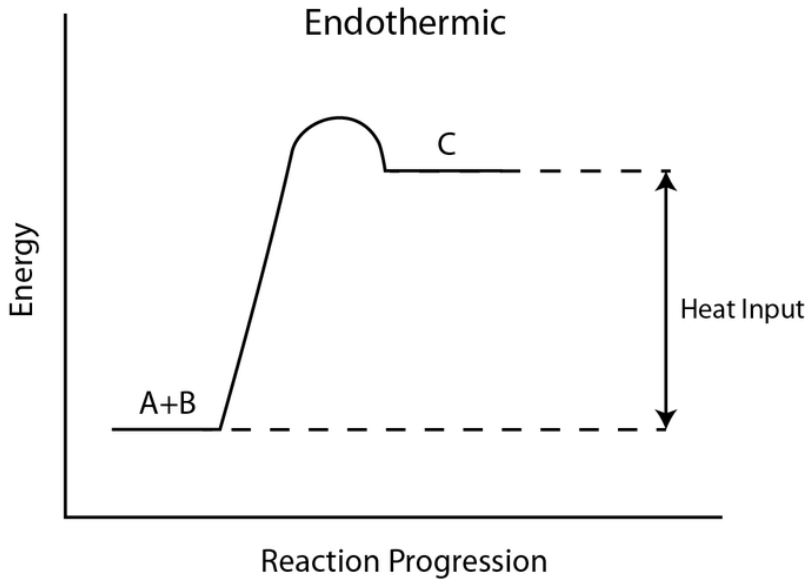


Figure 6.8.1: Activation energy in an endergonic reaction: In this endergonic reaction, activation energy is still required to transform the reactants A + B into the product C. This figure implies that the activation energy is in the form of heat energy.

Heat Energy

The source of the activation energy needed to push reactions forward is typically heat energy from the surroundings. Heat energy (the total bond energy of reactants or products in a chemical reaction) speeds up the motion of molecules, increasing the frequency and force with which they collide. It also moves atoms and bonds within the molecule slightly, helping them reach their transition state. For this reason, heating up a system will cause chemical reactants within that system to react more frequently. Increasing the pressure on a system has the same effect. Once reactants have absorbed enough heat energy from their surroundings to reach the transition state, the reaction will proceed.

The activation energy of a particular reaction determines the rate at which it will proceed. The higher the activation energy, the slower the chemical reaction will be. The example of iron rusting illustrates an inherently slow reaction. This reaction occurs slowly over time because of its high E_A. Additionally, the burning of many fuels, which is strongly exergonic, will take place at a negligible rate unless their activation energy is overcome by sufficient heat from a spark. Once they begin to burn, however, the chemical reactions release enough heat to continue the burning process, supplying the activation energy for surrounding fuel molecules.

Like these reactions outside of cells, the activation energy for most cellular reactions is too high for heat energy to overcome at efficient rates. In other words, in order for important cellular reactions to occur at significant rates (number of reactions per unit time), their activation energies must be lowered; this is referred to as catalysis. This is a very good thing as far as living cells are concerned. Important macromolecules, such as proteins, DNA, and RNA, store considerable energy, and their breakdown is exergonic. If cellular temperatures alone provided enough heat energy for these exergonic reactions to overcome their activation barriers, the essential components of a cell would disintegrate.

The Arrhenius Equation

The Arrhenius equations relates the rate of a chemical reaction to the magnitude of the activation energy:

$$k=Ae^{E_a/RT}$$

where

- k is the reaction rate coefficient or constant
- A is the frequency factor of the reaction. It is determined experimentally.
- R is the Universal Gas constant
- T is the temperature in Kelvin

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Key Points

- Reactions require an input of energy to initiate the reaction; this is called the activation energy (E_A).
- Activation energy is the amount of energy required to reach the transition state.
- The source of the activation energy needed to push reactions forward is typically heat energy from the surroundings.
- For cellular reactions to occur fast enough over short time scales, their activation energies are lowered by molecules called catalysts.
- Enzymes are catalysts.

Key Terms

- **activation energy**: The minimum energy required for a reaction to occur.
- **catalysis**: The increase in the rate of a chemical reaction by lowering its activation energy.
- **transition state**: An intermediate state during a chemical reaction that has a higher energy than the reactants or the products.

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6.9: ATP - Adenosine Triphosphate

Learning Objectives

- Explain the role of ATP as the currency of cellular energy

ATP: Adenosine Triphosphate

Adenosine triphosphate (ATP) is the energy currency for cellular processes. ATP provides the energy for both energy-consuming endergonic reactions and energy-releasing exergonic reactions, which require a small input of activation energy. When the chemical bonds within ATP are broken, energy is released and can be harnessed for cellular work. The more bonds in a molecule, the more potential energy it contains. Because the bond in ATP is so easily broken and reformed, ATP is like a rechargeable battery that powers cellular process ranging from DNA replication to protein synthesis.

Molecular Structure

Adenosine triphosphate (ATP) is comprised of the molecule adenosine bound to three phosphate groups. Adenosine is a nucleoside consisting of the nitrogenous base adenine and the five-carbon sugar ribose. The three phosphate groups, in order of closest to furthest from the ribose sugar, are labeled alpha, beta, and gamma. Together, these chemical groups constitute an energy powerhouse. The two bonds between the phosphates are equal high-energy bonds (phosphoanhydride bonds) that, when broken, release sufficient energy to power a variety of cellular reactions and processes. The bond between the beta and gamma phosphate is considered “high-energy” because when the bond breaks, the products [adenosine diphosphate (ADP) and one inorganic phosphate group (P_i)] have a lower free energy than the reactants (ATP and a water molecule). ATP breakdown into ADP and P_i is called hydrolysis because it consumes a water molecule (hydro-, meaning “water”, and lysis, meaning “separation”).

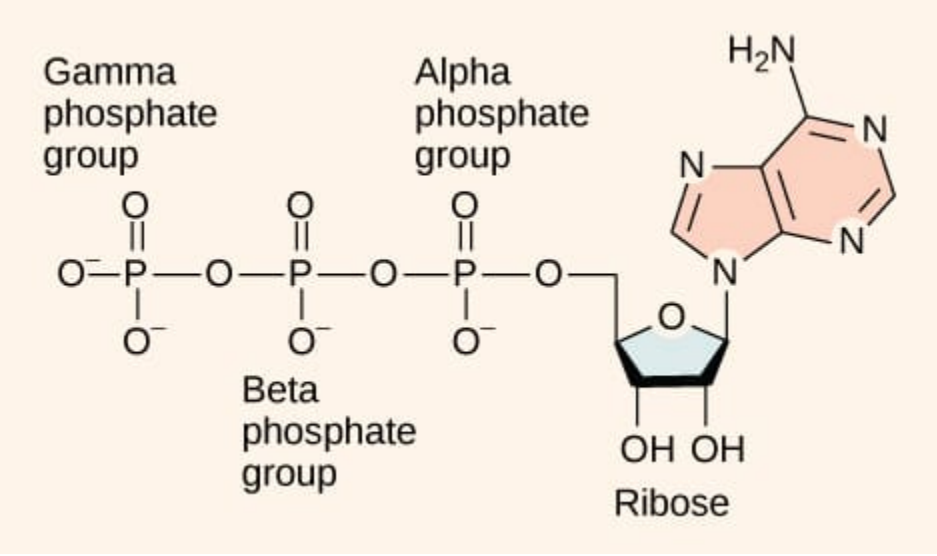


Figure 6.9.1: Adenosine Triphosphate (ATP): ATP is the primary energy currency of the cell. It has an adenosine backbone with three phosphate groups attached.

ATP Hydrolysis and Synthesis

ATP is hydrolyzed into ADP in the following reaction:

$ATP + H_2O \rightarrow ADP + P_i + \text{free energy}$

Like most chemical reactions, the hydrolysis of ATP to ADP is reversible. The reverse reaction combines ADP + P_i to regenerate ATP from ADP. Since ATP hydrolysis releases energy, ATP synthesis must require an input of free energy.

ADP is combined with a phosphate to form ATP in the following reaction:

$ADP + P_i + \text{free energy} \rightarrow ATP + H_2O$

ATP and Energy Coupling

Exactly how much free energy (ΔG) is released with the hydrolysis of ATP, and how is that free energy used to do cellular work? The calculated ΔG for the hydrolysis of one mole of ATP into ADP and P_i is –7.3 kcal/mole (–30.5 kJ/mol). However, this is only true under standard conditions, and the ΔG for the hydrolysis of one mole of ATP in a living cell is almost double the value at standard conditions: 14 kcal/mol (–57 kJ/mol).

ATP is a highly unstable molecule. Unless quickly used to perform work, ATP spontaneously dissociates into ADP + P_i, and the free energy released during this process is lost as heat. To harness the energy within the bonds of ATP, cells use a strategy called energy coupling.

Energy Coupling in Sodium-Potassium Pumps

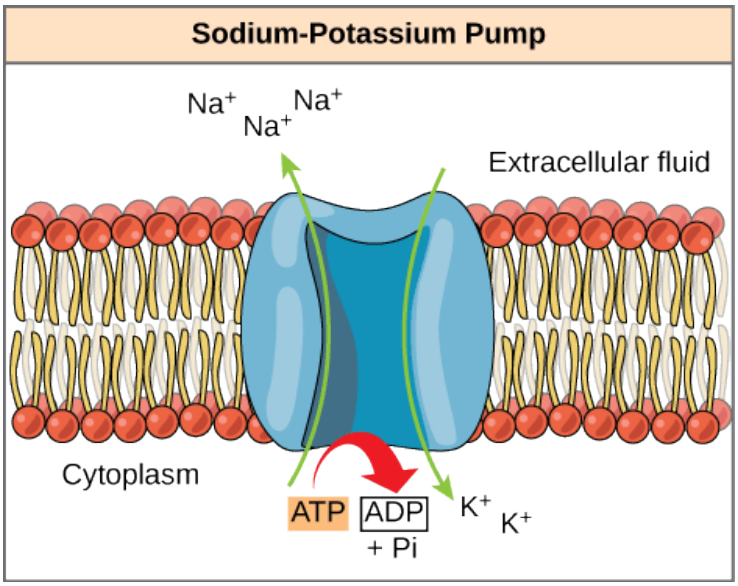


Figure 6.9.1: Energy Coupling: Sodium-potassium pumps use the energy derived from exergonic ATP hydrolysis to pump sodium and potassium ions across the cell membrane.

Cells couple the exergonic reaction of ATP hydrolysis with the endergonic reactions of cellular processes. For example, transmembrane ion pumps in nerve cells use the energy from ATP to pump ions across the cell membrane and generate an action potential. The sodium-potassium pump (Na^+/K^+pump) drives sodium out of the cell and potassium into the cell. When ATP is hydrolyzed, it transfers its gamma phosphate to the pump protein in a process called phosphorylation. The Na^+/K^+ pump gains the free energy and undergoes a conformational change, allowing it to release three Na^+ to the outside of the cell. Two extracellular K^+ ions bind to the protein, causing the protein to change shape again and discharge the phosphate. By donating free energy to the Na^+/K^+ pump, phosphorylation drives the endergonic reaction.

Energy Coupling in Metabolism

During cellular metabolic reactions, or the synthesis and breakdown of nutrients, certain molecules must be altered slightly in their conformation to become substrates for the next step in the reaction series. In the very first steps of cellular respiration, glucose is broken down through the process of glycolysis. ATP is required for the phosphorylation of glucose, creating a high-

energy but unstable intermediate. This phosphorylation reaction causes a conformational change that allows enzymes to convert the phosphorylated glucose molecule to the phosphorylated sugar fructose. Fructose is a necessary intermediate for glycolysis to move forward. In this example, the exergonic reaction of ATP hydrolysis is coupled with the endergonic reaction of converting glucose for use in the metabolic pathway.

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Key Points

- Adenosine triphosphate is composed of the nitrogenous base adenine, the five-carbon sugar ribose, and three phosphate groups.
- ATP is hydrolyzed to ADP in the reaction $ATP+H2O \rightarrow ADP+Pi+$ free energy; the calculated ΔG for the hydrolysis of 1 mole of ATP is -57 kJ/mol.
- ADP is combined with a phosphate to form ATP in the reaction $ADP+Pi+\text{free energy} \rightarrow ATP+H2O$.
- The energy released from the hydrolysis of ATP into ADP is used to perform cellular work, usually by coupling the exergonic reaction of ATP hydrolysis with endergonic reactions.
- Sodium-potassium pumps use the energy derived from exergonic ATP hydrolysis to pump sodium and potassium ions across the cell membrane while phosphorylation drives the endergonic reaction.

Key Terms

- **energy coupling**: Energy coupling occurs when the energy produced by one reaction or system is used to drive another reaction or system.
- **endergonic**: Describing a reaction that absorbs (heat) energy from its environment.
- **exergonic**: Describing a reaction that releases energy (heat) into its environment.
- **free energy**: Gibbs free energy is a thermodynamic potential that measures the useful or process-initiating work obtainable from a thermodynamic system at a constant temperature and pressure (isothermal, isobaric).
- **hydrolysis**: A chemical process of decomposition involving the splitting of a bond by the addition of water.

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6.10: Enzymes - Active Site and Substrate Specificity

Learning Objectives

- Describe models of substrate binding to an enzyme's active site.

Enzyme Active Site and Substrate Specificity

Enzymes bind with chemical reactants called substrates. There may be one or more substrates for each type of enzyme, 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, both become modified, and leave the reaction as two products.

The enzyme's active site binds to the substrate. Since enzymes are proteins, this site is composed of a unique combination of amino acid residues (side chains or R groups). Each amino acid residue can be large or small; weakly acidic or basic; hydrophilic or hydrophobic; and positively-charged, negatively-charged, or neutral. The positions, sequences, structures, and properties of these residues create a very specific chemical environment within the active site. A specific chemical substrate matches this site like a jigsaw puzzle piece and makes the enzyme specific to its substrate.

Active Sites and Environmental Conditions

Environmental conditions can affect an enzyme's active site and, therefore, the rate at which a chemical reaction can proceed. Increasing the environmental temperature generally increases reaction rates because the molecules are moving more quickly and are more likely to come into contact with each other.

However, increasing or decreasing the temperature outside of an optimal range can affect chemical bonds within the enzyme and change its shape. If the enzyme changes shape, the active site may no longer bind to the appropriate substrate and the rate of reaction will decrease. Dramatic changes to the temperature and pH will eventually cause enzymes to denature.

Induced Fit and Enzyme Function

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 more refined view called induced fit. As the enzyme and substrate come together, their interaction causes a mild shift in the enzyme's structure that confirms an ideal binding arrangement between the enzyme and the substrate. This dynamic binding maximizes the enzyme's ability to catalyze its reaction.

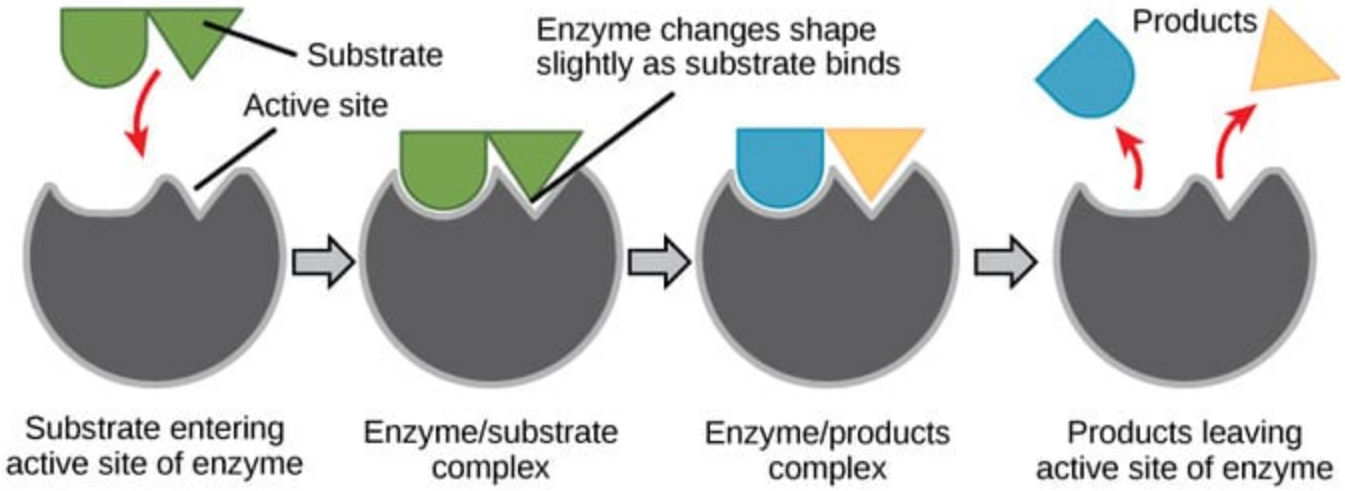


Figure 6.10.1: Induced Fit: According to the induced fit model, both enzyme and substrate undergo dynamic conformational changes upon binding. The enzyme contorts the substrate into its transition state, thereby increasing the rate of the reaction.

Enzyme-Substrate Complex

When an enzyme binds its substrate, it forms an enzyme-substrate complex. This complex lowers the activation energy of the reaction and promotes its rapid progression by providing certain ions or chemical groups that actually form covalent bonds with molecules as a necessary step of the reaction process. Enzymes also promote chemical reactions by bringing substrates together in an optimal orientation, lining up the atoms and bonds of one molecule with the atoms and bonds of the other molecule. This can contort the substrate molecules and facilitate bond-breaking. The active site of an enzyme also creates an ideal environment, such as a slightly acidic or non-polar environment, for the reaction to occur. The enzyme will always return to its original state at the completion of the reaction. One of the important properties of enzymes is that they remain ultimately unchanged by the reactions they catalyze. After an enzyme is done catalyzing a reaction, it releases its products (substrates).

Key Points

- The enzyme ‘s active site binds to the substrate.
- Increasing the temperature generally increases the rate of a reaction, but dramatic changes in temperature and pH can denature an enzyme, thereby abolishing its action as a catalyst.
- The induced fit model states an substrate binds to an active site and both change shape slightly, creating an ideal fit for catalysis.
- When an enzyme binds its substrate it forms an enzyme-substrate complex.
- Enzymes promote chemical reactions by bringing substrates together in an optimal orientation, thus creating an ideal chemical environment for the reaction to occur.
- The enzyme will always return to its original state at the completion of the reaction.

Key Terms

- **substrate**: A reactant in a chemical reaction is called a substrate when acted upon by an enzyme.
- **induced fit**: Proposes that the initial interaction between enzyme and substrate is relatively weak, but that these weak interactions rapidly induce conformational changes in the enzyme that strengthen binding.
- **active site**: The active site is the part of an enzyme to which substrates bind and where a reaction is catalyzed.

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6.11: Enzymes - Control of Metabolism Through Enzyme Regulation

Learning Objectives

- Explain the effect of an enzyme on chemical equilibrium

Control of Metabolism Through Enzyme Regulation

Cellular needs and conditions vary from cell to cell and change within individual cells over time. For example, a stomach cell requires a different amount of energy than a skin cell, fat storage cell, blood cell, or nerve cell. The same stomach cell may also need more energy immediately after a meal and less energy between meals.

A cell's function is encapsulated by the chemical reactions it can carry out. Enzymes lower the activation energies of chemical reactions; in cells, they promote those reactions that are specific to the cell's function. Because enzymes ultimately determine which chemical reactions a cell can carry out and the rate at which they can proceed, they are key to cell functionality.

Competitive and Noncompetitive Inhibition

The cell uses specific molecules to regulate enzymes in order to promote or inhibit certain chemical reactions. Sometimes it is necessary to inhibit an enzyme to reduce a reaction rate, and there is more than one way for this inhibition to occur. In competitive inhibition, an inhibitor molecule is similar enough to a substrate that it can bind to the enzyme's active site to stop it from binding to the substrate. It "competes" with the substrate to bind to the enzyme.

In noncompetitive inhibition, an inhibitor molecule binds to the enzyme at a location other than the active site (an allosteric site). The substrate can still bind to the enzyme, but the inhibitor changes the shape of the enzyme so it is no longer in optimal position to catalyze the reaction.

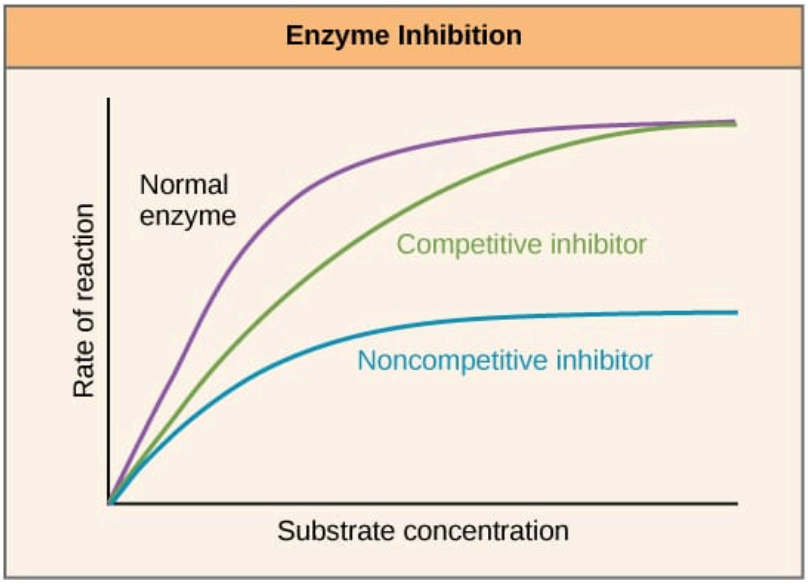


Figure 6.11.1: Enzyme inhibition: Competitive and noncompetitive inhibition affect the rate of reaction differently. Competitive inhibitors affect the initial rate, but do not affect the maximal rate, whereas noncompetitive inhibitors affect the maximal rate.

Allosteric Inhibition and Activation

In noncompetitive allosteric inhibition, inhibitor molecules bind to an enzyme at the allosteric site. Their binding induces a conformational change that reduces the affinity of the enzyme's active site for its substrate. The binding of this allosteric inhibitor changes the conformation of the enzyme and its active site, so the substrate is not able to bind. This prevents the enzyme from lowering the activation energy of the reaction, and the reaction rate is reduced.

However, allosteric inhibitors are not the only molecules that bind to allosteric sites. Allosteric activators can increase reaction rates. They bind to an allosteric site which induces a conformational change that *increases* the affinity of the enzyme's active site for its substrate. This increases the reaction rate.

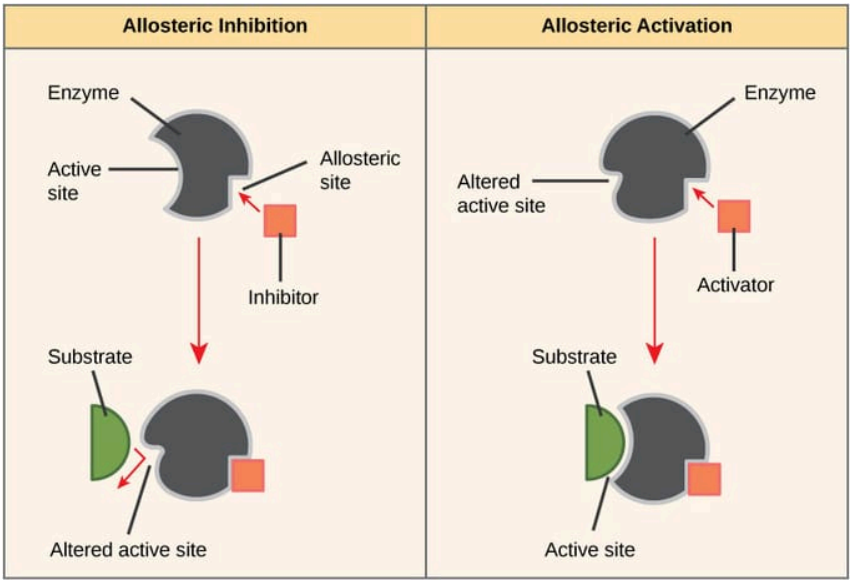


Figure 6.11.1: Allosteric inhibitors and activators: Allosteric inhibitors modify the active site of the enzyme so that substrate binding is reduced or prevented. In contrast, allosteric activators modify the active site of the enzyme so that the affinity for the substrate increases.

Cofactors and Coenzymes

Many enzymes only work if bound to non-protein helper molecules called cofactors and coenzymes. Binding to these molecules promotes optimal conformation and function for their respective enzymes. These molecules bind temporarily through ionic or hydrogen bonds or permanently through stronger covalent bonds.

Cofactors are inorganic ions such as iron (Fe^{2+}) and magnesium (Mg^{2+}). For example, DNA polymerase requires a zinc ion (Zn^{2+}) to build DNA molecules. Coenzymes are organic helper molecules with a basic atomic structure made up of carbon and hydrogen. The most common coenzymes are dietary vitamins. Vitamin C is a coenzyme for multiple enzymes that take part in building collagen, an important component of connective tissue. Pyruvate dehydrogenase is a complex of several enzymes that requires one cofactor and five different organic coenzymes to catalyze its chemical reaction. The availability of various cofactors and coenzymes regulates enzyme function.

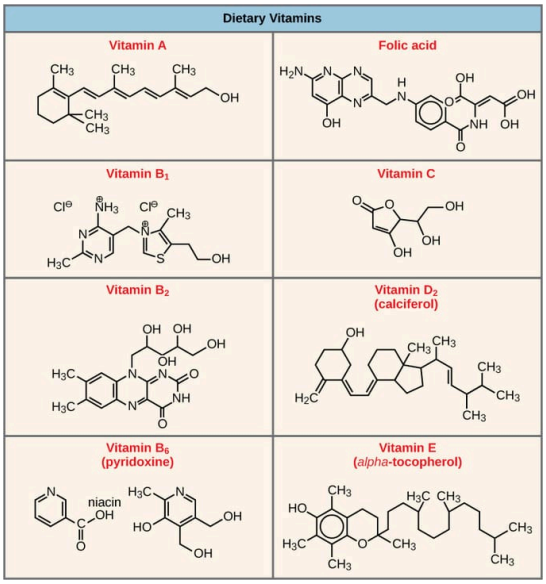


Figure 6.11.1: Vitamins: Vitamins are important coenzymes or precursors of coenzymes and are required for enzymes to function properly. Multivitamin capsules usually contain mixtures of all the vitamins at different percentages.

Enzyme Compartmentalization

In eukaryotic cells, molecules such as enzymes are usually compartmentalized into different organelles. This organization contributes to enzyme regulation because certain cellular processes are contained in separate organelles. For example, the enzymes involved in the later stages of cellular respiration carry out reactions exclusively in the mitochondria. The enzymes involved in the digestion of cellular debris and foreign materials are located within lysosomes.

Feedback Inhibition in Metabolic Pathways

Feedback inhibition is when a reaction product is used to regulate its own further production. Cells have evolved to use feedback inhibition to regulate enzyme activity in metabolism, by using the products of the enzymatic reactions to inhibit further enzyme activity. Metabolic reactions, such as anabolic and catabolic processes, must proceed according to the demands of the cell. In order to maintain chemical equilibrium and meet the needs of the cell, some metabolic products inhibit the enzymes in the chemical pathway while some reactants activate them.

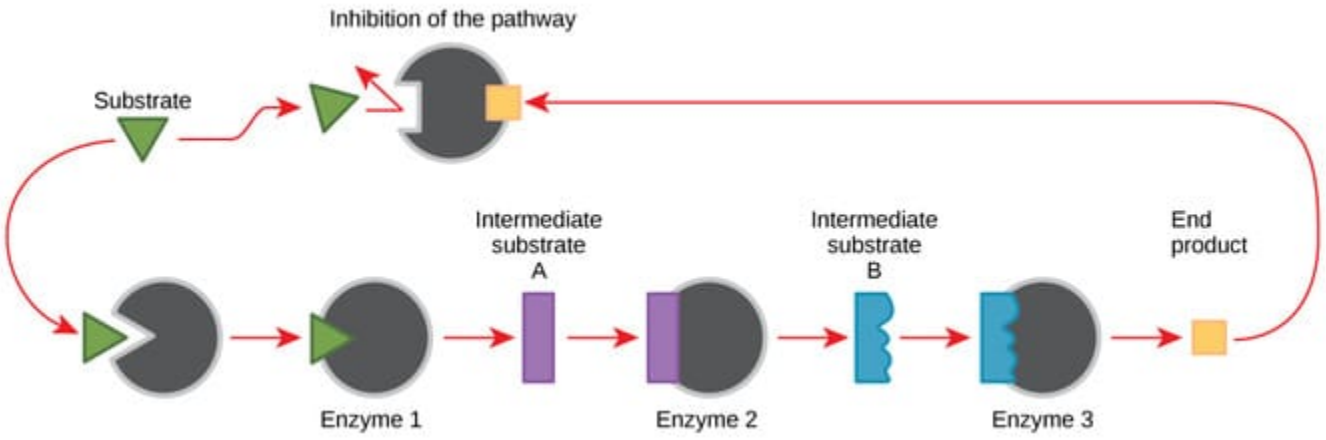


Figure 6.11.1: Feedback inhibition: Metabolic pathways are a series of reactions catalyzed by multiple enzymes. Feedback inhibition, where the end product of the pathway inhibits an earlier step, is an important regulatory mechanism in cells.

The production of both amino acids and nucleotides is controlled through feedback inhibition. For an example of feedback inhibition, consider ATP. It is the product of the catabolic metabolism of sugar (cellular respiration), but it also acts as an allosteric

regulator for the same enzymes that produced it. ATP is an unstable molecule that can spontaneously dissociate into ADP; if too much ATP were present, most of it would go to waste. This feedback inhibition prevents the production of additional ATP if it is already abundant. However, while ATP is an inhibitor, ADP is an allosteric activator. When levels of ADP are high compared to ATP levels, ADP triggers the catabolism of sugar to produce more ATP.

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Key Points

- In competitive inhibition, an inhibitor molecule competes with a substrate by binding to the enzyme ‘s active site so the substrate is blocked.
- In noncompetitive inhibition (also known as allosteric inhibition), an inhibitor binds to an allosteric site; the substrate can still bind to the enzyme, but the enzyme is no longer in optimal position to catalyze the reaction.
- Allosteric inhibitors induce a conformational change that changes the shape of the active site and reduces the affinity of the enzyme’s active site for its substrate.
- Allosteric activators induce a conformational change that changes the shape of the active site and increases the affinity of the enzyme’s active site for its substrate.
- Feedback inhibition involves the use of a reaction product to regulate its own further production.
- Inorganic cofactors and organic coenzymes promote optimal enzyme orientation and function.
- Vitamins act as coenzymes (or precursors to coenzymes) and are necessary for enzymes to function.

Key Terms

- **coenzyme**: An organic molecule that is necessary for an enzyme to function.
- **allosteric site**: A site other than the active site on an enzyme.
- **cofactor**: An inorganic molecule that is necessary for an enzyme to function.

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7: CELLULAR RESPIRATION

Cellular respiration is a set of metabolic reactions and processes that take place in the cells of organisms to convert biochemical energy from nutrients into adenosine triphosphate (ATP), and then release waste products.

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7.1: Energy in Living Systems - Transforming Chemical Energy

Learning Objectives

- Discuss the importance of cellular respiration

Introduction: Cellular Respiration

An electrical energy plant converts energy from one form to another form that can be more easily used. For example, geothermal energy plants start with underground thermal energy (heat) and transform it into electrical energy that will be transported to homes and factories.



Figure 7.1.1: Energy Plant: This geothermal energy plant transforms thermal energy from deep in the ground into electrical energy, which can be easily used.

Like a generating plant, living organisms must take in energy from their environment and convert it into to a form their cells can use. Organisms ingest large molecules, like carbohydrates, proteins, and fats, and convert them into smaller molecules like carbon dioxide and water. This process is called cellular respiration, a form of catabolism, and makes energy available for the cell to use. The energy released by cellular respiration is temporarily captured by the formation of adenosine triphosphate (ATP) within the cell. ATP is the principle form of stored energy used for cellular functions and is frequently referred to as the energy currency of the cell.

The nutrients broken down through cellular respiration lose electrons throughout the process and are said to be oxidized. When oxygen is used to help drive the oxidation of nutrients the process is called aerobic respiration. Aerobic respiration is common among the eukaryotes, including humans, and takes place mostly within the mitochondria. Respiration occurs within the cytoplasm of prokaryotes. Several prokaryotes and a few eukaryotes use an inorganic molecule other than oxygen to drive the oxidation of their nutrients in a process called anaerobic respiration. Electron acceptors for anaerobic respiration include nitrate, sulfate, carbon dioxide, and several metal ions.

The energy released during cellular respiration is then used in other biological processes. These processes build larger molecules that are essential to an organism's survival, such as amino acids, DNA, and proteins. Because they synthesize new molecules, these processes are examples of anabolism.

Key Points

- Organisms ingest organic molecules like the carbohydrate glucose to obtain the energy needed for cellular functions.
- The energy in glucose can be extracted in a series of chemical reactions known as cellular respiration.
- Cellular respiration produces energy in the form of ATP, which is the universal energy currency for cells.

Key Terms

- **aerobic respiration**: the process of converting the biochemical energy in nutrients to ATP in the presence of oxygen
- **adenosine triphosphate**: a multifunctional nucleoside triphosphate used in cells as a coenzyme, often called the “molecular unit of energy currency” in intracellular energy transfer
- **cellular respiration**: the set of the metabolic reactions and processes that take place in the cells of organisms to convert biochemical energy from nutrients into adenosine triphosphate (ATP)
- **catabolism**: the breakdown of large molecules into smaller ones usually accompanied by the release of energy

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7.2: Energy in Living Systems - Electrons and Energy

Learning Objectives

- Describe the role played by electrons in energy production and storage

Electrons and Energy

The removal of an electron from a molecule via a process called oxidation results in a decrease in the potential energy stored in the oxidized compound. When oxidation occurs in the cell, the electron (sometimes as part of a hydrogen atom) does not remain un-bonded in the cytoplasm. Instead, the electron shifts to a second compound, reducing the second compound (oxidation of one species always occurs in tandem with reduction of another).

The shift of an electron from one compound to another removes some potential energy from the first compound (the oxidized compound) and increases the potential energy of the second compound (the reduced compound). The transfer of electrons between molecules via oxidation and reduction is important because most of the energy stored in atoms is in the form of high-energy electrons; it is this energy that is used to fuel cellular functions. The transfer of energy in the form of electrons allows the cell to transfer and use energy in an incremental fashion: in small packages rather than as a single, destructive burst.

Electron carriers

In living systems, a small class of molecules functions as electron shuttles: they bind and carry high-energy electrons between compounds in cellular pathways. The principal electron carriers we will consider are derived from the vitamin B group, which are derivatives of nucleotides. These compounds can be easily reduced (that is, they accept electrons) or oxidized (they lose electrons). Nicotinamide adenine dinucleotide (NAD) is derived from vitamin B3, niacin. NAD^+ is the oxidized form of niacin; NADH is the reduced form after it has accepted two electrons and a proton (which together are the equivalent of a hydrogen atom with an extra electron). It is noteworthy that NAD^+*must* accept two electrons at once; it cannot serve as a one-electron carrier.

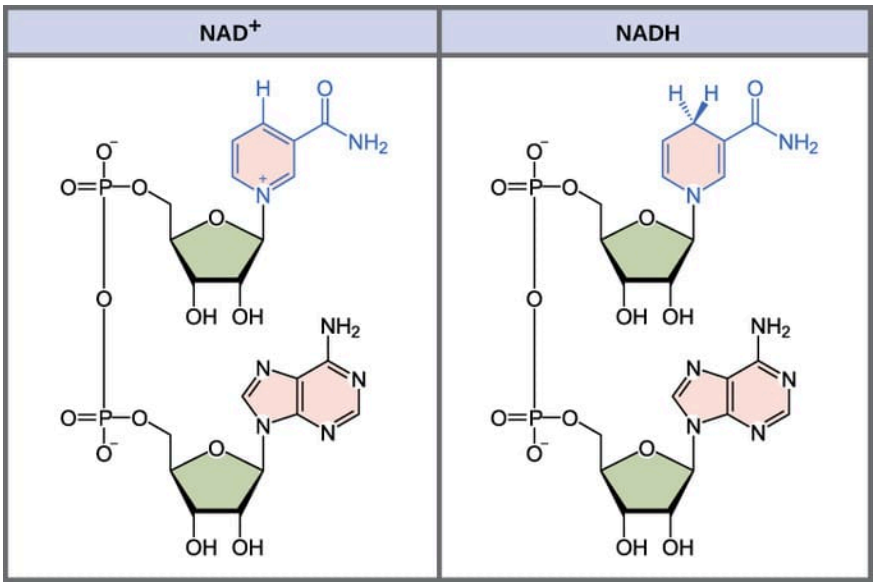


Figure 7.2.1: The structure of NADH and NAD+: The oxidized form of the electron carrier (NAD+) is shown on the left and the reduced form (NADH) is shown on the right. The nitrogenous base in NADH has one more hydrogen ion and two more electrons than in NAD+.

NAD^+ can accept electrons from an organic molecule according to the general equation:

RH (Reducing agent) + NAD^+ (Oxidizing agent) → NADH (Reduced) + R (Oxidized)

When electrons are added to a compound, the compound is reduced. A compound that reduces another is called a reducing agent. In the above equation, RH is a reducing agent and NAD^+ is reduced to NADH. When electrons are removed from a compound, the compound is oxidized. In the above equation, NAD^+ is an oxidizing agent and RH is oxidized to R. The molecule NADH is critical for cellular respiration and other metabolic pathways.

Similarly, flavin adenine dinucleotide (FAD^+) is derived from vitamin B_2, also called riboflavin. Its reduced form is $FADH_2$. A second variation of NAD, NADP, contains an extra phosphate group. Both NAD^+ and FAD^+ are extensively used in energy extraction from sugars, and NADP plays an important role in anabolic reactions and photosynthesis.

Key Points

- When electrons are added to a compound, the compound is reduced; a compound that reduces another is called a reducing agent.
- When electrons are removed from a compound, the compound is considered oxidized; a compound that oxidizes another is called an oxidizing agent.
- The transfer of energy in the form of electrons allows the cell to transfer and use energy in an incremental fashion.
- The principle electron carriers are NAD+ and NADH because they can be easily oxidized and reduced, respectively.
- NAD+ is the oxidized form of the niacin and NADH is the reduced form after it has accepted two electrons and a proton.

Key Terms

- **oxidation**: A reaction in which the atoms of an element lose electrons and the valence of the element increases.
- **reduction**: A reaction in which electrons are gained and valence is reduced; often by the removal of oxygen or the addition of hydrogen.
- **nicotinamide adenine dinucleotide**: (NAD) An organic coenzyme involved in biological oxidation and reduction reactions.
- **electron shuttle**: molecules that bind and carry high-energy electrons between compounds in cellular pathways

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7.3: Energy in Living Systems - ATP in Metabolism

Learning Objectives

- Compare the two methods by which cells utilize ATP for energy.

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 lead to excessive thermal motion that could damage and then destroy the cell. Rather, a cell must be able to handle that energy in a way that enables the cell to store energy safely and release it for use as needed. Living cells accomplish this by using the compound adenosine triphosphate (ATP). ATP is often called the “energy currency” of the cell and can be used to fill any energy need of the cell.

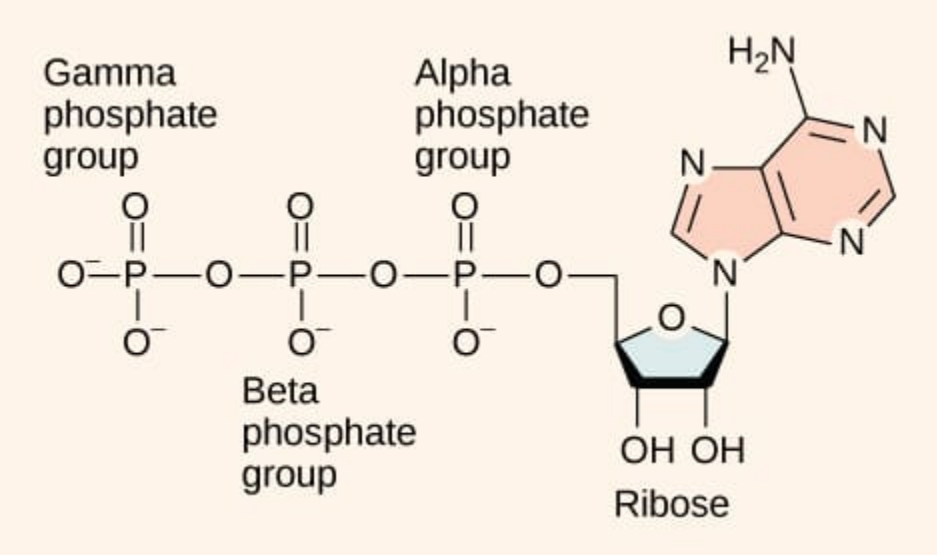


Figure 7.3.1: Adenosine triphosphate.: ATP (adenosine triphosphate) has three phosphate groups that can be removed by hydrolysis to form ADP (adenosine diphosphate) or AMP (adenosine monophosphate).The negative charges on the phosphate group naturally repel each other, requiring energy to bond them together and releasing energy when these bonds are broken.

ATP Structure and Function

The core of ATP is a molecule of adenosine monophosphate (AMP), which is composed of an adenine molecule bonded to a ribose molecule and to a single phosphate group. 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 the formation of adenosine diphosphate (ADP); the addition of a third phosphate group forms adenosine triphosphate (ATP).

The addition of a phosphate group to a molecule requires energy. Phosphate groups are negatively charged and, thus, repel one another when they are arranged in a 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 dephosphorylation, releases energy.

Energy from ATP

Hydrolysis is the process of breaking complex macromolecules apart. During hydrolysis, water is split, or lysed, and the resulting hydrogen atom (H^+) and a hydroxyl group (OH^-) are added to the larger molecule. The hydrolysis of ATP produces ADP, together

with an inorganic phosphate ion (P_i), and the release of free energy. To carry out life processes, ATP is continuously broken down into ADP, and, like a rechargeable battery, ADP is continuously regenerated into ATP by the reattachment of a third phosphate group. Water, which was broken down into its hydrogen atom and hydroxyl group during ATP hydrolysis, is regenerated when a third phosphate is added to the ADP molecule, reforming ATP.

Obviously, energy must be infused into the system to regenerate ATP. In nearly every living thing on earth, the energy comes from the metabolism of glucose. In this way, ATP is a direct link between the limited set of exergonic pathways of glucose catabolism and the multitude of endergonic pathways that power living cells.

Phosphorylation

When ATP is broken down by the removal of its terminal phosphate group, energy is released and can be used to do work by the cell. Often the released phosphate is directly transferred to another molecule, such as a protein, activating it. For example, ATP supplies the energy to move the contractile muscle proteins during the mechanical work of muscle contraction. Recall the active transport work of the sodium-potassium pump in cell membranes. Phosphorylation by ATP alters the structure of the integral protein that functions as the pump, changing its affinity for sodium and potassium. In this way, the cell performs work, using energy from ATP to pump ions against their electrochemical gradients.

Sometimes phosphorylation of an enzyme leads to its inhibition. For example, the pyruvate dehydrogenase (PDH) complex could be phosphorylated by pyruvate dehydrogenase kinase (PDHK). This reaction leads to inhibition of PDH and its inability to convert pyruvate into acetyl-CoA.

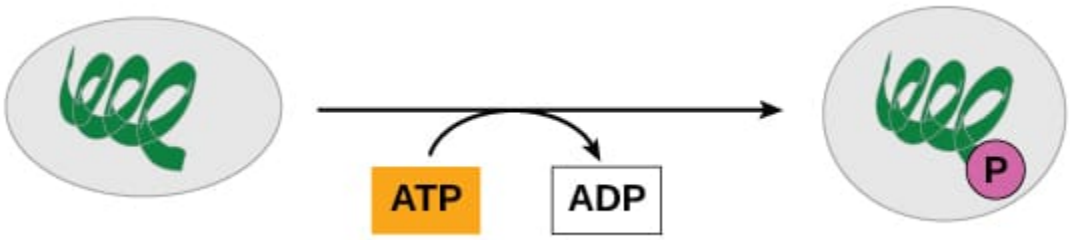


Figure 7.3.1: Protein phosphorylation: In phosphorylation reactions, the gamma phosphate of ATP is attached to a protein.

Energy from ATP hydrolysis

The energy from ATP can also be used to drive chemical reactions by coupling ATP hydrolysis with another reaction process in an enzyme. In many cellular chemical reactions, enzymes bind to several substrates or reactants to form a temporary intermediate complex that allow the substrates and reactants to more readily react with each other. In reactions where ATP is involved, ATP is one of the substrates and ADP is a product. During an endergonic chemical reaction, ATP forms an intermediate complex with the substrate and enzyme in the reaction. This intermediate complex allows the ATP to transfer its third phosphate group, with its energy, to the substrate, a process called phosphorylation. Phosphorylation refers to the addition of the phosphate (~P). When the intermediate complex breaks apart, the energy is used to modify the substrate and convert it into a product of the reaction. The ADP molecule and a free phosphate ion are released into the medium and are available for recycling through cell metabolism. This is illustrated by the following generic reaction:

A + enzyme + ATP → [A enzyme –P] B + enzyme + ADP + phosphate ion

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Key Points

- Cells require a constant supply of energy to survive, but cannot store this energy as free energy as this would result in elevated temperatures and would destroy the cell.
- Cells store energy in the form of adenosine triphosphate, or ATP.
- Energy is released when the terminal phosphate group is removed from ATP.
- To utilize the energy stored as ATP, cells either couple ATP hydrolysis to an energetically unfavorable reaction to allow it to proceed or transfer one of the phosphate groups from ATP to a protein substrate, causing it to change conformations and hence energetic preference.

Key Terms

- **phosphorylation**: the addition of a phosphate group to a compound; often catalyzed by enzymes
- **adenosine triphosphate**: a multifunctional nucleoside triphosphate used in cells as a coenzyme, often called the “molecular unit of energy currency” in intracellular energy transfer
- **phosphate**: Any salt or ester of phosphoric acid

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7.4: Glycolysis - Importance of Glycolysis

Learning Objectives

- Explain the importance of glycolysis to cells

Nearly all of the energy used by living cells comes to them from the energy in the bonds of the sugar glucose. Glucose enters heterotrophic cells in two ways. One method is through secondary active transport in which the transport takes place against the glucose concentration gradient. The other mechanism uses a group of integral proteins called GLUT proteins, also known as glucose transporter proteins. These transporters assist in the facilitated diffusion of glucose. Glycolysis is the first pathway used in the breakdown of glucose to extract energy. It takes place in the cytoplasm of both prokaryotic and eukaryotic cells. It was probably one of the earliest metabolic pathways to evolve since it is used by nearly all of the organisms on earth. The process does not use oxygen and is, therefore, anaerobic.

Glycolysis is the first of the main metabolic pathways of cellular respiration to produce energy in the form of ATP. Through two distinct phases, the six-carbon ring of glucose is cleaved into two three-carbon sugars of pyruvate through a series of enzymatic reactions. The first phase of glycolysis requires energy, while the second phase completes the conversion to pyruvate and produces ATP and NADH for the cell to use for energy. Overall, the process of glycolysis produces a net gain of two pyruvate molecules, two ATP molecules, and two NADH molecules for the cell to use for energy. Following the conversion of glucose to pyruvate, the glycolytic pathway is linked to the Krebs Cycle, where further ATP will be produced for the cell's energy needs.

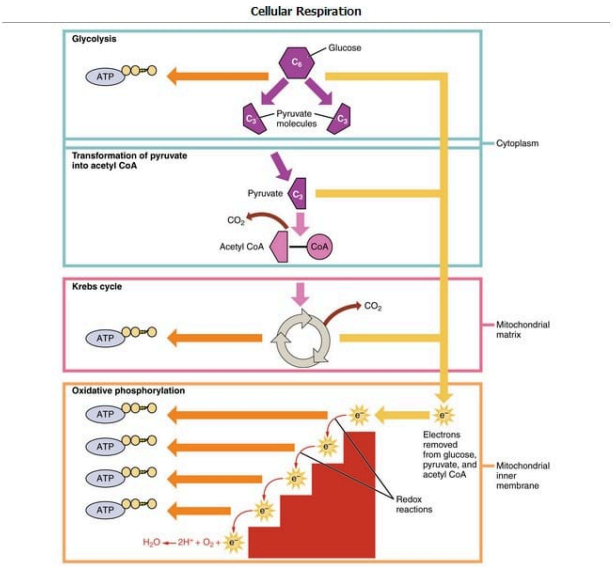


Figure 7.4.1: Cellular Respiration: Glycolysis is the first pathway of cellular respiration that oxidizes glucose molecules. It is followed by the Krebs cycle and oxidative phosphorylation to produce ATP.

Key Points

- Glycolysis is present in nearly all living organisms.
- Glucose is the source of almost all energy used by cells.
- Overall, glycolysis produces two pyruvate molecules, a net gain of two ATP molecules, and two NADH molecules.

Key Terms

- **glycolysis**: the cellular metabolic pathway of the simple sugar glucose to yield pyruvic acid and ATP as an energy source
- **heterotroph**: an organism that requires an external supply of energy in the form of food, as it cannot synthesize its own

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7.5: Glycolysis - The Energy-Requiring Steps of Glycolysis

Learning Objectives

- Outline the energy-requiring steps of glycolysis

First Half of Glycolysis (Energy-Requiring Steps)

In the first half of glycolysis, two adenosine triphosphate (ATP) molecules are used in the phosphorylation of glucose, which is then split into two three-carbon molecules as described in the following steps.

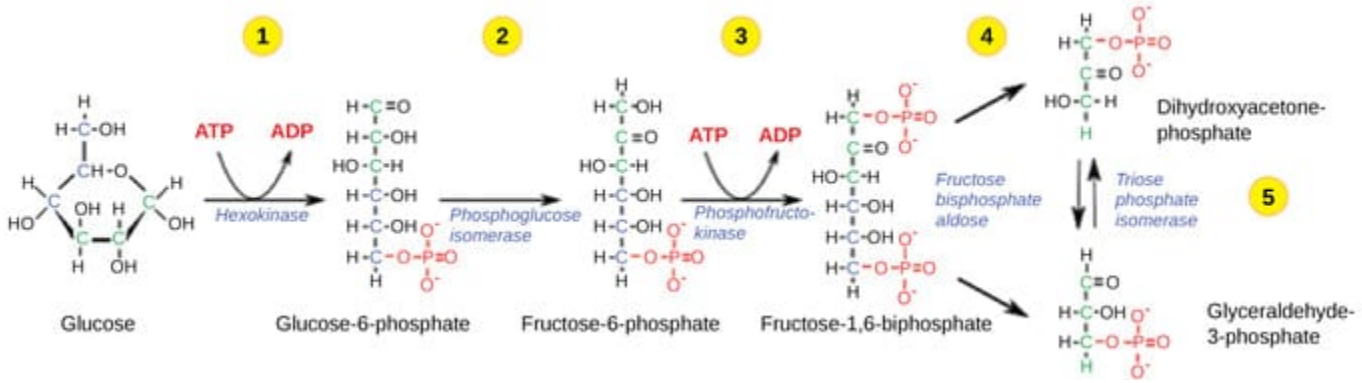


Figure 7.5.1: The first half of glycolysis: investment: The first half of glycolysis uses two ATP molecules in the phosphorylation of glucose, which is then split into two three-carbon molecules.

Step 1. The first step in glycolysis is catalyzed by hexokinase, an enzyme with broad specificity that catalyzes the phosphorylation of six-carbon sugars. Hexokinase phosphorylates glucose using ATP as the source of the phosphate, producing glucose-6-phosphate, a more reactive form of glucose. This reaction prevents the phosphorylated glucose molecule from continuing to interact with the GLUT proteins. It can no longer leave the cell because the negatively-charged phosphate will not allow it to cross the hydrophobic interior of the plasma membrane.

Step 2. In the second step of glycolysis, an isomerase converts glucose-6-phosphate into one of its isomers, fructose-6-phosphate. An enzyme that catalyzes the conversion of a molecule into one of its isomers is an isomerase. (This change from phosphoglucose to phosphofructose allows the eventual split of the sugar into two three-carbon molecules).

Step 3. The third step is the phosphorylation of fructose-6-phosphate, catalyzed by the enzyme phosphofructokinase. A second ATP molecule donates a high-energy phosphate to fructose-6-phosphate, producing fructose-1,6-bisphosphate. In this pathway, phosphofructokinase is a rate-limiting enzyme. It is active when the concentration of ADP is high; it is less active when ADP levels are low and the concentration of ATP is high. Thus, if there is “sufficient” ATP in the system, the pathway slows down. This is a type of end-product inhibition, since ATP is the end product of glucose catabolism.

Step 4. The newly-added high-energy phosphates further destabilize fructose-1,6-bisphosphate. The fourth step in glycolysis employs an enzyme, aldolase, to cleave 1,6-bisphosphate into two three-carbon isomers: dihydroxyacetone-phosphate and glyceraldehyde-3-phosphate.

Step 5. In the fifth step, an isomerase transforms the dihydroxyacetone-phosphate into its isomer, glyceraldehyde-3-phosphate. Thus, the pathway will continue with two molecules of a single isomer. At this point in the pathway, there is a net investment of energy from two ATP molecules in the breakdown of one glucose molecule.

Key Points

- ATP molecules donate high energy phosphate groups during the two phosphorylation steps, step 1 with hexokinase and step

3 with phosphofructokinase, in the first half of glycolysis.
- In steps 2 and 5, isomerases convert molecules into their isomers to allow glucose to be split eventually into two molecules of glyceraldehyde-3-phosphate, which continues into the second half of glycolysis.
- The enzyme aldolase in step 4 of glycolysis cleaves the six-carbon sugar 1,6-bisphosphate into two three-carbon sugar isomers, dihydroxyacetone-phosphate and glyceraldehyde-3-phosphate.

Key Terms

- **glucose**: a simple monosaccharide (sugar) with a molecular formula of C6H12O6; it is a principal source of energy for cellular metabolism
- **adenosine triphosphate**: a multifunctional nucleoside triphosphate used in cells as a coenzyme, often called the “molecular unit of energy currency” in intracellular energy transfer

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7.6: Glycolysis - The Energy-Releasing Steps of Glycolysis

Learning Objectives

- Outline the energy-releasing steps of glycolysis

Second Half of Glycolysis (Energy-Releasing Steps)

So far, glycolysis has cost the cell two ATP molecules and produced two small, three-carbon sugar molecules. Both of these molecules will proceed through the second half of the pathway where sufficient energy will be extracted to pay back the two ATP molecules used as an initial investment while also producing a profit for the cell of two additional ATP molecules and two even higher-energy NADH molecules.

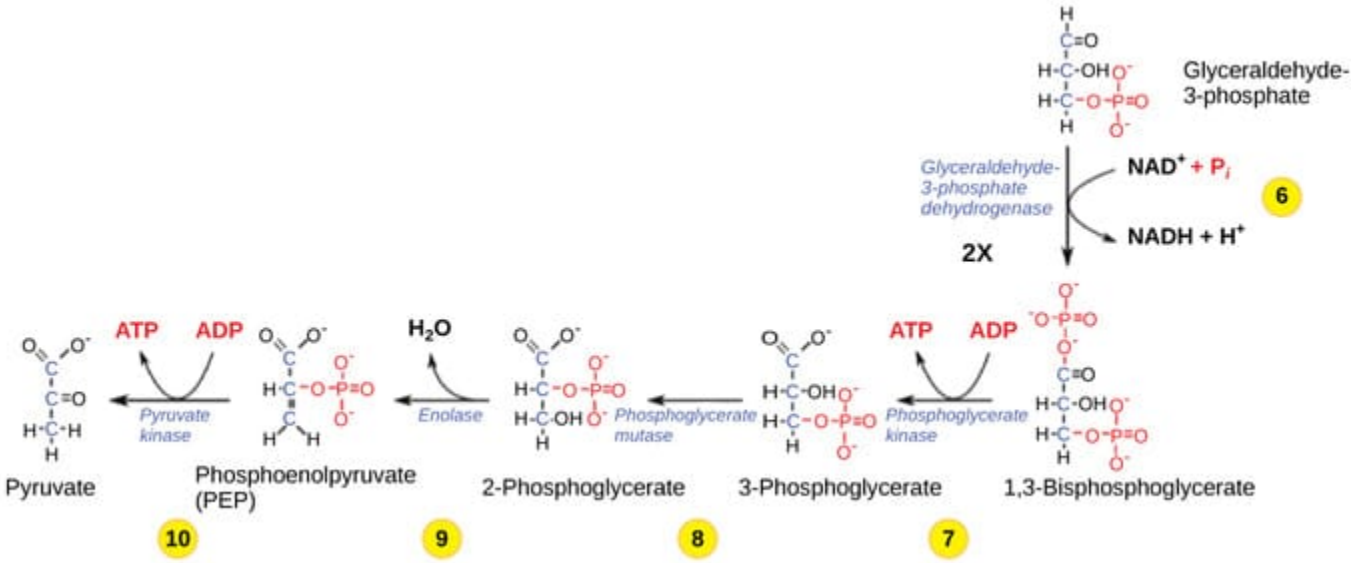


Figure 7.6.1: The second half of glycolysis: return on investment: The second half of glycolysis involves phosphorylation without ATP investment (step 6) and produces two NADH and four ATP molecules per glucose.

Step 6. The sixth step in glycolysis oxidizes the sugar (glyceraldehyde-3-phosphate), extracting high-energy electrons, which are picked up by the electron carrier NAD^+, producing NADH. The sugar is then phosphorylated by the addition of a second phosphate group, producing 1,3-bisphosphoglycerate. Note that the second phosphate group does not require another ATP molecule.

Here, again, there is a potential limiting factor for this pathway. The continuation of the reaction depends upon the availability of the oxidized form of the electron carrier NAD^+. Thus, NADH must be continuously oxidized back into NAD^+ in order to keep this step going. If NAD^+ is not available, the second half of glycolysis slows down or stops. If oxygen is available in the system, the NADH will be oxidized readily, though indirectly, and the high-energy electrons from the hydrogen released in this process will be used to produce ATP. In an environment without oxygen, an alternate pathway (fermentation) can provide the oxidation of NADH to NAD^+.

Step 7. In the seventh step, catalyzed by phosphoglycerate kinase (an enzyme named for the reverse reaction), 1,3-bisphosphoglycerate donates a high-energy phosphate to ADP, forming one molecule of ATP. (This is an example of substrate-level phosphorylation.) A carbonyl group on the 1,3-bisphosphoglycerate is oxidized to a carboxyl group, and 3-phosphoglycerate is formed.

Step 8. In the eighth step, the remaining phosphate group in 3-phosphoglycerate moves from the third carbon to the second carbon, producing 2-phosphoglycerate (an isomer of 3-phosphoglycerate). The enzyme catalyzing this step is a mutase

(isomerase).

Step 9. Enolase catalyzes the ninth step. This enzyme causes 2-phosphoglycerate to lose water from its structure; this is a dehydration reaction, resulting in the formation of a double bond that increases the potential energy in the remaining phosphate bond and produces phosphoenolpyruvate (PEP).

Step 10. The last step in glycolysis is catalyzed by the enzyme pyruvate kinase (the enzyme in this case is named for the reverse reaction of pyruvate's conversion into PEP) and results in the production of a second ATP molecule by substrate-level phosphorylation and the compound pyruvic acid (or its salt form, pyruvate). Many enzymes in enzymatic pathways are named for the reverse reactions since the enzyme can catalyze both forward and reverse reactions (these may have been described initially by the reverse reaction that takes place in vitro, under non-physiological conditions).

Key Points

- The net energy release in glycolysis is a result of two molecules of glyceraldehyde-3- phosphate entering the second half of glycolysis where they are converted to pyruvic acid.
- Substrate -level phosphorylation, where a substrate of glycolysis donates a phosphate to ADP, occurs in two steps of the second-half of glycolysis to produce ATP.
- The availability of NAD+ is a limiting factor for the steps of glycolysis; when it is unavailable, the second half of glycolysis slows or shuts down.

Key Terms

- **NADH**: nicotinamide adenine dinucleotide (NAD) carrying two electrons and bonded with a hydrogen (H) ion; the reduced form of NAD

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7.7: Glycolysis - Outcomes of Glycolysis

Learning Objectives

- Describe the energy obtained from one molecule of glucose going through glycolysis

Outcomes of Glycolysis

Glycolysis starts with one molecule of glucose and ends with two pyruvate (pyruvic acid) molecules, a total of four ATP molecules, and two molecules of NADH. Two ATP molecules were used in the first half of the pathway to prepare the six-carbon ring for cleavage, so the cell has a net gain of two ATP molecules and 2 NADH molecules for its use. If the cell cannot catabolize the pyruvate molecules further (via the citric acid cycle or Krebs cycle), it will harvest only two ATP molecules from one molecule of glucose.

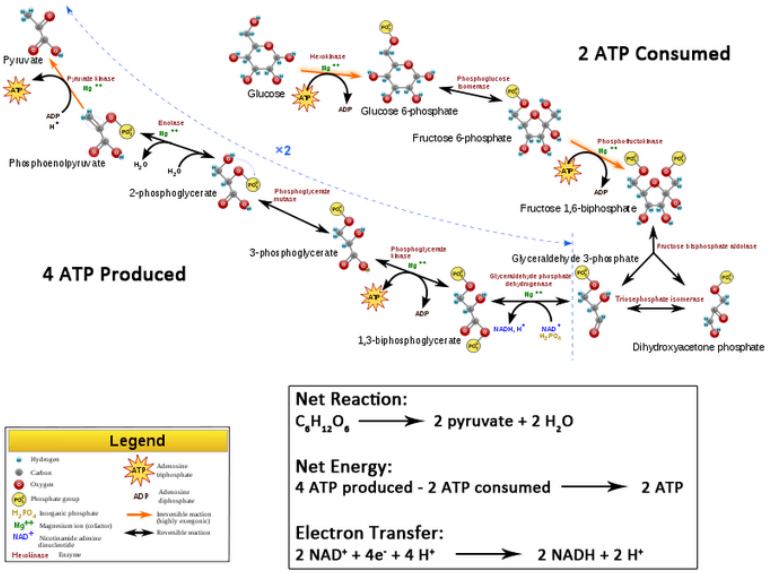


Figure 7.7.1: Glycolysis produces 2 ATP, 2 NADH, and 2 pyruvate molecules: Glycolysis, or the aerobic catabolic breakdown of glucose, produces energy in the form of ATP, NADH, and pyruvate, which itself enters the citric acid cycle to produce more energy.

Mature mammalian red blood cells do not have mitochondria and are not capable of aerobic respiration, the process in which organisms convert energy in the presence of oxygen. Instead, glycolysis is their sole source of ATP. Therefore, if glycolysis is interrupted, the red blood cells lose their ability to maintain their sodium-potassium pumps, which require ATP to function, and eventually, they die. For example, since the second half of glycolysis (which produces the energy molecules) slows or stops in the absence of NAD+, when NAD+ is unavailable, red blood cells will be unable to produce a sufficient amount of ATP in order to survive.

Additionally, the last step in glycolysis will not occur if pyruvate kinase, the enzyme that catalyzes the formation of pyruvate, is not available in sufficient quantities. In this situation, the entire glycolysis pathway will continue to proceed, but only two ATP molecules will be made in the second half (instead of the usual four ATP molecules). Thus, pyruvate kinase is a rate-limiting enzyme for glycolysis.

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Key Points

- Although four ATP molecules are produced in the second half, the net gain of glycolysis is only two ATP because two ATP molecules are used in the first half of glycolysis.
- Enzymes that catalyze the reactions that produce ATP are rate-limiting steps of glycolysis and must be present in sufficient quantities for glycolysis to complete the production of four ATP, two NADH, and two pyruvate molecules for each glucose molecule that enters the pathway.
- Red blood cells require glycolysis as their sole source of ATP in order to survive, because they do not have mitochondria.
- Cancer cells and stem cells also use glycolysis as the main source of ATP (process known as aerobic glycolysis, or Warburg effect).

Key Terms

- **pyruvate**: any salt or ester of pyruvic acid; the end product of glycolysis before entering the TCA cycle

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7.8: Oxidation of Pyruvate and the Citric Acid Cycle - Breakdown of Pyruvate

Learning Objectives

- Explain why cells break down pyruvate

Breakdown of Pyruvate

In order for pyruvate, the product of glycolysis, to enter the next pathway, it must undergo several changes to become acetyl Coenzyme A (acetyl CoA). Acetyl CoA is a molecule that is further converted to oxaloacetate, which enters the citric acid cycle (Krebs cycle). The conversion of pyruvate to acetyl CoA is a three-step process.

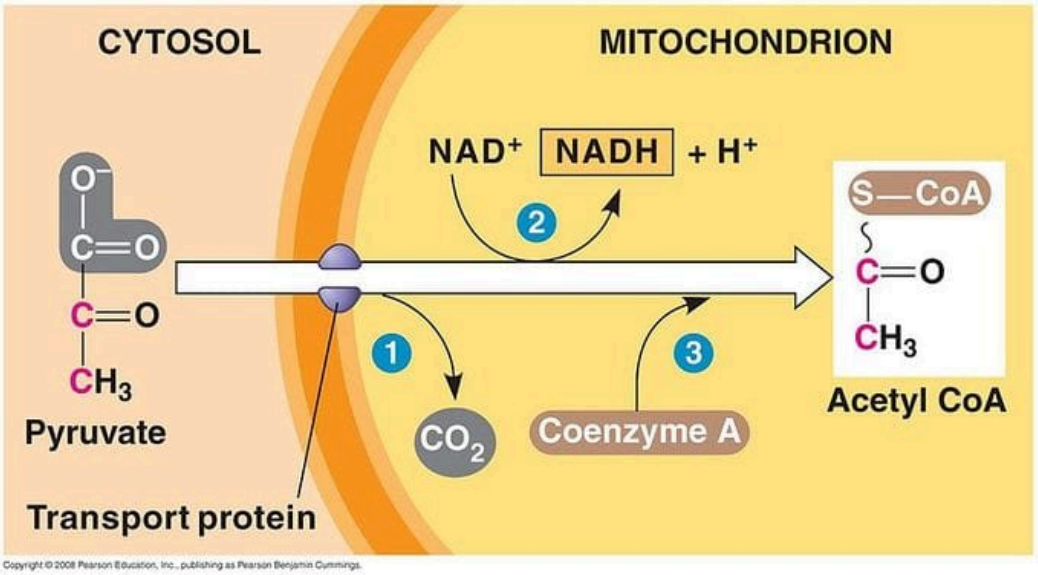


Figure 7.8.1: Breakdown of Pyruvate: Each pyruvate molecule loses a carboxylic group in the form of carbon dioxide. The remaining two carbons are then transferred to the enzyme CoA to produce Acetyl CoA.

Step 1. A carboxyl group is removed from pyruvate, releasing a molecule of carbon dioxide into the surrounding medium. (Note: carbon dioxide is one carbon attached to two oxygen atoms and is one of the major end products of cellular respiration.) The result of this step is a two-carbon hydroxyethyl group bound to the enzyme pyruvate dehydrogenase; the lost carbon dioxide is the first of the six carbons from the original glucose molecule to be removed. This step proceeds twice for every molecule of glucose metabolized (remember: there are two pyruvate molecules produced at the end of glycolysis); thus, two of the six carbons will have been removed at the end of both of these steps.

Step 2. The hydroxyethyl group is oxidized to an acetyl group, and the electrons are picked up by NAD^+, forming NADH (the reduced form of NAD+). The high- energy electrons from NADH will be used later by the cell to generate ATP for energy.

Step 3. The enzyme-bound acetyl group is transferred to CoA, producing a molecule of acetyl CoA. This molecule of acetyl CoA is then further converted to be used in the next pathway of metabolism, the citric acid cycle.

Key Points

- In the conversion of pyruvate to acetyl CoA, each pyruvate molecule loses one carbon atom with the release of carbon dioxide.

- During the breakdown of pyruvate, electrons are transferred to NAD+ to produce NADH, which will be used by the cell to produce ATP.
- In the final step of the breakdown of pyruvate, an acetyl group is transferred to Coenzyme A to produce acetyl CoA.

Key Terms

- **acetyl CoA**: a molecule that conveys the carbon atoms from glycolysis (pyruvate) to the citric acid cycle to be oxidized for energy production

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7.9: Oxidation of Pyruvate and the Citric Acid Cycle - Acetyl CoA to CO_2

Learning Objectives

- Describe the fate of the acetyl CoA carbons in the citric acid cycle

Acetyl CoA to CO_2

Acetyl CoA links glycolysis and pyruvate oxidation with the citric acid cycle. In the presence of oxygen, acetyl CoA delivers its acetyl group to a four-carbon molecule, oxaloacetate, to form citrate, a six-carbon molecule with three carboxyl groups. During this first step of the citric acid cycle, the CoA enzyme, which contains a sulfhydryl group (-SH), is recycled and becomes available to attach another acetyl group. The citrate will then harvest the remainder of the extractable energy from what began as a glucose molecule and continue through the citric acid cycle.

In the citric acid cycle, the two carbons that were originally the acetyl group of acetyl CoA are released as carbon dioxide, one of the major products of cellular respiration, through a series of enzymatic reactions. For each acetyl CoA that enters the citric acid cycle, two carbon dioxide molecules are released in reactions that are coupled with the production of NADH molecules from the reduction of NAD^+ molecules.

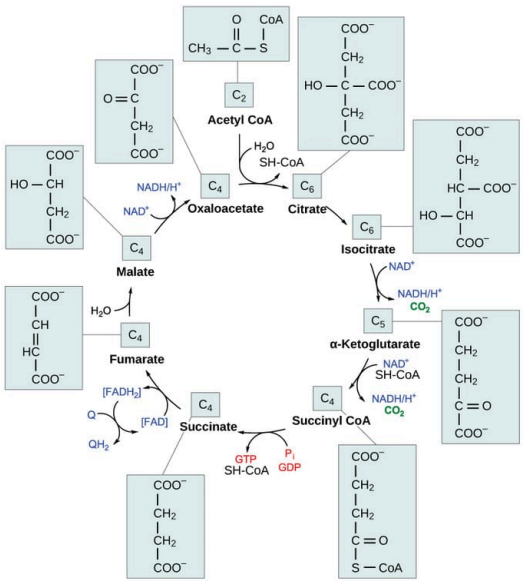


Figure 7.9.1: Acetyl CoA and the Citric Acid Cycle: For each molecule of acetyl CoA that enters the citric acid cycle, two carbon dioxide molecules are released, removing the carbons from the acetyl group.

In addition to the citric acid cycle, named for the first intermediate formed, citric acid, or citrate, when acetate joins to the oxaloacetate, the cycle is also known by two other names. The TCA cycle is named for tricarboxylic acids (TCA) because citric acid (or citrate) and isocitrate, the first two intermediates that are formed, are tricarboxylic acids. Additionally, the cycle is known as the Krebs cycle, named after Hans Krebs, who first identified the steps in the pathway in the 1930s in pigeon flight muscle.

Key Points

- The citric acid cycle is also known as the Krebs cycle or the TCA (tricarboxylic acid) cycle.
- Acetyl CoA transfers its acetyl group to oxaloacetate to form citrate and begin the citric acid cycle.

- The release of carbon dioxide is coupled with the reduction of NAD^+ to NADH in the citric acid cycle.

Key Terms

- **TCA cycle**: an alternative name for the Krebs cycle or citric acid cycle
- **Krebs cycle**: a series of enzymatic reactions that occurs in all aerobic organisms; it involves the oxidative metabolism of acetyl units and serves as the main source of cellular energy
- **oxaloacetate**: a four carbon molecule that receives an acetyl group from acetyl CoA to form citrate, which enters the citric acid cycle

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7.10: Oxidation of Pyruvate and the Citric Acid Cycle - Citric Acid Cycle

Learning Objectives

- List the steps of the Krebs (or citric acid) cycle

Citric Acid Cycle (Krebs Cycle)

Like the conversion of pyruvate to acetyl CoA, the citric acid cycle takes place in the matrix of the mitochondria. Almost all of the enzymes of the citric acid cycle are soluble, with the single exception of the enzyme succinate dehydrogenase, which is embedded in the inner membrane of the mitochondrion. 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 redox, dehydration, hydration, and decarboxylation reactions that produce two carbon dioxide molecules, one GTP/ATP, and reduced forms of NADH and FADH2. This is considered an aerobic pathway because the NADH and FADH2 produced must transfer their electrons to the next pathway in the system, which will use oxygen. If this transfer does not occur, the oxidation steps of the citric acid cycle also do not occur. Note that the citric acid cycle produces very little ATP directly and does not directly consume oxygen.

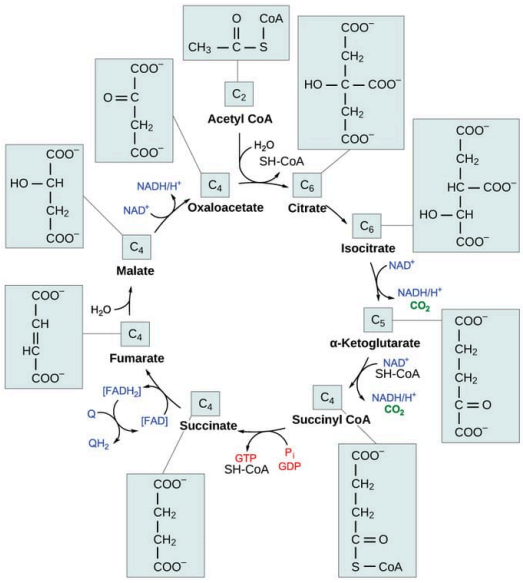


Figure 7.10.1: The citric acid cycle: In the citric acid cycle, the acetyl group from acetyl CoA is attached to a four-carbon oxaloacetate molecule to form a six-carbon citrate molecule. Through a series of steps, citrate is oxidized, releasing two carbon dioxide molecules for each acetyl group fed into the cycle. In the process, three NAD+ molecules are reduced to NADH, one FAD molecule is reduced to FADH2, and one ATP or GTP (depending on the cell type) is produced (by substrate-level phosphorylation). Because the final product of the citric acid cycle is also the first reactant, the cycle runs continuously in the presence of sufficient reactants.

Steps in the Citric Acid Cycle

Step 1. The first step is a condensation step, combining the two-carbon acetyl group (from acetyl CoA) with a four-carbon oxaloacetate molecule to form a six-carbon molecule of citrate. CoA is bound to a sulfhydryl group (-SH) and diffuses away to eventually combine with another acetyl group. This step is irreversible because it is highly exergonic. The rate of this reaction is controlled by negative feedback and the amount of ATP available. If ATP levels increase, the rate of this reaction decreases. If ATP is in short supply, the rate increases.

Step 2. Citrate loses one water molecule and gains another as citrate is converted into its isomer, isocitrate.

Steps 3 and 4. In step three, isocitrate is oxidized, producing a five-carbon molecule, α-ketoglutarate, together with a molecule of $CO_2$and two electrons, which reduce NAD+ to NADH. This step is also regulated by negative feedback from ATP and NADH and by a positive effect of ADP. Steps three and four are both oxidation and decarboxylation steps, which release electrons that reduce NAD^+ to NADH and release carboxyl groups that form CO_2 molecules. α-Ketoglutarate is the product of step three, and a succinyl group is the product of step four. CoA binds the succinyl group to form succinyl CoA. The enzyme that catalyzes step four is regulated by feedback inhibition of ATP, succinyl CoA, and NADH.

Step 5. A phosphate group is substituted for coenzyme A, and a high- energy bond is formed. This energy is used in substrate-level phosphorylation (during the conversion of the succinyl group to succinate) to form either guanine triphosphate (GTP) or ATP. There are two forms of the enzyme, called isoenzymes, for this step, depending upon the type of animal tissue in which they are found. One form is found in tissues that use large amounts of ATP, such as heart and skeletal muscle. This form produces ATP. The second form of the enzyme is found in tissues that have a high number of anabolic pathways, such as liver. This form produces GTP. GTP is energetically equivalent to ATP; however, its use is more restricted. In particular, protein synthesis primarily uses GTP.

Step 6. Step six is a dehydration process that converts succinate into fumarate. Two hydrogen atoms are transferred to FAD, producing $FADH_2$. The energy contained in the electrons of these atoms is insufficient to reduce NAD^+ but adequate to reduce FAD. Unlike NADH, this carrier remains attached to the enzyme and transfers the electrons to the electron transport chain directly. This process is made possible by the localization of the enzyme catalyzing this step inside the inner membrane of the mitochondrion.

Step 7. Water is added to fumarate during step seven, and malate is produced. The last step in the citric acid cycle regenerates oxaloacetate by oxidizing malate. Another molecule of NADH is produced.

Products of the Citric Acid Cycle

Two carbon atoms come into the citric acid cycle from each acetyl group, representing four out of the six carbons of one glucose molecule. Two carbon dioxide molecules are released on each turn of the cycle; however, these do not necessarily contain the most recently-added carbon atoms. The two acetyl carbon atoms will eventually be released on later turns of the cycle; thus, all six carbon atoms from the original glucose molecule are eventually incorporated into carbon dioxide. Each turn of the cycle forms three NADH molecules and one $FADH_2$ molecule. These carriers will connect with the last portion of aerobic respiration to produce ATP molecules. One GTP or ATP 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 amphibolic (both catabolic and anabolic).

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Key Points

- The four-carbon molecule, oxaloacetate, that began the cycle is regenerated after the eight steps of the citric acid cycle.
- The eight steps of the citric acid cycle are a series of redox, dehydration, hydration, and decarboxylation reactions.
- Each turn of the cycle forms one GTP or ATP as well as three NADH molecules and one FADH2 molecule, which will be used in further steps of cellular respiration to produce ATP for the cell.

Key Terms

- **citric acid cycle**: a series of chemical reactions used by all aerobic organisms to generate energy through the oxidization of acetate derived from carbohydrates, fats, and proteins into carbon dioxide
- **Krebs cycle**: a series of enzymatic reactions that occurs in all aerobic organisms; it involves the oxidative metabolism of acetyl units and serves as the main source of cellular energy
- **mitochondria**: in cell biology, a mitochondrion (plural mitochondria) is a membrane-enclosed organelle, often described as “cellular power plants” because they generate most of the ATP

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7.11: Oxidative Phosphorylation - Electron Transport Chain

Learning Objectives

- Describe how electrons move through the electron transport chain

Oxidative phosphorylation is a highly efficient method of producing large amounts of ATP, the basic unit of energy for metabolic processes. During this process electrons are exchanged between molecules, which creates a chemical gradient that allows for the production of ATP. The most vital part of this process is the electron transport chain, which produces more ATP than any other part of cellular respiration.

Electron Transport Chain

The electron transport chain is the final component of aerobic respiration and is the only part of glucose metabolism that uses atmospheric oxygen. Electron transport is a series of redox reactions that resemble a relay race. Electrons are passed rapidly from one component to the next to the endpoint of the chain, where the electrons reduce molecular oxygen, producing water. This requirement for oxygen in the final stages of the chain can be seen in the overall equation for cellular respiration, which requires both glucose and oxygen.

A complex is a structure consisting of a central atom, molecule, or protein weakly connected to surrounding atoms, molecules, or proteins. The electron transport chain is an aggregation of four of these complexes (labeled I through IV), together with associated mobile electron carriers. The electron transport chain is present in multiple copies in the inner mitochondrial membrane of eukaryotes and the plasma membrane of prokaryotes.

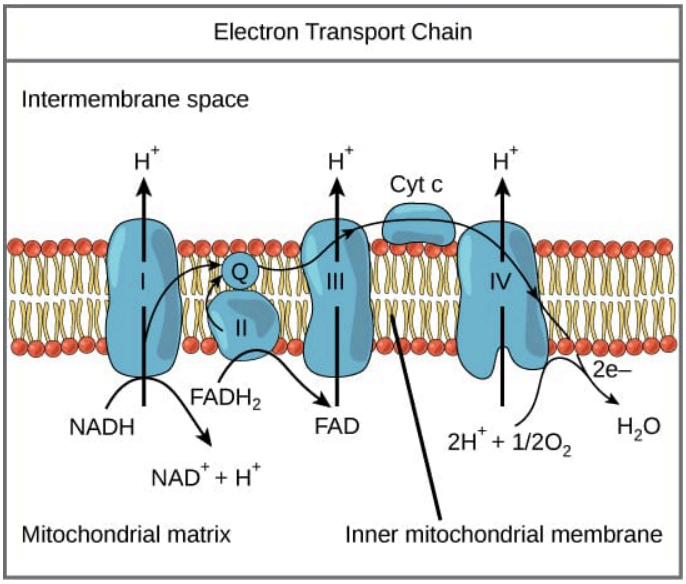


Figure 7.11.1: The electron transport chain: The electron transport chain is a series of electron transporters embedded in the inner mitochondrial membrane that shuttles electrons from NADH and $FADH_2$ to molecular oxygen. In the process, protons are pumped from the mitochondrial matrix to the intermembrane space, and oxygen is reduced to form water.

Complex I

To start, two electrons are carried to the first complex aboard NADH. Complex I is composed of flavin mononucleotide (FMN) and an enzyme containing iron-sulfur (Fe-S). FMN, which is derived from vitamin B_2 (also called riboflavin), is one of several prosthetic groups or co-factors in the electron transport chain. A prosthetic group is a non-protein molecule required for the activity of a protein. Prosthetic groups can be organic or inorganic and are non-peptide molecules bound to a protein that facilitate its

function.

Prosthetic groups include co-enzymes, which are the prosthetic groups of enzymes. The enzyme in complex I is NADH dehydrogenase, a very large protein containing 45 amino acid chains. Complex I can pump four hydrogen ions across the membrane from the matrix into the intermembrane space; it is in this way that the hydrogen ion gradient is established and maintained between the two compartments separated by the inner mitochondrial membrane.

Q and Complex II

Complex II directly receives $FADH_2$, which does not pass through complex I. The compound connecting the first and second complexes to the third is ubiquinone (Q). The Q molecule is lipid soluble and freely moves through the hydrophobic core of the membrane. Once it is reduced to QH_2, ubiquinone delivers its electrons to the next complex in the electron transport chain. Q receives the electrons derived from NADH from complex I and the electrons derived from $FADH_2$ from complex II, including succinate dehydrogenase. This enzyme and $FADH_2$ form a small complex that delivers electrons directly to the electron transport chain, bypassing the first complex. Since these electrons bypass, and thus do not energize, the proton pump in the first complex, fewer ATP molecules are made from the $FADH_2$ electrons. The number of ATP molecules ultimately obtained is directly proportional to the number of protons pumped across the inner mitochondrial membrane.

Complex III

The third complex is composed of cytochrome b, another Fe-S protein, Rieske center (2Fe-2S center), and cytochrome c proteins; this complex is also called cytochrome oxidoreductase. Cytochrome proteins have a prosthetic heme group. The heme molecule is similar to the heme in hemoglobin, but it carries electrons, not oxygen. As a result, the iron ion at its core is reduced and oxidized as it passes the electrons, fluctuating between different oxidation states: Fe^{2+} (reduced) and Fe^{3+} (oxidized). The heme molecules in the cytochromes have slightly different characteristics due to the effects of the different proteins binding them, which makes each complex. Complex III pumps protons through the membrane and passes its electrons to cytochrome c for transport to the fourth complex of proteins and enzymes. Cytochrome c is the acceptor of electrons from Q; however, whereas Q carries pairs of electrons, cytochrome c can accept only one at a time.

Complex IV

The fourth complex is composed of cytochrome proteins c, a, and a_3. This complex contains two heme groups (one in each of the cytochromes a and a_3) and three copper ions (a pair of Cu_A and one Cu_B in cytochrome a_3). The cytochromes hold an oxygen molecule very tightly between the iron and copper ions until the oxygen is completely reduced. The reduced oxygen then picks up two hydrogen ions from the surrounding medium to produce water (H_2O). The removal of the hydrogen ions from the system also contributes to the ion gradient used in the process of chemiosmosis.

Key Points

- Oxidative phosphorylation is the metabolic pathway in which electrons are transferred from electron donors to electron acceptors in redox reactions; this series of reactions releases energy which is used to form ATP.
- There are four protein complexes (labeled complex I-IV) in the electron transport chain, which are involved in moving electrons from NADH and $FADH_2$ to molecular oxygen.
- Complex I establishes the hydrogen ion gradient by pumping four hydrogen ions across the membrane from the matrix into the intermembrane space.
- Complex II receives $FADH_2$, which bypasses complex I, and delivers electrons directly to the electron transport chain.
- Ubiquinone (Q) accepts the electrons from both complex I and complex II and delivers them to complex III.
- Complex III pumps protons through the membrane and passes its electrons to cytochrome c for transport to the fourth complex of proteins and enzymes.
- Complex IV reduces oxygen; the reduced oxygen then picks up two hydrogen ions from the surrounding medium to make water.

Key Terms

- **prosthetic group**: The non-protein component of a conjugated protein.
- **complex**: A structure consisting of a central atom, molecule, or protein weakly connected to surrounding atoms, molecules, or proteins.
- **ubiquinone**: A lipid soluble substance that is a component of the electron transport chain and accepts electrons from complexes I and II.

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7.12: Oxidative Phosphorylation - Chemiosmosis and Oxidative Phosphorylation

Learning Objectives

- Describe how the energy obtained from the electron transport chain powers chemiosmosis and discuss the role of hydrogen ions in the synthesis of ATP

During chemiosmosis, electron carriers like NADH and FADH donate electrons to the electron transport chain. The electrons cause conformation changes in the shapes of the proteins to pump H+ across a selectively permeable cell membrane. The uneven distribution of H^+ ions across the membrane establishes both concentration and electrical gradients (thus, an electrochemical gradient) owing to the hydrogen ions' positive charge and their aggregation on one side of the membrane.

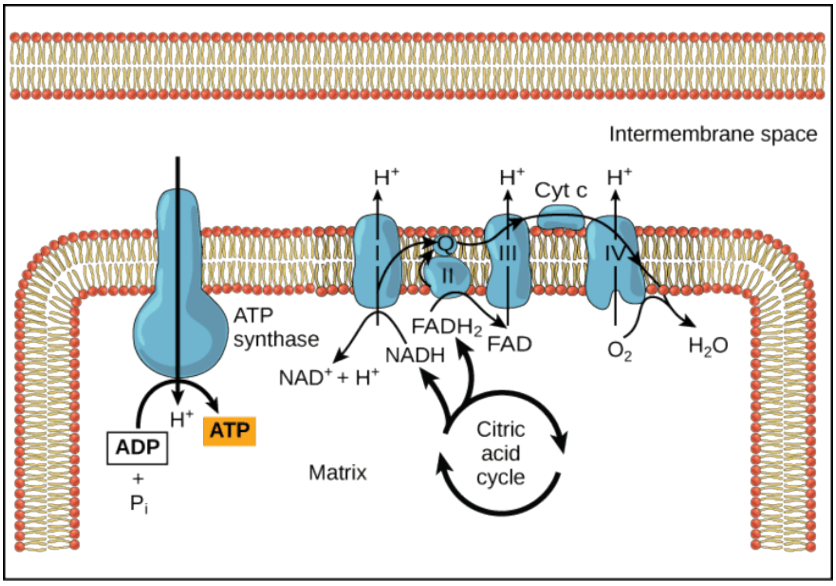


Figure 7.12.1: Chemiosmosis: In oxidative phosphorylation, the hydrogen ion gradient formed by the electron transport chain is used by ATP synthase to form ATP.

If the membrane were open to diffusion by the hydrogen ions, the ions would tend to spontaneously diffuse back across into the matrix, driven by their electrochemical gradient. However, many ions cannot diffuse through the nonpolar regions of phospholipid membranes without the aid of ion channels. Similarly, hydrogen ions in the matrix space can only pass through the inner mitochondrial membrane through a membrane protein called ATP synthase. This protein acts as a tiny generator turned by the force of the hydrogen ions diffusing through it, down their electrochemical gradient. The turning of this molecular machine harnesses the potential energy stored in the hydrogen ion gradient to add a phosphate to ADP, forming ATP.

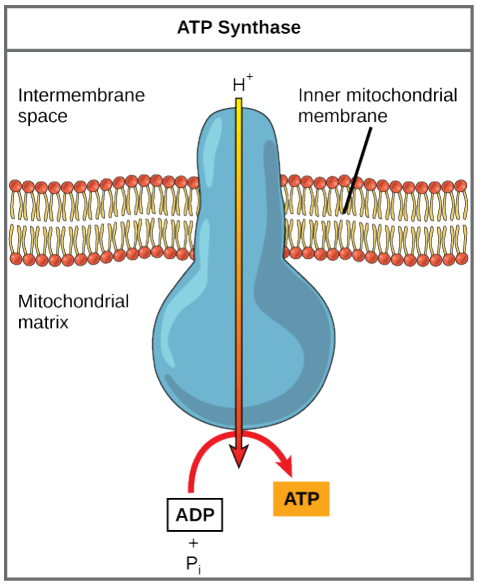


Figure 7.12.1: ATP Synthase: ATP synthase is a complex, molecular machine that uses a proton (H+) gradient to form ATP from ADP and inorganic phosphate (Pi).

Chemiosmosis is used to generate 90 percent of the ATP made during aerobic glucose catabolism. The production of ATP using the process of chemiosmosis in mitochondria is called oxidative phosphorylation. It is also the method used in the light reactions of photosynthesis to harness the energy of sunlight in the process of photophosphorylation. The overall result of these 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 pathway, the electrons are used to reduce an oxygen molecule to oxygen ions. The extra electrons on the oxygen attract hydrogen ions (protons) from the surrounding medium and water is formed.

Key Points

- During chemiosmosis, the free energy from the series of reactions that make up the electron transport chain is used to pump hydrogen ions across the membrane, establishing an electrochemical gradient.
- Hydrogen ions in the matrix space can only pass through the inner mitochondrial membrane through a membrane protein called ATP synthase.
- As protons move through ATP synthase, ADP is turned into ATP.
- The production of ATP using the process of chemiosmosis in mitochondria is called oxidative phosphorylation.

Key Terms

- **ATP synthase**: An important enzyme that provides energy for the cell to use through the synthesis of adenosine triphosphate (ATP).
- **oxidative phosphorylation**: A metabolic pathway that uses energy released by the oxidation of nutrients to produce adenosine triphosphate (ATP).
- **chemiosmosis**: The movement of ions across a selectively permeable membrane, down their electrochemical gradient.

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7.13: Oxidative Phosphorylation - ATP Yield

ese atoms were originally part of a glucose molecule. At the end of the pathway, the electrons are used to reduce an oxygen molecule to oxygen ions. The extra electrons on the oxygen attract hydrogen ions (protons) from the surrounding medium and water is formed.

ATP Yield

The amount of energy (as ATP) gained from glucose catabolism varies across species and depends on other related cellular processes.

LEARNING OBJECTIVES

Describe the origins of variability in the amount of ATP that is produced per molecule of glucose consumed

KEY TAKEAWAYS

Key Points

- While glucose catabolism always produces energy, the amount of energy (in terms of ATP equivalents) produced can vary, especially across different species.
- The number of hydrogen ions the electron transport chain complexes can pump through the membrane varies between species.
- NAD^+ provides more ATP than FAD^+ in the electron transport chain and can lead to variance in ATP production.
- The use of intermediates from glucose catabolism in other biosynthetic pathways, such as amino acid synthesis, can lower the yield of ATP.

Key Terms

- **catabolism**: Destructive metabolism, usually including the release of energy and breakdown of materials.

ATP Yield

In a eukaryotic cell, the process of cellular respiration can metabolize one molecule of glucose into 30 to 32 ATP. The process of glycolysis only produces two ATP, while all the rest are produced during the electron transport chain. Clearly, the electron transport chain is vastly more efficient, but it can only be carried out in the presence of oxygen.

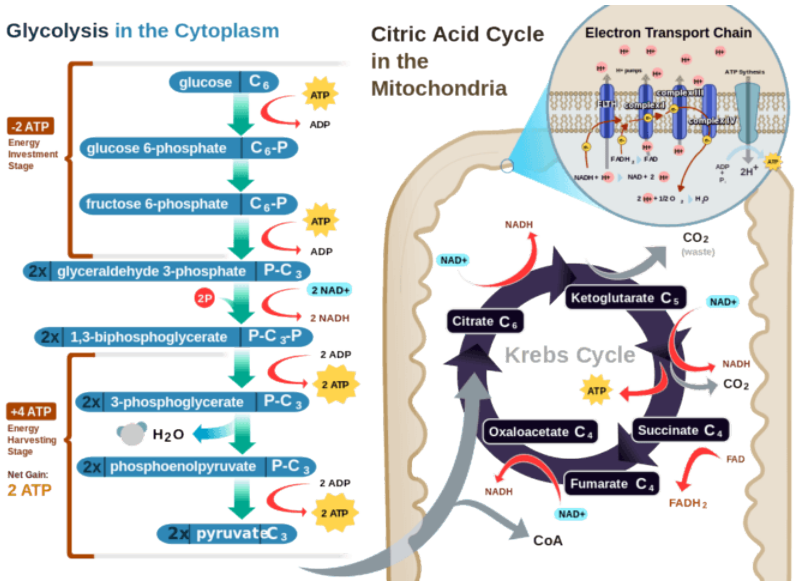


Figure 7.13.1: Cellular respiration in a eukaryotic cell: Glycolysis on the left portion of this illustration can be seen to yield 2 ATP molecules, while the Electron Transport Chain portion at the upper right will yield the remaining 30-32 ATP molecules under the presence of oxygen.

The number of ATP molecules generated via the catabolism of glucose can vary substantially. For example, the number of hydrogen ions the electron transport chain complexes can pump through the membrane varies between species. Another source of variance occurs during the shuttle of electrons across the membranes of the mitochondria. The NADH generated from glycolysis cannot easily enter mitochondria. Thus, electrons are picked up on the inside of mitochondria by either NAD^+ or FAD^+. These FAD^+ molecules can transport fewer ions; consequently, fewer ATP molecules are generated when FAD^+ acts as a carrier. NAD^+ is used as the electron transporter in the liver, and FAD^+ acts in the brain.

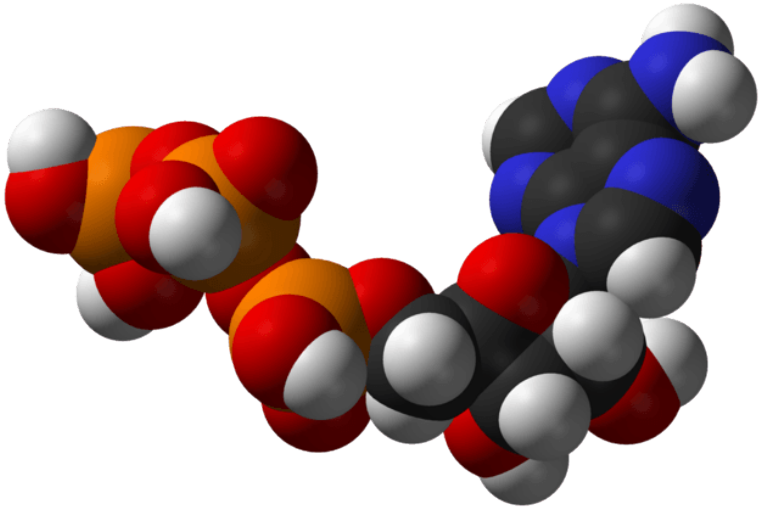


Figure 7.13.1: Adenosine triphosphate: ATP is the main source of energy in many living organisms.

Another factor that affects the yield of ATP molecules generated from glucose is the fact 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, but the result is not always ideal. For example, sugars other than glucose are fed into the glycolytic pathway for energy extraction. Moreover, the five-carbon sugars that form nucleic acids are made from intermediates in glycolysis. Certain nonessential amino acids can be made from intermediates of both glycolysis and the citric acid cycle. Lipids, such as cholesterol and triglycerides, are also made from intermediates in these pathways, and both amino acids and triglycerides are broken down for energy through these pathways. Overall, in living systems, these pathways of glucose catabolism extract about 34 percent of the energy contained in glucose.

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7.14: Metabolism without Oxygen - Anaerobic Cellular Respiration

Learning Objectives

- Describe the process of anaerobic cellular respiration.

Anaerobic Cellular Respiration

The production of energy requires oxygen. The electron transport chain, where the majority of ATP is formed, requires a large input of oxygen. However, many organisms have developed strategies to carry out metabolism without oxygen, or can switch from aerobic to anaerobic cell respiration when oxygen is scarce.

During cellular respiration, 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 as a final electron acceptor. Both methods are called anaerobic cellular respiration, where organisms convert energy for their use in the absence of oxygen.

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, reduce sulfate to hydrogen sulfide to regenerate NAD^+ from NADH.

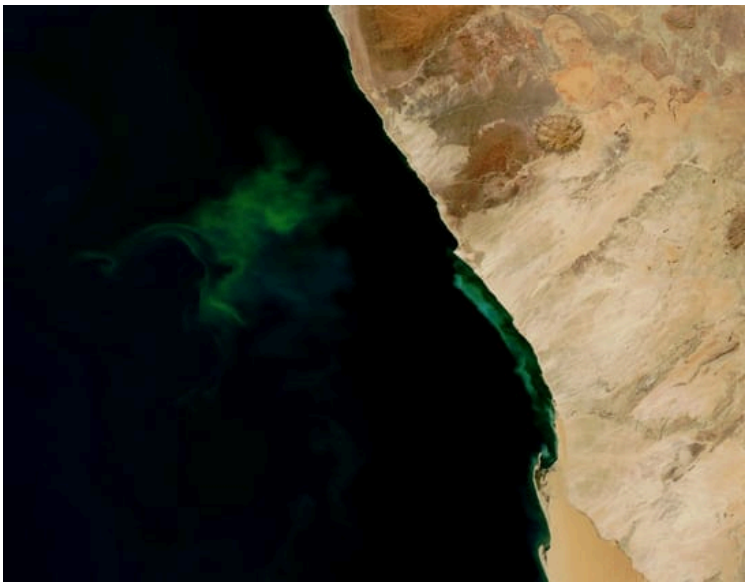


Figure 7.14.1: Anaerobic bacteria: The green color seen in these coastal waters is from an eruption of hydrogen sulfide-producing bacteria. These anaerobic, sulfate-reducing bacteria release hydrogen sulfide gas as they decompose algae in the water.

Eukaryotes can also undergo anaerobic respiration. Some examples include alcohol fermentation in yeast and lactic acid fermentation in mammals.

Lactic Acid Fermentation

The fermentation method used by animals and certain bacteria (like those in yogurt) is called lactic acid fermentation. This type of fermentation is used routinely in mammalian red blood cells and in skeletal muscle that has an insufficient oxygen supply to

allow aerobic respiration to continue (that is, in muscles used to the point of fatigue). The excess amount of lactate in those muscles is what causes the burning sensation in your legs while running. This pain is a signal to rest the overworked muscles so they can recover. In these muscles, lactic acid accumulation must be removed by the blood circulation and the lactate brought to the liver for further metabolism. The chemical reactions of lactic acid fermentation are the following:

Pyruvic acid + NADH $\leftrightarrow$ lactic acid + NAD^+

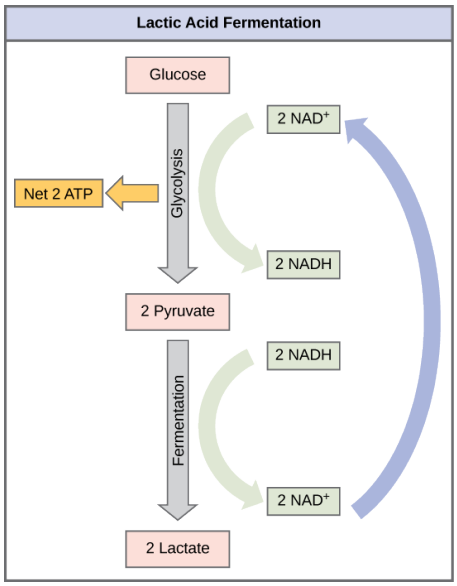


Figure 7.14.1: Lactic acid fermentation: Lactic acid fermentation is common in muscle cells that have run out of oxygen.

The enzyme used in this reaction is lactate dehydrogenase (LDH). The reaction can proceed in either direction, but the reaction from left to right is inhibited by acidic conditions. Such lactic acid accumulation was once believed to cause muscle stiffness, fatigue, and soreness, although more recent research disputes this hypothesis. Once the lactic acid has been removed from the muscle and circulated to the liver, it can be reconverted into pyruvic acid and further catabolized for energy.

Alcohol Fermentation

Another familiar fermentation process is alcohol fermentation, which produces ethanol, an alcohol. The use of alcohol fermentation can be traced back in history for thousands of years. The chemical reactions of alcoholic fermentation are the following (Note: CO_2 does not participate in the second reaction):

Pyruvic acid $\rightarrow$ CO2 + acetaldehyde + NADH $\rightarrow$ ethanol + NAD^+



Figure 7.14.1: Alcohol Fermentation: Fermentation of grape juice into wine produces CO2 as a byproduct. Fermentation tanks have valves so that the pressure inside the tanks created by the carbon dioxide produced can be released.

The first reaction is catalyzed by pyruvate decarboxylase, a cytoplasmic enzyme, with a coenzyme of thiamine pyrophosphate (TPP, derived from vitamin B_1 and also called thiamine). A carboxyl group is removed from pyruvic acid, releasing carbon dioxide as a gas. The loss of carbon dioxide reduces the size of the molecule by one carbon, making acetaldehyde. The second reaction is catalyzed by alcohol dehydrogenase to oxidize NADH to NAD^+ and reduce acetaldehyde to ethanol.

The fermentation of pyruvic acid by yeast produces the ethanol found in alcoholic beverages. Ethanol tolerance of yeast is variable, ranging from about 5 percent to 21 percent, depending on the yeast strain and environmental conditions.

Other Types of Fermentation

Various methods of fermentation are used by assorted 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.Other fermentation methods also 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*, are obligate anaerobes. Obligate anaerobes live and grow in the absence of molecular oxygen. Oxygen is a poison to these microorganisms, killing them on 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.

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Key Points

- Anaerobic respiration is a type of respiration where oxygen is not used; instead, organic or inorganic molecules are used as final electron acceptors.
- Fermentation includes processes that use an organic molecule to regenerate NAD^+ from NADH.
- Types of fermentation include lactic acid fermentation and alcohol fermentation, in which ethanol is produced.
- All forms of fermentation except lactic acid fermentation produce gas, which plays a role in the laboratory identification of bacteria.
- Some types of prokaryotes are facultatively anaerobic, which means that they can switch between aerobic respiration and fermentation, depending on the availability of oxygen.

Key Terms

- **archaea**: A group of single-celled microorganisms. They have no cell nucleus or any other membrane-bound organelles within their cells.
- **anaerobic respiration**: A form of respiration using electron acceptors other than oxygen.
- **fermentation**: An anaerobic biochemical reaction. When this reaction occurs in yeast, enzymes catalyze the conversion of sugars to alcohol or acetic acid with the evolution of carbon dioxide.

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7.15: Connections of Carbohydrate, Protein, and Lipid Metabolic Pathways - Connecting Other Sugars to Glucose Metabolism

Learning Objectives

- Identify the types of sugars involved in glucose metabolism

You have learned about the catabolism of glucose, which provides energy to living cells. But living things consume more than glucose for food. How does a turkey sandwich end up as ATP in your cells? This happens because all of the catabolic pathways for carbohydrates, proteins, and lipids eventually connect into glycolysis and the citric acid cycle pathways.

Metabolic pathways should be thought of as porous; that is, substances enter from other pathways, and intermediates leave for other pathways. These pathways are not closed systems. Many of the substrates, intermediates, and products in a particular pathway are reactants in other pathways. Like sugars and amino acids, the catabolic pathways of lipids are also connected to the glucose catabolism pathways.

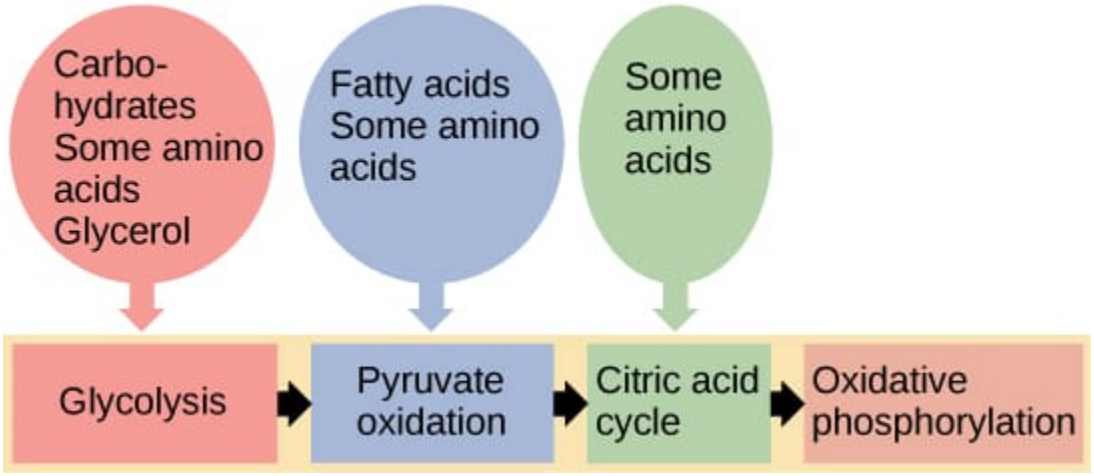


Figure 7.15.1: Glycogen Pathway: Glycogen from the liver and muscles, hydrolyzed into glucose-1-phosphate, together with fats and proteins, can feed into the catabolic pathways for carbohydrates.

Glycogen, a polymer of glucose, is an energy-storage molecule in animals. When there is adequate ATP present, excess glucose is shunted into glycogen for storage. Glycogen is made and stored in both the liver and muscles. The glycogen is hydrolyzed into the glucose monomer, glucose-1-phosphate (G-1-P), if blood sugar levels drop. The presence of glycogen as a source of glucose allows ATP to be produced for a longer period of time during exercise. Glycogen is broken down into G-1-P and converted into glucose-6-phosphate (G-6-P) in both muscle and liver cells; this product enters the glycolytic pathway.

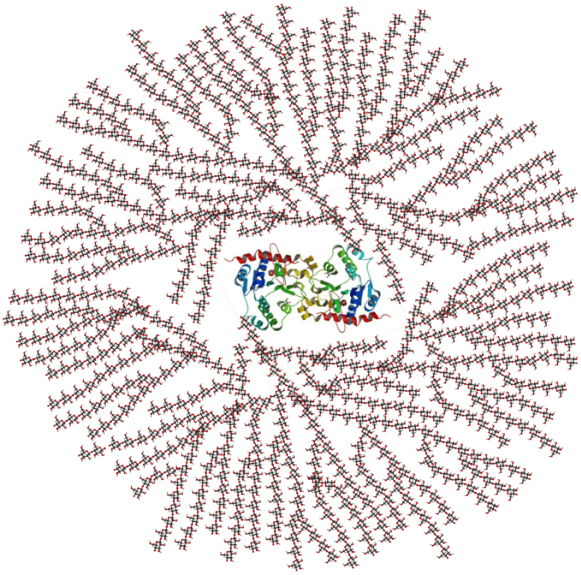


Figure 7.15.1: Glycogen Structure: Schematic two-dimensional cross-sectional view of glycogen: A core protein of glycogenin is surrounded by branches of glucose units. The entire globular granule may contain around 30,000 glucose units.

Galactose is the sugar in milk. Infants have an enzyme in the small intestine that metabolizes lactose to galactose and glucose. In areas where milk products are regularly consumed, adults have also evolved this enzyme. Galactose is converted in the liver to G-6-P and can thus enter the glycolytic pathway.

Fructose is one of the three dietary monosaccharides (along with glucose and galactose) which are absorbed directly into the bloodstream during digestion. Fructose is absorbed from the small intestine and then passes to the liver to be metabolized, primarily to glycogen. The catabolism of both fructose and galactose produces the same number of ATP molecules as glucose.

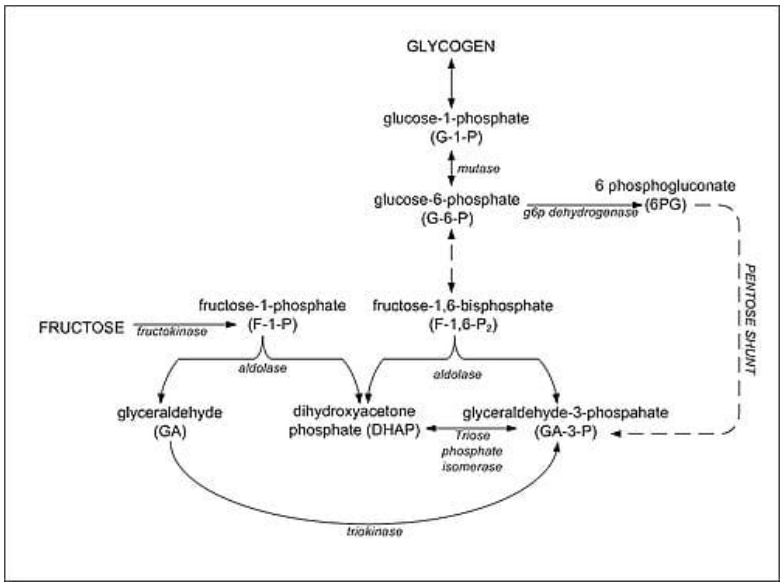


Figure 7.15.1: Fructose Metabolism: Although the metabolism of fructose and glucose share many of the same intermediate structures, they have very different metabolic fates in human metabolism.

Sucrose is a disaccharide with a molecule of glucose and a molecule of fructose bonded together with a glycosidic linkage. The catabolism of sucrose breaks it down to monomers of glucose and fructose. The glucose can directly enter the glycolytic pathway while fructose must first be converted to glycogen, which can be broken down to G-1-P and enter the glycolytic pathway as described above.

Key Points

- When blood sugar levels drop, glycogen is broken down into glucose -1-phosphate, which is then converted to glucose-6-phosphate and enters glycolysis for ATP production.
- In the liver, galactose is converted to glucose-6-phosphate in order to enter the glycolytic pathway.
- Fructose is converted into glycogen in the liver and then follows the same pathway as glycogen to enter glycolysis.
- Sucrose is broken down into glucose and fructose; glucose enters the pathway directly while fructose is converted to glycogen.

Key Terms

- **disaccharide**: A sugar, such as sucrose, maltose, or lactose, consisting of two monosaccharides combined together.
- **glycogen**: A polysaccharide that is the main form of carbohydrate storage in animals; converted to glucose as needed.
- **monosaccharide**: A simple sugar such as glucose, fructose, or deoxyribose that has a single ring.

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7.16: Connections of Carbohydrate, Protein, and Lipid Metabolic Pathways - Connecting Proteins to Glucose Metabolism

Learning Objectives

- Describe the role played by proteins in glucose metabolism

Metabolic pathways should be thought of as porous; that is, substances enter from other pathways and intermediates leave for other pathways. These pathways are not closed systems. Many of the substrates, intermediates, and products in a particular pathway are reactants in other pathways. Proteins are a good example of this phenomenon. They can be broken down into their constituent amino acids and used at various steps of the pathway of glucose catabolism.

Proteins are hydrolyzed by a variety of enzymes in cells. Most of the time, the amino acids are recycled into the synthesis of new proteins or are used as precursors in the synthesis of other important biological molecules, such as hormones, nucleotides, or neurotransmitters. However, if there are excess amino acids, or if the body is in a state of starvation, some amino acids will be shunted into the pathways of glucose catabolism.

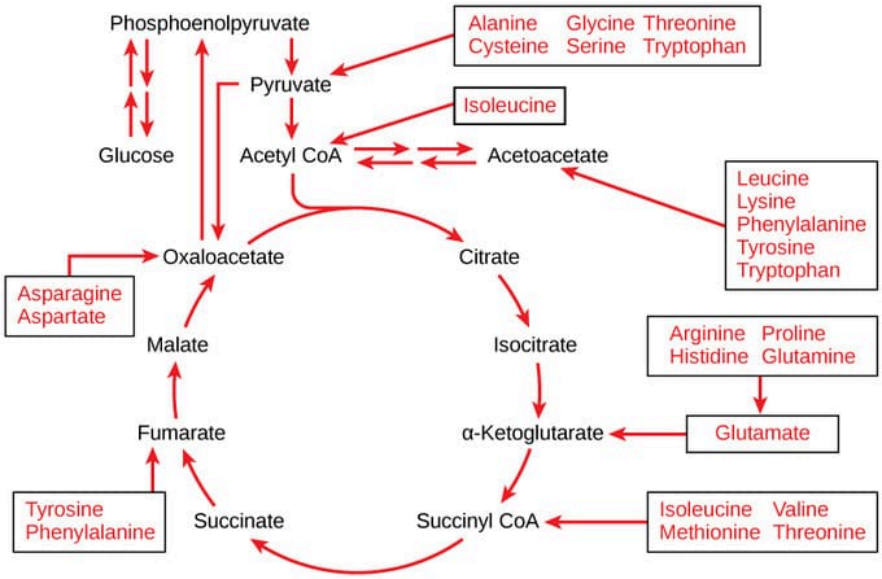


Figure 7.16.1: Connection of Amino Acids to Glucose Metabolism Pathways: The carbon skeletons of certain amino acids (indicated in boxes) are derived from proteins and can feed into pyruvate, acetyl CoA, and the citric acid cycle.

Each amino acid must have its amino group removed (deamination) prior to the carbon chain's entry into these pathways. When the amino group is removed from an amino acid, it is converted into ammonia through the urea cycle. The remaining atoms of the amino acid result in a keto acid: a carbon chain with one ketone and one carboxylic acid group. In mammals, the liver synthesizes urea from two ammonia molecules and a carbon dioxide molecule. Thus, urea is the principal waste product in mammals produced from the nitrogen originating in amino acids; it leaves the body in urine. The keto acid can then enter the citric acid cycle.

When deaminated, amino acids can enter the pathways of glucose metabolism as pyruvate, acetyl CoA, or several components of the citric acid cycle. For example, deaminated asparagine and aspartate are converted into oxaloacetate and enter glucose catabolism in the citric acid cycle. Deaminated amino acids can also be converted into another intermediate molecule before entering the pathways. Several amino acids can enter glucose catabolism at multiple locations.

Key Points

- Amino acids must be deaminated before entering any of the pathways of glucose catabolism: the amino group is converted to ammonia, which is used by the liver in the synthesis of urea.
- Deaminated amino acids can be converted into pyruvate, acetyl CoA, or some components of the citric acid cycle to enter the pathways of glucose catabolism.
- Several amino acids can enter the glucose catabolism pathways at multiple locations.

Key Terms

- **catabolism**: Destructive metabolism, usually including the release of energy and breakdown of materials.
- **keto acid**: Any carboxylic acid that also contains a ketone group.
- **deamination**: The removal of an amino group from a compound.

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7.17: Connections of Carbohydrate, Protein, and Lipid Metabolic Pathways - Connecting Lipids to Glucose Metabolism

Learning Objectives

- Explain the connection of lipids to glucose metabolism

Like sugars and amino acids, the catabolic pathways of lipids are also connected to the glucose catabolism pathways. The lipids that are connected to the glucose pathways are cholesterol and triglycerides.

Cholesterol

Cholesterol contributes to cell membrane flexibility and is a precursor to steroid hormones. The synthesis of cholesterol starts with acetyl groups, which are transferred from acetyl CoA, and proceeds in only one direction; the process cannot be reversed. Thus, synthesis of cholesterol requires an intermediate of glucose metabolism.

Triglycerides

Triglycerides, a form of long-term energy storage in animals, are made of glycerol and three fatty acids. Animals can make most of the fatty acids they need. Triglycerides can be both made and broken down through parts of the glucose catabolism pathways. Glycerol can be phosphorylated to glycerol-3-phosphate, which continues through glycolysis.

Fatty acids are catabolized in a process called beta-oxidation that takes place in the matrix of the mitochondria and converts their fatty acid chains into two carbon units of acetyl groups, while producing NADH and $FADH_2$. The acetyl groups are picked up by CoA to form acetyl CoA that proceeds into the citric acid cycle as it combines with oxaloacetate. The NADH and $FADH_2$ are then used by the electron transport chain.

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Key Points

- Many types of lipids exist, but cholesterol and triglycerides are the lipids that enter the pathways of glucose catabolism.
- Through the process of phosphorylation, glycerol can be converted to glycerol-3-phosphate during the glycolytic pathway.
- When fatty acids are broken down into acetyl groups through beta-oxidation, the acetyl groups are used by CoA to form acetyl-CoA, which enters the citric acid cycle to produce ATP.
- Beta-oxidation produces $FADH_2$ and NADH, which are used by the electron transport chain for ATP production.

Key Terms

- **beta-oxidation**: A process that takes place in the matrix of the mitochondria and catabolizes fatty acids by converting them to acetyl groups while producing NADH and FADH2.
- **lipid**: A group of organic compounds including fats, oils, waxes, sterols, and triglycerides; characterized by being insoluble in water; account for most of the fat present in the human body.

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7.18: Regulation of Cellular Respiration - Regulatory Mechanisms for Cellular Respiration

Learning Objectives

- Explain the mechanisms that regulate cellular respiration.

Regulatory Mechanisms

Various mechanisms are used to control cellular respiration. As such, some type of control exists at each stage of glucose metabolism. Access of glucose to the cell can be regulated using the GLUT proteins that transport glucose. In addition, different forms of the GLUT protein control passage of glucose into the cells of specific tissues.

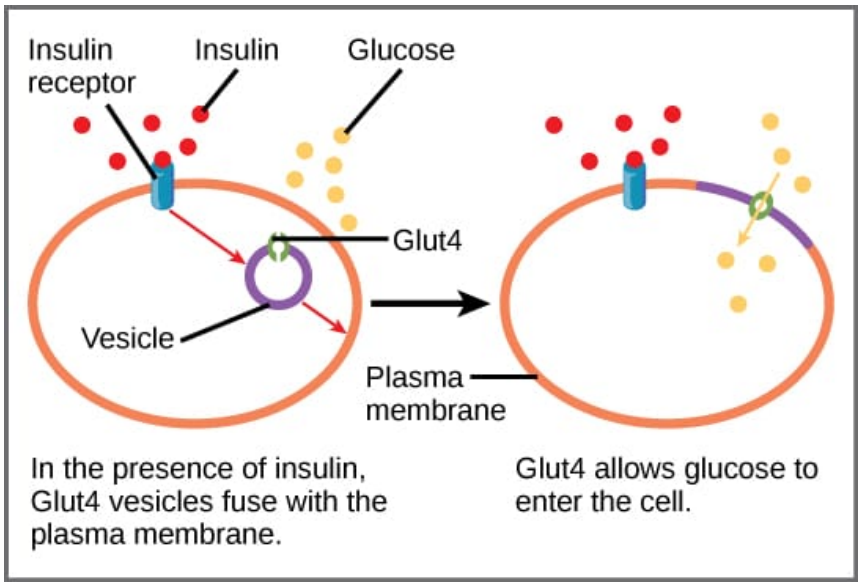


Figure 7.18.1: Glucose Transport: GLUT4 is a glucose transporter that is stored in vesicles. A cascade of events that occurs upon insulin binding to a receptor in the plasma membrane causes GLUT4-containing vesicles to fuse with the plasma membrane so that glucose may be transported into the cell.

Some reactions are controlled by having two different enzymes: one each for the two directions of a reversible reaction. Reactions that are catalyzed by only one enzyme can go to equilibrium, stalling the reaction. In contrast, if two different enzymes (each specific for a given direction) are necessary for a reversible reaction, the opportunity to control the rate of the reaction increases and equilibrium is not reached.

A number of enzymes involved in each of the pathways (in particular, the enzyme catalyzing the first committed reaction of the pathway) are controlled by attachment of a molecule to an allosteric (non-active) site on the protein. This site has an effect on the enzyme's activity, often by changing the conformation of the protein. The molecules most commonly used in this capacity are the nucleotides ATP, ADP, AMP, NAD^+, and NADH. These regulators, known as allosteric effectors, may increase or decrease enzyme activity, depending on the prevailing conditions, altering the steric structure of the enzyme, usually affecting the configuration of the active site. This alteration of the protein's (the enzyme's) structure either increases or decreases its affinity for its substrate, with the effect of increasing or decreasing the rate of the reaction. The attachment of a molecule to the allosteric site serves to send a signal to the enzyme, providing feedback. This feedback type of control is effective as long as the chemical affecting it is bound to the enzyme. Once the overall concentration of the chemical decreases, it will diffuse away from the protein, and the control is relaxed.

Key Points

- Varying forms of the GLUT protein control the passage of glucose into the cells of specific tissues, thereby regulating cellular respiration.
- Reactions that are catalyzed by only one enzyme can go to equilibrium, which can cause the reaction to stall.
- If two different enzymes are necessary for a reversible reaction, there is greater opportunity to control the rate of the reaction and, as a result, equilibrium is reached less often.
- Enzymes are often controlled by binding of a molecule to an allosteric site on the protein.

Key Terms

- **enzyme**: a globular protein that catalyses a biological chemical reaction
- **allosteric**: a compound that binds to an inactive site, affecting the activity of an enzyme by changing the conformation of the protein (can activate or deactivate)
- **metabolism**: the complete set of chemical reactions that occur in living cells

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7.19: Regulation of Cellular Respiration - Control of Catabolic Pathways

Learning Objectives

- Explain how catabolic pathways are controlled

Control of Catabolic Pathways

Enzymes, proteins, electron carriers, and pumps that play roles in glycolysis, the citric acid cycle, and the electron transport chain tend to catalyze non-reversible reactions. In other words, if the initial reaction takes place, the pathway is committed to proceeding with the remaining reactions. Whether a particular enzyme activity is released depends upon the energy needs of the cell (as reflected by the levels of ATP, ADP, and AMP).

Glycolysis

The control of glycolysis begins with the first enzyme in the pathway, hexokinase. This enzyme catalyzes the phosphorylation of glucose, which helps to prepare the compound for cleavage in a later step. The presence of the negatively-charged phosphate in the molecule also prevents the sugar from leaving the cell. When hexokinase is inhibited, glucose diffuses out of the cell and does not become a substrate for the respiration pathways in that tissue. The product of the hexokinase reaction is glucose-6-phosphate, which accumulates when a later enzyme, phosphofructokinase, is inhibited.

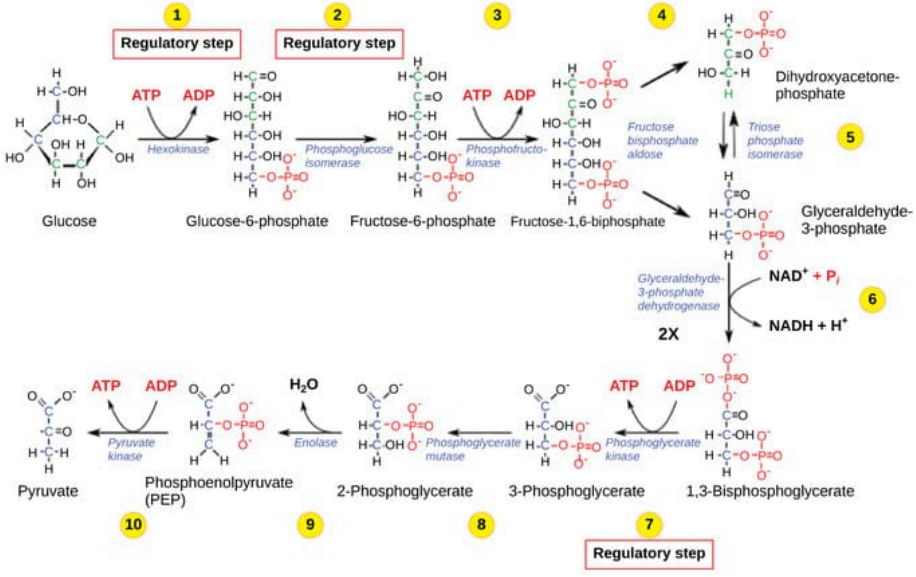


Figure 7.19.1: Glycolysis: The glycolysis pathway is primarily regulated at the three key enzymatic steps (1, 2, and 7) as indicated. Note that the first two steps that are regulated occur early in the pathway and involve hydrolysis of ATP.

Phosphofructokinase is the main enzyme controlled in glycolysis. High levels of ATP, citrate, or a lower, more acidic pH decrease the enzyme's activity. An increase in citrate concentration can occur because of a blockage in the citric acid cycle. Fermentation, with its production of organic acids like lactic acid, frequently accounts for the increased acidity in a cell; however, the products of fermentation do not typically accumulate in cells.

The last step in glycolysis is catalyzed by pyruvate kinase. The pyruvate produced can proceed to be catabolized or converted into the amino acid alanine. If no more energy is needed and alanine is in adequate supply, the enzyme is inhibited. The enzyme's activity is increased when fructose-1,6-bisphosphate levels increase. (Recall that fructose-1,6-bisphosphate is an intermediate

in the first half of glycolysis.) The regulation of pyruvate kinase involves phosphorylation, resulting in a less-active enzyme. Dephosphorylation by a phosphatase reactivates it. Pyruvate kinase is also regulated by ATP (a negative allosteric effect).

If more energy is needed, more pyruvate will be converted into acetyl CoA through the action of pyruvate dehydrogenase. If either acetyl groups or NADH accumulate, there is less need for the reaction and the rate decreases. Pyruvate dehydrogenase is also regulated by phosphorylation: a kinase phosphorylates it to form an inactive enzyme, and a phosphatase reactivates it. The kinase and the phosphatase are also regulated.

Citric Acid Cycle

The citric acid cycle is controlled through the enzymes that catalyze the reactions that make the first two molecules of NADH. These enzymes are isocitrate dehydrogenase and α-ketoglutarate dehydrogenase. When adequate ATP and NADH levels are available, the rates of these reactions decrease. When more ATP is needed, as reflected in rising ADP levels, the rate increases. α-Ketoglutarate dehydrogenase will also be affected by the levels of succinyl CoA, a subsequent intermediate in the cycle, causing a decrease in activity. A decrease in the rate of operation of the pathway at this point is not necessarily negative as the increased levels of the α-ketoglutarate not used by the citric acid cycle can be used by the cell for amino acid (glutamate) synthesis.

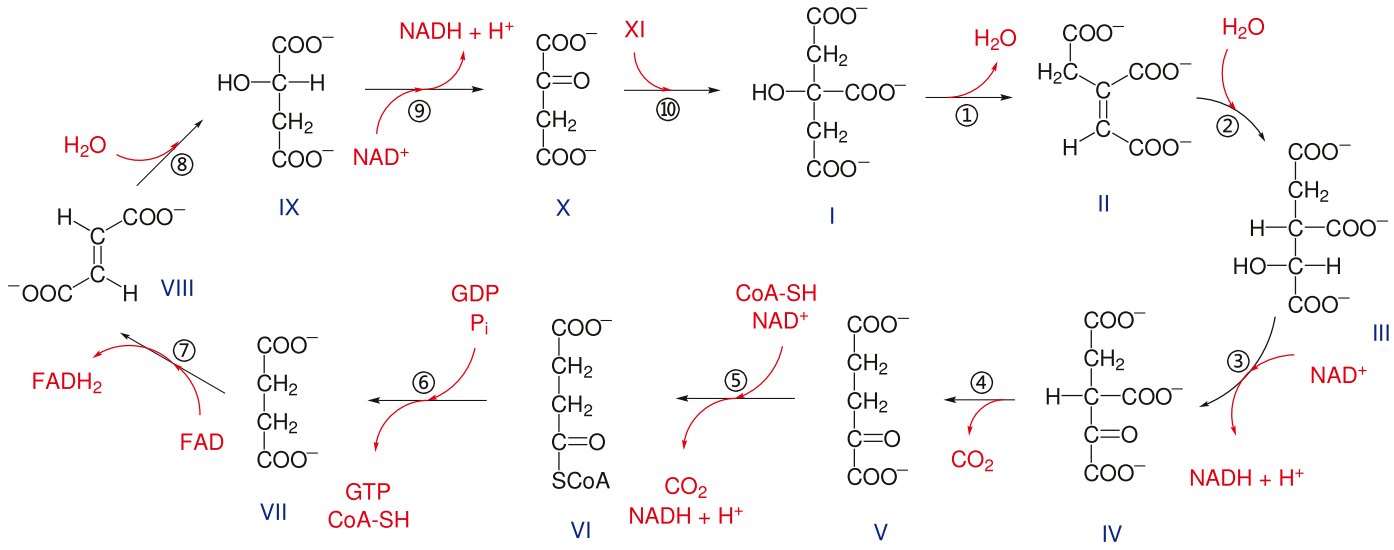


Figure 7.19.1: Citric Acid Cycle: Enzymes, isocitrate dehydrogenase and α-ketoglutarate dehydrogenase, catalyze the reactions that make the first two molecules of NADH in the citric acid cycle. Rates of the reaction decrease when sufficient ATP and NADH levels are reached.

Electron Transport Chain

Specific enzymes of the electron transport chain are unaffected by feedback inhibition, but the rate of electron transport through the pathway is affected by the levels of ADP and ATP. Greater ATP consumption by a cell is indicated by a buildup of ADP. As ATP usage decreases, the concentration of ADP decreases: ATP begins to build up in the cell. This change in the relative concentration of ADP to ATP triggers the cell to slow down the electron transport chain.

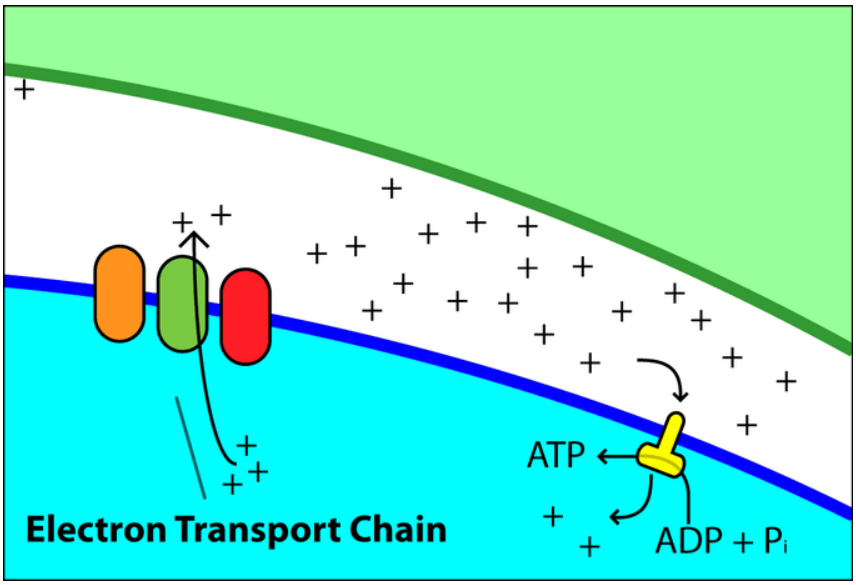


Figure 7.19.1: Electron Chain Transport: Levels of ADP and ATP affect the rate of electron transport through this type of chain transport.

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Key Points

- Glycolysis, the citric acid cycle, and the electron transport chain are catabolic pathways that bring forth non-reversible reactions.
- Glycolysis control begins with hexokinase, which catalyzes the phosphorylation of glucose; its product is glucose-6-phosphate, which accumulates when phosphofructokinase is inhibited.
- The citric acid cycle is controlled through the enzymes that break down the reactions that make the first two molecules of NADH.

- The rate of electron transport through the electron transport chain is affected by the levels of ADP and ATP, whereas specific enzymes of the electron transport chain are unaffected by feedback inhibition.

Key Terms

- **phosphofructokinase**: any of a group of kinase enzymes that convert fructose phosphates to biphosphate
- **glycolysis**: the cellular metabolic pathway of the simple sugar glucose to yield pyruvic acid and ATP as an energy source
- **kinase**: any of a group of enzymes that transfers phosphate groups from high-energy donor molecules, such as ATP, to specific target molecules (substrates); the process is termed phosphorylation

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8: PHOTOSYNTHESIS

- Topic hierarchy

8.1: Overview of Photosynthesis - The Purpose and Process of Photosynthesis
8.2: Overview of Photosynthesis - Main Structures and Summary of Photosynthesis
8.3: Overview of Photosynthesis - The Two Parts of Photosynthesis
8.4: The Light-Dependent Reactions of Photosynthesis - Introduction to Light Energy
8.5: The Light-Dependent Reactions of Photosynthesis - Absorption of Light
8.6: The Light-Dependent Reactions of Photosynthesis - Processes of the Light-Dependent Reactions
8.7: The Light-Independent Reactions of Photosynthesis - AM and C4 Photosynthesis
8.8: The Light-Independent Reactions of Photosynthesis - The Calvin Cycle
8.9: The Light-Independent Reactions of Photosynthesis - The Carbon Cycle

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8.1: Overview of Photosynthesis - The Purpose and Process of Photosynthesis

Learning Objectives

- Describe the process of photosynthesis

The Importance of Photosynthesis

The processes of all organisms—from bacteria to humans—require energy. To get this energy, many organisms access stored energy by eating food. Carnivores eat other animals and herbivores eat plants. But where does the stored energy in food originate? All of this energy can be traced back to the process of photosynthesis and light energy from the sun.

Photosynthesis is essential to all life on earth. It is the only biological process that captures energy from outer space (sunlight) and converts it into chemical energy in the form of G3P (
Glyceraldehyde 3-phosphate) which in turn can be made into sugars and other molecular compounds. Plants use these compounds in all of their metabolic processes; plants do not need to consume other organisms for food because they build all the molecules they need. Unlike plants, animals need to consume other organisms to consume the molecules they need for their metabolic processes.

The Process of Photosynthesis

During photosynthesis, molecules in leaves capture sunlight and energize electrons, which are then stored in the covalent bonds of carbohydrate molecules. That energy within those covalent bonds will be released when they are broken during cell respiration. How long lasting and stable are those covalent bonds? The energy extracted today by the burning of coal and petroleum products represents sunlight energy captured and stored by photosynthesis almost 200 million years ago.

Plants, algae, and a group of bacteria called cyanobacteria are the only organisms capable of performing photosynthesis. Because they use light to manufacture their own food, they are called photoautotrophs (“self-feeders using light”). Other organisms, such as animals, fungi, and most other bacteria, are termed heterotrophs (“other feeders”) because they must rely on the sugars produced by photosynthetic organisms for their energy needs. A third very interesting group of bacteria synthesize sugars, not by using sunlight’s energy, but by extracting energy from inorganic chemical compounds; hence, they are referred to as chemoautotrophs.

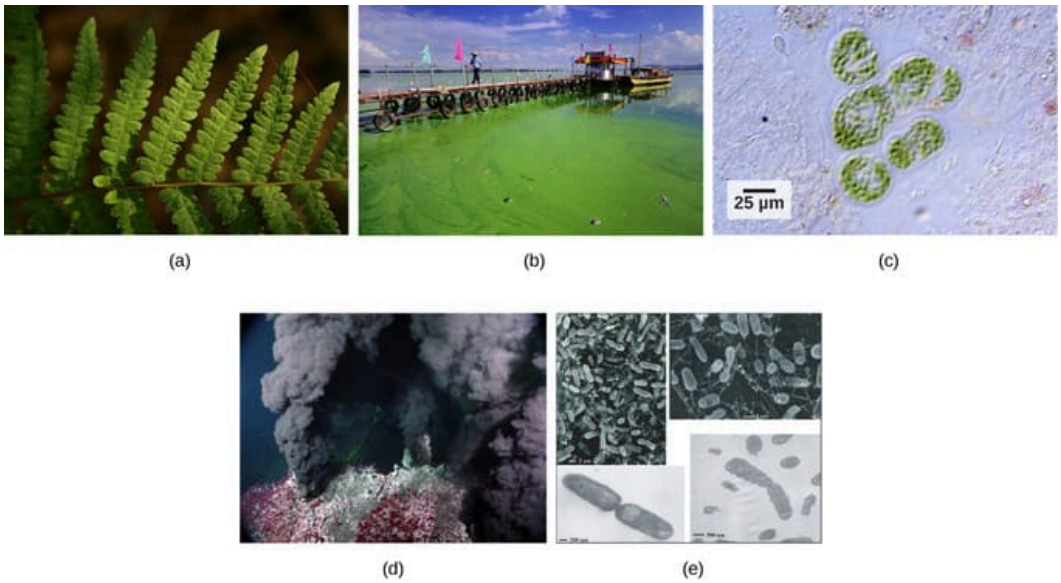


Figure 8.1.1: Photosynthetic and Chemosynthetic Organisms: Photoautotrophs, including (a) plants, (b) algae, and (c) cyanobacteria, synthesize their organic compounds via photosynthesis using sunlight as an energy source. Cyanobacteria and planktonic algae can grow over enormous areas in water, at times completely covering the surface. In a (d) deep sea vent, chemoautotrophs, such as these (e) thermophilic bacteria, capture energy from inorganic compounds to produce organic compounds. The ecosystem surrounding the vents has a diverse array of animals, such as tubeworms, crustaceans, and octopuses that derive energy from the bacteria.

The importance of photosynthesis is not just that it can capture sunlight's energy. A lizard sunning itself on a cold day can use the sun's energy to warm up. Photosynthesis is vital because it evolved as a way to store the energy in solar radiation (the "photo-" part) as high-energy electrons in the carbon-carbon bonds of carbohydrate molecules (the "-synthesis" part). Those carbohydrates are the energy source that heterotrophs use to power the synthesis of ATP via respiration. Therefore, photosynthesis powers 99 percent of Earth's ecosystems. When a top predator, such as a wolf, preys on a deer, the wolf is at the end of an energy path that went from nuclear reactions on the surface of the sun, to light, to photosynthesis, to vegetation, to deer, and finally to wolf.

Key Points

- Photosynthesis evolved as a way to store the energy in solar radiation as high-energy electrons in carbohydrate molecules.
- Plants, algae, and cyanobacteria, known as photoautotrophs, are the only organisms capable of performing photosynthesis.
- Heterotrophs, unable to produce their own food, rely on the carbohydrates produced by photosynthetic organisms for their energy needs.

Key Terms

- **photosynthesis**: the process by which plants and other photoautotrophs generate carbohydrates and oxygen from carbon dioxide, water, and light energy in chloroplasts
- **photoautotroph**: an organism that can synthesize its own food by using light as a source of energy
- **chemoautotroph**: a simple organism, such as a protozoan, that derives its energy from chemical processes rather than photosynthesis

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8.2: Overview of Photosynthesis - Main Structures and Summary of Photosynthesis

Learning Objectives

- Describe the main structures involved in photosynthesis and recall the chemical equation that summarizes the process of photosynthesis

Overview of Photosynthesis

Photosynthesis is a multi-step process that requires sunlight, carbon dioxide, and water as substrates. It produces oxygen and glyceraldehyde-3-phosphate (G3P or GA3P), simple carbohydrate molecules that are high in energy and can subsequently be converted into glucose, sucrose, or other sugar molecules. These sugar molecules contain covalent bonds that store energy. Organisms break down these molecules to release energy for use in cellular work.

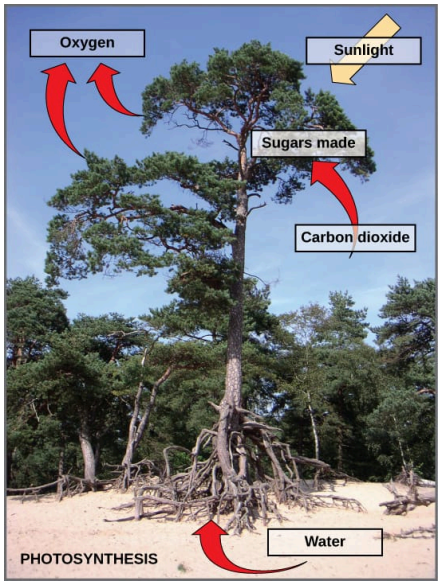


Figure 8.2.1: Photosynthesis: Photosynthesis uses solar energy, carbon dioxide, and water to produce energy-storing carbohydrates. Oxygen is generated as a waste product of photosynthesis.

The energy from sunlight drives the reaction of carbon dioxide and water molecules to produce sugar and oxygen, as seen in the chemical equation for photosynthesis. Though the equation looks simple, it is carried out through many complex steps. Before learning the details of how photoautotrophs convert light energy into chemical energy, it is important to become familiar with the structures involved.

Photosynthesis Equation							
Carbon dioxide	+	Water	SUNLIGHT →	Sugar	+	Oxygen	
$6CO_2$		$6H_2O$		$C_6H_{12}O_6$		$6O_2$	

Figure 8.2.1: Chemical equation for photosynthesis: The basic equation for photosynthesis is deceptively simple. In reality, the process includes many steps involving intermediate reactants and products. Glucose, the primary energy source in cells, is made from two three-carbon GA3P molecules.

Photosynthesis and the Leaf

In plants, photosynthesis generally takes place in leaves, which consist of several layers of cells. The process of photosynthesis occurs in a middle layer called the mesophyll. The gas exchange of carbon dioxide and oxygen occurs through small, regulated openings called stomata (singular: stoma), which also play a role in the plant's regulation of water balance. The stomata are typically located on the underside of the leaf, which minimizes water loss. Each stoma is flanked by guard cells that regulate the opening and closing of the stomata by swelling or shrinking in response to osmotic changes.

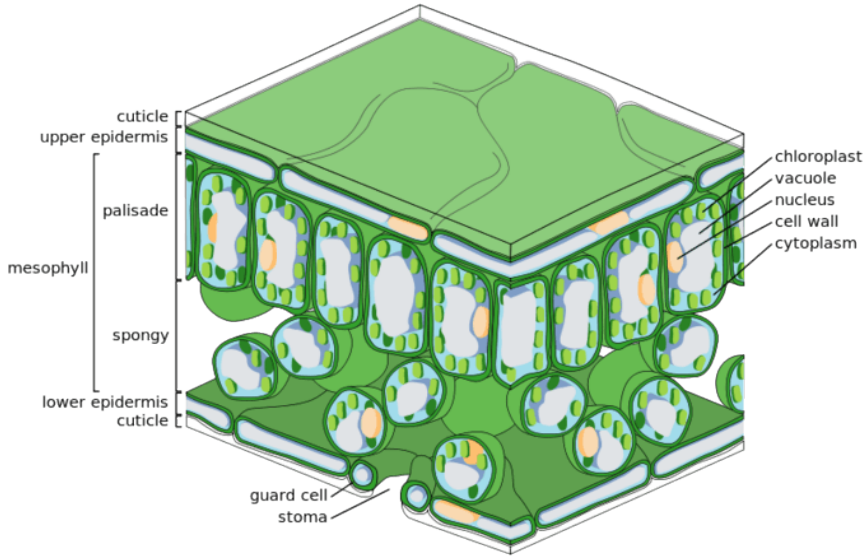


Figure 8.2.1: Structure of a leaf (cross-section): Photosynthesis takes place in the mesophyll. The palisade layer contains most of the chloroplast and principal region in which photosynthesis is carried out. The airy spongy layer is the region of storage and gas exchange. The stomata regulate carbon dioxide and water balance.

Photosynthesis within the Chloroplast

In all autotrophic eukaryotes, photosynthesis takes place inside an organelle called a chloroplast. For plants, chloroplast-containing cells exist in the mesophyll. Chloroplasts have a double membrane envelope composed of an outer membrane and an inner membrane. Within the double membrane are stacked, disc-shaped structures called thylakoids.

Embedded in the thylakoid membrane is chlorophyll, a pigment that absorbs certain portions of the visible spectrum and captures energy from sunlight. Chlorophyll gives plants their green color and is responsible for the initial interaction between light and plant material, as well as numerous proteins that make up the electron transport chain. The thylakoid membrane encloses an internal space called the thylakoid lumen. A stack of thylakoids is called a granum, and the liquid-filled space surrounding the granum is the stroma or "bed."

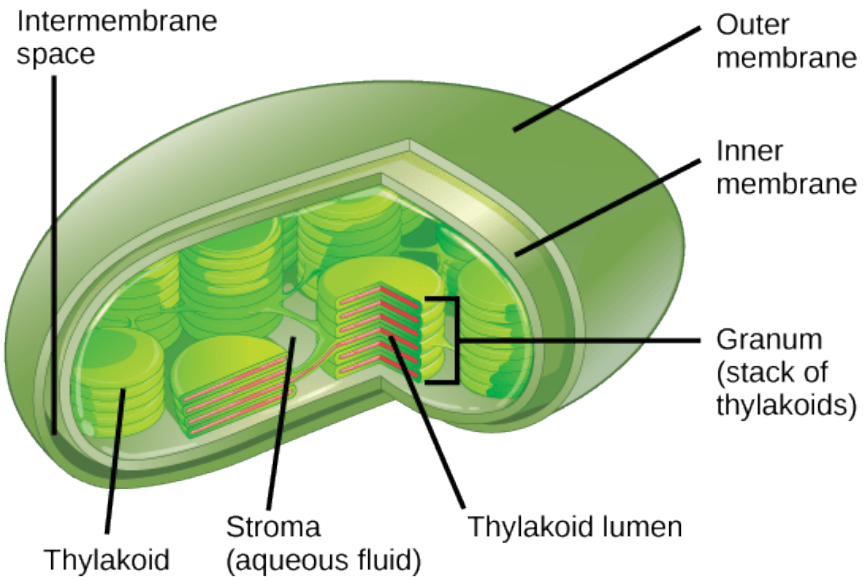


Figure 8.2.1: Structure of the Chloroplast: Photosynthesis takes place in chloroplasts, which have an outer membrane and an inner membrane. Stacks of thylakoids called grana form a third membrane layer.

Key Points

- The chemical equation for photosynthesis is $6CO_2 + 6H_2O \rightarrow C_6H_{12}O_6 + 6O_2$.$6CO_2 + 6H_2O \rightarrow C_6H_{12}O_6 + 6O_2$.
- In plants, the process of photosynthesis takes place in the mesophyll of the leaves, inside the chloroplasts.
- Chloroplasts contain disc-shaped structures called thylakoids, which contain the pigment chlorophyll.
- Chlorophyll absorbs certain portions of the visible spectrum and captures energy from sunlight.

Key Terms

- **chloroplast**: An organelle found in the cells of green plants and photosynthetic algae where photosynthesis takes place.
- **mesophyll**: A layer of cells that comprises most of the interior of the leaf between the upper and lower layers of epidermis.
- **stoma**: A pore in the leaf and stem epidermis that is used for gaseous exchange.

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8.3: Overview of Photosynthesis - The Two Parts of Photosynthesis

Learning Objectives

- Distinguish between the two parts of photosynthesis

Light-Dependent Reactions

Just as the name implies, light-dependent reactions require sunlight. In the light-dependent reactions, energy from sunlight is absorbed by chlorophyll and converted into stored chemical energy, in the form of the electron carrier molecule NADPH (nicotinamide adenine dinucleotide phosphate) and the energy currency molecule ATP (adenosine triphosphate). The light-dependent reactions take place in the thylakoid membranes in the granum (stack of thylakoids), within the chloroplast.

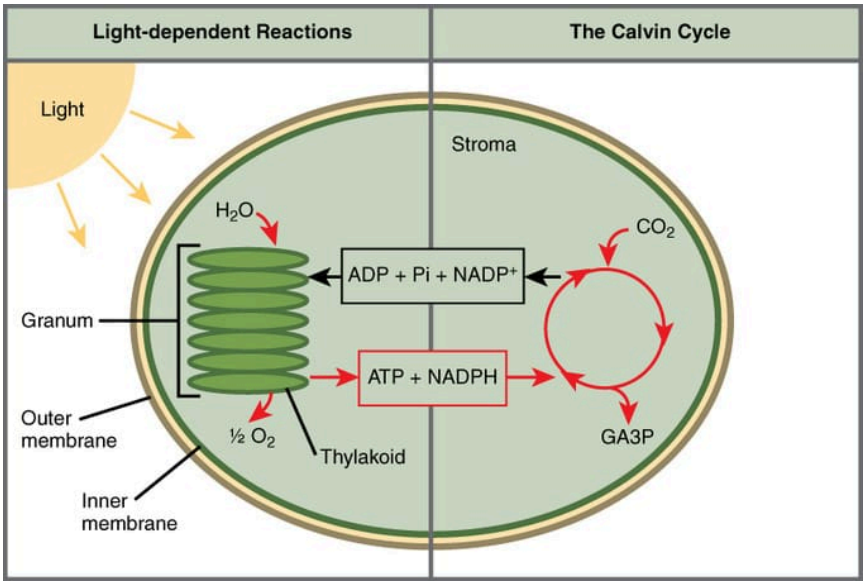


Figure 8.3.1: The two stages of photosynthesis: Photosynthesis takes place in two stages: light-dependent reactions and the Calvin cycle (light-independent reactions). Light-dependent reactions, which take place in the thylakoid membrane, use light energy to make ATP and NADPH. The Calvin cycle, which takes place in the stroma, uses energy derived from these compounds to make GA3P from CO2.

Photosystems

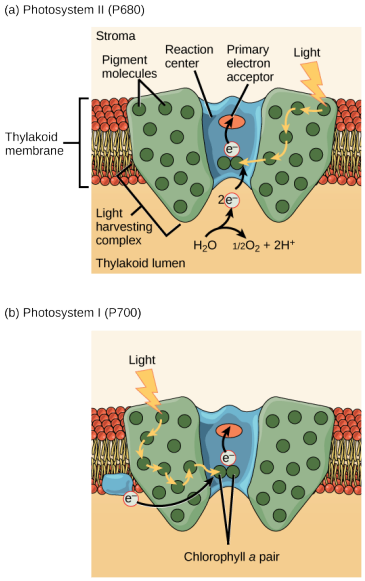


Figure 8.3.1: Photosystems I & II: As explained above, the photosystems manipulate electrons with energy harvested from light.

The process that converts light energy into chemical energy takes place in a multi-protein complex called a photosystem. Two types of photosystems are embedded in the thylakoid membrane: photosystem II (PSII) and photosystem I (PSI). Each photosystem plays a key role in capturing the energy from sunlight by exciting electrons. These energized electrons are transported by “energy carrier” molecules, which power the light-independent reactions.

Photosystems consist of a light-harvesting complex and a reaction center. Pigments in the light-harvesting complex pass light energy to two special chlorophyll *a* molecules in the reaction center. The light excites an electron from the chlorophyll *a* pair, which passes to the primary electron acceptor. The excited electron must then be replaced. In photosystem II, the electron comes from the splitting of water, which releases oxygen as a waste product. In photosystem I, the electron comes from the chloroplast electron transport chain.

The two photosystems oxidize different sources of the low-energy electron supply, deliver their energized electrons to different places, and respond to different wavelengths of light.

Light-Independent Reactions

In the light-independent reactions or Calvin cycle, the energized electrons from the light-dependent reactions provide the energy to form carbohydrates from carbon dioxide molecules. The light-independent reactions are sometimes called the Calvin cycle because of the cyclical nature of the process.

Although the light-independent reactions do not use light as a reactant (and as a result can take place at day or night), they require the products of the light-dependent reactions to function. The light-independent molecules depend on the energy carrier molecules, ATP and NADPH, to drive the construction of new carbohydrate molecules. After the energy is transferred, the energy carrier molecules return to the light-dependent reactions to obtain more energized electrons. In addition, several enzymes of the light-independent reactions are activated by light.

Photosynthesis takes place in two sequential stages:

1. The light-dependent reactions;
2. The light-independent reactions, or Calvin Cycle.

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Key Points

- In light-dependent reactions, the energy from sunlight is absorbed by chlorophyll and converted into chemical energy in the form of electron carrier molecules like ATP and NADPH.
- Light energy is harnessed in Photosystems I and II, both of which are present in the thylakoid membranes of chloroplasts.
- In light-independent reactions (the Calvin cycle), carbohydrate molecules are assembled from carbon dioxide using the chemical energy harvested during the light-dependent reactions.

Key Terms

- **photosystem**: Either of two biochemical systems active in chloroplasts that are part of photosynthesis.

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8.4: The Light-Dependent Reactions of Photosynthesis - Introduction to Light Energy

Learning Objectives

- Explain the difference between short and long wavelengths.

What Is Light Energy?

The sun emits an enormous amount of electromagnetic radiation (solar or light energy). Humans can see only a fraction of this energy, which is referred to as “visible light.” The manner in which solar energy travels is described as waves. Scientists can determine the amount of energy of a wave by measuring its wavelength, the distance between consecutive points of a wave, such as from crest to crest or from trough to trough.

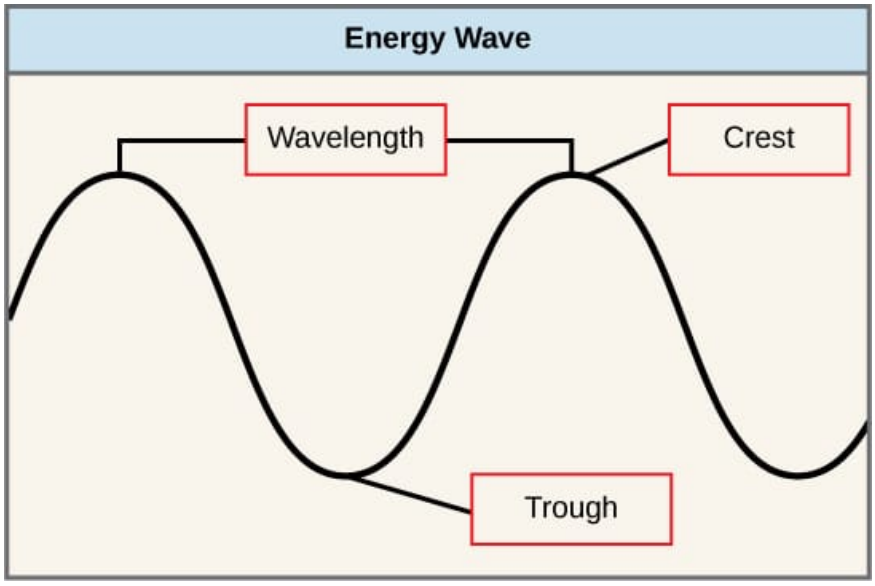


Figure 8.4.1: Wavelengths: The wavelength of a single wave is the distance between two consecutive points of similar position (two crests or two troughs) along the wave.

Visible light constitutes only one of many types of electromagnetic radiation emitted from the sun and other stars. The electromagnetic spectrum is the range of all possible frequencies of radiation. The electromagnetic spectrum shows several types of electromagnetic radiation originating from the sun, including X-rays and ultraviolet (UV) rays. The higher-energy waves can penetrate tissues and damage cells and DNA, which explains why both X-rays and UV rays can be harmful to living organisms. Scientists differentiate the various types of radiant energy from the sun within the electromagnetic spectrum.The difference between wavelengths relates to the amount of energy carried by them.

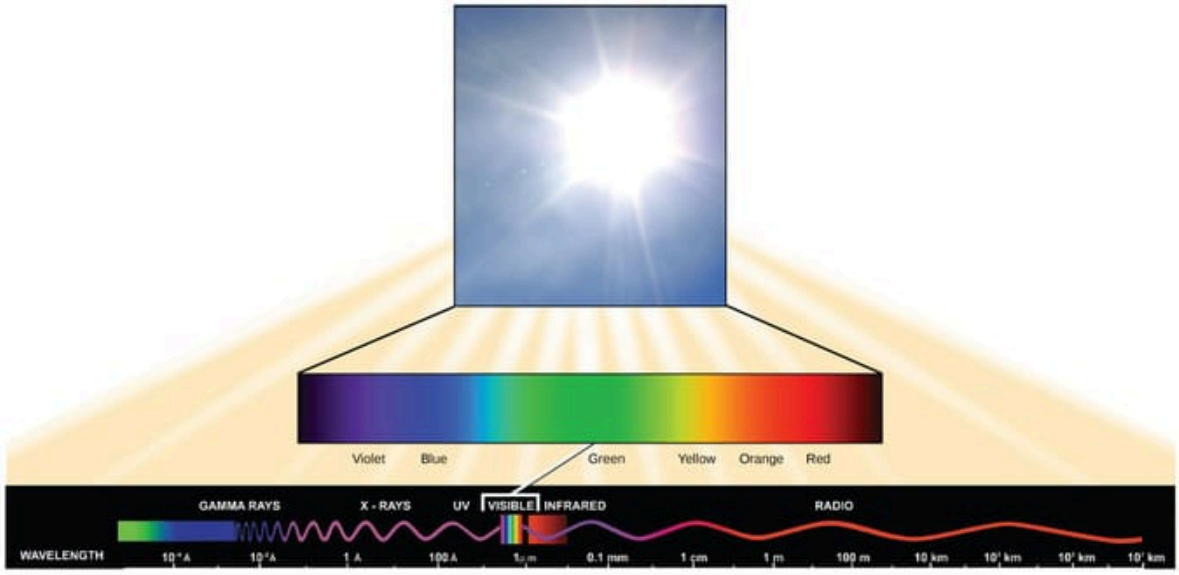


Figure 8.4.1: The Electromagnetic Spectrum: The sun emits energy in the form of electromagnetic radiation. This radiation exists at different wavelengths, each of which has its own characteristic energy. All electromagnetic radiation, including visible light, is characterized by its wavelength.

Each type of electromagnetic radiation travels at a particular wavelength. The longer the wavelength, the less energy is carried. Short, tight waves carry the most energy. This may seem illogical, but think of it in terms of a person moving a heavy rope. It takes little effort by a person to move a rope in long, wide waves. To make a rope move in short, tight waves, a person would need to apply significantly more energy.

Key Points

- The amount of energy of a wave can be determined by measuring its wavelength, the distance between consecutive points of a wave.
- Visible light is a type of radiant energy within the electromagnetic spectrum; other types of electromagnetic radiation include UV, infrared, gamma, and radio rays as well as X-rays.
- The difference between wavelengths relates to the amount of energy carried by them; short, tight waves carry more energy than long, wide waves.

Key Terms

- **electromagnetic spectrum**: the entire range of wavelengths of all known radiations consisting of oscillating electric and magnetic fields, including gamma rays, visible light, infrared, radio waves, and X-rays
- **wavelength**: the length of a single cycle of a wave, as measured by the distance between one peak or trough of a wave and the next; it corresponds to the velocity of the wave divided by its frequency
- **visible light**: the part of the electromagnetic spectrum, between infrared and ultraviolet, that is visible to the human eye

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8.5: The Light-Dependent Reactions of Photosynthesis - Absorption of Light

Learning Objectives

- Differentiate between chlorophyll and carotenoids.

Absorption of Light

Light energy initiates the process of photosynthesis when pigments absorb the light. Organic pigments have a narrow range of energy levels that they can absorb. Energy levels lower than those represented by red light are insufficient to raise an orbital electron to an excited, or quantum, state. Energy levels higher than those in blue light will physically tear the molecules apart, a process called bleaching. For example, retinal pigments can only "see" (absorb) 700 nm to 400 nm light; this is visible light. For the same reasons, plant pigment molecules absorb only light in the wavelength range of 700 nm to 400 nm; plant physiologists refer to this range for plants as photosynthetically-active radiation.

The visible light seen by humans as the color white light actually exists in a rainbow of colors in the electromagnetic spectrum, with violet and blue having shorter wavelengths and, thus, higher energy. At the other end of the spectrum, toward red, the wavelengths are longer and have lower energy.

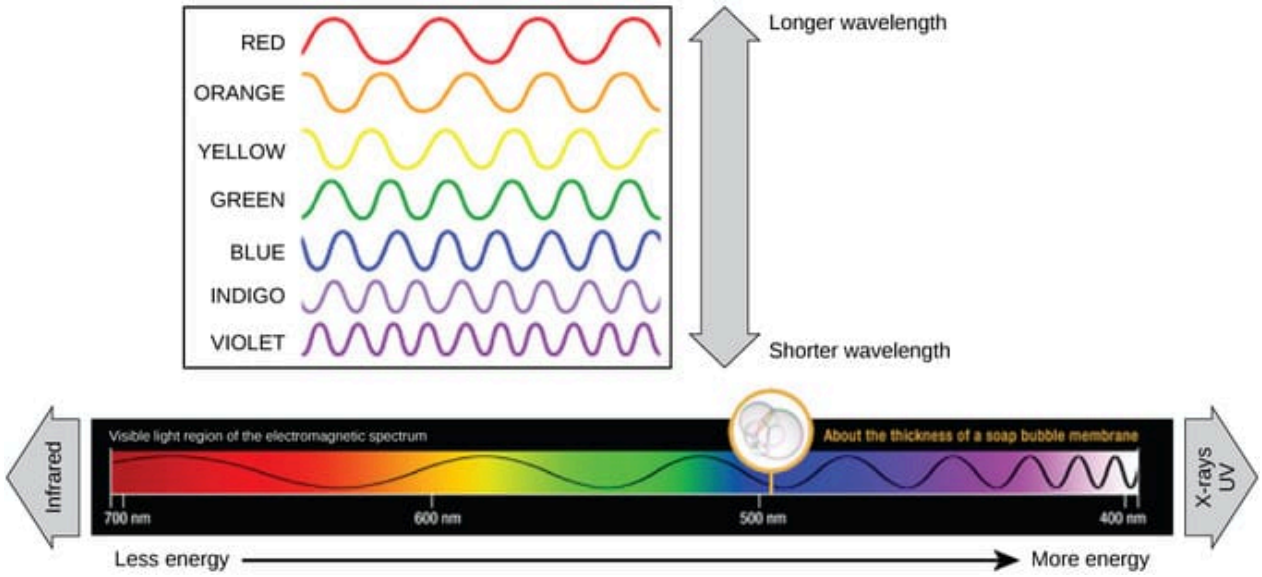


Figure 8.5.1: Visible Light: The colors of visible light do not carry the same amount of energy. Violet has the shortest wavelength and, therefore, carries the most energy, whereas red has the longest wavelength and carries the least amount of energy.

Understanding Pigments

Different kinds of pigments exist, each of which has evolved to absorb only certain wavelengths or colors of visible light. Pigments reflect or transmit the wavelengths they cannot absorb, making them appear in the corresponding color.

Chlorophylls and carotenoids are the two major classes of photosynthetic pigments found in plants and algae; each class has multiple types of pigment molecules. There are five major chlorophylls: *a*, *b*, *c* and *d,* along with a related molecule found in prokaryotes called bacteriochlorophyll.

With dozens of different forms, carotenoids are a much larger group of pigments. The carotenoids found in fruit, such as the

red of tomato (lycopene), the yellow of corn seeds (zeaxanthin), or the orange of an orange peel (β-carotene), are used to attract seed-dispersing organisms. In photosynthesis, carotenoids function as photosynthetic pigments that are very efficient molecules for the disposal of excess energy. When a leaf is exposed to full sun, the light-dependent reactions are required to process an enormous amount of energy; if that energy is not handled properly, it can do significant damage. Therefore, many carotenoids are stored in the thylakoid membrane to absorb excess energy and safely release that energy as heat.

Each type of pigment can be identified by the specific pattern of wavelengths it absorbs from visible light, which is the absorption spectrum. Chlorophyll *a* absorbs light in the blue-violet region, while chlorophyll *b* absorbs red-blue light. Neither *a* or *b* absorb green light; because green is reflected or transmitted, chlorophyll appears green. Carotenoids absorb light in the blue-green and violet region and reflect the longer yellow, red, and orange wavelengths.

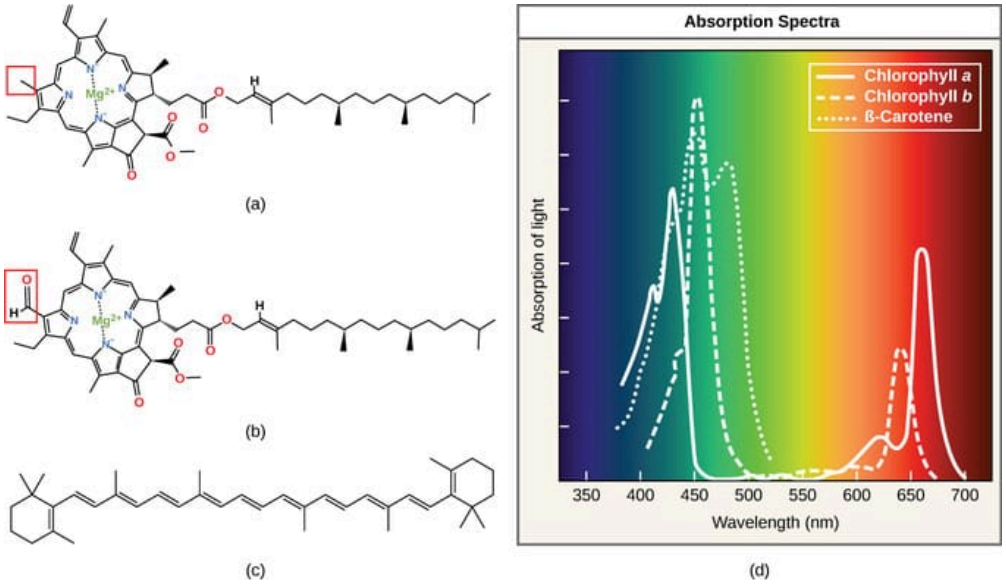


Figure 8.5.1: Chlorophyll a and b: (a) Chlorophyll *a*, (b) chlorophyll *b*, and (c) β-carotene are hydrophobic organic pigments found in the thylakoid membrane. Chlorophyll *a* and *b*, which are identical except for the part indicated in the red box, are responsible for the green color of leaves. β-carotene is responsible for the orange color in carrots. Each pigment has (d) a unique absorbance spectrum.

Many photosynthetic organisms have a mixture of pigments. In this way organisms can absorb energy from a wider range of wavelengths. Not all photosynthetic organisms have full access to sunlight. Some organisms grow underwater where light intensity and quality decrease and change with depth. Other organisms grow in competition for light. Plants on the rainforest floor must be able to absorb any light that comes through because the taller trees absorb most of the sunlight and scatter the remaining solar radiation



Figure 8.5.1: Pigments in Plants: Plants that commonly grow in the shade have adapted to low levels of light by changing the relative concentrations of their chlorophyll pigments.

When studying a photosynthetic organism, scientists can determine the types of pigments present by using a spectrophotometer. These instruments can differentiate which wavelengths of light a substance can absorb. Spectrophotometers measure transmitted light and compute its absorption. By extracting pigments from leaves and placing these samples into a spectrophotometer, scientists can identify which wavelengths of light an organism can absorb.

Key Points

- Plant pigment molecules absorb only light in the wavelength range of 700 nm to 400 nm; this range is referred to as photosynthetically-active radiation.
- Violet and blue have the shortest wavelengths and the most energy, whereas red has the longest wavelengths and carries the least amount of energy.
- Pigments reflect or transmit the wavelengths they cannot absorb, making them appear in the corresponding color.
- Chorophylls and carotenoids are the major pigments in plants; while there are dozens of carotenoids, there are only five important chorophylls: *a*, *b*, *c*, *d,* and bacteriochlorophyll.
- Chlorophyll *a* absorbs light in the blue-violet region, chlorophyll *b* absorbs red-blue light, and both *a* and *b* reflect green light (which is why chlorophyll appears green).
- Carotenoids absorb light in the blue-green and violet region and reflect the longer yellow, red, and orange wavelengths; these pigments also dispose excess energy out of the cell.

Key Terms

- **chlorophyll**: Any of a group of green pigments that are found in the chloroplasts of plants and in other photosynthetic organisms such as cyanobacteria.
- **carotenoid**: Any of a class of yellow to red plant pigments including the carotenes and xanthophylls.
- **spectrophotometer**: An instrument used to measure the intensity of electromagnetic radiation at different wavelengths.

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8.6: The Light-Dependent Reactions of Photosynthesis - Processes of the Light-Dependent Reactions

Learning Objectives

- Describe how light energy is converted into ATP and NADPH.

How Light-Dependent Reactions Work

The overall function of light-dependent reactions, the first stage of photosynthesis, is to convert solar energy into chemical energy in the form of NADPH and ATP, which are used in light-independent reactions and fuel the assembly of sugar molecules. Protein complexes and pigment molecules work together to produce NADPH and ATP.

Producing Chemical Energy

Light energy is converted into chemical energy in a multiprotein complex called a photosystem. Two types of photosystems, photosystem I (PSI) and photosystem II (PSII), are found in the thylakoid membrane inside the chloroplast. Each photosystem consists of multiple antenna proteins that contain a mixture of 300–400 chlorophyll *a* and *b* molecules, as well as other pigments like carotenoids. Cytochrome b6f complex and ATP synthase are also major protein complexes in the thylakoid membrane that work with the photosystems to create ATP and NADPH.

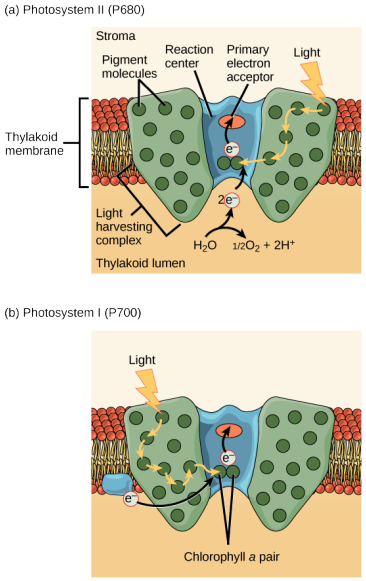


Figure 8.6.1: Photosystems I & II: A photosystem consists of a light-harvesting complex and a reaction center. Pigments in the light-harvesting complex pass light energy to two special chlorophyll a molecules in the reaction center. The light excites an electron from the chlorophyll a pair, which passes to the primary electron acceptor. The excited electron must then be replaced. In (a) photosystem II, the electron comes from the splitting of water, which releases oxygen as a waste product. In (b) photosystem I, the electron comes from the chloroplast electron transport chain.

The two photosystems absorb light energy through proteins containing pigments, such as chlorophyll. The light-dependent reactions begin in photosystem II. In PSII, energy from sunlight is used to split water, which releases two electrons, two hydrogen atoms, and one oxygen atom. When a chlorophyll *a* molecule within the reaction center of PSII absorbs a photon, the electron in this molecule attains a higher energy level. Because this state of an electron is very unstable, the electron is transferred to another molecule creating a chain of redox reactions called an electron transport chain (ETC). The electron flow goes from PSII to cytochrome b6f to PSI; as electrons move between these two photosystems, they lose energy. Because the electrons have lost

energy prior to their arrival at PSI, they must be re-energized by PSI. Therefore, another photon is absorbed by the PSI antenna. That energy is transmitted to the PSI reaction center. This reaction center, known as P700, is oxidized and sends a high-energy electron to reduce NADP+ to NADPH. This process illustrates oxygenic photosynthesis, wherein the first electron donor is water and oxygen is created as a waste product.

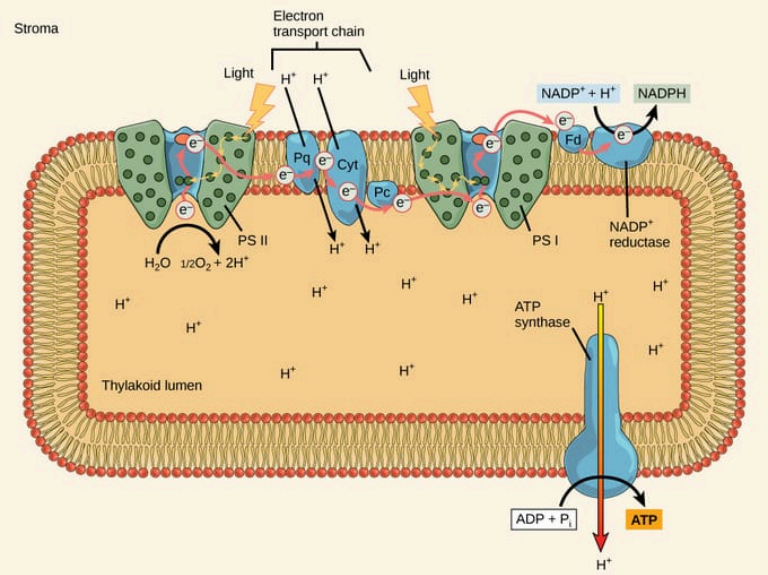


Figure 8.6.1: Photosystem II: In the photosystem II (PSII) reaction center, energy from sunlight is used to extract electrons from water. The electrons travel through the chloroplast electron transport chain to photosystem I (PSI), which reduces NADP+ to NADPH. The electron transport chain moves protons across the thylakoid membrane into the lumen. At the same time, splitting of water adds protons to the lumen while reduction of NADPH removes protons from the stroma. The net result is a low pH in the thylakoid lumen and a high pH in the stroma. ATP synthase uses this electrochemical gradient to make ATP.

Cytochrome b6f and ATP synthase work together to create ATP. This process, called photophosphorylation, occurs in two different ways. In non-cyclic photophosphorylation, cytochrome b6f uses the energy of electrons from PSII to pump hydrogen ions from the lumen (an area of high concentration) to the stroma (an area of low concentration). The energy released by the hydrogen ion stream allows ATP synthase to attach a third phosphate group to ADP, which forms ATP. This flow of hydrogen ions through ATP synthase is called chemiosmosis because the ions move from an area of high to an area of low concentration through a semi-permeable structure. In cyclic photophosphorylation, cytochrome b6f uses the energy of electrons from both PSII and PSI to create more ATP and to stop the production of NADPH. Cyclic phosphorylation is important to maintain the right proportions of NADPH and ATP, which will carry out light-independent reactions later on.

The net-reaction of all light-dependent reactions in oxygenic photosynthesis is: $2H_2O + 2NADP+ + 3ADP + 3Pi \rightarrow O_2 + 2NADPH + 3ATP$

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Key Points

- Light energy splits water and extracts electrons in photosystem II (PSII); then electrons are moved from PSII to cytochrome b6f to photosystem I (PSI) and reduce in energy.
- Electrons are re-energized in PSI and those high energy electrons reduce $NADP^+$ to NADPH.
- In non-cyclic photophosphorylation, cytochrome b6f uses the energy of electrons from PSII to pump hydrogen ions from the lumen to the stroma; this energy allows ATP synthase to attach a third phosphate group to ADP, which forms ATP.
- In cyclic photophosphorylation, cytochrome b6f uses the energy of electrons from both PSII and PSI to create more ATP and to stop the production of NADPH, maintaining the right proportions of NADPH and ATP.

Key Terms

- **photosystem**: Either of two biochemical systems, active in chloroplasts, that are part of photosynthesis.
- **photophosphorylation**: The addition of a phosphate (PO43-) group to a protein or other organic molecule by photosynthesis.
- **chemiosmosis**: The movement of ions across a selectively permeable membrane, down their electrochemical gradient.

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8.7: The Light-Independent Reactions of Photosynthesis - AM and C4 Photosynthesis

Learning Objectives

- Compare C4 and CAM photosynthesis

Photosynthesis in desert plants has evolved adaptations that conserve water. In harsh, dry heat, every drop of water must be used to survive. Because stomata must open to allow for the uptake of CO_2, water escapes from the leaf during active photosynthesis. Desert plants have evolved processes to conserve water and deal with harsh conditions. A more efficient use of CO_2 allows plants to adapt to living with less water.

Some plants such as cacti can prepare materials for photosynthesis during the night by a temporary carbon fixation and storage process, because opening the stomata at this time conserves water due to cooler temperatures. In addition, cacti have evolved the ability to carry out low levels of photosynthesis without opening stomata at all, a mechanism for surviving extremely dry periods.



Figure 8.7.1: Cactus: The harsh conditions of the desert have led plants like these cacti to evolve variations of the light-independent reactions of photosynthesis. These variations increase the efficiency of water usage, helping to conserve water and energy.

CAM Photosynthesis

Xerophytes, such as cacti and most succulents, also use
phosphoenolpyruvate (PEP) carboxylase to capture carbon dioxide in a process called crassulacean acid metabolism (CAM). In contrast to C_4 metabolism, which *physically* separates the CO_2 fixation to PEP from the Calvin cycle, CAM *temporally* separates these two processes.

CAM plants have a different leaf anatomy from C_3 plants, and fix the CO_2 at night, when their stomata are open. CAM plants store the CO_2 mostly in the form of malic acid via carboxylation of phosphoenolpyruvate to oxaloacetate, which is then reduced to malate. Decarboxylation of malate during the day releases CO_2 inside the leaves, thus allowing carbon fixation to 3-phosphoglycerate by RuBisCO. Sixteen thousand species of plants use CAM.

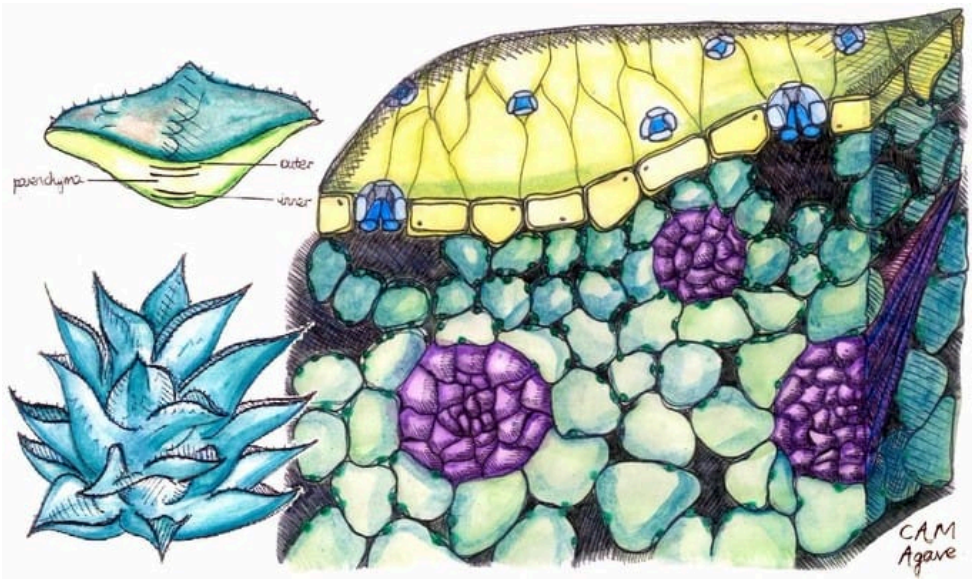
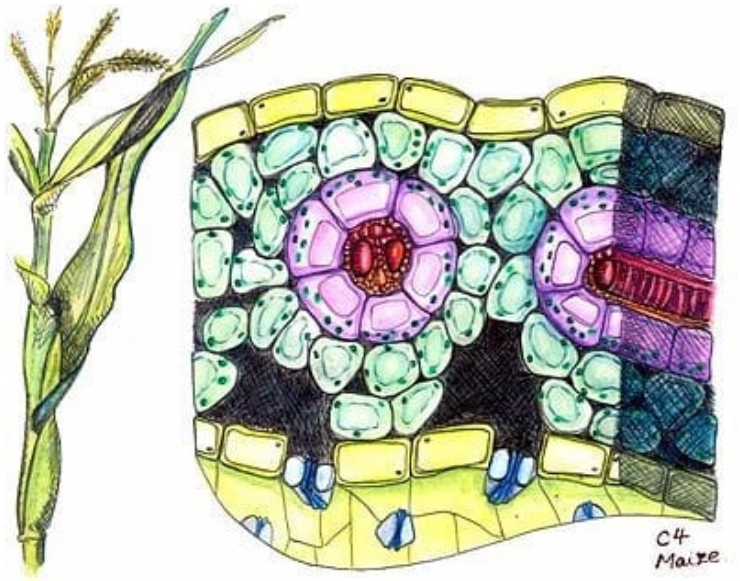


Figure 8.7.1: Cross section of agave, a CAM plant: Cross section of a CAM (crassulacean acid metabolism) plant, specifically of an agave leaf. Vascular bundles shown. Drawing based on microscopic images courtesy of Cambridge University Plant Sciences Department.

C_4 Carbon Fixation

The C4 pathway bears resemblance to CAM; both act to concentrate CO_2 around RuBisCO, thereby increasing its efficiency. CAM concentrates it temporally, providing CO_2 during the day and not at night, when respiration is the dominant reaction.

C_4 plants, in contrast, concentrate CO_2 spatially, with a RuBisCO reaction centre in a “bundle sheath cell” that is inundated with CO_2. Due to the inactivity required by the CAM mechanism, C_4 carbon fixation has a greater efficiency in terms of PGA synthesis.



Cross section of maize, a C_4 plant

Cross section of a C4 plant, specifically of a maize leaf. Drawing based on microscopic images courtesy of Cambridge University Plant Sciences Department.

C_4 plants can produce more sugar than C_3 plants in conditions of high light and temperature. Many important crop plants are C_4 plants, including maize, sorghum, sugarcane, and millet. Plants that do not use PEP-carboxylase in carbon fixation are called C3 plants because the primary carboxylation reaction, catalyzed by RuBisCO, produces the three-carbon 3-phosphoglyceric acids directly in the Calvin-Benson cycle. Over 90% of plants use C_3 carbon fixation, compared to 3% that use C_4 carbon fixation; however, the evolution of C_4 in over 60 plant lineages makes it a striking example of convergent evolution.

Key Points

- The process of photosynthesis in desert plants has evolved mechanisms to conserve water.
- Plants that use crassulacean acid metabolism (CAM) photosynthesis fix CO_2 at night, when their stomata are open.
- Plants that use C4 carbon fixation concentrate carbon dioxide spatially, using “bundle sheath cells” which are inundated with CO_2.

Key Terms

- **crassulacean acid metabolism**: A carbon fixation pathway that evolved in some plants as an adaptation to arid conditions, in which the stomata in the leaves remain shut during the day to reduce evapotranspiration, but open at night to collect carbon dioxide (CO2).
- **C4 carbon fixation**: A form of photosynthesis in which plants concentrate CO2 spatially, with a RuBisCO reaction centre in a “bundle sheath cell” that is inundated with CO2

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8.8: The Light-Independent Reactions of Photosynthesis - The Calvin Cycle

Learning Objectives

- Describe the Calvin Cycle

The Calvin Cycle

In plants, carbon dioxide (CO_2) enters the leaves through stomata, where it diffuses over short distances through intercellular spaces until it reaches the mesophyll cells. Once in the mesophyll cells, CO_2 diffuses into the stroma of the chloroplast, the site of light-independent reactions of photosynthesis. These reactions actually have several names associated with them. Other names for light-independent reactions include the Calvin cycle, the Calvin-Benson cycle, and dark reactions. The most outdated name is dark reactions, which can be misleading because it implies incorrectly that the reaction only occurs at night or is independent of light, which is why most scientists and instructors no longer use it.

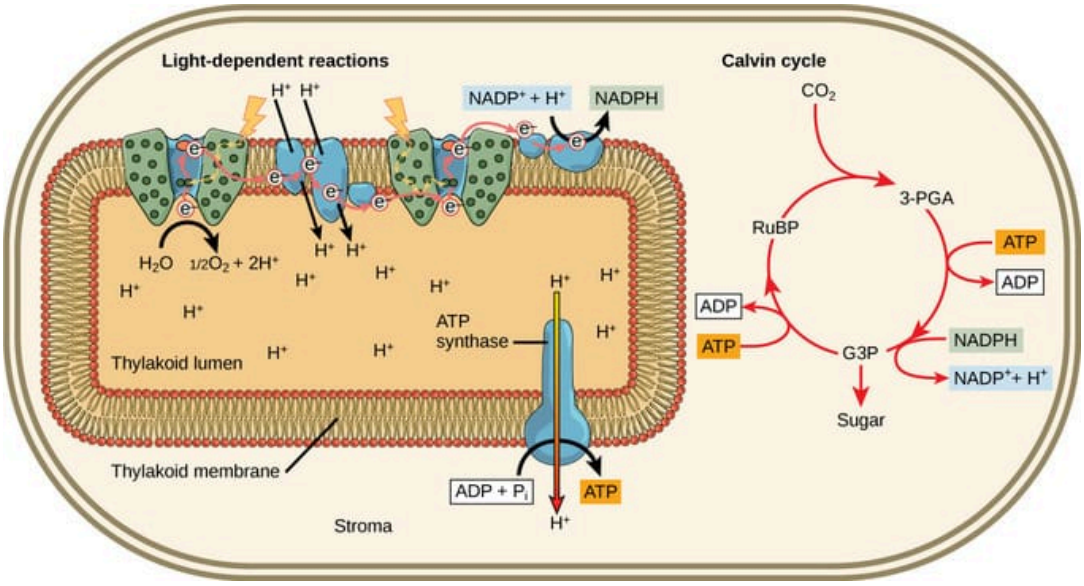


Figure 8.8.1: Light Reactions: Light-dependent reactions harness energy from the sun to produce chemical bonds, ATP, and NADPH. These energy-carrying molecules are made in the stroma where the Calvin cycle takes place. The Calvin cycle is not totally independent of light since it relies on ATP and NADH, which are products of the light-dependent reactions.

The light-independent reactions of the Calvin cycle can be organized into three basic stages: fixation, reduction, and regeneration.

Stage 1: Fixation

In the stroma, in addition to CO_2,two other components are present to initiate the light-independent reactions: an enzyme called ribulose bisphosphate carboxylase (RuBisCO) and three molecules of ribulose bisphosphate (RuBP). RuBP has five atoms of carbon, flanked by two phosphates. RuBisCO catalyzes a reaction between CO_2 and RuBP. For each CO_2 molecule that reacts with one RuBP, two molecules of 3-phosphoglyceric acid (3-PGA) form. 3-PGA has three carbons and one phosphate. Each turn of the cycle involves only one RuBP and one carbon dioxide and forms two molecules of 3-PGA. The number of carbon atoms remains the same, as the atoms move to form new bonds during the reactions (3 atoms from $3CO_2$ + 15 atoms from 3RuBP = 18 atoms in 3 atoms of 3-PGA). This process is called carbon fixation because CO_2 is “fixed” from an inorganic form into organic molecules.

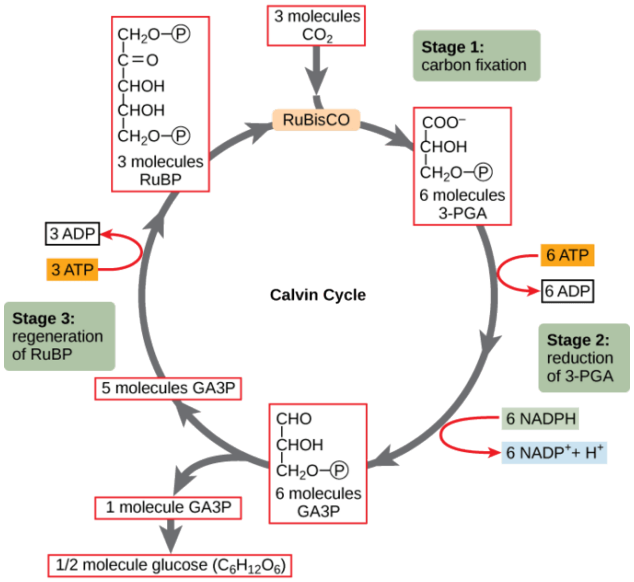


Figure 8.8.1: The Calvin Cycle: The Calvin cycle has three stages. In stage 1, the enzyme RuBisCO incorporates carbon dioxide into an organic molecule, 3-PGA. In stage 2, the organic molecule is reduced using electrons supplied by NADPH. In stage 3, RuBP, the molecule that starts the cycle, is regenerated so that the cycle can continue. Only one carbon dioxide molecule is incorporated at a time, so the cycle must be completed three times to produce a single three-carbon GA3P molecule, and six times to produce a six-carbon glucose molecule.

Stage 2: Reduction

ATP and NADPH are used to convert the six molecules of 3-PGA into six molecules of a chemical called glyceraldehyde 3-phosphate (G3P). This is a reduction reaction because it involves the gain of electrons by 3-PGA. Recall that a reduction is the gain of an electron by an atom or molecule. Six molecules of both ATP and NADPH are used. For ATP, energy is released with the loss of the terminal phosphate atom, converting it to ADP; for NADPH, both energy and a hydrogen atom are lost, converting it into $NADP^+$. Both of these molecules return to the nearby light-dependent reactions to be reused and reenergized.

Stage 3: Regeneration

At this point, only one of the G3P molecules leaves the Calvin cycle and is sent to the cytoplasm to contribute to the formation of other compounds needed by the plant. Because the G3P exported from the chloroplast has three carbon atoms, it takes three "turns" of the Calvin cycle to fix enough net carbon to export one G3P. But each turn makes two G3Ps, thus three turns make six G3Ps. One is exported while the remaining five G3P molecules remain in the cycle and are used to regenerate RuBP, which enables the system to prepare for more CO_2 to be fixed. Three more molecules of ATP are used in these regeneration reactions.

Key Points

- The Calvin cycle refers to the light-independent reactions in photosynthesis that take place in three key steps.
- Although the Calvin Cycle is not directly dependent on light, it is indirectly dependent on light since the necessary energy carriers (ATP and NADPH) are products of light-dependent reactions.
- In fixation, the first stage of the Calvin cycle, light-independent reactions are initiated; CO2 is fixed from an inorganic to an organic molecule.
- In the second stage, ATP and NADPH are used to reduce 3-PGA into G3P; then ATP and NADPH are converted to ADP and $NADP^+$, respectively.
- In the last stage of the Calvin Cycle, RuBP is regenerated, which enables the system to prepare for more CO_2 to be fixed.

Key Terms

- **light-independent reaction**: chemical reactions during photosynthesis that convert carbon dioxide and other compounds into glucose, taking place in the stroma

- **rubisco**: (ribulose bisphosphate carboxylase) a plant enzyme which catalyzes the fixing of atmospheric carbon dioxide during photosynthesis by catalyzing the reaction between carbon dioxide and RuBP
- **ribulose bisphosphate**: an organic substance that is involved in photosynthesis, reacts with carbon dioxide to form 3-PGA

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8.9: The Light-Independent Reactions of Photosynthesis - The Carbon Cycle

Learning Objectives

- Describe the importance of the carbon cycle

The Carbon Cycle

Whether the organism is a bacterium, plant, or animal, all living things access energy by breaking down carbohydrate molecules. But if plants make carbohydrate molecules, why would they need to break them down, especially when it has been shown that the gas organisms release as a "waste product" (CO_2) acts as a substrate for the formation of more food in photosynthesis? Living things need energy to perform life functions. In addition, an organism can either make its own food or eat another organism; either way, the food still needs to be broken down. Finally, in the process of breaking down food, called cellular respiration, heterotrophs release needed energy and produce "waste" in the form of CO_2 gas.



Figure 8.9.1: Photosynthesis and Aerobic Respiration: Photosynthesis consumes carbon dioxide and produces oxygen. Aerobic respiration consumes oxygen and produces carbon dioxide. These two processes play an important role in the carbon cycle.

In nature, there is no such thing as waste. Every single atom of matter and energy is conserved, recycling over and over, infinitely. Substances change form or move from one type of molecule to another, but their constituent atoms never disappear.

CO_2 is no more a form of waste than oxygen is wasteful to photosynthesis. Both are byproducts of reactions that move on to other reactions. Photosynthesis absorbs light energy to build carbohydrates in chloroplasts, and aerobic cellular respiration releases energy by using oxygen to metabolize carbohydrates in the cytoplasm and mitochondria. Photosynthesis consumes carbon dioxide and produces oxygen. Aerobic respiration consumes oxygen and produces carbon dioxide. Both processes use electron transport chains to capture the energy necessary to drive other reactions. These two powerhouse processes, photosynthesis and cellular respiration, function in biological, cyclical harmony to allow organisms to access life-sustaining energy that originates millions of miles away in the sun.

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Key Points

- Every single atom of energy is conserved by changing form or moving from one type of energy to another, so waste does not

exist in nature.
- Photosynthesis absorbs light energy to build carbohydrates, and aerobic cellular respiration releases energy by using oxygen to metabolize carbohydrates.
- Photosynthesis consumes carbon dioxide and produces oxygen, and aerobic respiration consumes oxygen and produces carbon dioxide.
- Both photosynthesis and cellular respiration use electron transport chains to capture the energy necessary to drive other reactions.

Key Terms

- **heterotroph**: an organism that requires an external supply of energy in the form of food, as it cannot synthesize its own
- **cellular respiration**: the set of the metabolic reactions and processes that take place in the cells of organisms to convert biochemical energy from nutrients into adenosine triphosphate (ATP)
- **aerobic**: living or occurring only in the presence of oxygen

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9: CELL COMMUNICATION

9.1: Signaling Molecules and Cellular Receptors - Signaling Molecules and Cellular Receptors

9.2: Signaling Molecules and Cellular Receptors - Forms of Signaling

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9.1: Signaling Molecules and Cellular Receptors - Signaling Molecules and Cellular Receptors

Learning Objectives

- Explain the importance of cell communication

Introduction: Signaling Molecules and Cellular Receptors

Imagine what life would be like if you and the people around you could not communicate. You would not be able to express your wishes to others, nor could you ask questions to find out more about your environment. Social organization is dependent on communication between the individuals that comprise that society; without communication, society would fall apart.



Figure 9.1.1: Communication is Key: Have you ever become separated from a friend while in a crowd? If so, you know the challenge of searching for someone when surrounded by thousands of other people. If you and your friend have cell phones, your chances of finding each other are good. A cell phone's ability to send and receive messages makes it an ideal communication device.

As with people, it is vital for individual cells to be able to interact with their environment. This is true whether a cell is growing by itself in a pond or is one of many cells that form a larger organism. In order to properly respond to external stimuli, cells have developed complex mechanisms of communication that can receive a message, transfer the information across the plasma membrane, and then produce changes within the cell in response to the message.

In multicellular organisms, cells send and receive chemical messages constantly to coordinate the actions of distant organs, tissues, and cells. The ability to send messages quickly and efficiently enables cells to coordinate and fine-tune their functions.

While the necessity for cellular communication in larger organisms seems obvious, even single-celled organisms communicate with each other. Yeast cells signal each other to aid mating. Some forms of bacteria coordinate their actions in order to form large complexes called biofilms or to organize the production of toxins to remove competing organisms. The ability of cells to communicate through chemical signals originated in single cells and was essential for the evolution of multicellular organisms. The efficient and error-free function of communication systems is vital for all forms of life.

Key Points

- The ability of cells to communicate through chemical signals originated in single cells and was essential for the evolution of multicellular organisms.
- In multicellular organisms, cells send and receive chemical messages constantly to coordinate the actions of distant organs, tissues, and cells.
- Cells can receive a message, transfer the information across the plasma membrane, and then produce changes within the cell in response to the message.
- Single-celled organisms, like yeast and bacteria, communicate with each other to aid in mating and coordination.
- Cellular communication has developed as a means to communicate with the environment, produce biological changes, and, if necessary, ensure survival.

Key Terms

- **biofilm**: a thin film of mucus created by and containing a colony of bacteria and other microorganisms

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9.2: Signaling Molecules and Cellular Receptors - Forms of Signaling

Learning Objectives

- Describe four types of signaling found in multicellular organisms

Forms of Signaling

There are four categories of chemical signaling found in multicellular organisms: paracrine signaling, endocrine signaling, autocrine signaling, and direct signaling across gap junctions. The main difference between the different categories of signaling is the distance that the signal travels through the organism to reach the target cell. It is also important to note that not all cells are affected by the same signals.

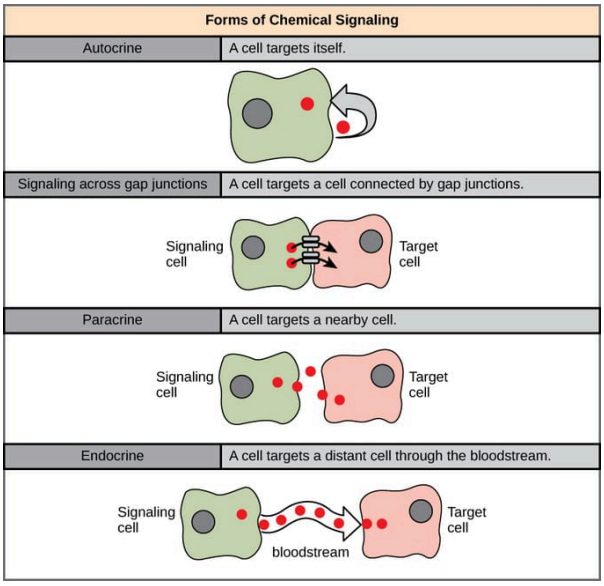


Figure 9.2.1: Forms of Chemical Signaling: In chemical signaling, a cell may target itself (autocrine signaling), a cell connected by gap junctions, a nearby cell (paracrine signaling), or a distant cell (endocrine signaling). Paracrine signaling acts on nearby cells, endocrine signaling uses the circulatory system to transport ligands, and autocrine signaling acts on the signaling cell. Signaling via gap junctions involves signaling molecules moving directly between adjacent cells.

Paracrine Signaling

Signals that act locally between cells that are close together are called paracrine signals. Paracrine signals move by diffusion through the extracellular matrix. These types of signals usually elicit quick responses that last only a short amount of time. In order to keep the response localized, paracrine ligand molecules are normally quickly degraded by enzymes or removed by neighboring cells. Removing the signals will reestablish the concentration gradient for the signal, allowing them to quickly diffuse through the intracellular space if released again.

One example of paracrine signaling is the transfer of signals across synapses between nerve cells. A nerve cell consists of a cell body, several short, branched extensions called dendrites that receive stimuli, and a long extension called an axon, which transmits signals to other nerve cells or muscle cells. The junction between nerve cells where signal transmission occurs is called a synapse. A synaptic signal is a chemical signal that travels between nerve cells. Signals within the nerve cells are propagated by fast-moving electrical impulses. When these impulses reach the end of the axon, the signal continues on to a dendrite of the next cell by the release of chemical ligands called neurotransmitters by the presynaptic cell (the cell emitting the signal). The

neurotransmitters are transported across the very small distances between nerve cells, which are called chemical synapses. The small distance between nerve cells allows the signal to travel quickly; this enables an immediate response.

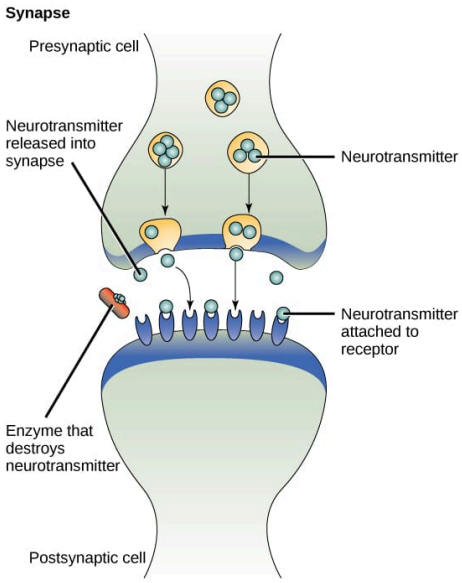


Figure 9.2.1: Synapsis: The distance between the presynaptic cell and the postsynaptic cell—called the synaptic gap—is very small and allows for rapid diffusion of the neurotransmitter. Enzymes in the synapatic cleft degrade some types of neurotransmitters to terminate the signal.

Endocrine Signaling

Signals from distant cells are called endocrine signals; they originate from endocrine cells. In the body, many endocrine cells are located in endocrine glands, such as the thyroid gland, the hypothalamus, and the pituitary gland. These types of signals usually produce a slower response, but have a longer-lasting effect. The ligands released in endocrine signaling are called hormones, signaling molecules that are produced in one part of the body, but affect other body regions some distance away.

Hormones travel the large distances between endocrine cells and their target cells via the bloodstream, which is a relatively slow way to move throughout the body. Because of their form of transport, hormones get diluted and are present in low concentrations when they act on their target cells. This is different from paracrine signaling in which local concentrations of ligands can be very high.

Autocrine Signaling

Autocrine signals are produced by signaling cells that can also bind to the ligand that is released. This means the signaling cell and the target cell can be the same or a similar cell (the prefix auto- means self, a reminder that the signaling cell sends a signal to itself). This type of signaling often occurs during the early development of an organism to ensure that cells develop into the correct tissues and take on the proper function. Autocrine signaling also regulates pain sensation and inflammatory responses. Further, if a cell is infected with a virus, the cell can signal itself to undergo programmed cell death, killing the virus in the process. In some cases, neighboring cells of the same type are also influenced by the released ligand. In embryological development, this process of stimulating a group of neighboring cells may help to direct the differentiation of identical cells into the same cell type, thus ensuring the proper developmental outcome.

Direct Signaling Across Gap Junctions

Gap junctions in animals and plasmodesmata in plants are connections between the plasma membranes of neighboring cells. These water-filled channels allow small signaling molecules, called intracellular mediators, to diffuse between the two cells. Small molecules, such as calcium ions (Ca^{2+}), are able to move between cells, but large molecules, like proteins and DNA, cannot fit through the channels. The specificity of the channels ensures that the cells remain independent, but can quickly and easily transmit signals. The transfer of signaling molecules communicates the current state of the cell that is directly next to the target cell; this allows a group of cells to coordinate their response to a signal that only one of them may have received. In plants,

plasmodesmata are ubiquitous, making the entire plant into a giant communication network.

Key Points

- Cells communicate via various types of signaling that allow chemicals to travel to target sites in order to elicit a response.
- Paracrine signaling occurs between local cells where the signals elicit quick responses and last only a short amount of time due to the degradation of the paracrine ligands.
- Endocrine signaling occurs between distant cells and is mediated by hormones released from specific endocrine cells that travel to target cells, producing a slower, long-lasting response.
- Autocrine signals are produced by signaling cells that can also bind to the ligand that is released, which means the signaling cell and the target cell can be the same or a similar cell.
- Direct signaling can occur by transferring signaling molecules across gap junctions between neighboring cells.

Key Terms

- **endocrine signaling**: signals from distant cells that originate from endocrine cells, usually producing a slow response, but having a long-lasting effect
- **autocrine signaling**: produced by signaling cells that can also bind to the ligand that is released: the signaling cell and the target cell can be the same or a similar cell (prefix auto- means self)
- **paracrine signaling**: a form of cell signaling in which the target cell is near (para = near) the signal-releasing cell

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9.3: Signaling Molecules and Cellular Receptors - Types of Receptors

Learning Objectives

- Compare internal receptors with cell-surface receptors

Types of Receptors

Receptors are protein molecules in the target cell or on its surface that bind ligands. There are two types of receptors: internal receptors and cell-surface receptors.

Internal receptors

Internal receptors, also known as intracellular or cytoplasmic receptors, are found in the cytoplasm of the cell and respond to hydrophobic ligand molecules that are able to travel across the plasma membrane. Once inside the cell, many of these molecules bind to proteins that act as regulators of mRNA synthesis to mediate gene expression. Gene expression is the cellular process of transforming the information in a cell's DNA into a sequence of amino acids that ultimately forms a protein. When the ligand binds to the internal receptor, a conformational change exposes a DNA-binding site on the protein. The ligand-receptor complex moves into the nucleus, binds to specific regulatory regions of the chromosomal DNA, and promotes the initiation of transcription. Internal receptors can directly influence gene expression without having to pass the signal on to other receptors or messengers.

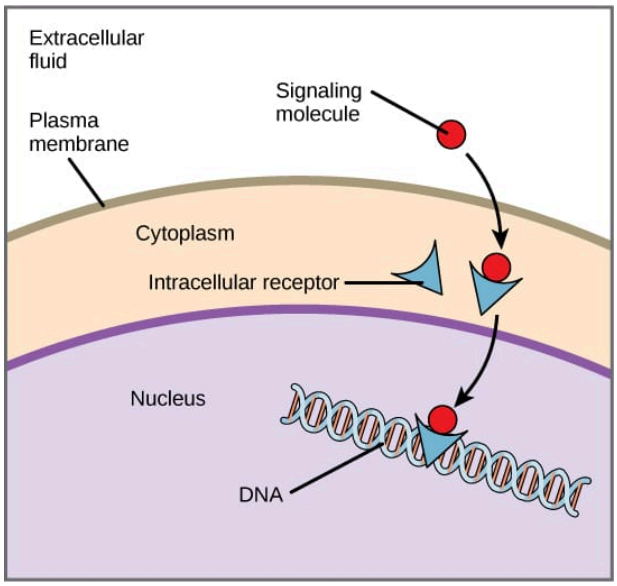


Figure 9.3.1: Intracellular Receptors: Hydrophobic signaling molecules typically diffuse across the plasma membrane and interact with intracellular receptors in the cytoplasm. Many intracellular receptors are transcription factors that interact with DNA in the nucleus and regulate gene expression.

Cell-Surface Receptors

Cell-surface receptors, also known as transmembrane receptors, are cell surface, membrane-anchored, or integral proteins that bind to external ligand molecules. This type of receptor spans the plasma membrane and performs signal transduction, converting an extracellular signal into an intracellular signal. Ligands that interact with cell-surface receptors do not have to enter the cell that they affect. Cell-surface receptors are also called cell-specific proteins or markers because they are specific to individual cell

types.

Each cell-surface receptor has three main components: an external ligand-binding domain (extracellular domain), a hydrophobic membrane-spanning region, and an intracellular domain inside the cell. The size and extent of each of these domains vary widely, depending on the type of receptor.

Cell-surface receptors are involved in most of the signaling in multicellular organisms. There are three general categories of cell-surface receptors: ion channel-linked receptors, G-protein-linked receptors, and enzyme-linked receptors.

Ion Channel-Linked Receptors

Ion channel-linked receptors bind a ligand and open a channel through the membrane that allows specific ions to pass through. To form a channel, this type of cell-surface receptor has an extensive membrane-spanning region. In order to interact with the phospholipid fatty acid tails that form the center of the plasma membrane, many of the amino acids in the membrane-spanning region are hydrophobic in nature. Conversely, the amino acids that line the inside of the channel are hydrophilic to allow for the passage of water or ions. When a ligand binds to the extracellular region of the channel, there is a conformational change in the protein's structure that allows ions such as sodium, calcium, magnesium, and hydrogen to pass through.

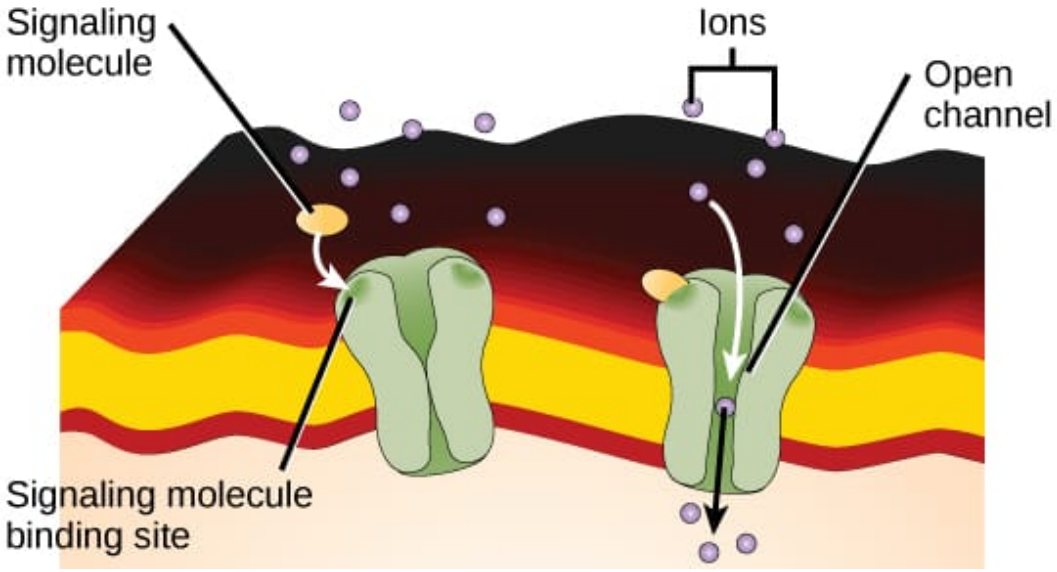


Figure 9.3.1: Gated-Ion Channels: Gated ion channels form a pore through the plasma membrane that opens when the signaling molecule binds. The open pore then allows ions to flow into or out of the cell.

G-Protein Linked Receptors

G-protein-linked receptors bind a ligand and activate a membrane protein called a G-protein. The activated G-protein then interacts with either an ion channel or an enzyme in the membrane. All G-protein-linked receptors have seven transmembrane domains, but each receptor has its own specific extracellular domain and G-protein-binding site.

Cell signaling using G-protein-linked receptors occurs as a cyclic series of events. Before the ligand binds, the inactive G-protein can bind to a newly-revealed site on the receptor specific for its binding. Once the G-protein binds to the receptor, the resultant shape change activates the G-protein, which releases GDP and picks up GTP. The subunits of the G-protein then split into the α subunit and the β subunit. One or both of these G-protein fragments may be able to activate other proteins as a result. Later, the GTP on the active α subunit of the G-protein is hydrolyzed to GDP and the β subunit is deactivated. The subunits reassociate to form the inactive G-protein, and the cycle starts over.

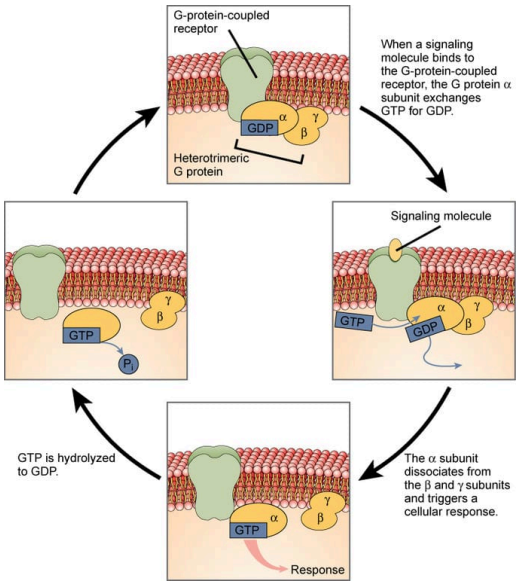


Figure 9.3.1: G-proteins: Heterotrimeric G proteins have three subunits: α, β, and γ. When a signaling molecule binds to a G-protein-coupled receptor in the plasma membrane, a GDP molecule associated with the α subunit is exchanged for GTP. The β and γ subunits dissociate from the α subunit, and a cellular response is triggered either by the α subunit or the dissociated β pair. Hydrolysis of GTP to GDP terminates the signal.

Enzyme-Linked Receptors

Enzyme-linked receptors are cell-surface receptors with intracellular domains that are associated with an enzyme. In some cases, the intracellular domain of the receptor itself is an enzyme or the enzyme-linked receptor has an intracellular domain that interacts directly with an enzyme. The enzyme-linked receptors normally have large extracellular and intracellular domains, but the membrane-spanning region consists of a single alpha-helical region of the peptide strand. When a ligand binds to the extracellular domain, a signal is transferred through the membrane and activates the enzyme, which sets off a chain of events within the cell that eventually leads to a response. An example of this type of enzyme-linked receptor is the tyrosine kinase receptor. The tyrosine kinase receptor transfers phosphate groups to tyrosine molecules. Signaling molecules bind to the extracellular domain of two nearby tyrosine kinase receptors, which then dimerize. Phosphates are then added to tyrosine residues on the intracellular domain of the receptors and can then transmit the signal to the next messenger within the cytoplasm.

Key Points

- Intracellular receptors are located in the cytoplasm of the cell and are activated by hydrophobic ligand molecules that can pass through the plasma membrane.
- Cell-surface receptors bind to an external ligand molecule and convert an extracellular signal into an intracellular signal.
- Three general categories of cell-surface receptors include: ion -channel, G- protein, and enzyme -linked protein receptors.
- Ion channel -linked receptors bind a ligand and open a channel through the membrane that allows specific ions to pass through.
- G-protein-linked receptors bind a ligand and activate a membrane protein called a G-protein, which then interacts with either an ion channel or an enzyme in the membrane.
- Enzyme-linked receptors are cell-surface receptors with intracellular domains that are associated with an enzyme.

Key Terms

- **integral protein**: a protein molecule (or assembly of proteins) that is permanently attached to the biological membrane
- **transcription**: the synthesis of RNA under the direction of DNA

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9.4: Signaling Molecules and Cellular Receptors - Signaling Molecules

Learning Objectives

- Compare and contrast the different types of signaling molecules: hydrophobic, water-soluble, and gas ligands

Signaling Molecules

Produced by signaling cells and the subsequent binding to receptors in target cells, ligands act as chemical signals that travel to the target cells to coordinate responses. The types of molecules that serve as ligands are incredibly varied and range from small proteins to small ions like calcium (Ca^{2+}).

Small Hydrophobic Ligands

Small hydrophobic ligands can directly diffuse through the plasma membrane and interact with internal receptors. Important members of this class of ligands are the steroid hormones. Steroids are lipids that have a hydrocarbon skeleton with four fused rings; different steroids have different functional groups attached to the carbon skeleton. Steroid hormones include the female sex hormone, estradiol, which is a type of estrogen; the male sex hormone, testosterone; and cholesterol, which is an important structural component of biological membranes and a precursor of steriod hormones. Other hydrophobic hormones include thyroid hormones and vitamin D. In order to be soluble in blood, hydrophobic ligands must bind to carrier proteins while they are being transported through the bloodstream.

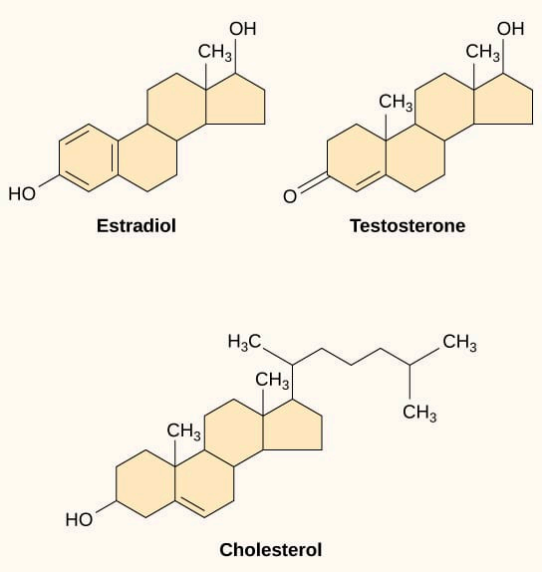


Figure 9.4.1: Steroid Hormones: Steroid hormones have similar chemical structures to their precursor, cholesterol. Because these molecules are small and hydrophobic, they can diffuse directly across the plasma membrane into the cell, where they interact with internal receptors.

Water-Soluble Ligands

Water-soluble ligands are polar and, therefore, cannot pass through the plasma membrane unaided; sometimes, they are too large to pass through the membrane at all. Instead, most water-soluble ligands bind to the extracellular domain of cell-surface receptors. Cell-surface receptors include: ion-channel, G-protein, and enzyme-linked protein receptors. The binding of these ligands to these receptors results in a series of cellular changes. These water soluble ligands are quite diverse and include small

molecules, peptides, and proteins.

Other Ligands

Nitric oxide (NO) is a gas that also acts as a ligand. It is able to diffuse directly across the plasma membrane; one of its roles is to interact with receptors in smooth muscle and induce relaxation of the tissue. NO has a very short half-life; therefore, it only functions over short distances. Nitroglycerin, a treatment for heart disease, acts by triggering the release of NO, which causes blood vessels to dilate (expand), thus restoring blood flow to the heart.

Key Points

- Signaling molecules can range from small proteins to small ions and can be hydrophobic, water-soluble, or even a gas.
- Hydrophobic signaling molecules (ligands) can diffuse through the plasma membrane and bind to internal receptors.
- Water-soluble ligands are unable to pass freely through the plasma membrane due to their polarity and must bind to an extracellular domain of a cell -surface receptor.
- Other types of ligands can include gases, such as nitric oxide, which can freely diffuse through the plasma membrane and bind to internal receptors.

Key Terms

- **ligand**: an ion, molecule, or functional group that binds to another chemical entity to form a larger complex
- **hydrophobic**: lacking an affinity for water; unable to absorb, or be wetted by water

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9.5: Propagation of the Cellular Signal - Binding Initiates a Signaling Pathway

Learning Objectives

- Recognize the relationship between a ligand's structure and its mechanism of action.

Cell-surface receptors, also known as transmembrane receptors, are membrane-anchored (integral) proteins that bind to external ligand molecules. This type of receptor spans the plasma membrane and performs signal transduction in which an extracellular signal is converted into an intracellular signal. Ligands that interact with cell-surface receptors do not have to enter the cell that they affect. Cell-surface receptors are also called cell-specific proteins or markers because they are specific to individual cell types. Each cell-surface receptor has three main components: an external ligand-binding domain, a hydrophobic membrane-spanning region, and an intracellular domain inside the cell. The ligand-binding domain is also called the extracellular domain. The size and extent of each of these domains vary widely, depending on the type of receptor. Cell-surface receptors are involved in most of the signaling in multicellular organisms.

There are three general categories of cell-surface receptors: ion channel-linked receptors, G-protein-linked receptors, and enzyme-linked receptors.

1. Ion channel-linked receptors bind a ligand and open a channel through the membrane that allows specific ions to pass through. To form a channel, this type of cell-surface receptor has an extensive membrane-spanning region. When a ligand binds to the extracellular region of the channel, there is a conformational change in the protein's structure that allows ions such as sodium, calcium, magnesium, and hydrogen to pass through.
2. G-protein-linked receptors bind a ligand and activate a membrane protein called a G-protein. The activated G-protein then interacts with either an ion channel or an enzyme in the membrane. All G-protein-linked receptors have seven transmembrane domains, but each receptor has its own specific extracellular domain and G-protein-binding site.
3. Enzyme-linked receptors are cell-surface receptors with intracellular domains that are associated with an enzyme. In some cases, the intracellular domain of the receptor itself is an enzyme. Other enzyme-linked receptors have a small intracellular domain that interacts directly with an enzyme. When a ligand binds to the extracellular domain, a signal is transferred through the membrane, activating the enzyme. Activation of the enzyme sets off a chain of events within the cell that eventually leads to a response.

After the ligand binds to the cell-surface receptor, the activation of the receptor's intracellular components sets off a chain of events that is called a signaling pathway or a signaling cascade. In a signaling pathway, second messengers, enzymes, and activated proteins interact with specific proteins, which are in turn activated in a chain reaction that eventually leads to a change in the cell's environment. The events in the cascade occur in a series, much like a current flows in a river. Interactions that occur before a certain point are defined as upstream events; events after that point are called downstream events.

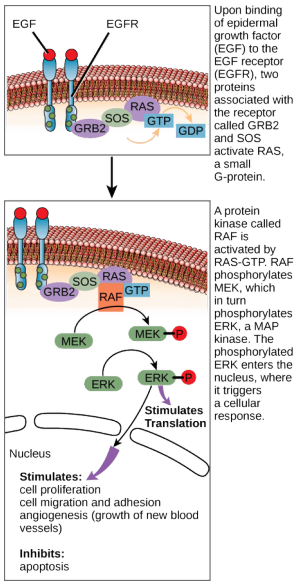


Figure 9.5.1: Ligand Initiated Signaling Pathway: An example of ligand initiated signaling pathways is when epidermal growth factor (EGF) binds to its receptor. A complex cascade of downstream events causes the cell to grow and divide.

Signaling pathways can get very complicated very quickly because most cellular proteins can affect different downstream events, depending on the conditions within the cell. A single pathway can branch off toward different endpoints based on the interplay between two or more signaling pathways. The same ligands are often used to initiate different signals in different cell types. This variation in response is due to differences in protein expression in different cell types. Another complicating element is signal integration of the pathways in which signals from two or more different cell-surface receptors merge to activate the same response in the cell. This process can ensure that multiple external requirements are met before a cell commits to a specific response.

The effects of extracellular signals can also be amplified by enzymatic cascades. At the initiation of the signal, a single ligand binds to a single receptor. However, activation of a receptor-linked enzyme can activate many copies of a component of the signaling cascade, which amplifies the signal.

Key Points

- Signaling pathways can be complicated since most cellular proteins can affect different downstream events.
- Cell -surface receptors are integral in signaling pathways.
- Ion channel -linked receptors open a channel once a ligand binds allowing specific ions to pass through the membrane.
- G-protein-linked receptors activate a membrane protein called a G-protein once a ligand binds.
- Enzyme -linked receptors are cell-surface receptors with intracellular domains.

Key Terms

- **ligand**: an ion, molecule, or functional group that binds to another chemical entity to form a larger complex
- **receptor**: a protein on a cell wall that binds with specific molecules so that they can be absorbed into the cell in order to control certain functions

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9.6: Propagation of the Cellular Signal - Methods of Intracellular Signaling

Learning Objectives

- Explain how the binding of a ligand initiates signal transduction throughout a cell

The induction of a signaling pathway depends on the modification of a cellular component by an enzyme. There are numerous enzymatic modifications that can occur which are recognized in turn by the next component downstream.

One of the most common chemical modifications that occurs in signaling pathways is the addition of a phosphate group (PO_4^{-3}) to a molecule such as a protein in a process called phosphorylation. The phosphate can be added to a nucleotide such as GMP to form GDP or GTP. Phosphates are also often added to serine, threonine, and tyrosine residues of proteins where they replace the hydroxyl group of the amino acid. The transfer of the phosphate is catalyzed by an enzyme called a kinase. Various kinases are named for the substrate they phosphorylate. Phosphorylation of serine and threonine residues often activates enzymes. Phosphorylation of tyrosine residues can either affect the activity of an enzyme or create a binding site that interacts with downstream components in the signaling cascade. Phosphorylation may activate or inactivate enzymes; the reversal of phosphorylation, dephosphorylation by a phosphatase, will reverse the effect.

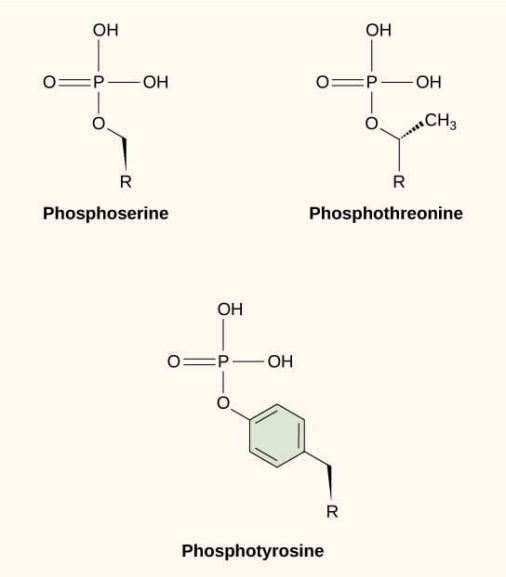


Figure 9.6.1: Example of phosphorylation: In protein phosphorylation, a phosphate group (PO4-3) is added to residues of the amino acids serine, threonine, and tyrosine.

The activation of second messengers is also a common event after the induction of a signaling pathway. They are small molecules that propagate a signal after it has been initiated by the binding of the signaling molecule to the receptor. These molecules help to spread a signal through the cytoplasm by altering the behavior of certain cellular proteins.

Calcium ion is a widely-used second messenger. The free concentration of calcium ions (Ca^{2+}) within a cell is very low because ion pumps in the plasma membrane continuously use adenosine-5′-triphosphate (ATP) to remove it. For signaling purposes, Ca^{2+} is stored in cytoplasmic vesicles, such as the endoplasmic reticulum, or accessed from outside the cell. When signaling occurs, ligand-gated calcium ion channels allow the higher levels of Ca^{2+} that are present outside the cell (or in intracellular storage compartments) to flow into the cytoplasm, which raises the concentration of cytoplasmic Ca^{2+}. The response to the increase in Ca^{2+} varies, depending on the cell type involved. For example, in the β-cells of the pancreas, Ca^{2+} signaling leads to the release of insulin, whereas in muscle cells, an increase in Ca^{2+} leads to muscle contractions.

Another second messenger utilized in many different cell types is cyclic AMP (cAMP). Cyclic AMP is synthesized by the enzyme adenylyl cyclase from ATP. The main role of cAMP in cells is to bind to and activate an enzyme called cAMP-dependent kinase (A-kinase). A-kinase regulates many vital metabolic pathways. It phosphorylates serine and threonine residues of its target proteins, activating them in the process. A-kinase is found in many different types of cells; the target proteins in each kind of cell are different. Differences give rise to the variation of the responses to cAMP in different cells.

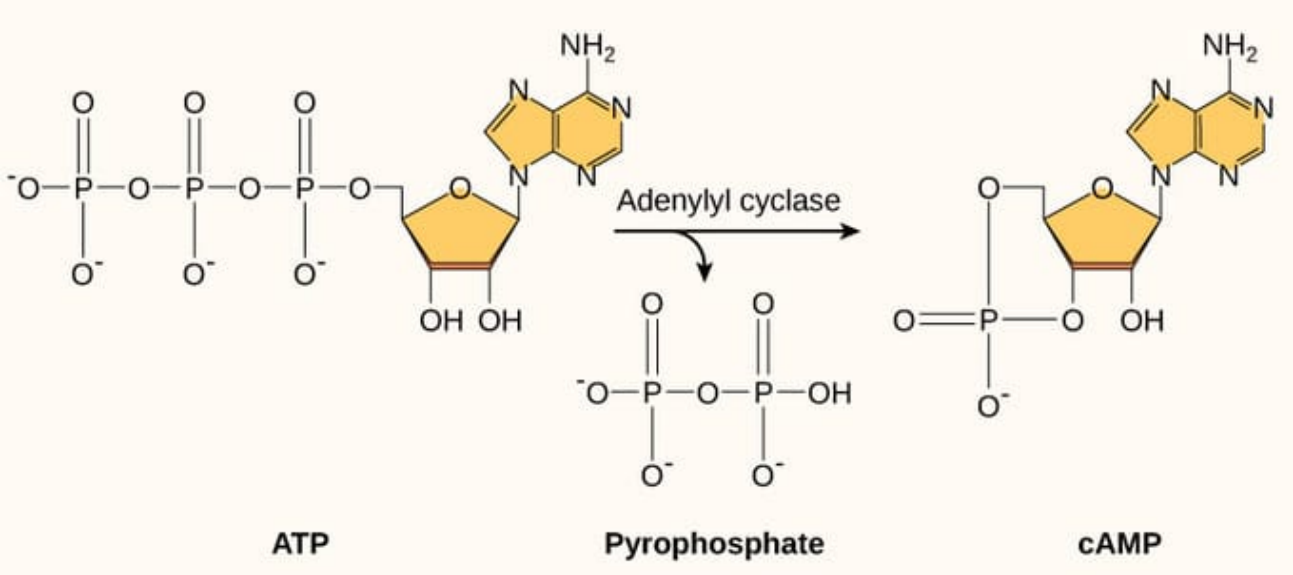


Figure 9.6.1: Example of cAMP as a second messenger: This diagram shows the mechanism for the formation of cyclic AMP (cAMP). cAMP serves as a second messenger to activate or inactivate proteins within the cell. Termination of the signal occurs when an enzyme called phosphodiesterase converts cAMP into AMP.

Present in small concentrations in the plasma membrane, inositol phospholipids are lipids that can also be converted into second messengers. Because these molecules are membrane components, they are located near membrane-bound receptors and can easily interact with them. Phosphatidylinositol (PI) is the main phospholipid that plays a role in cellular signaling. Enzymes known as kinases phosphorylate PI to form PI-phosphate (PIP) and PI-bisphosphate (PIP_2).

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Key Points

- Phosphorylation, the addition of a phosphate group to a molecule such as a protein, is one of the most common chemical modifications that occurs in signaling pathways.
- The activation of second messengers, small molecules that propagate a signal, is a common event after the induction of a signaling pathway.
- Calcium ion, cyclic AMP, and inositol phospholipids are examples of widely-used second messengers.

Key Terms

- **second messenger**: any substance used to transmit a signal within a cell, especially one which triggers a cascade of events by activating cellular components
- **phosphorylation**: the addition of a phosphate group to a compound; often catalyzed by enzymes

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9.7: Response to the Cellular Signal - Termination of the Signal Cascade

Learning Objectives

- Describe the process by which the signal cascade in cell communication is terminated

Termination of the Signal Cascade

Ligand binding to the receptor allows for signal transduction through the cell. The chain of events that conveys the signal through the cell is called a signaling pathway or cascade. Signaling pathways are often very complex because of the interplay between different proteins. A major component of cell signaling cascades is the phosphorylation of molecules by enzymes known as kinases. Phosphorylation adds a phosphate group to serine, threonine, and tyrosine residues in a protein, changing their shapes, and activating or inactivating the protein.

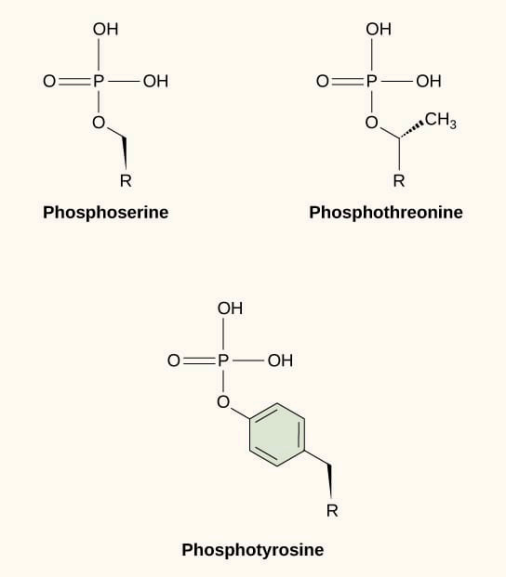


Figure 9.7.1: Phosphorylation: In protein phosphorylation, a phosphate group is added to residues of the amino acids serine, threonine, and tyrosine.

The aberrant signaling often seen in tumor cells is proof that the termination of a signal at the appropriate time can be just as important as the initiation of a signal. One method of terminating or stopping a specific signal is to degrade or remove the ligand so that it can no longer access its receptor. One reason that hydrophobic hormones like estrogen and testosterone trigger long-lasting events is because they bind carrier proteins. These proteins allow the insoluble molecules to be soluble in blood, but they also protect the hormones from degradation by circulating enzymes.

Inside the cell, many different enzymes reverse the cellular modifications that result from signaling cascades. For example, phosphatases are enzymes that remove the phosphate group attached to proteins by kinases in a process called dephosphorylation. Cyclic AMP (cAMP) is degraded into AMP by phosphodiesterase, and the release of calcium stores is reversed by the Ca^{2+} pumps that are located in the external and internal membranes of the cell.

Key Points

- The chain of events that conveys the signal through the cell is called a signaling pathway or cascade.
- Phosphorylation, a major component of signal cascades, adds a phosphate group to proteins, thereby changing their shapes

and activating or inactivating the protein.
- Degrading or removing the ligand so it can no longer access its receptor terminates the signal.
- Enzymes like phosphotases can remove phosphate groups on proteins during dephosphorylation and reverse the cellular modifications produced by signaling cascades.

Key Terms

- **signaling cascade**: the chain of events that conveys the signal through the cell
- **phosphorylation**: the addition of a phosphate group to a compound; often catalyzed by enzymes
- **dephosphorylation**: the removal of phosphate groups from a compound; often catalyzed by enzymes

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9.8: Response to the Cellular Signal - Cell Signaling and Gene Expression

Learning Objectives

- Describe the regulation of gene expression

Gene Expression

For a cell to function properly, necessary proteins must be synthesized at the proper time. All cells control or regulate the synthesis of proteins from information encoded in their DNA. The process of turning on a gene to produce RNA and protein is called gene expression.

Whether in a simple unicellular organism or a complex multi-cellular organism, each cell controls when and how its genes are expressed. For this to occur, there must be a mechanism to control when a gene is expressed to make RNA and protein; how much of the protein is made; and when it is time to stop making that protein because it is no longer needed. The regulation of gene expression conserves energy and space. It would require a significant amount of energy for an organism to express every gene at all times, so it is more energy efficient to turn on the genes only when they are required. In addition, only expressing a subset of genes in each cell saves space because DNA must be unwound from its tightly-coiled structure to transcribe and translate the DNA. Cells would have to be enormous if every protein were expressed in every cell all the time. The control of gene expression is extremely complex. Malfunctions in this process are detrimental to the cell and can lead to the development of many diseases, including cancer.

Prokaryotic versus Eukaryotic Gene Expression

To understand how gene expression is regulated, we must first understand how a gene codes for a functional protein in a cell. The process occurs in both prokaryotic and eukaryotic cells, just in slightly different manners. Prokaryotic organisms are single-celled organisms that lack a cell nucleus; their DNA floats freely in the cell cytoplasm. To synthesize a protein, the processes of transcription and translation occur almost simultaneously. When the resulting protein is no longer needed, transcription stops. As a result, the primary method to control what type of protein and how much of each protein is expressed in a prokaryotic cell is the regulation of DNA transcription. All of the subsequent steps occur automatically. When more protein is required, more transcription occurs. Therefore, in prokaryotic cells, the control of gene expression is mostly at the transcriptional level.

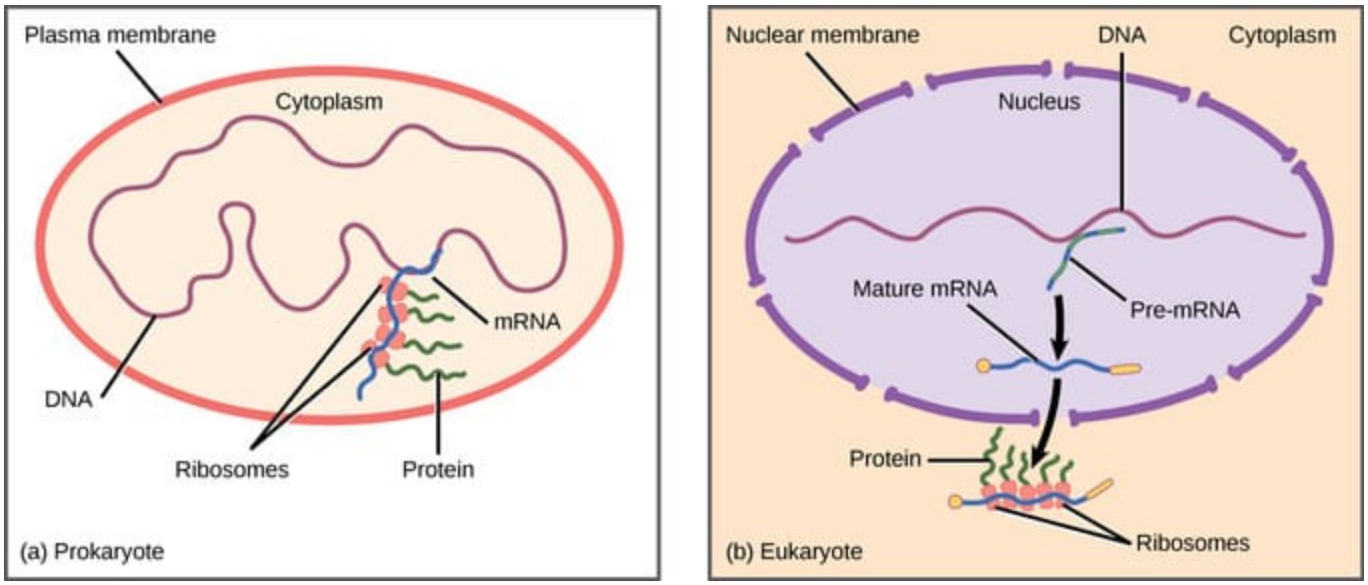


Figure 9.8.1: Prokaryotic & Eukaryotic Gene Expression: Prokaryotic transcription and translation occur simultaneously in the cytoplasm; regulation occurs at the transcriptional level. Eukaryotic gene expression is regulated during transcription and RNA processing, which take place in the nucleus, and during protein translation, which takes place in the cytoplasm. Further regulation may occur through post-translational modifications of proteins.

Eukaryotic cells, in contrast, have intracellular organelles that add to their complexity. In eukaryotic cells, the DNA is contained inside the cell's nucleus where it is transcribed into RNA. The newly-synthesized RNA is then transported out of the nucleus into the cytoplasm where ribosomes translate the RNA into protein. The processes of transcription and translation are physically separated by the nuclear membrane: transcription occurs only within the nucleus, and translation occurs only outside the nucleus in the cytoplasm. The regulation of gene expression can occur at all stages of the process. Regulation may occur when the DNA is uncoiled and loosened from nucleosomes to bind transcription factors (epigenetic level); when the RNA is transcribed (transcriptional level); when the RNA is processed and exported to the cytoplasm after it is transcribed (post-transcriptional level); when the RNA is translated into protein (translational level); or after the protein has been made (post-translational level).

Key Points

- Each cell controls when and how its genes are expressed.
- Malfunctions in the control of gene expression are detrimental to the cell and can lead to the development of many diseases, such as cancer.
- In prokaryotic cells, the control of gene expression is mostly at the transcriptional level.
- In eukaryotic cells, the control of gene expression is at the epigenetic, transcriptional, post-transcriptional, translational, and post-translational levels.

Key Terms

- **translation**: a process occurring in the ribosome in which a strand of messenger RNA (mRNA) guides assembly of a sequence of amino acids to make a protein
- **gene expression**: the transcription and translation of a gene into messenger RNA and, thus, into a protein
- **transcription**: the synthesis of RNA under the direction of DNA

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9.9: Response to the Cellular Signal - Cell Signaling and Cellular Metabolism

Learning Objectives

- Explain how cellular metabolism can be altered

Increase in Cellular Metabolism

As the environments of most organisms are constantly changing, the reactions of metabolism must be finely regulated to maintain a constant set of conditions within cells. Metabolic regulation also allows organisms to respond to signals and interact actively with their environments. Two closely-linked concepts are important for understanding how metabolic pathways are controlled. Firstly, the *regulation* of an enzyme in a pathway is how its activity is increased and decreased in response to signals. Secondly, the *control*exerted by this enzyme is the effect that these changes in its activity have on the overall rate of the pathway. For example, an enzyme may show large changes in activity (*i.e.* it is highly regulated), but if these changes have little effect on the rate of a metabolic pathway, then this enzyme is not involved in the control of the pathway.

The result of one such signaling pathway affects muscle cells and is a good example of an increase in cellular metabolism. The activation of β-adrenergic receptors in muscle cells by adrenaline leads to an increase in cyclic adenosine monophosphate (also known as cyclic AMP or cAMP) inside the cell. Also known as epinephrine, adrenaline is a hormone (produced by the adrenal gland attached to the kidney) that prepares the body for short-term emergencies. Cyclic AMP activates PKA (protein kinase A), which in turn phosphorylates two enzymes. The first enzyme promotes the degradation of glycogen by activating intermediate glycogen phosphorylase kinase (GPK) that in turn activates glycogen phosphorylase (GP), which catabolizes glycogen into glucose. (Recall that your body converts excess glucose to glycogen for short-term storage. When energy is needed, glycogen is quickly reconverted to glucose.) Phosphorylation of the second enzyme, glycogen synthase (GS), inhibits its ability to form glycogen from glucose. In this manner, a muscle cell obtains a ready pool of glucose by activating its formation via glycogen degradation and by inhibiting the use of glucose to form glycogen, thus preventing a futile cycle of glycogen degradation and synthesis. The glucose is then available for use by the muscle cell in response to a sudden surge of adrenaline—the “fight or flight” reflex.

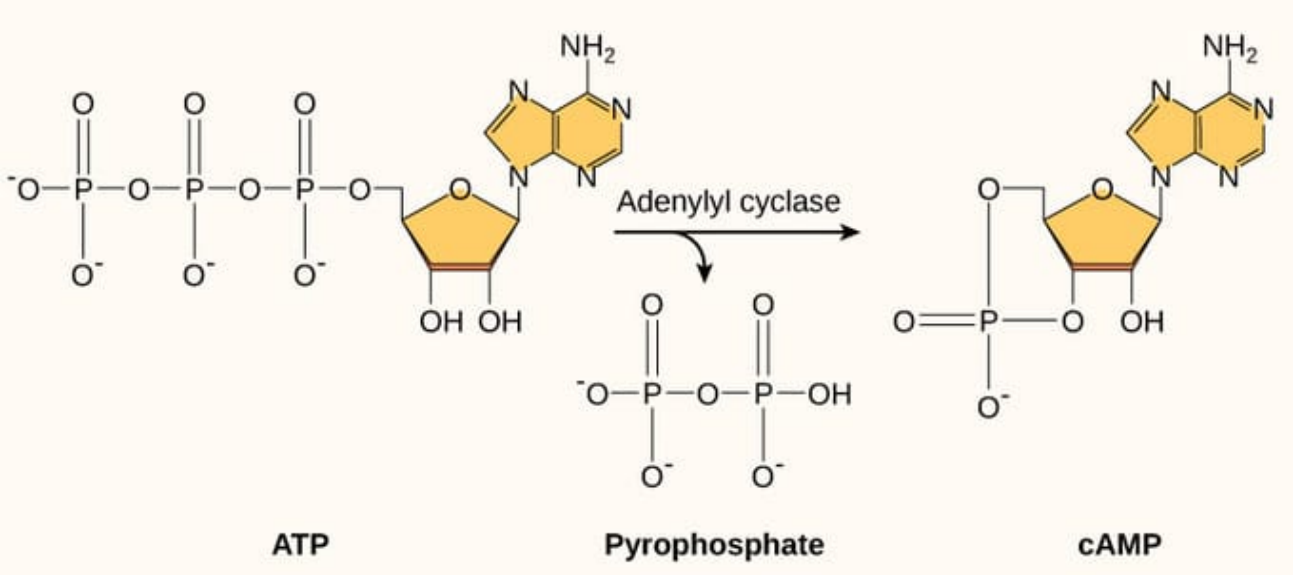


Figure 9.9.1: Formation of Cyclic AMP: This diagram shows the mechanism for the formation of cyclic AMP (cAMP). cAMP serves as a second messenger to activate or inactivate proteins within the cell.

Key Points

- The activation of β-adrenergic receptors in muscle cells by adrenaline leads to an increase in cyclic AMP.
- Cyclic AMP activates PKA (protein kinase A), which phosphorylates two enzymes.
- Phophorylation of the first enzyme promotes the degradation of glycogen by activating intermediate GPK that in turn activates GP, which catabolizes glycogen into glucose.
- Phosphorylation of the second enzyme, glycogen synthase (GS), inhibits its ability to form glycogen from glucose.
- The inhibition of glucose to form glycogen prevents a futile cycle of glycogen degradation and synthesis, so glucose is then available for use by the muscle cell.

Key Terms

- **cyclic adenosine monophosphate**: cAMP, a second messenger derived from ATP that is involved in the activation of protein kinases and regulates the effects of adrenaline
- **epinephrine**: (adrenaline) an amino acid-derived hormone secreted by the adrenal gland in response to stress
- **protein kinase A**: a family of enzymes whose activity is dependent on cellular levels of cyclic AMP (cAMP)

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9.10: Response to the Cellular Signal - Cell Signaling and Cell Growth

Learning Objectives

- Explain how cell growth is affected by growth factors.

Cell Growth

Cell signaling pathways play a major role in cell division. Cells do not normally divide unless they are stimulated by signals from other cells. The ligands that promote cell growth are called growth factors. Most growth factors bind to cell-surface receptors that are linked to tyrosine kinases. These cell-surface receptors are called receptor tyrosine kinases (RTKs). Activation of RTKs initiates a signaling pathway that includes a G-protein called RAS, which activates the MAP kinase pathway described earlier. The enzyme MAP kinase then stimulates the expression of proteins that interact with other cellular components to initiate cell division. In addition, uncontrolled cell growth leads to cancer; mutations in the genes encoding protein components of signaling pathways are often found in tumor cells.

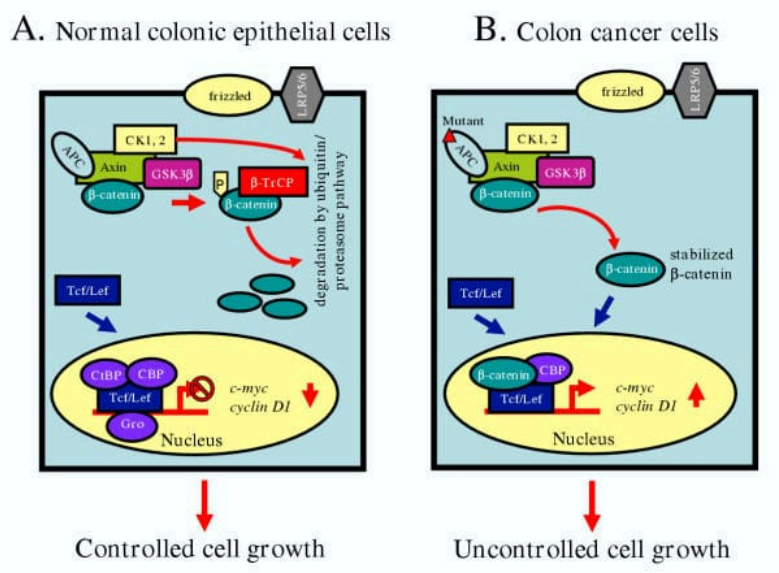


Figure 9.10.1: Uncontrolled Cell Growth: Colorectal cancer occurs after numerous mutations to a normal cell.

Cancer Biologists & Uncontrolled Cell Growth

Cancer biologists study the molecular origins of cancer with the goal of developing new prevention methods and treatment strategies that will inhibit the growth of tumors without harming the normal cells of the body. Signaling pathways control cell growth. These pathways are controlled by signaling proteins, which are, in turn, expressed by genes. Mutations in these genes can result in malfunctioning signaling proteins. This prevents the cell from regulating its cell cycle, triggering unrestricted cell division and cancer. The genes that regulate the signaling proteins are one type of oncogene: a gene that has the potential to cause cancer. The gene encoding RAS is an oncogene that was originally discovered when mutations in the RAS protein were linked to cancer. Further studies have indicated that 30 percent of cancer cells have a mutation in the RAS gene that leads to uncontrolled growth. If left unchecked, uncontrolled cell division can lead tumor formation and metastasis, the growth of cancer cells in new locations in the body.

Cancer biologists have been able to identify many other oncogenes that contribute to the development of cancer. For example, HER2 is a cell-surface receptor that is present in excessive amounts in 20 percent of human breast cancers. Cancer biologists

realized that gene duplication led to HER2 overexpression in 25 percent of breast cancer patients and developed a drug called Herceptin (trastuzumab), a monoclonal antibody that targets HER2 for removal by the immune system. Herceptin therapy helps to control signaling through HER2. Its use, in combination with chemotherapy, has helped to increase the overall survival rate of patients with metastatic breast cancer.

Key Points

- Normally, cells do not divide unless they are stimulated by signals from other cells.
- Most growth factors, which promote cell growth, bind to cell-surface receptors that are linked to tyrosine kinases.
- MAP kinase stimulates the expression of proteins that interact with other cellular components to initiate cell division.
- Uncontrolled cell growth leads to cancer.

Key Terms

- **receptor**: a protein on a cell wall that binds with specific molecules so that they can be absorbed into the cell in order to control certain functions
- **growth factor**: a naturally-occurring substance capable of stimulating cellular growth, proliferation, and cellular differentiation
- **oncogene**: any gene that contributes to the conversion of a normal cell into a cancerous cell when mutated or expressed at high levels

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9.11: Response to the Cellular Signal - Cell Signaling and Cell Death

Learning Objectives

- Describe how apoptosis is initiated

Apoptosis

When a cell is damaged, superfluous, or potentially dangerous to an organism, a cell can initiate a mechanism to trigger programmed cell death, or apoptosis. Apoptosis allows a cell to die in a controlled manner that prevents the release of potentially damaging molecules from inside the cell.

Internal Signaling

There are many internal checkpoints that monitor a cell's health; if abnormalities are observed, a cell can spontaneously initiate the process of apoptosis. However, in some cases such as a viral infection or uncontrolled cell division due to cancer, the cell's normal checks and balances fail.

External Signaling

External signaling can also initiate apoptosis. For example, most normal animal cells have receptors that interact with the extracellular matrix, a network of glycoproteins that provides structural support for cells in an organism. The binding of cellular receptors to the extracellular matrix initiates a signaling cascade within the cell. However, if the cell moves away from the extracellular matrix, the signaling ceases, and the cell undergoes apoptosis. This system keeps cells from traveling through the body and proliferating out of control, as happens with tumor cells that metastasize.

Another example of external signaling that leads to apoptosis occurs in T-cell development. T-cells are immune cells that bind to foreign macromolecules and particles, targeting them for destruction by the immune system. Normally, T-cells do not target "self" proteins (those of their own organism), a process that can lead to autoimmune diseases. In order to develop the ability to discriminate between self and non-self, immature T-cells undergo screening to determine whether they bind to so-called self proteins. If the T-cell receptor binds to self proteins, the cell initiates apoptosis to remove the potentially dangerous cell.

Apoptosis and Embryos

Apoptosis is also essential for normal embryological development. In vertebrates, for example, early stages of development include the formation of web-like tissue between individual fingers and toes. During the course of normal development, these unnecessary cells must be eliminated, enabling fully separated fingers and toes to form. A cell signaling mechanism triggers apoptosis, which destroys the cells between the developing digits.



Figure 9.11.1: Apoptosis: The histological section of a foot of a 15-day-old mouse embryo, visualized using light microscopy, reveals areas of tissue between the toes which apoptosis will eliminate before the mouse reaches its full gestational age at 27 days.

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Key Points

- Apoptosis allows a cell to die in a controlled manner by preventing the release of damaging molecules from inside the cell.
- Internal checkpoints to monitor a cell's health exist; if abnormalities are observed, a cell can also spontaneously initiate the process of apoptosis.
- In some cases, such as a viral infection or cancer, the cell's normal checks and balances fail.
- External signaling can also initiate apoptosis.
- Apoptosis is also essential for normal embryological development; unnecessary cells that appear during the early stages of development will eventually be eliminated through cell signaling.

Key Terms

- **apoptosis**: a process of programmed cell death
- **glycoprotein**: a protein with covalently-bonded carbohydrates

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9.12: Signaling in Single-Celled Organisms - Signaling in Yeast

Learning Objectives

- Describe how cell signaling occurs in single-celled organisms such as yeast

Signaling in Yeast

Yeasts are single-celled eukaryotes; therefore, they have a nucleus and organelles characteristic of more complex life forms. Comparisons of the genomes of yeasts, nematode worms, fruit flies, and humans illustrate the evolution of increasingly-complex signaling systems that allow for the efficient inner workings that keep humans and other complex life forms functioning correctly.

The components and processes found in yeast signals are similar to those of cell-surface receptor signals in multicellular organisms. Budding yeasts are able to participate in a process that is similar to sexual reproduction that entails two haploid cells combining to form a diploid cell. In order to find another haploid yeast cell that is prepared to mate, budding yeasts secrete a signaling molecule called mating factor. When mating factor binds to cell-surface receptors in other yeast cells that are nearby, they stop their normal growth cycles and initiate a cell signaling cascade that includes protein kinases and GTP-binding proteins that are similar to G-proteins.

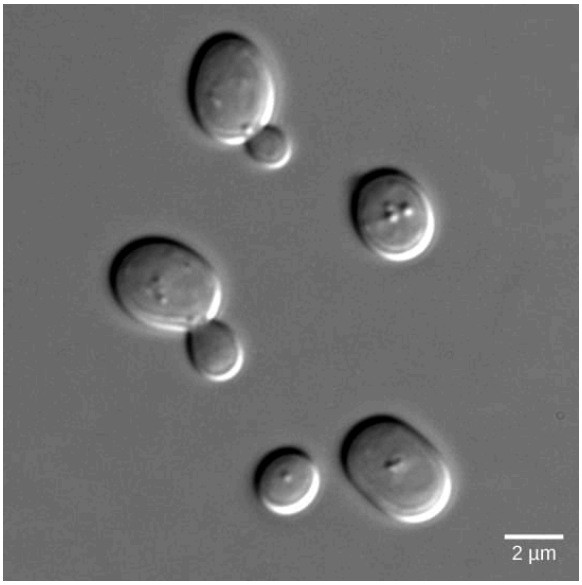


Figure 9.12.1: Budding Yeasts: Budding Saccharomyces cerevisiae yeast cells can communicate by releasing a signaling molecule called mating factor. In this micrograph, they are visualized using differential interference contrast microscopy, a light microscopy technique that enhances the contrast of the sample.

Cellular Communication in Yeasts

Kinases are a major component of cellular communication. Studies of these enzymes illustrate the evolutionary connectivity of different species. Yeasts have 130 types of kinases. More complex organisms such as nematode worms and fruit flies have 454 and 239 kinases, respectively. Of the 130 kinase types in yeast, 97 belong to the 55 subfamilies of kinases that are found in other eukaryotic organisms. The only obvious deficiency seen in yeasts is the complete absence of tyrosine kinases. It is hypothesized that phosphorylation of tyrosine residues is needed to control the more sophisticated functions of development, differentiation, and cellular communication used in multicellular organisms.

Because yeasts contain many of the same classes of signaling proteins as humans, these organisms are ideal for studying signaling cascades. Yeasts multiply quickly and are much simpler organisms than humans or other multicellular animals. Therefore, the signaling cascades are also simpler and easier to study, although they contain similar counterparts to human signaling

Key Points

- Budding yeasts participate in a process that is similar to sexual reproduction that entails two haploid cells combining to form a diploid cell.
- Budding yeasts secrete a signaling molecule called mating factor when trying to find another haploid yeast cell that is ready to mate.
- In yeast, a cell signaling cascade is initiated when a mating factor binds to cell-surface receptors in other yeast cells.
- A cell signaling cascade includes protein kinases and GTP-binding proteins that are similar to G-proteins.
- Yeasts have 130 types of kinases, but they do not contain tyrosine kinases, which are utilized by multicellular organisms to control complex forms of development and communication.

Key Terms

- **kinase**: any of a group of enzymes that transfers phosphate groups from high-energy donor molecules, such as ATP, to specific target molecules (substrates); the process is termed phosphorylation
- **GTP-binding protein**: a protein which binds GTP and catalyzes its conversion to GDP
- **G protein**: any of a class of proteins, found in cell membranes, that pass signals between hormone receptors and effector enzymes

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9.13: Signaling in Single-Celled Organisms - Signaling in Bacteria

Learning Objectives

- Describe how cell signaling occurs in single-celled organisms such as bacteria

Signaling in Bacteria

Signaling in bacteria, known as quorum sensing, enables bacteria to monitor extracellular conditions, ensure sufficient amounts of nutrients are present, and avoid hazardous situations. There are circumstances, however, when bacteria communicate with each other.

The first evidence of bacterial communication was observed in a bacterium that has a symbiotic relationship with Hawaiian bobtail squid. When the population density of the bacteria reached a certain level, specific gene expression was initiated: the bacteria produced bioluminescent proteins that emitted light. Because the number of cells present in the environment (the cell density) is the determining factor for signaling, bacterial signaling was named quorum sensing. Interestingly, in politics and business, a quorum is the minimum number of members required to be present to vote on an issue.

Quorum sensing uses autoinducers as signaling molecules. Autoinducers are signaling molecules secreted by bacteria to communicate with other bacteria of the same kind. The secreted autoinducers can be small, hydrophobic molecules, such as acyl-homoserine lactone (AHL), or larger peptide-based molecules. Each type of molecule has a different mode of action. When AHL enters target bacteria, it binds to transcription factors, which then switch gene expression on or off. The peptide autoinducers stimulate more complicated signaling pathways that include bacterial kinases. The changes in bacteria following exposure to autoinducers can be quite extensive. The pathogenic bacterium *Pseudomonas aeruginosa* has 616 different genes that respond to autoinducers.

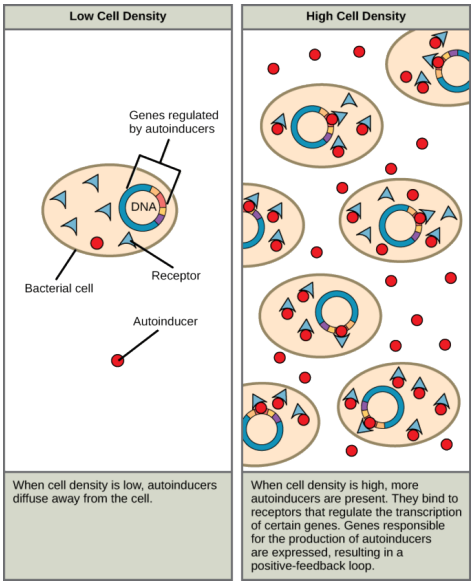


Figure 9.13.1: Autoinducers: Autoinducers are small molecules or proteins produced by bacteria that regulate gene expression.

Some species of bacteria that use quorum sensing form biofilms, which are complex colonies of bacteria (often containing several species) that exchange chemical signals to coordinate the release of toxins that attack the host. Bacterial biofilms can sometimes be found on medical equipment. When biofilms invade implants, such as hip or knee replacements or heart pacemakers, they can cause life-threatening infections.

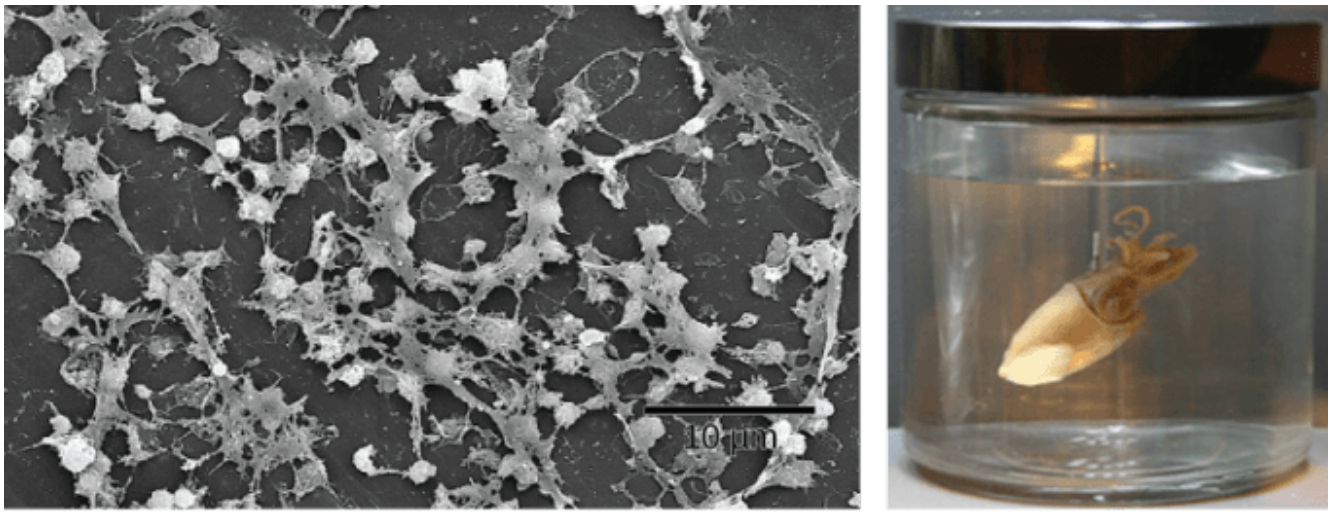


Figure 9.13.1: Bacterial Biofilms: Cell-cell communication enables these (a) Staphylococcus aureus bacteria to work together to form a biofilm inside a hospital patient's catheter, seen here via scanning electron microscopy. S. aureus is the main cause of hospital-acquired infections. (b) Hawaiian bobtail squid have a symbiotic relationship with the bioluminescent bacteria Vibrio fischeri. The luminescence makes it difficult to see the squid from below because it effectively eliminates its shadow. In return for camouflage, the squid provides food for the bacteria. Free-living V. fischeri do not produce luciferase, the enzyme responsible for luminescence, but V. fischeri living in a symbiotic relationship with the squid do. Quorum sensing determines whether the bacteria should produce the luciferase enzyme.

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Key Points

- Gene expression in bacteria is initiated when the population density of the bacteria reaches a certain level.

- Bacterial signaling is called quorum sensing because cell density is the determining factor for signaling.
- Quorum sensing uses autoinducers, which are secreted by bacteria to communicate with other bacteria of the same kind, as signaling molecules.
- Autoinducers may be small, hydrophobic molecules, or they can be larger peptide-based molecules; regardless, each type of molecule has a different mode of action.
- Some bacteria form biofilms, which are complex colonies of bacteria that exchange chemical signals to coordinate the release of toxins that attack the host.

Key Terms

- **quorum sensing**: a method of communication between bacterial cells by the release and sensing of small diffusible signal molecules
- **autoinducer**: any of several compounds, synthesized by bacteria, that have signalling functions in quorum sensing
- **biofilm**: a thin film of mucus created by and containing a colony of bacteria and other microorganisms

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10: CELL REPRODUCTION

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10.1A: The Role of the Cell Cycle

10.1B: Genomic DNA and Chromosomes

10.1C: Eukaryotic Chromosomal Structure and Compaction

10.2: The Cell Cycle

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10.1: CELL DIVISION

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- Topic hierarchy

10.1A: The Role of the Cell Cycle

10.1B: Genomic DNA and Chromosomes

10.1C: Eukaryotic Chromosomal Structure and Compaction

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10.1A: The Role of the Cell Cycle

Learning Objectives

- Explain the role of the cell cycle in carrying out the cell's essential functions

Introduction: Cell Division and Reproduction

A human, as well as every sexually-reproducing organism, begins life as a fertilized egg or zygote. Trillions of cell divisions subsequently occur in a controlled manner to produce a complex, multicellular human. In other words, that original single cell is the ancestor of every other cell in the body. Once a being is fully grown, cell reproduction is still necessary to repair or regenerate tissues. For example, new blood and skin cells are constantly being produced. All multicellular organisms use cell division for growth and the maintenance and repair of cells and tissues. Cell division is tightly regulated because the occasional failure of regulation can have life-threatening consequences. Single-celled organisms use cell division as their method of reproduction.

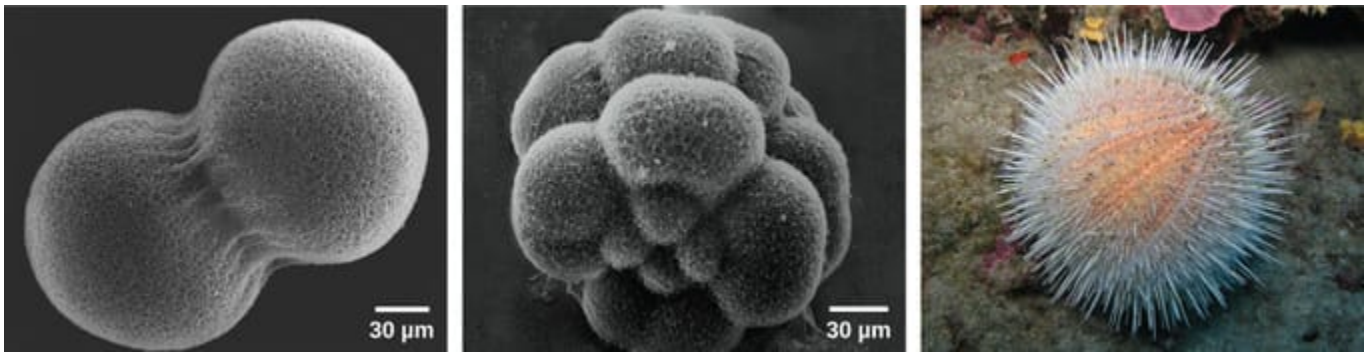


Figure 10.1A.1: Cell Division and Growth: A sea urchin begins life as a single cell that (a) divides to form two cells, visible by scanning electron microscopy. After four rounds of cell division, (b) there are 16 cells, as seen in this SEM image. After many rounds of cell division, the individual develops into a complex, multicellular organism, as seen in this (c) mature sea urchin.

While there are a few cells in the body that do not undergo cell division, most somatic cells divide regularly. A somatic cell is a general term for a body cell: all human cells, except for the cells that produce eggs and sperm (which are referred to as germ cells), are somatic cells. Somatic cells contain two copies of each of their chromosomes (one copy received from each parent). Cells in the body replace themselves over the lifetime of a person. For example, the cells lining the gastrointestinal tract must be frequently replaced when constantly "worn off" by the movement of food through the gut. But what triggers a cell to divide and how does it prepare for and complete cell division?

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 produces two identical (clone) cells. The cell cycle has two major phases: interphase and the mitotic phase. 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.

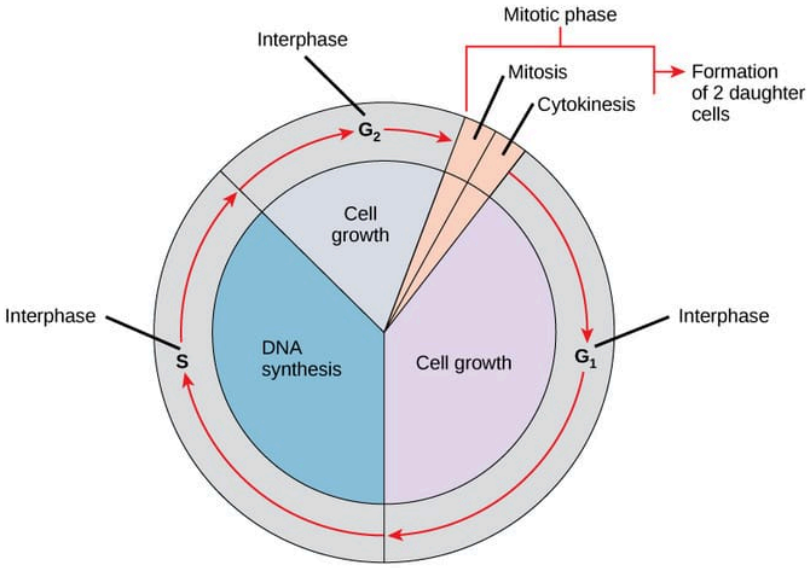


Figure 10.1A.1: The Cell Cycle: The cell cycle consists of interphase and the mitotic phase. During interphase, the cell grows and the nuclear DNA is duplicated. Interphase is followed by the mitotic phase. During the mitotic phase, the duplicated chromosomes are segregated and distributed into daughter nuclei. The cytoplasm is usually divided as well, resulting in two daughter cells

Key Points

- All multicellular organisms use cell division for growth and the maintenance and repair of cells and tissues.
- Single-celled organisms use cell division as their method of reproduction.
- Somatic cells divide regularly; all human cells (except for the cells that produce eggs and sperm) are somatic cells.
- Somatic cells contain two copies of each of their chromosomes (one copy from each parent).
- The cell cycle has two major phases: interphase and the mitotic phase.
- 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.

Key Terms

- **somatic cell**: any normal body cell of an organism that is not involved in reproduction; a cell that is not on the germline
- **interphase**: the stage in the life cycle of a cell where the cell grows and DNA is replicated
- **mitotic phase**: replicated DNA and the cytoplasmic material are divided into two identical cells

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10.1B: Genomic DNA and Chromosomes

Learning Objectives

- Explain the importance of a genome to an organism

Genomic DNA

Before discussing the steps a cell must undertake to replicate, a deeper understanding of the structure and function of a cell's genetic information is necessary. A cell's DNA, packaged as a double-stranded DNA molecule, 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. Bacteria can exchange these plasmids with other bacteria, sometimes receiving beneficial new genes that the recipient can add to their chromosomal DNA. Antibiotic resistance is one trait that often spreads through a bacterial colony through plasmid exchange.

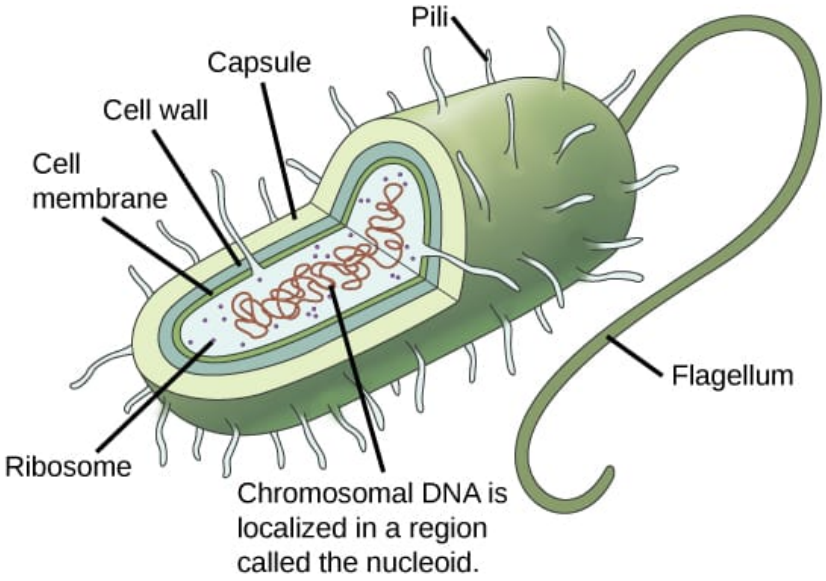


Figure $10.1B.1$: Prokaryotic Genome: Prokaryotes, including bacteria and archaea, have a single, circular chromosome located in a central region called the nucleoid.

In eukaryotes, the genome consists of several double-stranded linear DNA molecules packaged into chromosomes. Each species of eukaryotes has a characteristic number of chromosomes in the nuclei of its cells. Human body cells have 46 chromosomes, while human gametes (sperm or eggs) have 23 chromosomes each. A typical body cell, or 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 2n. Human cells that contain one set of chromosomes are called gametes, or sex cells; these are eggs and sperm, and are designated 1n, or haploid.

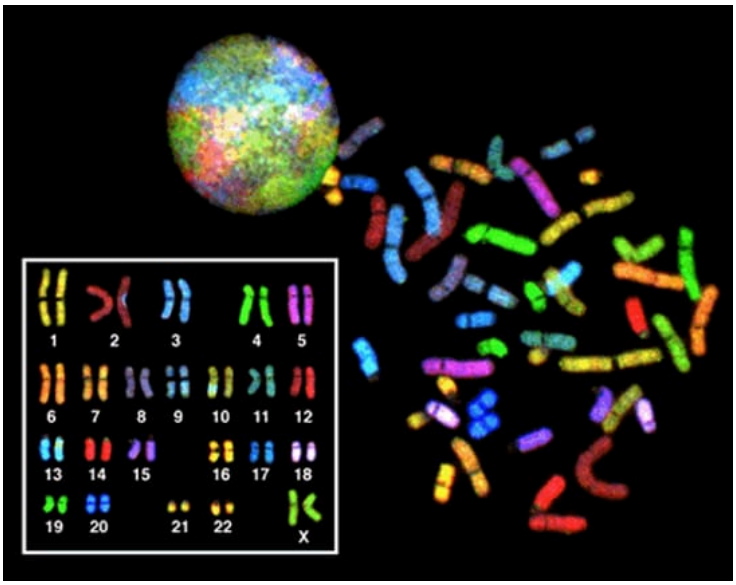


Figure $10.1B.1$: Eukaryotic Genome: There are 23 pairs of homologous chromosomes in a female human somatic cell. The condensed chromosomes are viewed within the nucleus (top), removed from a cell in mitosis and spread out on a slide (right), and artificially arranged according to length (left); an arrangement like this is called a karyotype. In this image, the chromosomes were exposed to fluorescent stains for differentiation of the different chromosomes. A method of staining called "chromosome painting" employs fluorescent dyes that highlight chromosomes in different colors.

Matched pairs of chromosomes in a diploid organism are called homologous ("same knowledge") 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, or traits, by coding for specific proteins. For example, hair color is a trait that can be blonde, brown, or black.

Each copy of a homologous pair of chromosomes originates from a different parent; therefore, the genes themselves are not identical. The variation of individuals within a species is due to the specific combination of the genes inherited from both parents. Even a slightly altered sequence of nucleotides within a gene can result in an alternative trait. For example, there are three possible gene sequences on the human chromosome that code 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 on both homologous chromosomes, with one on each (for example, AA, BB, or OO), or two different sequences, such as AB, AO, or BO.

Minor variations of traits, such as blood type, eye color, and handedness, contribute to the natural variation found within a species. However, if the entire DNA sequence from any pair of human homologous chromosomes is compared, the difference is less than one percent. The sex chromosomes, X and Y, are the single exception to the rule of homologous chromosome uniformity. Other than a small amount of homology that is necessary to accurately produce gametes, the genes found on the X and Y chromosomes are different.

Key Points

- A cell 's DNA, packaged as a double-stranded DNA molecule, 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.
- In eukaryotes, the genome consists of several double-stranded linear DNA molecules; each species of eukaryotes has a characteristic number of chromosomes in the nuclei of its cells.
- Matched pairs of chromosomes in a diploid organism are called homologous chromosomes, which are the same length and have specific nucleotide segments called genes in exactly the same location, or locus.
- Each copy of a homologous pair of chromosomes originates from a different parent, so the genes themselves are not identical.
- The difference between the DNA sequences in pairs of homologous chromosomes is less than one percent; the sex chromosomes, X and Y, are the single exception to this rule since their genes are different.

Key Terms

- **genome**: the cell's complete genetic information packaged as a double-stranded DNA molecule
- **nucleoid**: the irregularly-shaped region within a prokaryote cell where the genetic material is localized
- **gene**: a unit of heredity; the functional units of chromosomes that determine specific characteristics by coding for specific proteins
- **chromosome**: a structure in the cell nucleus that contains DNA, histone protein, and other structural proteins
- **locus**: a fixed position on a chromosome that may be occupied by one or more genes

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10.1C: Eukaryotic Chromosomal Structure and Compaction

Learning Objectives

- Describe the levels of chromsomal structure and compaction

Eukaryotic Chromosomal Structure and Compaction

If the DNA from all 46 chromosomes in a human cell nucleus was laid out end to end, it would measure approximately two meters. However, the diameter would be only 2 nm. Considering that the size of a typical human cell is about 10 µm (100,000 cells lined up to equal one meter), DNA must be tightly packaged to fit in the cell's nucleus. At the same time, it must also be readily accessible for the genes to be expressed. During some stages of the cell cycle, the long strands of DNA are condensed into compact chromosomes. There are a number of ways that chromosomes are compacted to fit in the cell's nucleus and be accessible for gene expression.

In the first level of compaction, short stretches of the DNA double helix wrap around a core of eight histone proteins at regular intervals along the entire length of the chromosome. The DNA-histone complex is called chromatin. The beadlike, histone DNA complex is called a nucleosome. DNA connecting the nucleosomes is called linker DNA. A DNA molecule in this form is about seven times shorter than the double helix without the histones. The beads are about 10 nm in diameter, in contrast with the 2-nm diameter of a DNA double helix. The next level of compaction occurs as the nucleosomes and the linker DNA between them are coiled into a 30-nm chromatin fiber. This coiling further shortens the chromosome so that it is now about 50 times shorter than the extended form. In the third level of packing, a variety of fibrous proteins is used to pack the chromatin. These fibrous proteins also ensure that each chromosome in a non-dividing cell occupies a particular area of the nucleus that does not overlap with that of any other chromosome.

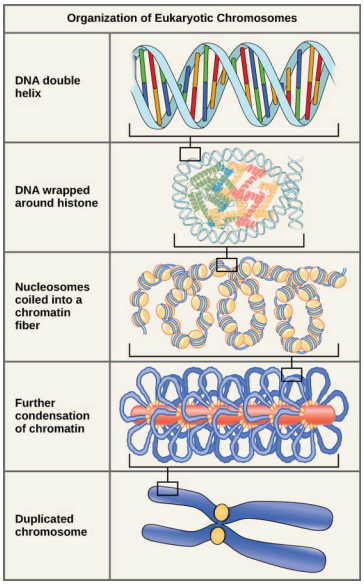


Figure $10.1C.1$: Levels of DNA Compaction: Double-stranded DNA wraps around histone proteins to form nucleosomes that have the appearance of "beads on a string." The nucleosomes are coiled into a 30-nm chromatin fiber. When a cell undergoes mitosis, the chromosomes condense even further.

DNA replicates in the S phase of interphase. After replication, the chromosomes are composed of two linked sister chromatids. When fully compact, the pairs of identically-packed chromosomes are bound to each other by cohesin proteins. The connection between the sister chromatids is closest in a region called the centromere. The conjoined sister chromatids, with a diameter of about 1 µm, are visible under a light microscope. The centromeric region is highly condensed and will appear as a constricted area.

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Key Points

- During some stages of the cell cycle, the long strands of DNA are condensed into compact chromosomes to fit in the cell's nucleus.
- In the first level of compaction, short stretches of the DNA double helix wrap around a core of eight histone proteins at regular intervals along the entire length of the chromosome.
- The DNA surrouding the histone core is called a nucleosome; the DNA-histone complex is called chromatin.
- The second level of compaction occurs as the nucleosomes and the linker DNA between them are coiled into a 30-nm chromatin fiber, which shortens the chromosome so it's about 50 times shorter than the extended form.
- After replication, the chromosomes are composed of two linked sister chromatids; when fully compact, the pairs of identically-packed chromosomes are bound to each other by cohesin proteins.
- The connection between the sister chromatids is closest in a region called the centromere; this region is highly condensed.

Key Terms

- **nucleosome**: any of the subunits that repeat in chromatin; a coil of DNA surrounding a histone core
- **histone**: any of various simple water-soluble proteins that are rich in the basic amino acids lysine and arginine and are complexed with DNA in the nucleosomes of eukaryotic chromatin
- **chromatin**: a complex of DNA, RNA, and proteins within the cell nucleus out of which chromosomes condense during cell division

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10.2: THE CELL CYCLE



- Topic hierarchy

10.2A: Interphase

10.2B: The Mitotic Phase and the G0 Phase

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10.2A: Interphase

Learning Objectives

- Describe the events that occur during Interphase

Interphase

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

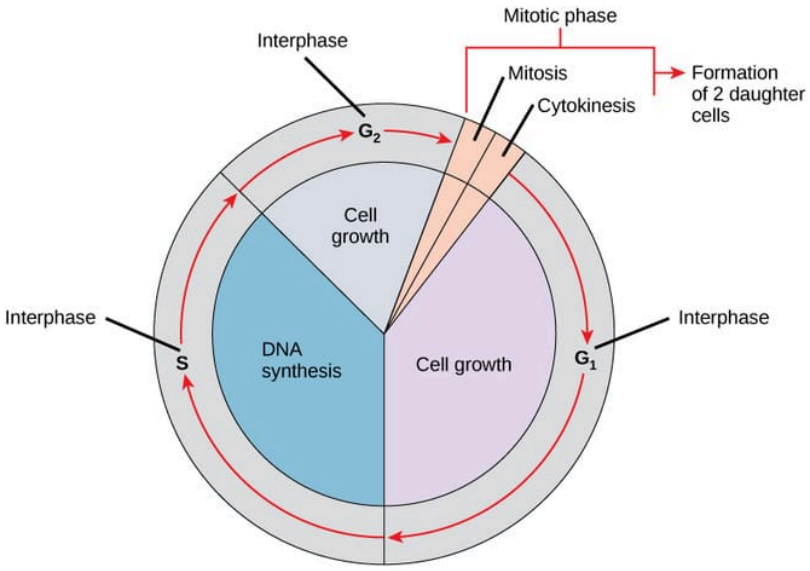


Figure 10.2A.1: The Stages of Interphase and the Cell Cycle: The cell cycle consists of interphase and the mitotic phase. During interphase, the cell grows and the nuclear DNA is duplicated. Interphase is followed by the mitotic phase. During the mitotic phase, the duplicated chromosomes are segregated and distributed into daughter nuclei. The cytoplasm is usually divided as well, resulting in two daughter cells.

G_1 Phase (First Gap)

The first stage of interphase is called the G_1 phase (first gap) because, from a microscopic aspect, little change is visible. However, during the G_1 stage, the cell is quite active at the biochemical level. The cell grows and accumulates the building blocks of chromosomal DNA and the associated proteins as well as sufficient energy reserves to complete the task of replicating each chromosome in the nucleus.

S Phase (Synthesis of DNA)

The synthesis phase of interphase takes the longest because of the complexity of the genetic material being duplicated. Throughout interphase, nuclear DNA remains in a semi-condensed chromatin configuration. In the S phase, DNA replication results in the formation of identical pairs of DNA molecules, sister chromatids, that are firmly attached to the centromeric region. 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. At the center of each animal cell, the centrosomes of animal cells are associated with a pair of rod-like objects, the centrioles, which are at right angles to each other. Centrioles help organize cell division. Centrioles are not present in the centrosomes of other eukaryotic species, such as plants and most fungi.

G_2 Phase (Second Gap)

In the G_2 phase, the cell replenishes its energy stores and synthesizes proteins necessary for chromosome manipulation. Some cell organelles are duplicated, and the cytoskeleton is dismantled to provide resources for the mitotic phase. 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.

Key Points

- There are three stages of interphase: G_1 (first gap), S (synthesis of new DNA), and G_2 (second gap).
- Cells spend most of their lives in interphase, specifically in the S phase where genetic material must be copied.
- The cell grows and carries out biochemical functions, such as protein synthesis, in the G_1 phase.
- During the S phase, DNA is duplicated into two sister chromatids, and centrosomes, which give rise to the mitotic spindle, are also replicated.
- In the G_2 phase, energy is replenished, new proteins are synthesized, the cytoskeleton is dismantled, and additional growth occurs.

Key Terms

- **interphase**: the stage in the life cycle of a cell where the cell grows and DNA is replicated
- **sister chromatid**: either of the two identical strands of a chromosome (DNA material) that separate during mitosis
- **mitotic spindle**: the apparatus that orchestrates the movement of chromosomes during mitosis

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10.2B: The Mitotic Phase and the G0 Phase

Learning Objectives

- Describe the events that occur at the different stages of mitosis

The Mitotic Phase

The mitotic phase is a multistep process during which the duplicated chromosomes are aligned, separated, and move into two new, identical daughter cells. The first portion of the mitotic phase is called karyokinesis or nuclear division. The second portion of the mitotic phase, called cytokinesis, is the physical separation of the cytoplasmic components into the two daughter cells.

Karyokinesis (Mitosis)

Karyokinesis, also known as mitosis, is divided into a series of phases (prophase, prometaphase, metaphase, anaphase, and telophase) that result in the division of the cell nucleus.

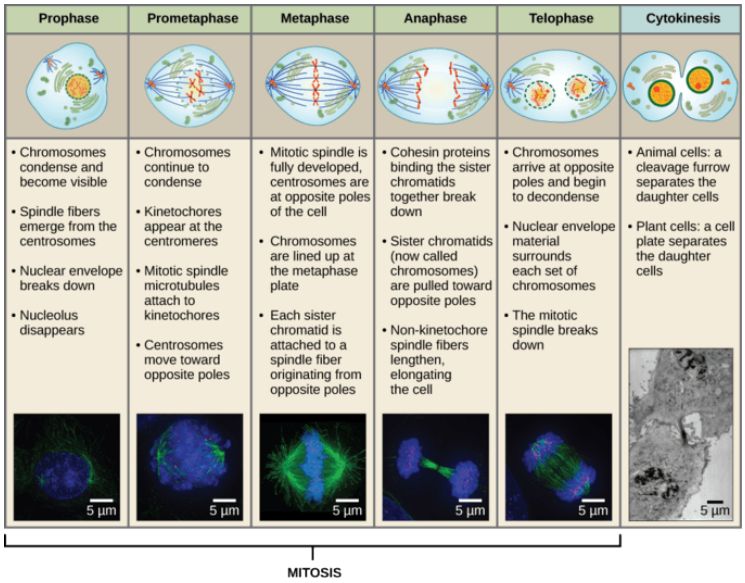


Figure $10.2B.1$: Stages of the Cell Cycle: Karyokinesis (or mitosis) is divided into five stages: prophase, prometaphase, metaphase, anaphase, and telophase. The images at the bottom were taken by fluorescence microscopy (hence, the black background) of cells artificially stained by fluorescent dyes: blue fluorescence indicates DNA (chromosomes) and green fluorescence indicates microtubules (spindle apparatus).

During prophase, the “first phase,” the nuclear envelope starts to dissociate into small vesicles. The membranous organelles (such as the Golgi apparatus and endoplasmic reticulum) fragment and disperse toward the periphery of the cell. The nucleolus disappears and the centrosomes begin to move to opposite poles of the cell. Microtubules that will eventually form the mitotic spindle extend between the centrosomes, pushing them farther apart as the microtubule fibers lengthen. The sister chromatids begin to coil more tightly with the aid of condensin proteins and become visible under a light microscope.

During prometaphase, the “first change phase,” many processes that began in prophase continue to advance. The remnants of the nuclear envelope fragment. 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 discrete. Each sister chromatid develops a protein structure called a kinetochore in the centromeric region. The proteins of the kinetochore attract and bind mitotic spindle microtubules.

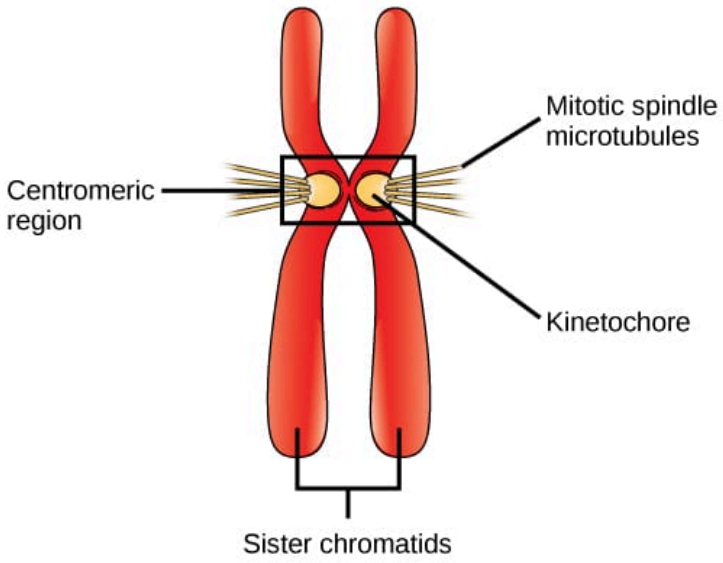


Figure $10.2B.1$: Kinetochore and Mitotic Spindle: During prometaphase, mitotic spindle microtubules from opposite poles attach to each sister chromatid at the kinetochore. In anaphase, the connection between the sister chromatids breaks down and the microtubules pull the chromosomes toward opposite poles.

During metaphase, the “change phase,” all the chromosomes are aligned on 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 by cohesin proteins. At this time, the chromosomes are maximally condensed.

During anaphase, the “upward phase,” the cohesin proteins degrade, and the sister chromatids separate at the centromere. Each chromatid, now called a chromosome, is pulled rapidly toward the centrosome to which its microtubule is attached. The cell becomes visibly elongated (oval shaped) as the polar microtubules slide against each other at the metaphase plate where they overlap.

During telophase, the “distance phase,” the chromosomes reach the opposite poles and begin to decondense (unravel), relaxing into a chromatin configuration. The mitotic spindles are depolymerized into tubulin monomers that will be used to assemble cytoskeletal components for each daughter cell. Nuclear envelopes form around the chromosomes and nucleosomes appear within the nuclear area.

Cytokinesis

Cytokinesis, or “cell motion,” is the second main stage of the mitotic phase during which cell division is completed via the physical separation of the cytoplasmic components into two daughter cells. Division is not complete until the cell components have been apportioned and completely separated into the 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, which lack cell walls, cytokinesis follows 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; eventually the membrane is cleaved in two.

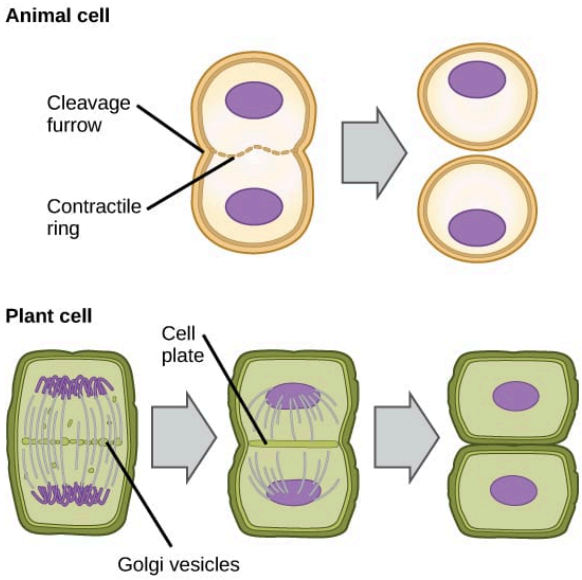


Figure $10.2B.1$: Cytokinesis: During cytokinesis in animal cells, a ring of actin filaments forms at the metaphase plate. The ring contracts, forming a cleavage furrow, which divides the cell in two. In plant cells, Golgi vesicles coalesce at the former metaphase plate, forming a phragmoplast. A cell plate formed by the fusion of the vesicles of the phragmoplast grows from the center toward the cell walls and the membranes of the vesicles fuse to form a plasma membrane that divides the cell in two.

In plant cells, 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 into vesicles and dispersing throughout the dividing cell. During telophase, these Golgi vesicles are transported on microtubules to form a phragmoplast (a vesicular structure) at the metaphase plate. There, the vesicles fuse and coalesce 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 walls at the periphery of the cell. Enzymes use the glucose that has accumulated between the membrane layers to build a new cell wall. The Golgi membranes become parts of the plasma membrane on either side of the new cell wall.

G_0 Phase

Not all cells adhere to the classic cell cycle pattern in which a newly-formed daughter cell immediately enters the preparatory phases of interphase, closely followed by the mitotic phase. Cells in G_0 phase are not actively preparing to divide. The cell is in a quiescent (inactive) stage that occurs when cells exit 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.

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Key Points

- During prophase, the nucleus disappears, spindle fibers form, and DNA condenses into chromosomes (sister chromatids).
- During metaphase, the sister chromatids align along the equator of the cell by attaching their centromeres to the spindle fibers.
- During anaphase, sister chromatids are separated at the centromere and are pulled towards opposite poles of the cell by the mitotic spindle.
- During telophase, chromosomes arrive at opposite poles and unwind into thin strands of DNA, the spindle fibers disappear, and the nuclear membrane reappears.
- Cytokinesis is the actual splitting of the cell membrane; animal cells pinch apart, while plant cells form a cell plate that becomes the new cell wall.
- Cells enter the G_0 (inactive) phase after they exit the cell cycle when they are not actively preparing to divide; some cells remain in G_0 phase permanently.

Key Terms

- **karyokinesis**: (mitosis) the first portion of mitotic phase in which division of the cell nucleus takes place
- **centrosome**: an organelle near the nucleus in the cytoplasm of most organisms that controls the organization of its microtubules and gives rise to the mitotic spindle
- **cytokinesis**: the second portion of the mitotic phase in which the cytoplasm of a cell divides following the division of the nucleus

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10.3: CONTROL OF THE CELL CYCLE



- Topic hierarchy

10.3A: Regulation of the Cell Cycle by External Events

10.3B: Regulation of the Cell Cycle at Internal Checkpoints

10.3C: Regulator Molecules of the Cell Cycle

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10.3A: Regulation of the Cell Cycle by External Events

Learning Objectives

- Describe external events that can affect cell cycle regulation

Regulation of the Cell Cycle by External Events

Unlike the life of organisms, which is a straight progression from birth to death, the life of a cell takes place in a cyclical pattern. Each cell is produced as part of its parent cell. When a daughter cell divides, it turns into two new cells, which would lead to the assumption that each cell is capable of being immortal as long as its descendants can continue to divide. However, all cells in the body only live as long as the organism lives. Some cells do live longer than others, but eventually all cells die when their vital functions cease. Most cells in the body exist in the state of interphase, the non-dividing stage of the cell life cycle. When this stage ends, cells move into the dividing part of their lives called mitosis.

Both the initiation and inhibition of cell division are triggered by events external to the cell when it is about to begin the replication process. An event may be as simple as the death of a nearby cell or as sweeping as the release of growth-promoting hormones, such as human growth hormone (HGH). A lack of HGH can inhibit cell division, resulting in dwarfism, whereas too much HGH can result in gigantism. Crowding of cells can also inhibit cell division. Another factor that can initiate cell division is the size of the cell; as a cell grows, it becomes inefficient due to its decreasing surface-to-volume ratio. The solution to this problem is to divide.



Figure 10.3A.1: Dwarfism: Commodore Nut (right) was a famous circus performer afflicted with dwarfism. This was a result of a lack of Human Growth Hormone.

Whatever the source of the message, the cell receives the signal, and a series of events within the cell allows it to proceed into interphase. Moving forward from this initiation point, every parameter required during each cell cycle phase must be met or the cycle cannot progress.

Key Points

- The death of nearby cells and the presence or absence of certain hormones can impact the cell cycle.
- The release of growth-promoting hormones, such as HGH, can initiate cell division, and a lack of these hormones can inhibit cell division.

- Cell growth initiates cell division because cells must divide as the surface-to-volume ratio decreases; cell crowding inhibits cell division.
- Key conditions must be met before the cell can move into interphase.

Key Terms

- **gigantism**: a condition caused by an over-production of growth hormone, resulting in excessive bone growth
- **growth hormone**: any polypeptide hormone secreted by the pituitary gland that promotes growth and regulates the metabolism of carbohydrates, proteins, and lipids
- **dwarfism**: a condition caused by a lack of growth hormone, resulting in short stature and limbs that are disproportionately small in relation to the body

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10.3B: Regulation of the Cell Cycle at Internal Checkpoints

Learning Objectives

- Explain the effects of internal checkpoints on the regulation of the cell cycle

Regulation at Internal Checkpoints

It is essential that the daughter cells are 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 an abnormal cell. To prevent a compromised cell from continuing to divide, internal control mechanisms operate at three main cell cycle checkpoints. A checkpoint is one of several points in the eukaryotic cell cycle at which the progression of a cell to the next stage in the cycle can be halted until conditions are favorable (e.g. the DNA is repaired). These checkpoints occur near the end of G_1, at the G_2/M transition, and during metaphase.

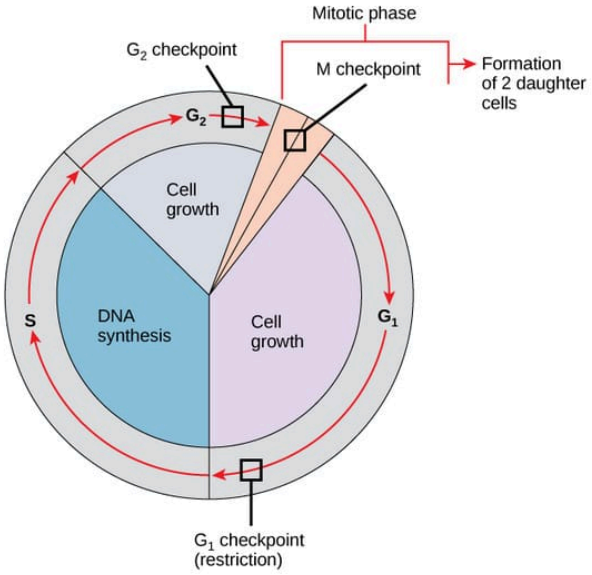


Figure $10.3B.1$: Internal Checkpoints During the Cell Cycle: The cell cycle is controlled at three checkpoints. The integrity of the DNA is assessed at the G1 checkpoint. Proper chromosome duplication is assessed at the G2 checkpoint. Attachment of each kinetochore to a spindle fiber is assessed at 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 (in yeast), is a point at which the cell irreversibly commits to the cell division process. External influences, such as growth factors, play a large role in carrying the cell past the G_1 checkpoint. The cell will only pass the checkpoint if it is an appropriate size and has adequate energy reserves. At this point, the cell also checks for DNA damage. A cell that does not meet all the requirements will not progress to the S phase. The cell can halt the cycle and attempt to remedy the problematic condition, or the cell can advance into G_0 (inactive) phase and await further signals when conditions improve.

If a cell meets the requirements for the G_1 checkpoint, the cell will enter S phase and begin DNA replication. This transition, as with all of the major checkpoint transitions in the cell cycle, is signaled by cyclins and cyclin dependent kinases (CDKs). Cyclins are cell-signaling molecules that regulate the cell cycle.

The G_2 Checkpoint

The G_2 checkpoint bars entry into the mitotic phase if certain conditions are not met. As with 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 accurately replicated without mistakes or damage. If the checkpoint mechanisms detect problems with the DNA, the cell cycle is halted and the cell attempts to either complete DNA replication or repair the damaged DNA. If the DNA has been correctly replicated, cyclin dependent kinases (CDKs) signal the beginning of mitotic cell division.

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 whether 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 at least two spindle fibers arising from opposite poles of the cell.

Key Points

- A checkpoint is one of several points in the eukaryotic cell cycle at which the progression of a cell to the next stage in the cycle can be halted until conditions are favorable.
- Damage to DNA and other external factors are evaluated at the G1 checkpoint; if conditions are inadequate, the cell will not be allowed to continue to the S phase of interphase.
- The G2 checkpoint ensures all of the chromosomes have been replicated and that the replicated DNA is not damaged before cell enters mitosis.
- The M checkpoint determines whether all the sister chromatids are correctly attached to the spindle microtubules before the cell enters the irreversible anaphase stage.

Key Terms

- **restriction point**: (G1 checkpoint) a point in the animal cell cycle at which the cell becomes “committed” to the cell cycle, which is determined by external factors and signals
- **spindle checkpoint**: (M checkpoint) prevents separation of the duplicated chromosomes until each chromosome is properly attached to the spindle apparatus
- **cyclin**: any of a group of proteins that regulates the cell cycle by forming a complex with kinases
- **G2 checkpoint**: ensures all of the chromosomes have been replicated and that the replicated DNA is not damaged

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10.3C: Regulator Molecules of the Cell Cycle

Learning Objectives

- Differentiate among the molecules that regulate the cell cycle

Regulator Molecules of the Cell Cycle

In addition to the internally controlled checkpoints, there are two groups of intracellular molecules that regulate the cell cycle. These regulatory molecules either promote progress of the cell to the next phase (positive regulation) or halt the cycle (negative regulation). Regulator molecules may act individually or they can influence the activity or production of other regulatory proteins. Therefore, the failure of a single regulator may have almost no effect on the cell cycle, especially if more than one mechanism controls the same event. Conversely, the effect of a deficient or non-functioning regulator can be wide-ranging and possibly fatal to the cell if multiple processes are affected.

Positive Regulation of the Cell Cycle

Two groups of proteins, called cyclins and cyclin-dependent kinases (Cdks), are responsible for the progress of the cell through the various checkpoints. The levels of the four cyclin proteins fluctuate throughout the cell cycle in a predictable pattern. Increases in the concentration of cyclin proteins are triggered by both external and internal signals. After the cell moves to the next stage of the cell cycle, the cyclins that were active in the previous stage are degraded.

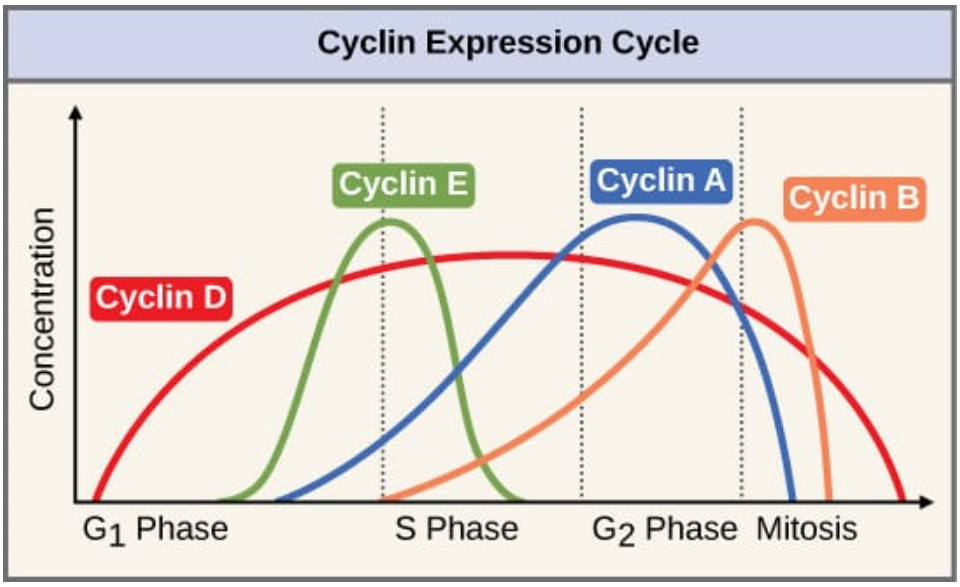


Figure $10.3C.1$: Cyclin Concentrations at Checkpoints: The concentrations of cyclin proteins change throughout the cell cycle. There is a direct correlation between cyclin accumulation and the three major cell cycle checkpoints. Also, note the sharp decline of cyclin levels following each checkpoint (the transition between phases of the cell cycle) as cyclin is degraded by cytoplasmic enzymes.

Cyclins regulate the cell cycle only when they are tightly bound to Cdks. To be fully active, the Cdk/cyclin complex must also be phosphorylated in specific locations. Like all kinases, Cdks are enzymes (kinases) that phosphorylate other proteins. Phosphorylation activates the protein by changing its shape. The proteins phosphorylated by Cdks are involved in advancing the cell to the next phase.. The levels of Cdk proteins are relatively stable throughout the cell cycle; however, the concentrations of cyclin fluctuate and determine when Cdk/cyclin complexes form. The different cyclins and Cdks bind at specific points in the cell cycle and thus regulate different checkpoints.

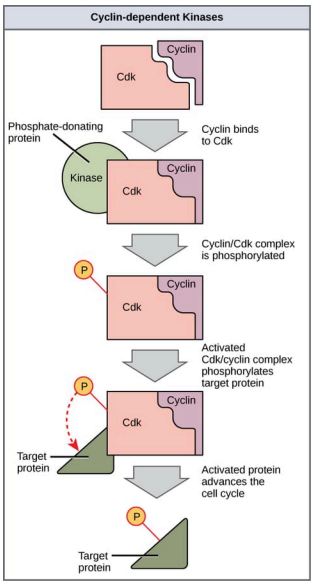


Figure $10.3C.1$: Activation of Cdks: Cyclin-dependent kinases (Cdks) are protein kinases that, when fully activated, can phosphorylate and activate other proteins that advance the cell cycle past a checkpoint. To become fully activated, a Cdk must bind to a cyclin protein and then be phosphorylated by another kinase.

Although the cyclins are the main regulatory molecules that determine the forward momentum of the cell cycle, there are several other mechanisms that fine tune the progress of the cycle with negative, rather than positive, effects. These mechanisms essentially block the progression of the cell cycle until problematic conditions are resolved. Molecules that prevent the full activation of Cdks are called Cdk inhibitors. Many of these inhibitor molecules directly or indirectly monitor a particular cell cycle event. The block placed on Cdks by inhibitor molecules will not be removed until the specific event being monitored is completed.

Negative Regulation of the Cell Cycle

The second group of cell cycle regulatory molecules are negative regulators. Negative regulators halt the cell cycle. Remember that in positive regulation, active molecules cause the cycle to progress.

The best understood negative regulatory molecules are retinoblastoma protein (Rb), p53, and p21. Retinoblastoma proteins are a group of tumor-suppressor proteins common in many cells. Much of what is known about cell cycle regulation comes from research conducted with cells that have lost regulatory control. All three of these regulatory proteins were discovered to be damaged or non-functional in cells that had begun to replicate uncontrollably (became cancerous). In each case, the main cause of the unchecked progress through the cell cycle was a faulty copy of the regulatory protein.

Rb, p53, and p21 act primarily at the G_1 checkpoint. p53 is a multi-functional protein that has a major impact on the cell's commitment to division; it acts when there is damaged DNA in cells that are undergoing the preparatory processes during G_1. If damaged DNA is detected, p53 halts the cell cycle and recruits enzymes to repair the DNA. If the DNA cannot be repaired, p53 can trigger apoptosis (cell suicide) to prevent the duplication of damaged chromosomes. As p53 levels rise, the production of p21 is triggered. p21 enforces the halt in the cycle dictated by p53 by binding to and inhibiting the activity of the Cdk/cyclin complexes. As a cell is exposed to more stress, higher levels of p53 and p21 accumulate, making it less likely that the cell will move into the S phase.

Rb exerts its regulatory influence on other positive regulator proteins. Rb monitors cell size. In the active, dephosphorylated state, Rb binds to proteins called transcription factors, most commonly to E2F. Transcription factors "turn on" specific genes, allowing the production of proteins encoded by that gene. When Rb is bound to E2F, production of proteins necessary for the G_1/S transition is blocked. As the cell increases in size, Rb is slowly phosphorylated until it becomes inactivated. Rb releases E2F, which can now turn on the gene that produces the transition protein and this particular block is removed. For the cell to move past each of the checkpoints, all positive regulators must be "turned on" and all negative regulators must be "turned off."

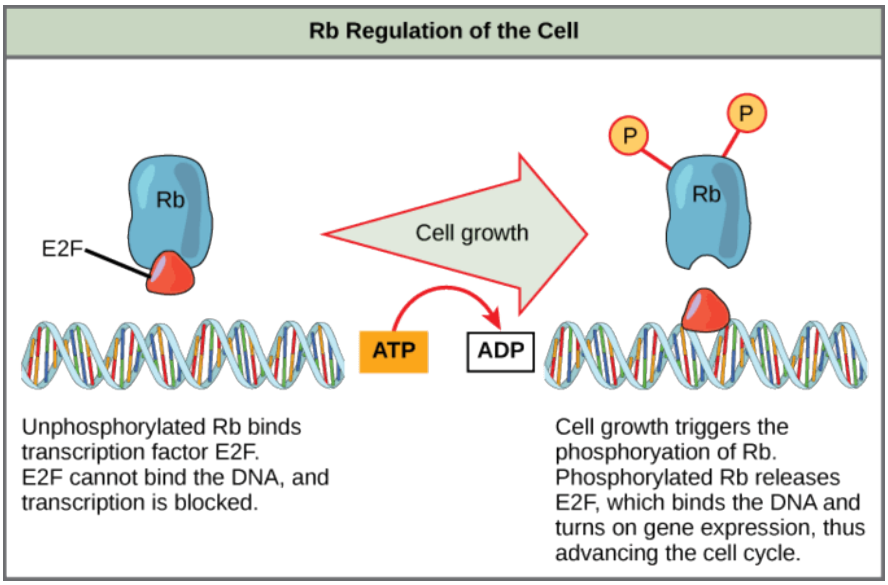


Figure $10.3C.1$: Function of the Rb Regulator Molecule: Rb halts the cell cycle by binding E2F. Rb releases its hold on E2F in response to cell growth to advance the cell cycle.

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Key Points

- Two groups of proteins, cyclins and cyclin-dependent kinases (Cdks), are responsible for promoting the cell cycle.
- Cyclins regulate the cell cycle only when they are bound to Cdks; to be fully active, the Cdk/cyclin complex must be phosphorylated, which allows it to phosphorylate other proteins that advance the cell cycle.
- Negative regulator molecules (Rb, p53, and p21) act primarily at the G_1 checkpoint and prevent the cell from moving forward to division until damaged DNA is repaired.
- p53 halts the cell cycle and recruits enzymes to repair damaged DNA; if DNA cannot be repaired, p53 triggers apoptosis to prevent duplication.
- Production of p21 is triggered by p53; p21 halts the cycle by binding to and inhibiting the activity of the Cdk/cyclin complex.
- Dephosphorylated Rb binds to E2F, which halts the cell cycle; when the cell grows, Rb is phosphorylated and releases E2F, which advances the cell cycle.

Key Terms

- **cyclin**: any of a group of proteins that regulates the cell cycle by forming a complex with kinases
- **cyclin-dependent kinase**: (CDK) a member of a family of protein kinases first discovered for its role in regulating the cell cycle through phosphorylation
- **retinoblastoma protein**: (Rb) a group of tumor-suppressor proteins that regulates the cell cycle by monitoring cell size

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10.4: CANCER AND THE CELL CYCLE



- Topic hierarchy

10.4A: Proto-oncogenes

10.4B: Tumor Suppressor Genes

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10.4A: Proto-oncogenes

Learning Objectives

- Explain regulation of the cell cycle by proto-oncogenes

Proto-oncogenes

The genes that code for the positive cell cycle regulators are called proto-oncogenes. Proto-oncogenes are normal genes that, when mutated in certain ways, become oncogenes: genes that cause a cell to become cancerous. There are several ways by which a proto-oncogene can be converted into an oncogene. Consider what might happen to the cell cycle in a cell with a recently-acquired oncogene. In most instances, the alteration of the DNA sequence will result in a less functional (or non-functional) protein. The result is detrimental to the cell and will likely prevent the cell from completing the cell cycle; however, the organism is not harmed because the mutation will not be carried forward. If a cell cannot reproduce, the mutation is not propagated and the damage is minimal.

Occasionally, however, a gene mutation causes a change that increases the activity of a positive regulator. For example, a mutation that allows the Cdk gene to be activated without being partnered with cyclin could push the cell cycle past a checkpoint before all of the required conditions are met. If the resulting daughter cells are too damaged to undergo further cell divisions, the mutation would not be propagated and no harm would come to the organism. However, if the atypical daughter cells are able to undergo further cell divisions, subsequent generations of cells will probably accumulate even more mutations, some possibly in additional genes that regulate the cell cycle.

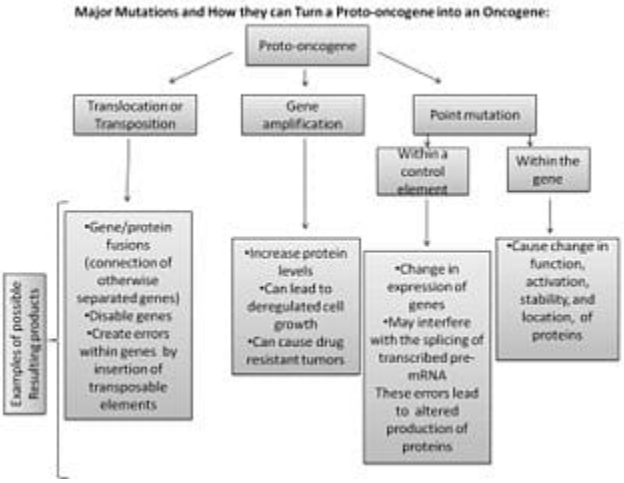


Figure 10.4A.1: Proto-oncogene Conversion to Oncogene: Examples of ways to convert proto-oncogenes into cancer-causing genes (oncogenes).

The Cdk gene in the above example is only one of many genes that are considered proto-oncogenes. In addition to the cell cycle regulatory proteins, any protein that influences the cycle can be altered in such a way as to override cell cycle checkpoints. An oncogene is any gene that, when altered, leads to an increase in the rate of cell cycle progression.

Key Points

- Proto- oncogenes positively regulate the cell cycle.
- Mutations may cause proto-oncogenes to become oncogenes, disrupting normal cell division and causing cancers to form.
- Some mutations prevent the cell from reproducing, which keeps the mutations from being passed on.
- If a mutated cell is able to reproduce because the cell division regulators are damaged, then the mutation will be passed on, possibly accumulating more mutations with successive divisions.

Key Terms

- **proto-oncogene**: a gene that promotes the specialization and division of normal cells that becomes an oncogene following mutation
- **mutation**: any heritable change of the base-pair sequence of genetic material
- **oncogene**: any gene that contributes to the conversion of a normal cell into a cancerous cell when mutated or expressed at high levels

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10.4B: Tumor Suppressor Genes

Learning Objectives

- Describe the role played by tumor suppressor genes in the cell cycle

Like proto- oncogenes, many of the negative cell cycle regulatory proteins were discovered in cells that had become cancerous. Tumor suppressor genes are segments of DNA that code for negative regulator proteins: the type of regulators that, when activated, can prevent the cell from undergoing uncontrolled division. The collective function of the best-understood tumor suppressor gene proteins, Rb, p53, and p21, is to put up a roadblock to cell cycle progression until certain events are completed. A cell that carries a mutated form of a negative regulator might not be able to halt the cell cycle if there is a problem. Tumor suppressors are similar to brakes in a vehicle: malfunctioning brakes can contribute to a car crash.

Mutated p53 genes have been identified in more than one-half of all human tumor cells. This discovery is not surprising in light of the multiple roles that the p53 protein plays at the G_1 checkpoint. A cell with a faulty p53 may fail to detect errors present in the genomic DNA. Even if a partially-functional p53 does identify the mutations, it may no longer be able to signal the necessary DNA repair enzymes. Either way, damaged DNA will remain uncorrected. At this point, a functional p53 will deem the cell unsalvageable and trigger programmed cell death (apoptosis). The damaged version of p53 found in cancer cells, however, cannot trigger apoptosis.

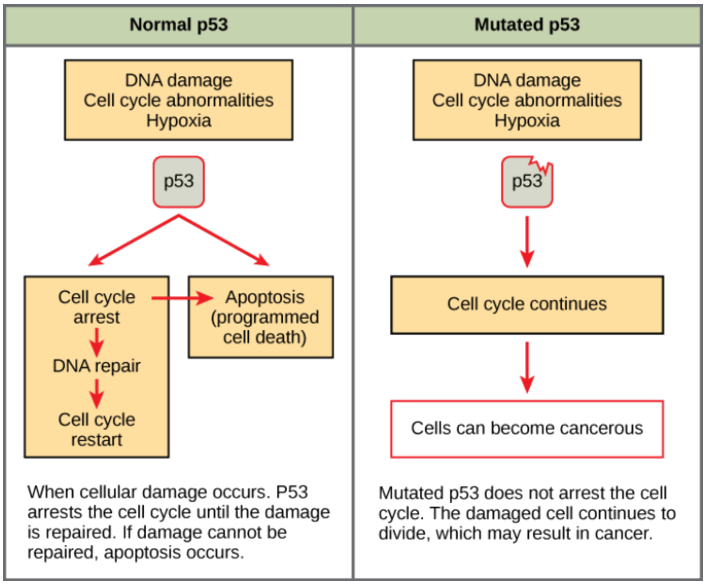


Figure $10.4B.1$: Function of Normal and Mutated p53 genes: The role of normal p53 is to monitor DNA and the supply of oxygen (hypoxia is a condition of reduced oxygen supply). If damage is detected, p53 triggers repair mechanisms. If repairs are unsuccessful, p53 signals apoptosis. A cell with an abnormal p53 protein cannot repair damaged DNA and cannot signal apoptosis. Cells with abnormal p53 can become cancerous.

The loss of p53 function has other repercussions for the cell cycle. Mutated p53 might lose its ability to trigger p21 production. Without adequate levels of p21, there is no effective block on Cdk activation. Essentially, without a fully functional p53, the G_1 checkpoint is severely compromised and the cell proceeds directly from G_1 to S regardless of internal and external conditions. At the completion of this shortened cell cycle, two daughter cells are produced that have inherited the mutated p53 gene. Given the non-optimal conditions under which the parent cell reproduced, it is likely that the daughter cells will have acquired other mutations in addition to the faulty tumor suppressor gene. Cells such as these daughter cells quickly accumulate both oncogenes and non-functional tumor suppressor genes. Again, the result is tumor growth.

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Key Points

- Tumor suppressor genes are segments of DNA that code for negative regulator proteins, which keep the cell from undergoing uncontrolled division.
- Mutated p53 genes are believed to be responsible for causing tumor growth because they turn off the regulatory mechanisms that keep cells from dividing out of control.
- Sometimes cells with negative regulators can halt their transmission by inducing pre-programmed cell death called apoptosis.
- Without a fully functional p53, the G1 checkpoint of interphase is severely compromised and the cell proceeds directly from G1 to S; this creates two daughter cells that have inherited the mutated p53 gene.

Key Terms

- **apoptosis**: a process of programmed cell death

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10.5: PROKARYOTIC CELL DIVISION

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- Topic hierarchy

10.5A: Binary Fission

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10.5A: Binary Fission

Learning Objectives

- Describe the process of binary fission in prokaryotes

Prokaryotes, such as bacteria, propagate by binary fission. For unicellular organisms, cell division is the only method used to produce new individuals. In both prokaryotic and eukaryotic cells, the outcome of cell reproduction is a pair of daughter cells that are genetically identical to the parent cell. In unicellular organisms, daughter cells are individuals.

Due to the relative simplicity of the prokaryotes, the cell division process, or binary fission, is a less complicated and much more rapid process than cell division in eukaryotes. The single, circular DNA chromosome of bacteria is not enclosed in a nucleus, but instead occupies a specific location, the nucleoid, within the cell. Although the DNA of the nucleoid is associated with proteins that aid in packaging the molecule into a compact size, there are no histone proteins and thus, no nucleosomes in prokaryotes. The packing proteins of bacteria are, however, related to the cohesin and condensin proteins involved in the chromosome compaction of eukaryotes.

The bacterial chromosome is attached to the plasma membrane at about the midpoint of the cell. The starting point of replication, the origin, is close to the binding site of the chromosome at the plasma membrane. Replication of the DNA is bidirectional, moving away from the origin on both strands of the loop simultaneously. As the new double strands are formed, each origin point moves away from the cell wall attachment toward the opposite ends of the cell. As the cell elongates, the growing membrane aids in the transport of the chromosomes. After the chromosomes have cleared the midpoint of the elongated cell, cytoplasmic separation begins. The formation of a ring composed of repeating units of a protein, FtsZ, directs the partition between the nucleoids. Formation of the FtsZ ring triggers the accumulation of other proteins that work together to recruit new membrane and cell wall materials to the site. A septum is formed between the nucleoids, extending gradually from the periphery toward the center of the cell. When the new cell walls are in place, the daughter cells separate.

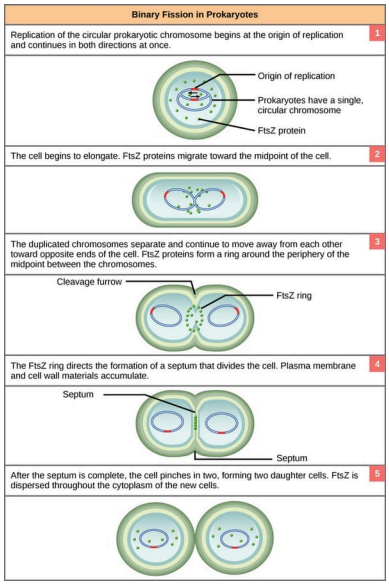


Figure 10.5A.1: Binary Fission: These images show the steps of binary fission in prokaryotes.

Mitotic Spindle Apparatus

The precise timing and formation of the mitotic spindle is critical to the success of eukaryotic cell division. Prokaryotic cells, on the other hand, do not undergo karyokinesis and, therefore, have no need for a mitotic spindle. However, the FtsZ protein that plays such a vital role in prokaryotic cytokinesis is structurally and functionally very similar to tubulin, the building block of the microtubules that make up the mitotic spindle fibers that are necessary for eukaryotes. FtsZ proteins can form filaments, rings,

and other three-dimensional structures that resemble the way tubulin forms microtubules, centrioles, and various cytoskeletal components. In addition, both FtsZ and tubulin employ the same energy source, GTP (guanosine triphosphate), to rapidly assemble and disassemble complex structures.

FtsZ and tubulin are homologous structures derived from common evolutionary origins. In this example, FtsZ is the ancestor protein to tubulin (a modern protein). While both proteins are found in extant organisms, tubulin function has evolved and diversified tremendously since evolving from its FtsZ prokaryotic origin. A survey of mitotic assembly components found in present-day unicellular eukaryotes reveals crucial intermediary steps to the complex membrane-enclosed genomes of multicellular eukaryotes.

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Key Points

- In bacterial replication, the DNA is attached to the plasma membrane at about the midpoint of the cell.
- The origin, or starting point of bacterial replication, is close to the binding site of the DNA to the plasma membrane.
- Replication of the bacterial DNA is bidirectional, which means it moves away from the origin on both strands simultaneously.
- The formation of the FtsZ ring, a ring composed of repeating units of protein, triggers the accumulation of other proteins that work together to acquire and bring new membrane and cell wall materials to the site.
- When new cell walls are in place, due to the formation of a septum, the daughter cells separate to form individual cells.

Key Terms

- **mitotic spindle**: the apparatus that orchestrates the movement of DNA during mitosis
- **karyokinesis**: (mitosis) the first portion of mitotic phase where division of the cell nucleus takes place
- **binary fission**: the process whereby a cell divides asexually to produce two daughter cells

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11: MEIOSIS AND SEXUAL REPRODUCTION

11.1: The Process of Meiosis - Introduction to Meiosis
11.2: The Process of Meiosis - Meiosis I
11.3: The Process of Meiosis - Meiosis II
11.4: The Process of Meiosis - Comparing Meiosis and Mitosis
11.5: Sexual Reproduction - Advantages and Disadvantages of Sexual Reproduction
11.6: Sexual Reproduction - Life Cycles of Sexually Reproducing Organisms

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11.1: The Process of Meiosis - Introduction to Meiosis

Learning Objectives

- Describe the importance of meiosis in sexual reproduction

Introduction: Meiosis and Sexual Reproduction

The ability to reproduce *in kind* is a basic characteristic of all living things. In kind means that the offspring of any organism closely resemble their parent or parents. Sexual reproduction requires fertilization: the union of two cells from two individual organisms. Haploid cells contain one set of chromosomes. Cells containing two sets of chromosomes are called diploid. The number of sets of chromosomes in a cell is called its ploidy level. If the reproductive cycle is to continue, then 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. Therefore, sexual reproduction includes a nuclear division that reduces the number of chromosome sets.



Figure 11.1.1: Offspring Closely Resemble Their Parents: *In kind* means that the offspring of any organism closely resemble their parent or parents. The hippopotamus gives birth to hippopotamus calves (a). Joshua trees produce seeds from which Joshua tree seedlings emerge (b). Adult flamingos lay eggs that hatch into flamingo chicks (c).

Sexual reproduction is the production of haploid cells (gametes) and the fusion (fertilization) of two gametes to form a single, unique diploid cell called a zygote. All animals and most plants produce these gametes, or eggs and sperm. In most plants and animals, through tens of rounds of mitotic cell division, this diploid cell will develop into an adult organism.

Haploid cells that are part of the sexual reproductive cycle are produced by a type of cell division called meiosis. 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, so the resulting cells have half the chromosomes as the original. To achieve this reduction in chromosomes, 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 major process and the stages are designated with a “I” or a “II.” Thus, meiosis I is the first round of meiotic division and consists of prophase I, prometaphase I, and so on. Meiosis II, the second round of meiotic division, includes prophase II, prometaphase II, and so on.

Key Points

- Sexual reproduction is the production of haploid cells and the fusion of two of those cells to form a diploid cell.
- Before sexual reproduction can occur, the number of chromosomes in a diploid cell must decrease by half.

- Meiosis produces cells with half the number of chromosomes as the original cell.
- Haploid cells used in sexual reproduction, gametes, are formed during meiosis, which consists of one round of chromosome replication and two rounds of nuclear division.
- Meiosis I is the first round of meiotic division, while meiosis II is the second round.

Key Terms

- **haploid**: of a cell having a single set of unpaired chromosomes
- **gamete**: a reproductive cell, male (sperm) or female (egg), that has only half the usual number of chromosomes
- **diploid**: of a cell, having a pair of each type of chromosome, one of the pair being derived from the ovum and the other from the spermatozoon

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11.2: The Process of Meiosis - Meiosis I

Learning Objectives

- Describe the stages and results of meiosis I

Meiosis I

Meiosis is preceded by an interphase consisting of three stages. The G_1 phase (also called the first gap phase) initiates this stage and is focused on cell growth. The S phase is next, during which the DNA of the chromosomes is replicated. This replication produces two identical copies, called sister chromatids, that are held together at the centromere by cohesin proteins. The centrosomes, which are the structures that organize the microtubules of the meiotic spindle, also replicate. Finally, during the G_2 phase (also called the second gap phase), the cell undergoes the final preparations for meiosis.

Prophase I

During prophase I, chromosomes condense and become visible inside the nucleus. As the nuclear envelope begins to break down, homologous chromosomes move closer together. The synaptonemal complex, a lattice of proteins between the homologous chromosomes, forms at specific locations, spreading to cover the entire length of the chromosomes. The tight pairing of the homologous chromosomes is called synapsis. In synapsis, the genes on the chromatids of the homologous chromosomes are aligned with each other. The synaptonemal complex also supports the exchange of chromosomal segments between non-sister homologous chromatids in a process called crossing over. The crossover events are the first source of genetic variation produced by meiosis. A single crossover event between homologous non-sister chromatids leads to an exchange of DNA between chromosomes. Following crossover, the synaptonemal complex breaks down and the cohesin connection between homologous pairs is also removed. At the end of prophase I, the pairs are held together only at the chiasmata; they are called tetrads because the four sister chromatids of each pair of homologous chromosomes are now visible.

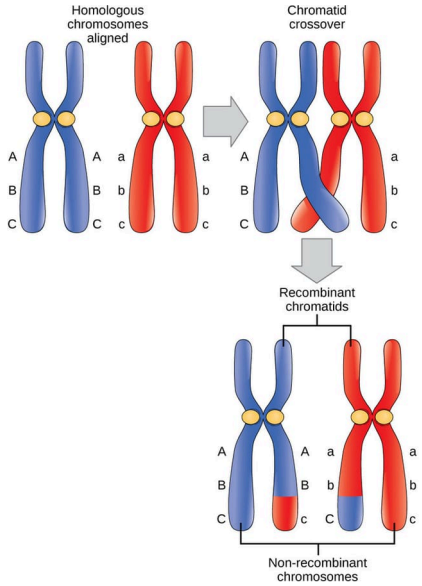


Figure 11.2.1: Crossover between homologous chromosomes: Crossover occurs between non-sister chromatids of homologous chromosomes. The result is an exchange of genetic material between homologous chromosomes.

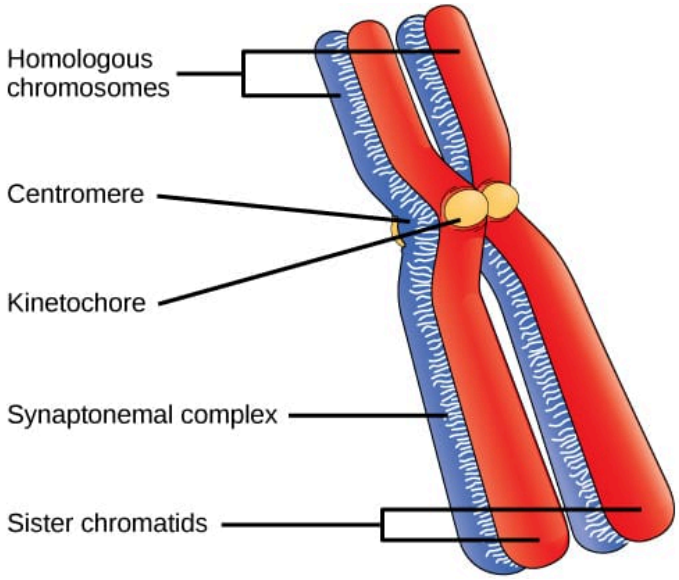


Figure 11.2.1: Synapsis holds pairs of homologous chromosomes together: Early in prophase I, homologous chromosomes come together to form a synapse. The chromosomes are bound tightly together and in perfect alignment by a protein lattice called a synaptonemal complex and by cohesin proteins at the centromere.

Prometaphase I

The key event in prometaphase I is the formation of the spindle fiber apparatus where spindle fiber microtubules attach to the kinetochore proteins at the centromeres. Microtubules grow from centrosomes placed at opposite poles of the cell. The microtubules move toward the middle of the cell and attach to one of the two fused homologous chromosomes at the kinetochores. At the end of prometaphase I, each tetrad is attached to microtubules from both poles, with one homologous chromosome facing each pole. In addition, the nuclear membrane has broken down entirely.

Metaphase I

During metaphase I, the tetrads move to the metaphase plate with kinetochores facing opposite poles. The homologous pairs orient themselves randomly at the equator. This event is the second mechanism that introduces variation into the gametes or spores. In each cell that undergoes meiosis, the arrangement of the tetrads is different. The number of variations is dependent on the number of chromosomes making up a set. There are two possibilities for orientation at the metaphase plate. The possible number of alignments, therefore, equals 2n, where n is the number of chromosomes per set. Given these two mechanisms, it is highly unlikely that any two haploid cells resulting from meiosis will have the same genetic composition.

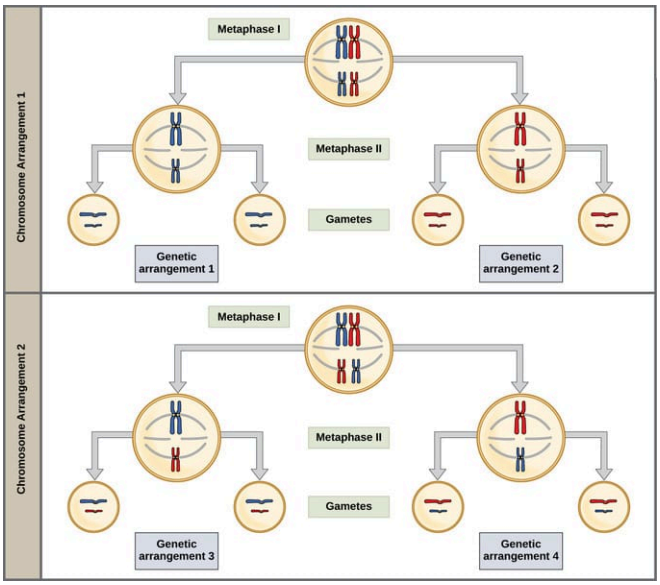


Figure 11.2.1: Meiosis I ensures unique gametes: Random, independent assortment during metaphase I can be demonstrated by considering a cell with a set of two chromosomes (n = 2). In this case, there are two possible arrangements at the equatorial plane in metaphase I. The total possible number of different gametes is 2n, where n equals the number of chromosomes in a set. In this example, there are four possible genetic combinations for the gametes. With n = 23 in human cells, there are over 8 million possible combinations of paternal and maternal chromosomes.

Anaphase I

In anaphase I, the microtubules pull the attached chromosomes apart. The sister chromatids remain tightly bound together at the centromere. The chiasmata are broken in anaphase I as the microtubules attached to the fused kinetochores pull the homologous chromosomes apart.

Telophase I and Cytokinesis

In telophase I, the separated chromosomes arrive at opposite poles. In some organisms, the chromosomes decondense and nuclear envelopes form around the chromatids in telophase I. Then cytokinesis, the physical separation of the cytoplasmic components into two daughter cells, occurs without reformation of the nuclei. In nearly all species of animals and some fungi, cytokinesis separates the cell contents via a cleavage furrow (constriction of the actin ring that leads to cytoplasmic division). In plants, a cell plate is formed during cell cytokinesis by Golgi vesicles fusing at the metaphase plate. This cell plate will ultimately lead to the formation of cell walls that separate the two daughter cells.

Two haploid cells are the end result of the first meiotic division. The cells are haploid because at each pole there is just one of each pair of the homologous chromosomes. Therefore, only one full set of the chromosomes is present. Although there is only one chromosome set, each homolog still consists of two sister chromatids.

Key Points

- Meiosis is preceded by interphase which consists of the G_1 phase (growth), the S phase (DNA replication), and the G_2 phase.
- During prophase I, the homologous chromosomes condense and become visible as the x shape we know, pair up to form a tetrad, and exchange genetic material by crossing over.
- During prometaphase I, microtubules attach at the chromosomes' kinetochores and the nuclear envelope breaks down.
- In metaphase I, the tetrads line themselves up at the metaphase plate and homologous pairs orient themselves randomly.
- In anaphase I, centromeres break down and homologous chromosomes separate.
- In telophase I, chromosomes move to opposite poles; during cytokinesis the cell separates into two haploid cells.

Key Terms

- **crossing over**: the exchange of genetic material between homologous chromosomes that results in recombinant chromosomes
- **tetrad**: two pairs of sister chromatids (a dyad pair) aligned in a certain way and often on the equatorial plane during the meiosis process
- **chromatid**: either of the two strands of a chromosome that separate during meiosis

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11.3: The Process of Meiosis - Meiosis II

Learning Objectives

- Describe the stages and results of Meiosis II

Meiosis II

Meiosis II initiates immediately after cytokinesis, usually before the chromosomes have fully decondensed. In contrast to meiosis I, meiosis II resembles a normal mitosis. In some species, cells enter a brief interphase, or interkinesis, before entering meiosis II. Interkinesis lacks an S phase, so chromosomes are not duplicated. The two cells produced in meiosis I go through the events of meiosis II together. During meiosis II, the sister chromatids within the two daughter cells separate, forming four new haploid gametes. The mechanics of meiosis II is similar to mitosis, except that each dividing cell has only one set of homologous chromosomes.

Prophase II

If the chromosomes decondensed in telophase I, they condense again. If nuclear envelopes were formed, they fragment into vesicles. The centrosomes that were duplicated during interphase I move away from each other toward opposite poles and new spindles are formed.

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.

Metaphase II

The sister chromatids are maximally condensed and aligned at the equator of the cell.

Anaphase II

The sister chromatids are pulled apart by the kinetochore microtubules and move toward opposite poles. Non-kinetochore microtubules elongate the cell.

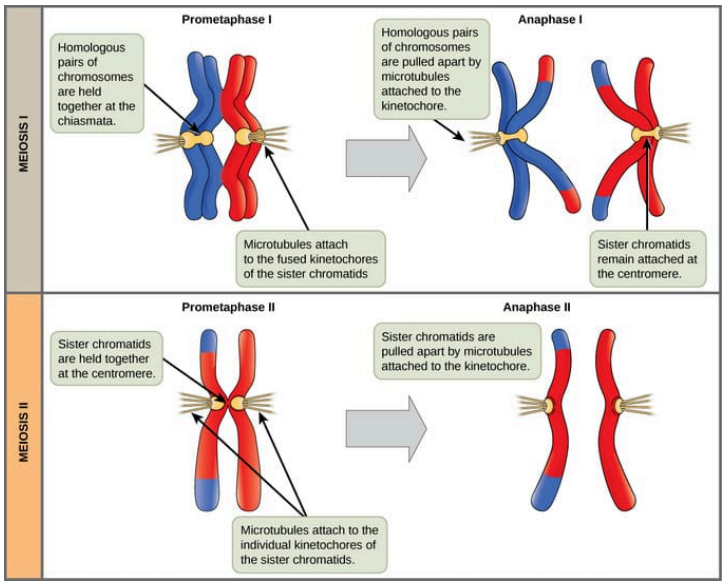


Figure 11.3.1: Meiosis I vs. Meiosis II: The process of chromosome alignment differs between meiosis I and meiosis II. In prometaphase I, microtubules attach to the fused kinetochores of homologous chromosomes, and the homologous chromosomes are arranged at the midpoint of the cell in metaphase I. In anaphase I, the homologous chromosomes are separated. In prometaphase II, microtubules attach to the kinetochores of sister chromatids, and the sister chromatids are arranged at the midpoint of the cells in metaphase II. In anaphase II, the sister chromatids are separated.

Telophase II and Cytokinesis

The chromosomes arrive at opposite poles and begin to decondense. Nuclear envelopes form around the chromosomes. Cytokinesis separates the two cells into four unique haploid cells. At this point, the newly-formed nuclei are both haploid. The cells produced are genetically unique because of the random assortment of paternal and maternal homologs and because of the recombining of maternal and paternal segments of chromosomes (with their sets of genes) that occurs during crossover.

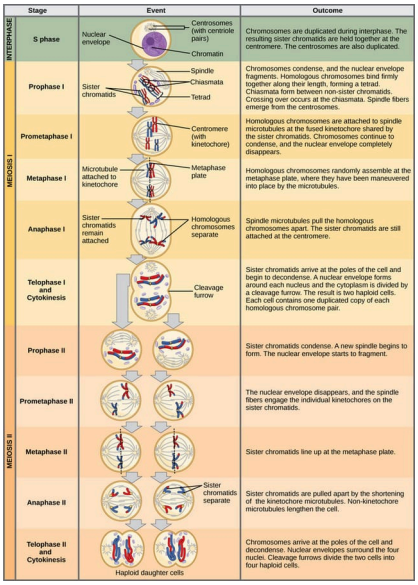


Figure 11.3.1: Complete Stages of Meiosis: An animal cell with a diploid number of four (2n = 4) proceeds through the stages of meiosis to form four haploid daughter cells.

Key Points

- During prophase II, chromsomes condense again, centrosomes that were duplicated during interphase I move away from each other toward opposite poles, and new spindles are formed.

- During prometaphase II, the nuclear envelopes are completely broken down, and each sister chromatid forms an individual kinetochore that attaches to microtubules from opposite poles.
- During metaphase II, sister chromatids are condensed and aligned at the equator of the cell.
- During anaphase II sister chromatids are pulled apart by the kinetochore microtubules and move toward opposite poles.
- During telophase II and cytokinesis, chromosomes arrive at opposite poles and begin to decondense; the two cells divide into four unique haploid cells.

Key Terms

- **meiosis II**: the second part of the meiotic process; the end result is production of four haploid cells from the two haploid cells produced in meiosis I

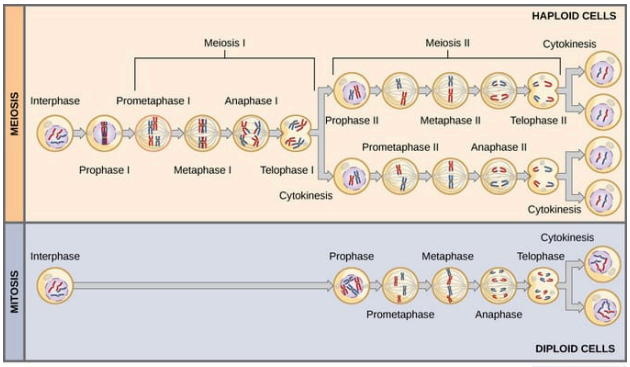
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11.4: The Process of Meiosis - Comparing Meiosis and Mitosis

Learning Objectives

- Compare and contrast mitosis and meiosis

Mitosis and meiosis are both forms of division of the nucleus in eukaryotic cells. They share some similarities, but also exhibit distinct differences that lead to very different outcomes. The purpose of mitosis is cell regeneration, growth, and asexual reproduction,while the purpose of meiosis is the production of gametes for sexual reproduction. Mitosis is a single nuclear division that results in two nuclei that are usually partitioned into two new daughter cells. The nuclei resulting from a mitotic division are genetically identical to the original nucleus. They have the same number of sets of chromosomes, one set in the case of haploid cells and two sets in the case of diploid cells. In most plants and all animal species, it is typically diploid cells that undergo mitosis to form new diploid cells. In contrast, meiosis consists of two nuclear divisions resulting in four nuclei that are usually partitioned into four new haploid daughter cells. The nuclei resulting from meiosis are not genetically identical and they contain one chromosome set only. This is half the number of chromosome sets in the original cell, which is diploid.



						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 11.4.1: Comparing Meiosis and Mitosis: 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.

The main differences between mitosis and meiosis occur in meiosis I. In meiosis I, the homologous chromosome pairs become associated with each other and are bound together with the synaptonemal complex. Chiasmata develop and crossover occurs between homologous chromosomes, which then line up along the metaphase plate in tetrads with kinetochore fibers from opposite spindle poles attached to each kinetochore of a homolog in a tetrad. All of these events occur only in meiosis I.

When the tetrad is broken up and the homologous chromosomes move to opposite poles, the ploidy level 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 during mitosis.

Meiosis II is much more similar to a mitotic division. In this case, the duplicated chromosomes (only one set, as the homologous pairs have now been separated into two different cells) line up on the metaphase plate with divided kinetochores attached to kinetochore fibers from opposite poles. During anaphase II and mitotic anaphase, the kinetochores divide and sister chromatids, now referred to as chromosomes, are pulled to opposite poles. The two daughter cells of mitosis, however, are identical, unlike the daughter cells produced by meiosis. They are different because there has 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. Meiosis II is, therefore, referred to as equatorial division.

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Key Points

- For the most part, in mitosis, diploid cells are partitioned into two new diploid cells, while in meiosis, diploid cells are partitioned into four new haploid cells.
- In mitosis, the daughter cells have the same number of chromosomes as the parent cell, while in meiosis, the daughter cells have half the number of chromosomes as the parent.
- The daughter cells produced by mitosis are identical, whereas the daughter cells produced by meiosis are different because crossing over has occurred.
- The events that occur in meiosis but not mitosis include homologous chromosomes pairing up, crossing over, and lining up along the metaphase plate in tetrads.
- Meiosis II and mitosis are not reduction division like meiosis I because the number of chromosomes remains the same; therefore, meiosis II is referred to as equatorial division.
- When the homologous chromosomes separate and move to opposite poles during meiosis I, the ploidy level is reduced from two to one, which is referred to as a reduction division.

Key Terms

- **reduction division**: the first of the two divisions of meiosis, a type of cell division
- **ploidy**: the number of homologous sets of chromosomes in a cell
- **equatorial division**: a process of nuclear division in which each chromosome divides equally such that the number of chromosomes remains the same from parent to daughter cells

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11.5: Sexual Reproduction - Advantages and Disadvantages of Sexual Reproduction

Learning Objectives

- Describe the benefits of sexual reproduction

An Introduction to Sexual Reproduction

Sexual reproduction was an early evolutionary innovation after the appearance of eukaryotic cells. During sexual reproduction, the genetic material of two individuals is combined to produce genetically-diverse offspring that differ from their parents. The fact that most eukaryotes reproduce sexually is evidence of its evolutionary success. In many animals, it is actually the only mode of reproduction. The genetic diversity of sexually-produced offspring is thought to give species a better chance of surviving in an unpredictable or changing environment.

Scientists recognize some real disadvantages to sexual reproduction. On the surface, creating offspring that are genetic clones of the parent appears to be a better system. If the parent organism is successfully occupying a habitat, offspring with the same traits would be similarly successful. Species that reproduce sexually must maintain two different types of individuals, males and females, which can limit the ability to colonize new habitats as both sexes must be present. Therefore, there is an obvious benefit to an organism that can produce offspring whenever circumstances are favorable by asexual budding, fragmentation, or asexual eggs. These methods of asexual reproduction do not require another organism of the opposite sex. Indeed, some organisms that lead a solitary lifestyle have retained the ability to reproduce asexually. In addition, in asexual populations, every individual is capable of reproduction. In sexual populations, the males are not producing the offspring themselves. In theory, an asexual population could grow twice as fast.

Nevertheless, multicellular organisms that exclusively depend on asexual reproduction are exceedingly rare. Why is sexuality (and meiosis) so common? This is one of the important unanswered questions in biology and has been the focus of much research beginning in the latter half of the twentieth century. There are several possible explanations, one of which is that the variation that sexual reproduction creates among offspring is very important to the survival and reproduction of the population. Thus, on average, a sexually-reproducing population will leave more descendants than an otherwise similar asexually-reproducing population. The only source of variation in asexual organisms is mutation. This is the ultimate source of variation in sexual organisms, but, 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, dividing the chromosomes among gametes.

The process of meiosis produces 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 sexual life cycles: diploid-dominant, demonstrated by most animals; haploid-dominant, demonstrated by all fungi and some algae; and the alternation of generations, demonstrated by plants and some algae.

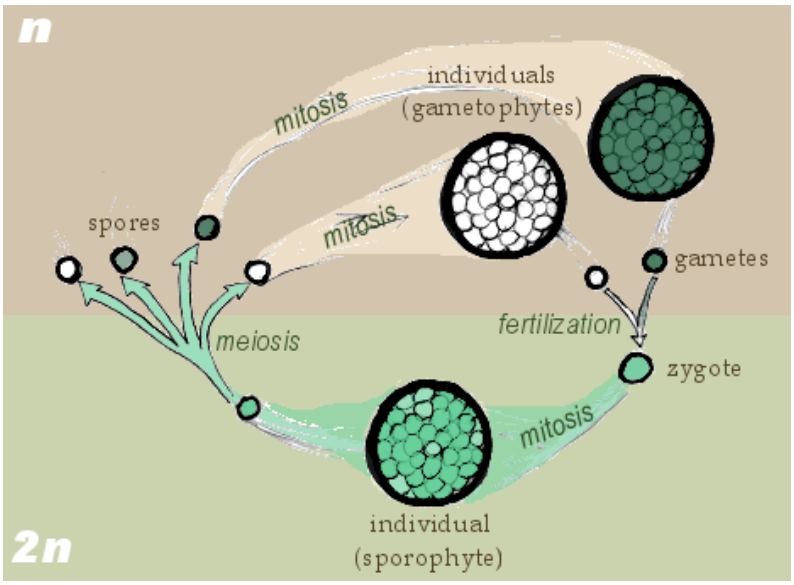


Figure 11.5.1: The Sexual Life Cycle: In animals, sexually-reproducing adults form haploid gametes from diploid germ cells. Fusion of the gametes gives rise to a fertilized egg cell, or zygote. The zygote will undergo multiple rounds of mitosis to produce a multicellular offspring.

The Red Queen Hypothesis

It is not in dispute that sexual reproduction provides evolutionary advantages to organisms that employ this mechanism to produce offspring. But why, even in the face of fairly stable conditions, does sexual reproduction persist when it is more difficult and costly for individual organisms? Variation is the outcome of sexual reproduction, but why are ongoing variations necessary? Possible answers to these questions are explained in the Red Queen hypothesis, first proposed by Leigh Van Valen in 1973.

All species co-evolve with other organisms; for example, predators evolve with their prey and parasites evolve with their hosts. 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 co-evolving species to maintain its own share of the resources is to also continually improve its fitness. As one species gains an advantage, this increases selection on the other species; they must also develop an advantage or they will be out-competed. No single species progresses too far ahead because genetic variation among the progeny of sexual reproduction provides all species with a mechanism to improve rapidly. Species that 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 co-evolution between competing species.

Key Points

- The variation that sexual reproduction creates among offspring is very important to the survival and reproduction of the population.
- In sexual reproduction, different mutations are continually reshuffled from one generation to the next when different parents combine their unique genomes; this results in an increase of genetic diversity.
- On average, a sexually-reproducing population will leave more offspring than an otherwise similar asexually-reproducing population.

Key Terms

- **sexual reproduction**: Sexual reproduction is the creation of a new organism by combining the genetic material of two organisms. There are two main processes during sexual reproduction: meiosis, involving the halving of the number of chromosomes, and fertilization, involving the fusion of two gametes and the restoration of the original number of chromosomes.
- **asexual reproduction**: any form of reproduction that involves neither meiosis nor fusion of gametes

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11.6: Sexual Reproduction - Life Cycles of Sexually Reproducing Organisms

Learning Objectives

- Explain the life cycles in sexual reproduction

In sexual reproduction, the genetic material of two individuals is combined to produce genetically diverse offspring that differ from their parents. Fertilization and meiosis alternate in sexual life cycles. What happens between these two events depends upon the organism. The process of meiosis, the division of the contents of the nucleus that divides the chromosomes among gametes, reduces the chromosome number by half, while fertilization, the joining of two haploid gametes, restores the diploid condition. There are three main categories of life cycles in eukaryotic organisms: diploid-dominant, haploid-dominant, and alternation of generations.

Diploid-Dominant Life Cycle

In the diploid-dominant life cycle, the multicellular diploid stage is the most obvious life stage, as occurs with most animals, including humans. Nearly all animals employ a diploid-dominant life cycle strategy in which the only haploid cells produced by the organism are the gametes. Early in the development of the embryo, specialized diploid cells, called germ cells, are produced within the gonads (e.g. testes and ovaries). Germ cells are capable of mitosis to perpetuate the cell line and meiosis to produce 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.

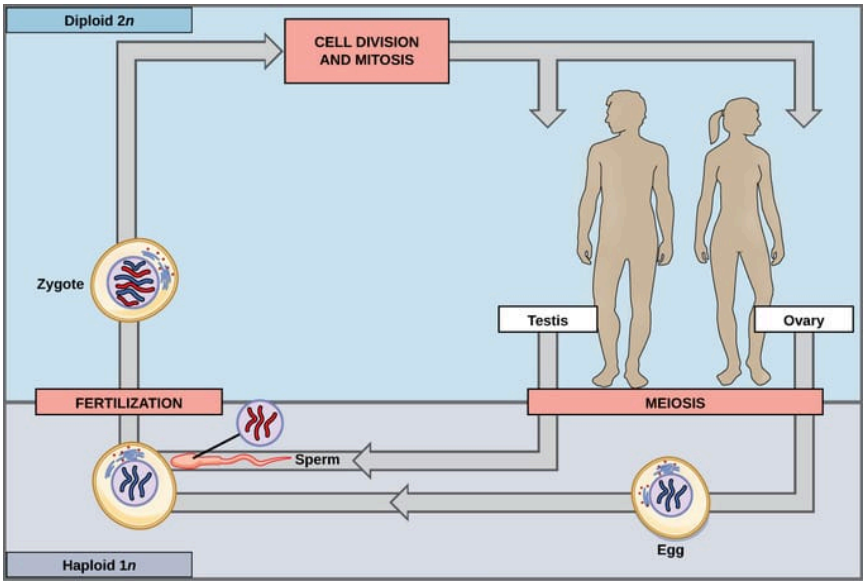


Figure 11.6.1: Diploid-Dominant Life Cycle: In animals, sexually-reproducing adults form haploid gametes from diploid germ cells. Fusion of the gametes gives rise to a fertilized egg cell, or zygote. The zygote will undergo multiple rounds of mitosis to produce a multicellular offspring. The germ cells are generated early in the development of the zygote.

Haploid-Dominant Life Cycle

Within haploid-dominant life cycles, the multicellular haploid stage is the most obvious life stage. Most fungi and algae employ a life cycle type in which the “body” of the organism, the ecologically important part of the life cycle, is haploid. The haploid cells that make up the tissues of the dominant multicellular stage are formed by mitosis. During sexual reproduction, specialized haploid cells from two individuals, designated the (+) and (–) mating types, join to form a diploid zygote. The zygote immediately

undergoes meiosis to form four haploid cells called spores. Although haploid like the “parents,” these spores contain a new genetic combination from two parents. The spores can remain dormant for various time periods. Eventually, when conditions are conducive, the spores form multicellular haploid structures by many rounds of mitosis.

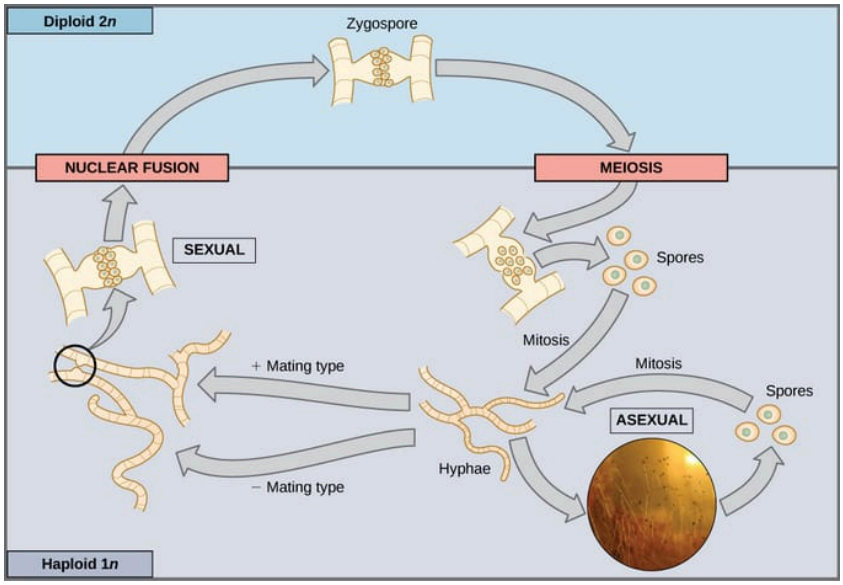


Figure 11.6.1: Haploid-Dominant Life Cycle: Fungi, such as black bread mold (Rhizopus nigricans), have haploid-dominant life cycles. The haploid multicellular stage produces specialized haploid cells by mitosis that fuse to form a diploid zygote. The zygote undergoes meiosis to produce haploid spores. Each spore gives rise to a multicellular haploid organism by mitosis.

Alternation of Generations

The third life-cycle type, employed by some algae and all plants, is a blend of the haploid-dominant and diploid-dominant extremes. Species with alternation of generations have both haploid and diploid multicellular organisms as part of their life cycle. The haploid multicellular plants are called gametophytes because they produce gametes from specialized cells. Meiosis is not directly involved in the production of gametes because the organism that produces the gametes is already a 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 subsequently develop into the gametophytes.

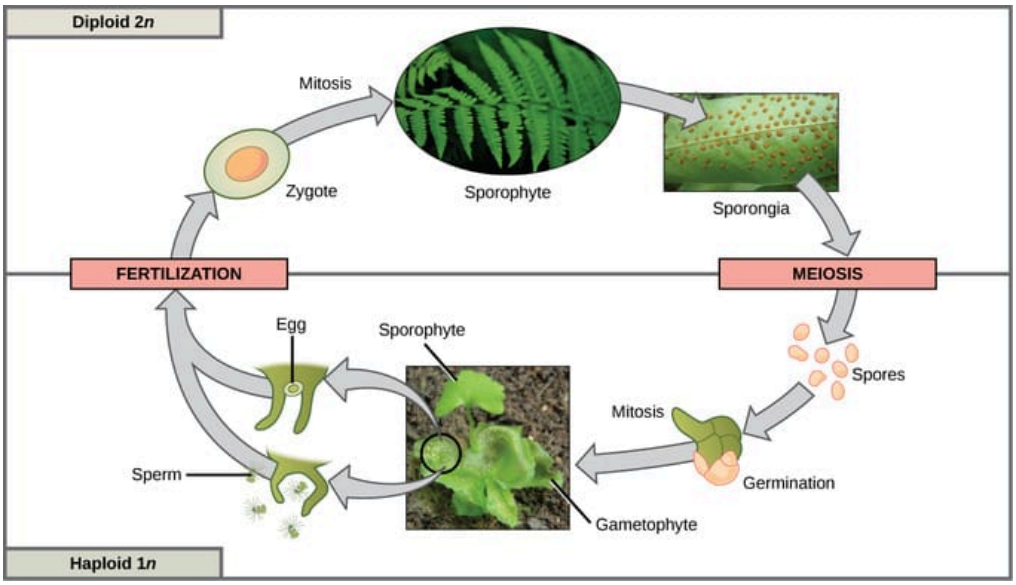


Figure 11.6.1: Alternation of Generations: Plants have a life cycle that alternates between a multicellular haploid organism and a multicellular diploid organism. In some plants, such as ferns, both the haploid and diploid plant stages are free-living. The diploid plant is called a sporophyte because it produces haploid spores by meiosis. The spores develop into multicellular, haploid plants called gametophytes because they produce gametes. The gametes of two individuals will fuse to form a diploid zygote that becomes the sporophyte.

Although all plants utilize some version of the alternation of generations, the relative size of the sporophyte and the gametophyte and the relationship between them vary greatly. In plants such as moss, the gametophyte organism is the free-living plant, while the sporophyte is physically dependent on the gametophyte. In other plants, such as ferns, both the gametophyte and sporophyte plants are free-living; however, the sporophyte is much larger. In seed plants, such as magnolia trees and daisies, the gametophyte is composed of only a few cells and, in the case of the female gametophyte, is completely retained within the sporophyte.

Sexual reproduction takes many forms in multicellular organisms. However, at some point in each type of life cycle, meiosis produces haploid cells that will fuse with the haploid cell of another organism. The mechanisms of variation (crossover, random assortment of homologous chromosomes, and random fertilization) are present in all versions of sexual reproduction. The fact that nearly every multicellular organism on earth employs sexual reproduction is strong evidence for the benefits of producing offspring with unique gene combinations, although there are other possible benefits as well.

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Key Points

- In the diploid – dominant cycle, the multicellular diploid stage is the most obvious life stage; the only haploid cells produced by the organism are the gametes.
- Most fungi and algae employ a haploid-dominant life cycle type in which the “body” of the organism is haploid; specialized haploid cells from two individuals join to form a diploid zygote.
- Observed in all plants and some algae, species with alternation of generations have both haploid and diploid multicellular organisms as part of their life cycle.

Key Terms

- **zygote**: a diploid fertilized egg cell
- **gametophyte**: a plant (or the haploid phase in its life cycle) that produces gametes by mitosis in order to produce a zygote
- **sporophyte**: a plant (or the diploid phase in its life cycle) that produces spores by meiosis in order to produce gametophytes

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12: MENDEL'S EXPERIMENTS AND HEREDITY

- Topic hierarchy

12.1: Mendels Experiments and the Laws of Probability

12.1A: Introduction to Mendelian Inheritance

12.1B: Mendel's Model System

12.1C: Mendelian Crosses

12.1D: Garden Pea Characteristics Revealed the Basics of Heredity

12.1E: Rules of Probability for Mendelian Inheritance

12.2: Patterns of Inheritance

12.2A: Genes as the Unit of Heredity

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12.3: Laws of Inheritance

12.3A: Mendel's Laws of Heredity

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12.3D: Mendel's Law of Independent Assortment

12.3E: Genetic Linkage and Violation of the Law of Independent Assortment

12.3F: Epistasis

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12.1: MENDELS EXPERIMENTS AND THE LAWS OF PROBABILITY

- Topic hierarchy

12.1A: Introduction to Mendelian Inheritance

12.1B: Mendel's Model System

12.1C: Mendelian Crosses

12.1D: Garden Pea Characteristics Revealed the Basics of Heredity

12.1E: Rules of Probability for Mendelian Inheritance

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12.1A: Introduction to Mendelian Inheritance

Learning Objectives

- Describe the traits of pea plants that were studied by Mendel

Gregor Mendel and the Study of Genetics

Genetics is the study of heredity, or the passing of traits from parents to offspring. Gregor Johann Mendel set the framework for genetics long before chromosomes or genes had been identified, at a time when meiosis was not well understood. For his work, Mendel is often referred to as the "father of modern genetics. " Mendel selected a simple biological system, garden peas, and conducted methodical, quantitative analyses using large sample sizes.



Figure 12.1A.1: Gregor Mendel: Gregor Johann Mendel was a German-speaking Moravian scientist and Augustinian friar who gained posthumous fame as the founder of the modern science of genetics.

Mendel entered the Augustinian St. Thomas's Abbey and began his training as a priest. He began studying heredity using mice, but his bishop did not like one of his friars studying animal sex, so he switched to plants. Mendel grew and studied around 29,000 garden pea plants in a monastery's garden, where he analyzed seven characteristics of the garden pea plants: flower color (purple or white), seed texture (wrinkled or round), seed color (yellow or green), stem length (long or short), pod color (yellow or green), pod texture (inflated or constricted), and flower position (axial or terminal). Based on the appearance, or phenotypes, of the seven traits, Mendel developed genotypes for those traits.

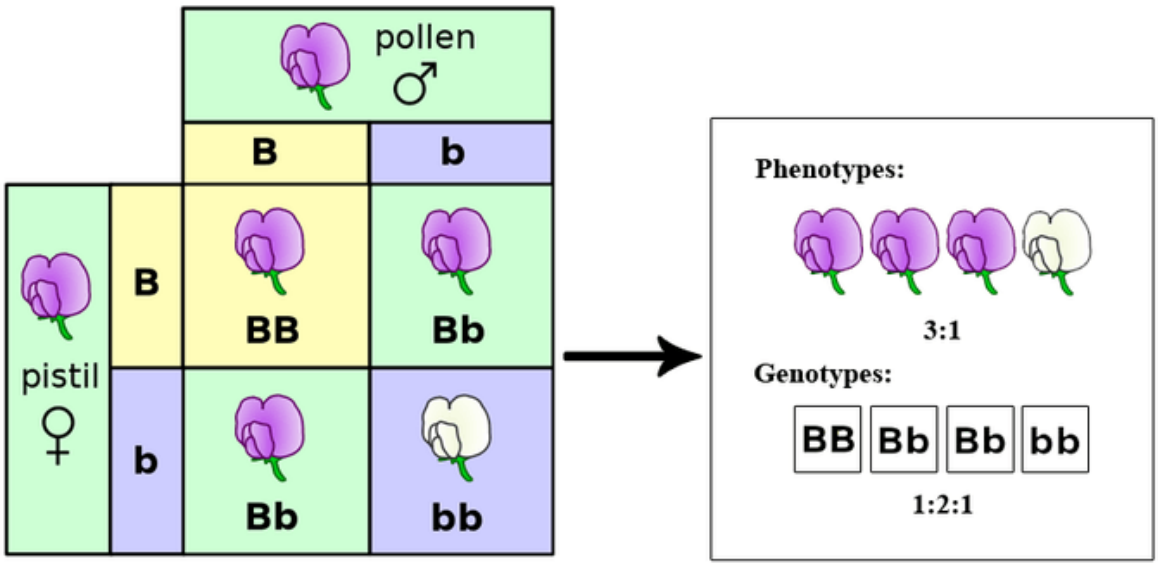


Figure 12.1A.1: Appearance and genetic makeup of garden pea plant flowers: Based on Mendel's experiments, the genotype of the pea flowers could be determined from the phenotypes of the flowers.

Because of Mendel's work, the fundamental principles of heredity were revealed, which are often referred to as Mendel's Laws of Inheritance. We now know that genes, carried on chromosomes, are the basic functional units of heredity with the capability to be replicated, expressed, or mutated. Today, the postulates put forth by Mendel form the basis of classical, or Mendelian, genetics. Not all genes are transmitted from parents to offspring according to Mendelian genetics, but Mendel's experiments serve as an excellent starting point for thinking about inheritance.

Mendel made all of his observations and findings crossing individual plants. We can now view a human karyotype of all of the chromosomes in an individual to visualize chromosomal abnormalities in offspring, even before birth. Shortly after Mendel proposed that traits were determined by what are now known as genes, other researchers observed that different traits were often inherited together, and thereby deduced that the genes were physically linked by being located on the same chromosome. Mendel's work was the beginning of many of the advances in molecular biology over the years.

Key Points

- Mendel studied seven characteristics of the garden pea plants: flower color, seed texture, seed color, stem length, pod color, pod texture, and flower position to develop his Laws of Inheritance.
- Genetics is the study of genes passed from parents to offspring.
- Genes are the basic fundamental units of heredity.

Key Terms

- **genetics**: The branch of biology that deals with the transmission and variation of inherited characteristics, in particular chromosomes and DNA.

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12.1B: Mendel's Model System

Learning Objectives

- Describe the scientific reasons for the success of Mendel's experimental work

Mendel's Model System

Mendel's seminal work was accomplished using the garden pea, *Pisum sativum*, to study inheritance. Pea plant reproduction is easily manipulated; large quantities of garden peas could be cultivated simultaneously, allowing Mendel to conclude that his results did not occur simply by chance. The garden pea also grows to maturity within one season; several generations could be evaluated over a relatively short time.

Pea plants have both male and female parts and can easily be grown in large numbers. For this reason, garden pea plants can either self-pollinate or cross-pollinate with other pea plants. In the absence of outside manipulation, this species naturally self-fertilizes: ova (the eggs) within individual flowers are fertilized by pollen (containing the sperm cell) from the same flower. The sperm and the eggs that produce the next generation of plants both come from the same parent. What's more, the flower petals remain sealed tightly until after pollination, preventing pollination from other plants. The result is highly inbred, or "true-breeding," pea plants. These are plants that always produce offspring that look like the parent. Today, we know that these "true-breeding" plants are homozygous for most traits.

A gardener or researcher, such as Mendel, can cross-pollinate these same plants by manually applying sperm from one plant to the pistil (containing the ova) of another plant. Now the sperm and eggs come from different parent plants. When Mendel cross-pollinated a true-breeding plant that only produced yellow peas with a true-breeding plant that only produced green peas, he found that the first generation of offspring is always all yellow peas. The green pea trait did not show up. However, if this first generation of yellow pea plants were allowed to self-pollinate, the following or second generation had a ratio of 3:1 yellow to green peas.

In this and all the other pea plant traits Mendel followed, one form of the trait was "dominant" over another so it masked the presence of the other "recessive" form in the first generation after cross-breeding two homozygous plants.. Even if the phenotype (visible form) is hidden, the genotype (allele controlling that form of the trait) can be passed on to next generation and produce the recessive form in the second generation. By experimenting with true-breeding pea plants, Mendel avoided the appearance of unexpected (recombinant) traits in offspring that might occur if the plants were not true breeding.



Figure $12.1B.1$: Mendel's Experiments With Peas: Experimenting with thousands of garden peas, Mendel uncovered the fundamentals of genetics.

Key Points

- Mendel used true-breeding plants in his experiments. These plants, when self-fertilized, always produce offspring with the same phenotype.
- Pea plants are easily manipulated, grow in one season, and can be grown in large quantities; these qualities allowed Mendel to conduct methodical, quantitative analyses using large sample sizes.
- Based on his experiments with the garden peas, Mendel found that one phenotype was always dominant over another recessive phenotype for the same trait.

Key Terms

- **phenotype**: the observable characteristics of an organism, often resulting from its genetic information or a combination of genetic information and environmental factors
- **genotype**: the specific genetic information of a cell or organism, usually a description of the allele or alleles relating to a specific gene.
- **true-breeding plant**: a plant that always produces offspring of the same phenotype when self-fertilized; one that is homozygous for the trait being followed.

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12.1C: Mendelian Crosses

Learning Objectives

- Identify Mendelian crosses

Mendelian Crosses

Mendel performed crosses, which involved mating two true-breeding individuals that have different traits. In the pea, which is a naturally self-pollinating plant, 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. In plants, pollen carries the male gametes (sperm) to the stigma, a sticky organ that traps pollen and allows the sperm to move down the pistil to the female gametes (ova) below. To prevent the pea plant that was receiving pollen from self-fertilizing and confounding his results, Mendel painstakingly removed all of the anthers from the plant's flowers before they had a chance to mature.

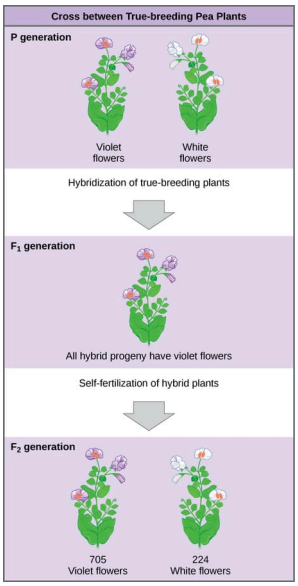


Figure $12.1C.1$: Mendelian Crosses: In one of his experiments on inheritance patterns, Mendel crossed plants that were true-breeding for violet flower color with plants true-breeding for white flower color (the P generation). The resulting hybrids in the F1 generation all had violet flowers. In the F2 generation, approximately three-quarters of the plants had violet flowers, while one-quarter had white flowers.

Plants used in first-generation crosses were called P_0, or parental generation one, plants. Mendel collected the seeds belonging to the P_0 plants that resulted from each cross and grew them the following season. These offspring were called the F_1, or the first filial (filial = offspring, daughter or son), generation. Once Mendel examined the characteristics in the F_1generation 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 and F_4generations, and so on, but it was the ratio of characteristics in the P_0–F_1–F_2 generations that were the most intriguing and became the basis for Mendel's postulates.

Key Points

- Mendel carefully controlled his experiments by removing the anthers from the pea plants before they matured.
- First generation pea plants were called parental generation, P_0, while the following generations were called filial, F_n, where n is the number of generations from P_0.
- The ratio of characteristics in the P_0–F_1–F_2 generations became the basis for Mendel's postulates.

Key Terms

- **filial**: of a generation or generations descending from a specific previous one
- **parental**: of the generation of organisms that produce a hybrid

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12.1D: Garden Pea Characteristics Revealed the Basics of Heredity

Learning Objectives

- Evaluate the results of F1 and F2 generations from Mendelian crosses of peas

Garden Pea Characteristics Revealed the Basics of Heredity

To fully examine each of the seven traits in garden peas, Mendel generated large numbers of F_1 and F_2 plants, reporting results from 19,959 F_2 plants alone. His findings were consistent.

What results did Mendel find in his crosses for flower color? First, Mendel confirmed that he had plants that bred true for white or violet flower color. Regardless of how many generations 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.

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_1hybrid 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 in the F_1 generation had completely disappeared.

Importantly, Mendel did not stop his experimentation there. He allowed the F_1 plants to self-fertilize and found that, of F_2-generation plants, 705 had violet flowers and 224 had white flowers. This was a ratio of 3.15 violet flowers per 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 about the same ratio regardless 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 Mendel examined, the F_1 and F_2generations behaved in the same way as they had 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 approximately 3:1.

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, respectively, dominant and recessive traits. Dominant traits 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-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 (not blended) in the plants of the F_1 generation. Mendel also proposed that plants possessed two copies of the trait for the flower-color characteristic and that each parent transmitted one of its two copies to its 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.

The Results of Mendel's Garden Pea Hybridizations				
Characteristic	**Contrasting P0 Traits**	**F1 Offspring Traits**	**F2 Offspring Traits**	**F2 Trait Ratios**
Flower color	Violet vs. white	100 percent violet	705 violet 224 white	3.15:1
Flower position	Axial vs. terminal	100 percent axial	651 axial 207 terminal	3.14:1
Plant height	Tall vs. dwarf	100 percent tall	787 tall 277 dwarf	2.84:1
Seed texture	Round vs. wrinkled	100 percent round	5,474 round 1,850 wrinkled	2.96:1
Seed color	Yellow vs. green	100 percent yellow	6,022 yellow 2,001 green	3.01:1
Pea pod texture	Inflated vs. constricted	100 percent inflated	882 inflated 299 constricted	2.95:1
Pea pod color	Green vs. yellow	100 percent green	428 green 152 yellow	2.82:1

Figure $12.1D.1$: Results of Mendel's Garden Pea Hybridizations: Mendel conducted thousands of experiments and found the same ratios of offspring every time, regardless of which trait he examined.

Key Points

- Dominant traits are inherited unchanged from one generation to the next.
- Recessive traits disappear in the first filial generation, but reappear in the second filial generation at a ratio of 3:1, dominant:recessive.
- In the F1 generation, Mendel found that one of the two options for each trait had disappeared (all offspring were identical phenotypes), while in the F_2 generation, the trait reappeared in 1/4 of the offspring (a 3:1 ratio).

Key Terms

- **hybrid**: offspring resulting from cross-breeding different entities, e.g. two different species or two purebred parent strains
- **recessive**: able to be covered up by a dominant trait
- **dominant**: a relationship between alleles of a gene, in which one allele masks the expression (phenotype) of another allele at the same locus

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12.1E: Rules of Probability for Mendelian Inheritance

Learning Objectives

- Calculate the probability of traits of pea plants using Mendelian crosses

Probability Basics

Probabilities are mathematical measures of likelihood. The empirical probability of an event is calculated by dividing the number of times the event occurs by the total number of opportunities for the event to occur. Empirical probabilities come from observations such as those of Mendel. An example of a genetic event is a round seed produced by a pea plant. Mendel demonstrated that the probability of the event "round seed" was guaranteed to occur in the F_1 offspring of true-breeding parents, one of which has round seeds and one of which has wrinkled seeds. When the F_1 plants were subsequently self-crossed, the probability of any given F_2 offspring having round seeds was now three out of four. In other words, in a large population of F_2 offspring chosen at random, 75 percent were expected to have round seeds, whereas 25 percent were expected to have wrinkled seeds. Using large numbers of crosses, Mendel was able to calculate probabilities and use these to predict the outcomes of other crosses.

The Product Rule

Mendel demonstrated that the pea-plant characteristics he studied were transmitted as discrete units from parent to offspring. Mendel also determined that different characteristics were transmitted independently of one another and could be considered in separate probability analyses. For instance, performing a cross between a plant with green, wrinkled seeds and a plant with yellow, round seeds produced offspring that had a 3:1 ratio of green:yellow seeds and a 3:1 ratio of round:wrinkled seeds. The characteristics of color and texture did not influence each other.

The product rule of probability can be applied to this phenomenon of the independent transmission of characteristics. It states that the probability of two independent events occurring together can be calculated by multiplying the individual probabilities of each event occurring alone. Imagine that you are rolling a six-sided die (D) and flipping a penny (P) at the same time. The die may roll any number from 1–6 (D#), whereas the penny may turn up heads (P_H) or tails (P_T). The outcome of rolling the die has no effect on the outcome of flipping the penny and vice versa. There are 12 possible outcomes, and each is expected to occur with equal probability: D_1P_H, D_1P_T, D_2P_H, D_2P_T, D_3P_H, D_3P_T, D_4P_H, D_4P_T, D_5P_H, D_5P_T, D_6P_H, D_6P_T.

Of the 12 possible outcomes, the die has a 2/12 (or 1/6) probability of rolling a two, and the penny has a 6/12 (or 1/2) probability of coming up heads. The probability that you will obtain the combined outcome 2 and heads is: (D_2) x (P_H) = (1/6) x (1/2) or 1/12. The word "and" is a signal to apply the product rule. Consider how the product rule is applied to a dihybrid: the probability of having both dominant traits in the F_2 progeny is the product of the probabilities of having the dominant trait for each characteristic.

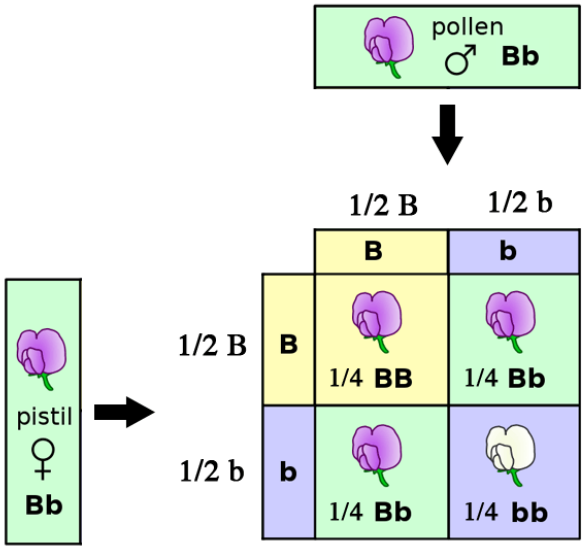


Figure 12.1E.1: Role of probability in segregation of alleles and fertilization: In a genetic cross, the probability of the dominant trait being expressed is dependent upon its frequency. In this case, both parents possessed a dominant and a recessive gene for the trait of flower color. The dominant trait is expressed in 3/4 of the offspring and the recessive trait is expressed in 1/4.

The Sum Rule

The sum rule is applied when considering two mutually-exclusive outcomes that can result from more than one pathway. It states that the probability of the occurrence of one event or the other, of two mutually-exclusive events, is the sum of their individual probabilities. The word “or” indicates that you should apply the sum rule. Let’s imagine you are flipping a penny (P) and a quarter (Q). What is the probability of one coin coming up heads and one coming up tails? This can be achieved by two cases: the penny is heads (P_H) and the quarter is tails (Q_T), or the quarter is heads (Q_H) and the penny is tails (P_T). Either case fulfills the outcome. We calculate the probability of obtaining one head and one tail as $[(P_H) \times (Q_T)] + [(Q_H) \times (P_T)] = [(1/2) \times (1/2)] + [(1/2) \times (1/2)] = 1/2$. You should also notice that we used the product rule to calculate the probability of P_H and Q_T and also the probability of P_T and Q_H, before we summed them. The sum rule can be applied to show the probability of having just one dominant trait in the F_2 generation of a dihybrid cross.

To use probability laws in practice, it is necessary to work with large sample sizes because small sample sizes are prone to deviations caused by chance. The large quantities of pea plants that Mendel examined allowed him to calculate the probabilities of the traits appearing in his F_2 generation. This discovery meant that when parental traits were known, the offspring’s traits could be predicted accurately even before fertilization.

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Key Points

- The Product Rule is used to determine the outcome of an event with two independent events; the probability of the event is the product of the probabilities of each individual event.
- The Sum Rule is used to determine the outcome of an event with two mutually exclusive events from multiple pathways; the probability of the event is the sum of the probabilities of each individual event.
- The Product Rule of probability is used to determine the probability of having both dominant traits in the F_2progeny; it is the product of the probabilities of having the dominant trait for each characteristic.
- The Sum Rule of probability is used to determine the probability of having one dominant trait in the F2 generation of a dihybrid cross; it is the sum of the probabilities of each individual with that trait.

Key Terms

- **sum rule**: the probability of the occurrence of one event or the other event, of two mutually exclusive events, is the sum of their individual probabilities
- **product rule**: the probability of two independent events occurring together can be calculated by multiplying the individual probabilities of each event occurring alone
- **probability**: a number, between 0 and 1, expressing the precise likelihood of an event happening

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12.2: PATTERNS OF INHERITANCE



- Topic hierarchy

12.2A: Genes as the Unit of Heredity

12.2B: Phenotypes and Genotypes

12.2C: The Punnett Square Approach for a Monohybrid Cross

12.2D: Alternatives to Dominance and Recessiveness

12.2E: Sex-Linked Traits

12.2F: Lethal Inheritance Patterns

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12.2A: Genes as the Unit of Heredity

Learning Objectives

- Describe the structure of a gene and how offspring inherit genes from each parent

Pairs of Unit Factors, or Genes

Mendel proposed that paired unit factors of heredity were transmitted faithfully from generation to generation by the dissociation and reassociation of paired factors during gametogenesis and fertilization, respectively. After he crossed peas with contrasting traits and found that the recessive trait resurfaced in the F_2 generation, Mendel deduced that hereditary factors must be inherited as discrete units. This finding contradicted the belief at that time that parental traits were blended in the offspring.

A gene is made up of short sections of DNA that are contained on a chromosome within the nucleus of a cell. Genes control the development and function of all organs and all working systems in the body. A gene has a certain influence on how the cell works; the same gene in many different cells determines a certain physical or biochemical feature of the whole body (e.g., eye color or reproductive functions). All human cells hold approximately 21,000 different genes.

Genetics is the science of the way traits are passed from parent to offspring. For all forms of life, continuity of the species depends upon the genetic code being passed from parent to offspring. Evolution by natural selection is dependent on traits being heritable. Genetics is very important in human physiology because all attributes of the human body are affected by a person's genetic code. It can be as simple as eye color, height, or hair color. Or it can be as complex as how well your liver processes toxins, whether you will be prone to heart disease or breast cancer, and whether you will be color blind.

Genetic inheritance begins at the time of conception. You inherited 23 chromosomes from your mother and 23 from your father. Together they form 22 pairs of autosomal chromosomes and a pair of sex chromosomes (either XX if you are female, or XY if you are male). Homologous chromosomes have the same genes in the same positions, but may have different alleles (varieties) of those genes. There can be many alleles of a gene within a population, but an individual within that population only has two copies and can be homozygous (both copies the same) or heterozygous (the two copies are different) for any given gene.



Figure 12.2A.1: Gene pairs enable genetic combinations: A child will inherit half of its genes (one of each of its 23 pairs) from its mother and the other half from its father.

Key Points

- A gene is a stretch of DNA that helps to control the development and function of all organs and working systems in the body.
- Genes are passed from parent to offspring; the combination of these genes affects all aspects of the human body, from eye and hair color to how well the liver can process toxins.
- A human will inherit 23 chromosomes from its mother and 23 from its father; together, these form 23 pairs of chromosomes that direct the inherited characteristics of the individual.
- If the two copies of a gene inherited from each parent are the same, that individual is said to be homozygous for the gene; if the two copies inherited from each parent are different, that individual is said to be heterozygous for the gene.

Key Terms

- **gene**: a unit of heredity; the functional units of chromosomes that determine specific characteristics by coding for specific proteins
- **chromosome**: a structure in the cell nucleus that contains DNA, histone protein, and other structural proteins
- **genetics**: the branch of biology that deals with the transmission and variation of inherited characteristics, in particular chromosomes and DNA

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12.2B: Phenotypes and Genotypes

Learning Objectives

- Distinguish between the phenotype and the genotype of an organism

Phenotypes and Genotypes

The observable traits expressed by an organism are referred to as its phenotype. An organism's underlying genetic makeup, consisting of both physically visible and non-expressed alleles, is called its genotype. Johann Gregor Mendel's (1822–1884) hybridization experiments demonstrate the difference between phenotype and genotype.

Mendel crossed or mated two true-breeding (self-pollinating) garden peas, *Pisum saivum*, 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_0, or parental generation one, plants. Mendel collected the seeds belonging to the P_0plants that resulted from each cross and grew them the following season. These offspring were called the F_1, or the first filial (filial = offspring, 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.

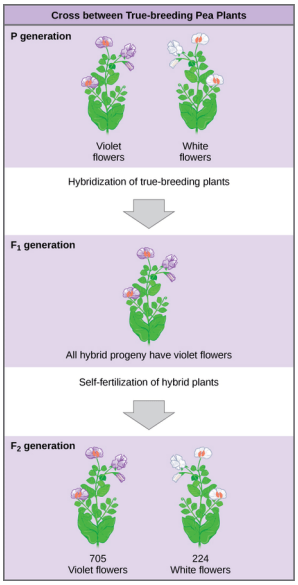


Figure 12.2B.1: Mendelian crosses: In one of his experiments on inheritance patterns, Mendel crossed plants that were true-breeding for violet flower color with plants true-breeding for white flower color (the P generation). The resulting hybrids in the F_1 generation all had violet flowers. In the F_2 generation, approximately three-quarters of the plants had violet flowers, and one-quarter had white flowers.

When true-breeding plants in which one parent had white flowers and one had violet flowers were cross-fertilized, all of the F1 hybrid offspring had violet flowers. That is, the hybrid offspring were phenotypically identical to the true-breeding parent with violet flowers. However, we know that the allele donated by the parent with white flowers was not simply lost because it reappeared in some of the F2 offspring. Therefore, the F1 plants must have been genotypically different from the parent with violet flowers.

In his 1865 publication, Mendel reported the results of his crosses involving seven different phenotypes, 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. To fully examine each characteristic, Mendel generated large numbers of F_1 and F_2 plants, reporting results from 19,959 F_2 plants alone. His findings were consistent. First, Mendel confirmed that he had plants that bred true for white or violet flower color. Regardless of how many generations 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.

Key Points

- Mendel used pea plants with seven distinct traits or phenotypes to determine the pattern of inheritance and the underlying genotypes.
- Mendel found that crossing two purebred pea plants which expressed different traits resulted in an F_1generation where all the pea plants expressed the same trait or phenotype.
- When Mendel allowed the F_1 plants to self-fertilize, the F_2 generation showed two different phenotypes, indicating that the F_1 plants had different genotypes.

Key Terms

- **phenotype**: the appearance of an organism based on a multifactorial combination of genetic traits and environmental factors, especially used in pedigrees
- **genotype**: the combination of alleles, situated on corresponding chromosomes, that determines a specific trait of an individual, such as “Aa” or “aa”

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12.2C: The Punnett Square Approach for a Monohybrid Cross

Learning Objectives

- Describe the Punnett square approach to a monohybrid cross

Punnett Square Approach to a Monohybrid Cross

When fertilization occurs between two true-breeding parents that differ in only one characteristic, the process is called a monohybrid cross, and the resulting offspring are monohybrids. Mendel performed seven monohybrid crosses involving contrasting traits for each characteristic. On the basis of his results in F_1 and F_2 generations, Mendel postulated that each parent in the monohybrid cross contributed one of two paired unit factors to each offspring and that every possible combination of unit factors was equally likely.

To demonstrate a monohybrid cross, consider the case of true-breeding pea plants with yellow versus green pea seeds. The dominant seed color is yellow; therefore, the parental genotypes were YY (homozygous dominant) for the plants with yellow seeds and yy (homozygous recessive) for the plants with green seeds, respectively. A Punnett square, devised by the British geneticist Reginald Punnett, can be drawn that applies the rules of probability to predict the possible outcomes of a genetic cross or mating and their expected frequencies.To prepare a Punnett square, all possible combinations of the parental alleles are listed along the top (for one parent) and side (for the other parent) of a grid, representing their meiotic segregation into haploid gametes. Then the combinations of egg and sperm are made in the boxes in the table to show which alleles are combining. Each box then represents the diploid genotype of a zygote, or fertilized egg, that could result from this mating. Because each possibility is equally likely, genotypic ratios can be determined from a Punnett square. If the pattern of inheritance (dominant or 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. All offspring are Yy and have yellow seeds.

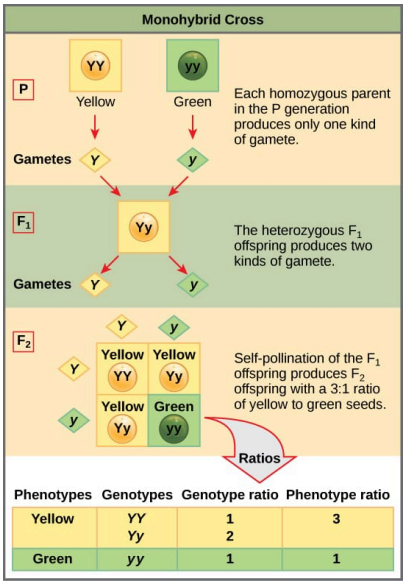


Figure $12.2C.1$: Punnett square analysis of a monohybrid cross: In the P generation, pea plants that are true-breeding for the dominant yellow phenotype are crossed with plants with the recessive green phenotype. This cross produces F1 heterozygotes with a yellow phenotype. Punnett square analysis can be used to predict the genotypes of the F2 generation.

A self-cross of one of the Yy heterozygous offspring can be represented in a 2 × 2 Punnett square because each parent can donate one of two different alleles. Therefore, the offspring can potentially have one of four allele combinations: YY, Yy, yY, or yy. Notice that there are two ways to obtain the Yy genotype: a Y from the egg and a y from the sperm, or a y from the egg and a Y from the sperm. Both of these possibilities must be counted. Recall that Mendel's pea-plant characteristics behaved in the same way in reciprocal crosses. Therefore, the two possible heterozygous combinations produce offspring that are genotypically and

phenotypically identical despite their dominant and recessive alleles deriving from different parents. They are grouped together. Because fertilization is a random event, we expect each combination to be equally likely and for the offspring to exhibit a ratio of YY:Yy:yy genotypes of 1:2:1. Furthermore, because the YY and Yy offspring have yellow seeds and are phenotypically identical, applying the sum rule of probability, we expect the offspring to exhibit a phenotypic ratio of 3 yellow:1 green. Indeed, working with large sample sizes, Mendel observed approximately this ratio in every F_2 generation resulting from crosses for individual traits.

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. Alternatively, if the dominant expressing organism is a heterozygote, the F_1 offspring will exhibit a 1:1 ratio of heterozygotes and recessive homozygotes. The test cross further validates Mendel's postulate that pairs of unit factors segregate equally.

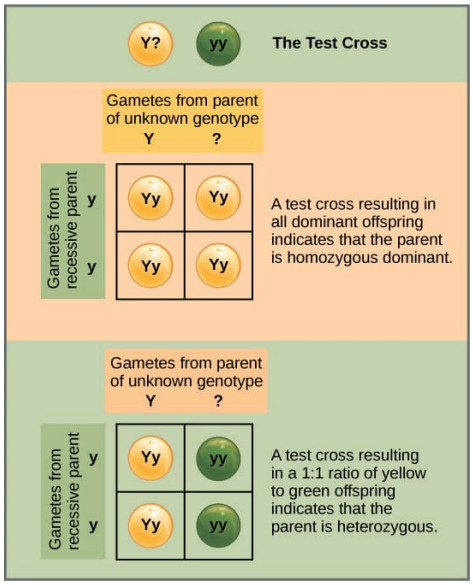


Figure $12.2C.1$: Example of a test cross: A test cross can be performed to determine whether an organism expressing a dominant trait is a homozygote or a heterozygote.

Key Points

- Fertilization between two true-breeding parents that differ in only one characteristic is called a monohybrid cross.
- For a monohybrid cross of two true-breeding parents, each parent contributes one type of allele resulting in all of the offspring with the same genotype.
- A test cross is a way to determine whether an organism that expressed a dominant trait was a heterozygote or a homozygote.

Key Terms

- **monohybrid**: a hybrid between two species that only have a difference of one gene
- **homozygous**: of an organism in which both copies of a given gene have the same allele
- **heterozygous**: of an organism which has two different alleles of a given gene
- **Punnett square**: a graphical representation used to determine the probability of an offspring expressing a particular genotype

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12.2D: Alternatives to Dominance and Recessiveness

Learning Objectives

- Discuss incomplete dominance, codominance, and multiple alleles as alternatives to dominance and recessiveness

Alternatives to Dominance and Recessiveness

Mendel's experiments with pea plants suggested that: (1) two "units" or alleles exist for every gene; (2) alleles maintain their integrity in each generation (no blending); and (3) in the presence of the dominant allele, the recessive allele is hidden and makes no contribution to the phenotype. Therefore, recessive alleles can be "carried" and not expressed by individuals. Such heterozygous individuals are sometimes referred to as "carriers." Further genetic studies in other plants and animals have shown that much more complexity exists, but that the fundamental principles of Mendelian genetics still hold true.

Mendel's results, that traits are inherited as dominant and recessive pairs, contradicted the view at that time that offspring exhibited a blend of their parents' traits. However, the heterozygote phenotype occasionally does appear to be intermediate between the two parents. For example, in the snapdragon, *Antirrhinum majus*, a cross between a homozygous parent with white flowers (C^WC^W) and a homozygous parent with red flowers (C^RC^R) will produce offspring with pink flowers (C^RC^W). This pattern of inheritance is described as incomplete dominance, denoting the expression of two contrasting alleles such that the individual displays an intermediate phenotype. The allele for red flowers is incompletely dominant over the allele for white flowers. However, the results of a heterozygote self-cross can still be predicted, just as with Mendelian dominant and recessive crosses. In this case, the genotypic ratio would be 1 C^RC^R:2 C^RC^W:1 C^WC^W, and the phenotypic ratio would be 1:2:1 for red:pink:white.



Figure 12.2*D*.1: Example of incomplete dominance: These pink flowers of a heterozygote snapdragon result from incomplete dominance.

A variation on incomplete dominance is codominance, in which both alleles for the same characteristic are simultaneously expressed in the heterozygote. An example of codominance is the MN blood groups of humans. The M and N alleles are expressed in the form of an M or N antigen present on the surface of red blood cells. Homozygotes ($L^ML^M$and L^NL^N) express either the M or the N allele, and heterozygotes (L^ML^N) express both alleles equally. In a self-cross between heterozygotes expressing a codominant trait, the three possible offspring genotypes are phenotypically distinct. However, the 1:2:1 genotypic ratio characteristic of a Mendelian monohybrid cross still applies.

Mendel implied that only two alleles, one dominant and one recessive, could exist for a given gene. We now know that this is an oversimplification. Although individual humans (and all diploid organisms) can only have two alleles for a given gene, multiple

alleles may exist at the population level such that many combinations of two alleles are observed. Note that when many alleles exist for the same gene, the convention is to denote the most common phenotype or genotype among wild animals as the wild type (often abbreviated "+"); this is considered the standard or norm. All other phenotypes or genotypes are considered variants of this standard, meaning that they deviate from the wild type. The variant may be recessive or dominant to the wild-type allele. An example of multiple alleles is coat color in rabbits. Here, four alleles exist for the c gene. The wild-type version, C^+C^+, is expressed as brown fur. The chinchilla phenotype, $c^{ch}c^{ch}$, is expressed as black-tipped white fur. The Himalayan phenotype, c^hc^h, has black fur on the extremities and white fur elsewhere. Finally, the albino, or "colorless" phenotype, cc, is expressed as white fur. In cases of multiple alleles, dominance hierarchies can exist. In this case, the wild-type allele is dominant over all the others, chinchilla is incompletely dominant over Himalayan and albino, and Himalayan is dominant over albino. This hierarchy, or allelic series, was revealed by observing the phenotypes of each possible heterozygote offspring.

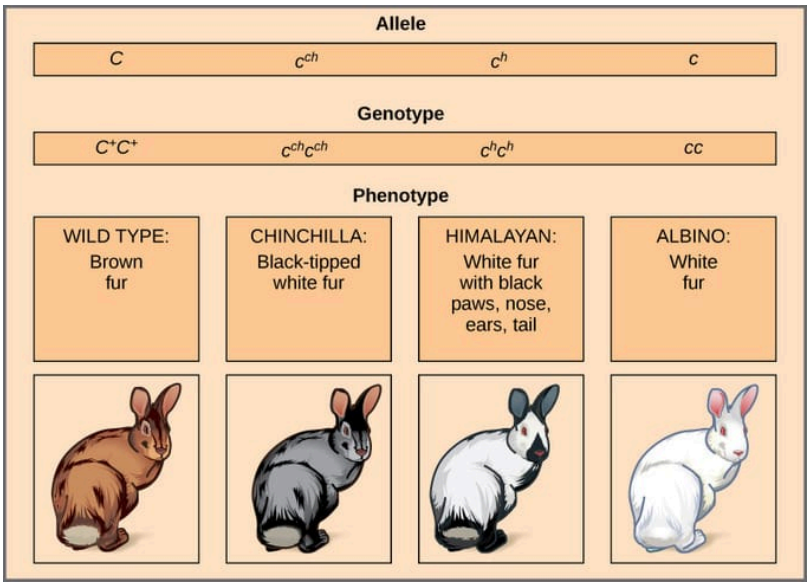


Figure 12.2D.1: Example of multiple alleles for rabbit coat color: Four different alleles exist for the rabbit coat color (C) gene.

The complete dominance of a wild-type phenotype over all other mutants often occurs as an effect of "dosage" of a specific gene product, such that the wild-type allele supplies the correct amount of gene product whereas the mutant alleles cannot. For the allelic series in rabbits, the wild-type allele may supply a given dosage of fur pigment, whereas the mutants supply a lesser dosage or none at all. Alternatively, one mutant allele can be dominant over all other phenotypes, including the wild type. This may occur when the mutant allele somehow interferes with the genetic message so that even a heterozygote with one wild-type allele copy expresses the mutant phenotype. One way in which the mutant allele can interfere is by enhancing the function of the wild-type gene product or changing its distribution in the body. One example of this is the Antennapedia mutation in *Drosophila*. In this case, the mutant allele expands the distribution of the gene product; as a result, the Antennapedia heterozygote develops legs on its head where its antennae should be.



Figure 12.2D.1: Example of a mutant allele interfering with the function of a wild-type gene: As seen in comparing the wild-type *Drosophila*(left) and the Antennapedia mutant (right), the Antennapedia mutant has legs on its head in place of antennae.

Key Points

- Incomplete dominance is the expression of two contrasting alleles such that the individual displays an intermediate phenotype.
- Codominance is a variation on incomplete dominance in which both alleles for the same characteristic are simultaneously expressed in the heterozygote.
- Diploid organisms can only have two alleles for a given gene; however, multiple alleles may exist at the population level such that many combinations of two alleles are observed.
- The complete dominance of a wild-type phenotype over all other mutants often occurs as an effect of “dosage” of a specific gene product: the wild-type allele supplies the correct amount of gene product whereas the mutant alleles cannot.
- One mutant allele can also be dominant over all other phenotypes, including the wild type.

Key Terms

- **allele**: one of a number of alternative forms of the same gene occupying a given position on a chromosome
- **incomplete dominance**: a condition in which the phenotype of the heterozygous genotype is distinct from and often intermediate to the phenotypes of the homozygous genotypes
- **codominance**: a condition in which both alleles of a gene pair in a heterozygote are fully expressed, with neither one being dominant or recessive to the other

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12.2E: Sex-Linked Traits

Learning Objectives

- Distinguish between sex-linked traits and other forms of inheritance

Sex Determination

In humans, as well as in many other animals and some plants, the sex of the individual is determined by sex chromosomes. However, there are other sex determination systems in nature. For example, temperature-dependent sex determination is relatively common,
and there are many other types of environmental sex determination. Some species, such as some snails, practice sex change adults start out male, then become female. In tropical clown fish, the dominant individual in a group becomes female while the others are male.

The sex chromosomes are one pair of non-homologous chromosomes. Until now, we have only considered inheritance patterns among non-sex chromosomes, or autosomes. In addition to 22 homologous pairs of autosomes, human females have a homologous pair of X chromosomes, whereas human males have an XY chromosome pair. Although the Y chromosome contains a small region of similarity to the X chromosome so that they can pair during meiosis, the Y chromosome is much shorter and contains many fewer genes. When a gene being examined is present on the X chromosome, but not on the Y chromosome, it is said to be X-linked.

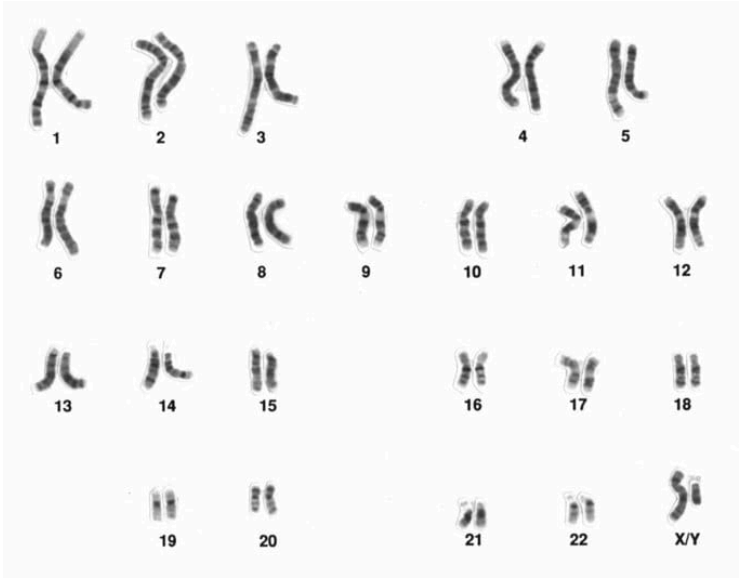


Figure $12.2E.1$: Human male karyotype: A human males possesses XY chromosomes, as seen in the bottom left of this karyotype. The Y chromosome is much shorter than the X chromosome, unlike all of the other homologous chromosome pairs.

X-Linked Traits

Insects also follow an XY sex-determination pattern and like humans, *Drosophila* males have an XY chromosome pair and females are XX. Eye color in *Drosophila* was one of the first X-linked traits to be identified, and Thomas Hunt Morgan mapped this trait to the X chromosome in 1910.

In fruit flies, the wild-type eye color is red (X^W) and is dominant to white eye color (X^w). Because this eye-color gene is located on the X chromosome only, reciprocal crosses do not produce the same offspring ratios. Males are said to be hemizygous, because they have only one allele for any X-linked characteristic. Hemizygosity makes the descriptions of dominance and recessiveness

irrelevant for XY males because each male only has one copy of the gene. *Drosophila* males lack a second allele copy on the Y chromosome; their genotype can only be X^WY or X^wY. In contrast, females have two allele copies of this gene and can be X^WX^W, X^WX^w, or X^wX^w.



Figure 12.2E.1: Eye color in Drosophila is an example of a X-linked trait: In *Drosophila*, the gene for eye color is located on the X chromosome. Clockwise from top left are brown, cinnabar, sepia, vermilion, white, and red. Red eye color is wild-type and is dominant to white eye color.

X-Linked Crosses

In an X-linked cross, the genotypes of F_1 and F_2 offspring depend on whether the recessive trait was expressed by the male or the female in the P_1 generation. With regard to *Drosophila* eye color, when the P_1 male expresses the white-eye phenotype and the female is homozygous red-eyed, all members of the F_1 generation exhibit red eyes. The F_1 females are heterozygous (X^WX^w), and the males are all X^WY, having received their X chromosome from the homozygous dominant P_1 female and their Y chromosome from the P_1 male.

A subsequent cross between the X^WX^w female and the X^WY male would produce only red-eyed females (with X^WX^W or X^WX^wgenotypes) and both red- and white-eyed males (with X^WY or X^wY genotypes). Now, consider a cross between a homozygous white-eyed female and a male with red eyes. The F_1 generation would exhibit only heterozygous red-eyed females (X^WX^w) and only white-eyed males (X^wY). Half of the F_2 females would be red-eyed (X^WX^w) and half would be white-eyed (X^wX^w). Similarly, half of the F_2 males would be red-eyed (X^WY) and half would be white-eyed (X^wY).

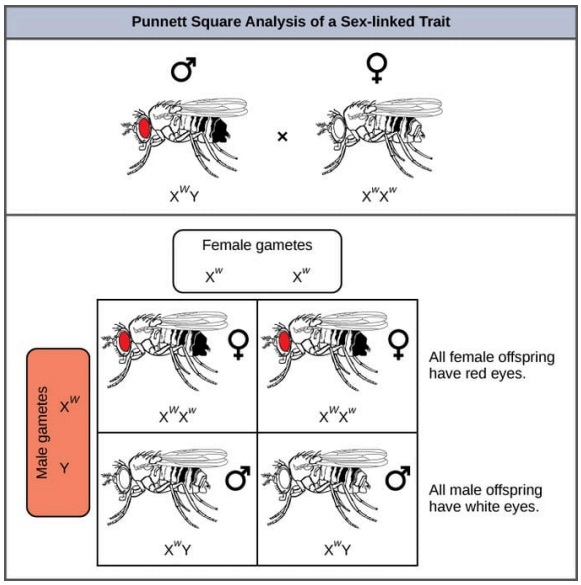


Figure $12.2E.1$: Punnett square analysis of *Drosophila* eye color: Punnett square analysis is used to determine the ratio of offspring from a cross between a red-eyed male fruit fly (X^WY) and a white-eyed female fruit fly (X^WX^W).

X-Linked Recessive Disorders in Humans

Sex-linkage studies provided the fundamentals for understanding X-linked recessive disorders in humans, which include red-green color blindness and Types A and B hemophilia. Because human males need to inherit only one recessive mutant X allele to be affected, X-linked disorders are disproportionately observed in males. Females must inherit recessive X-linked alleles from both of their parents in order to express the trait.

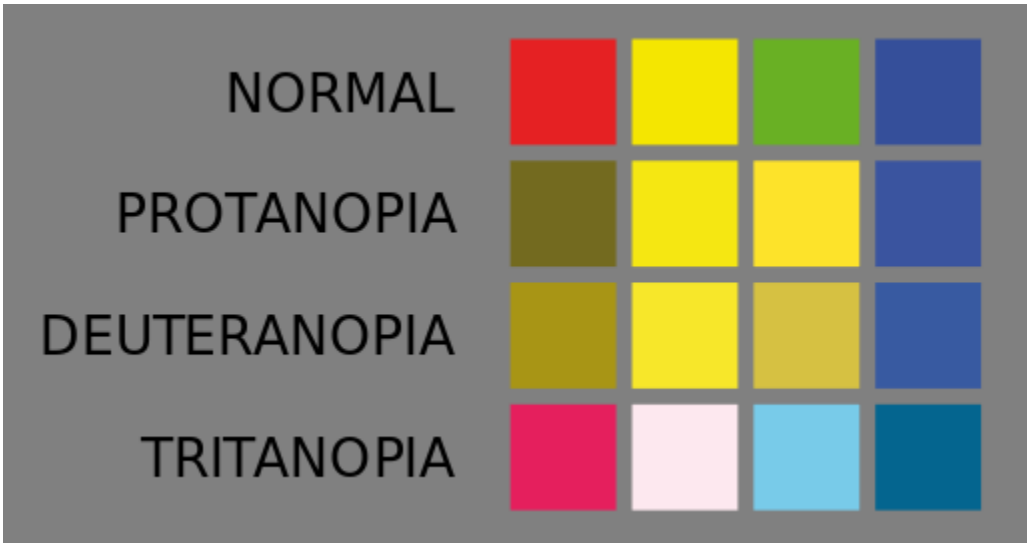


Figure $12.2E.1$: Color perception in different types of color blindness: In this chart you can see what people with different types of color blindness can see versus the normal color vision line at top.

Recessive Carriers

When they inherit one recessive X-linked mutant allele and one dominant X-linked wild-type allele, they are carriers of the trait and are typically unaffected. Carrier females can manifest mild forms of the trait due to the inactivation of the dominant allele located on one of the X chromosomes. However, female carriers can contribute the trait to their sons, resulting in the son exhibiting the trait, or they can contribute the recessive allele to their daughters, resulting in the daughters being carriers of the trait. Although some Y-linked recessive disorders exist, typically they are associated with infertility in males and are, therefore, not transmitted

to subsequent generations.

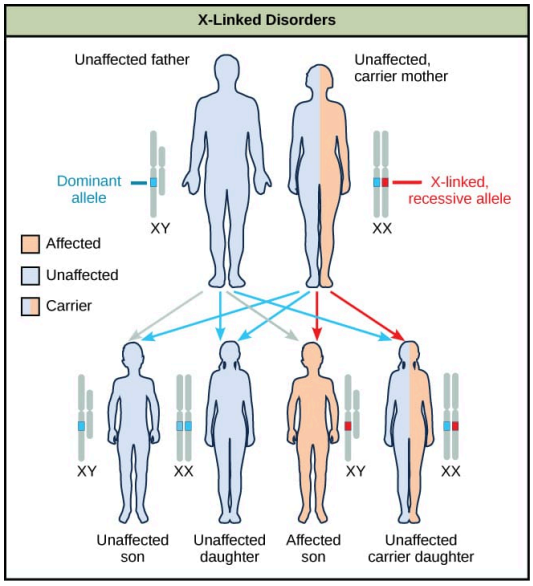


Figure $12.2E.1$: Inheritance of a recessive X-linked disorder: The son of a woman who is a carrier of a recessive X-linked disorder will have a 50 percent chance of being affected. A daughter will not be affected, but she will have a 50 percent chance of being a carrier like her mother.

Key Points

- In mammals, females have a homologous pair of X chromosomes, whereas males have an XY chromosome pair.
- The Y chromosome contains a small region of similarity to the X chromosome so that they can pair during meiosis, but the Y is much shorter and contains fewer genes.
- Males are said to be hemizygous because they have only one allele for any X-linked characteristic; males will exhibit the trait of any gene on the X-chromosome regardless of dominance and recessiveness.
- Most sex-linked traits are actually X-linked, such as eye color in *Drosophila* or color blindness in humans.

Key Terms

- **hemizygous**: Having some single copies of genes in an otherwise diploid cell or organism.
- **X-linked**: Associated with the X chromosome.
- **carrier**: A person or animal that transmits a disease to others without itself contracting the disease.
- **sex chromosomes**: A chromosome involved with determining the sex of an organism, typically one of two kinds.

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12.2F: Lethal Inheritance Patterns

Learning Objectives

- Describe recessive and dominant lethal inheritance patterns

Lethal Inheritance Patterns

A large proportion of genes in an individual's genome are essential for survival. Occasionally, a nonfunctional allele for an essential gene can arise by mutation and be transmitted in a population as long as individuals with this allele also have a wild-type, functional copy. The wild-type allele functions at a capacity sufficient to sustain life and is, therefore, considered to be dominant over the nonfunctional allele. However, consider two heterozygous parents that have a genotype of wild-type/nonfunctional mutant for a hypothetical essential gene. In one quarter of their offspring, we would expect to observe individuals that are homozygous recessive for the nonfunctional allele. Because the gene is essential, these individuals might fail to develop past fertilization, die in utero, or die later in life, depending on what life stage requires this gene. An inheritance pattern in which an allele is only lethal in the homozygous form and in which the heterozygote may be normal or have some altered non-lethal phenotype is referred to as recessive lethal.

For crosses between heterozygous individuals with a recessive lethal allele that causes death before birth when homozygous, only wild-type homozygotes and heterozygotes would be observed. The genotypic ratio would therefore be 2:1. In other instances, the recessive lethal allele might also exhibit a dominant (but not lethal) phenotype in the heterozygote. For instance, the recessive lethal Curly allele in Drosophila affects wing shape in the heterozygote form, but is lethal in the homozygote.

Dominant Lethal Alleles

A single copy of the wild-type allele is not always sufficient for normal functioning or even survival. The dominant lethal inheritance pattern is one in which an allele is lethal both in the homozygote and the heterozygote; this allele can only be transmitted if the lethality phenotype occurs after reproductive age. Individuals with mutations that result in dominant lethal alleles fail to survive even in the heterozygote form. Dominant lethal alleles are very rare because, as you might expect, the allele only lasts one generation and is not transmitted. However, just as the recessive lethal allele might not immediately manifest the phenotype of death, dominant lethal alleles also might not be expressed until adulthood. Once the individual reaches reproductive age, the allele may be unknowingly passed on, resulting in a delayed death in both generations. An example of this in humans is Huntington's disease in which the nervous system gradually wastes away. People who are heterozygous for the dominant Huntington allele (Hh) will inevitably develop the fatal disease. However, the onset of Huntington's disease may not occur until age 40, at which point the afflicted persons may have already passed the allele to 50 percent of their offspring.

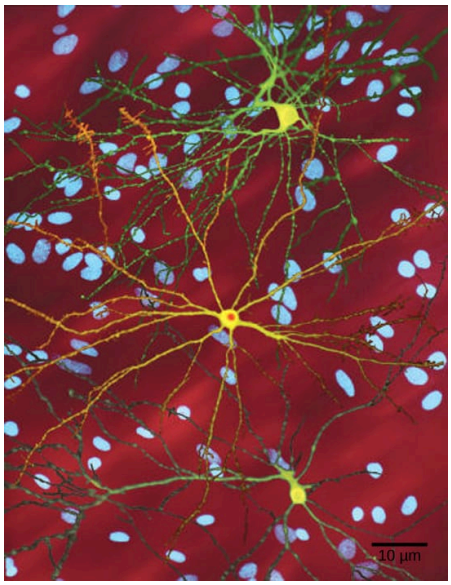


Figure $12.2F.1$: Effects of Huntington's disease on neurons: The neuron in the center of this micrograph (yellow) has nuclear inclusions characteristic of Huntington's disease (orange area in the center of the neuron). Huntington's disease occurs when an abnormal dominant allele for the Huntington gene is present.

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Key Points

- An inheritance pattern in which an allele is only lethal in the homozygous form and in which the heterozygote may be normal or have some altered non-lethal phenotype is referred to as recessive lethal.
- The dominant lethal inheritance pattern is one in which an allele is lethal both in the homozygote and the heterozygote; this allele can only be transmitted if the lethality phenotype occurs after reproductive age.
- Dominant lethal alleles are very rare because the allele only lasts one generation and is, therefore, not usually transmitted.
- In the case where dominant lethal alleles might not be expressed until adulthood, the allele may be unknowingly passed on, resulting in a delayed death in both generations.

Key Terms

- **mutation**: any heritable change of the base-pair sequence of genetic material
- **recessive lethal**: an inheritance pattern in which an allele is only lethal in the homozygous form and in which the heterozygote may be normal or have some altered non-lethal phenotype

- **dominant lethal**: an inheritance pattern is one in which an allele is lethal both in the homozygote and the heterozygote; this allele can only be transmitted if the lethality phenotype occurs after reproductive age

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12.3: LAWS OF INHERITANCE



- Topic hierarchy

12.3A: Mendel's Laws of Heredity

12.3B: Mendel's Law of Dominance

12.3C: Mendel's Law of Segregation

12.3D: Mendel's Law of Independent Assortment

12.3E: Genetic Linkage and Violation of the Law of Independent Assortment

12.3F: Epistasis

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12.3A: Mendel's Laws of Heredity

Learning Objectives

- Discuss the methods Mendel utilized in his research that led to his success in understanding the process of inheritance

Introduction

Mendelian inheritance (or Mendelian genetics or Mendelism) is a set of primary tenets relating to the transmission of hereditary characteristics from parent organisms to their children; it underlies much of genetics. The tenets were initially derived from the work of Gregor Mendel published in 1865 and 1866, which was "re-discovered" in 1900; they were initially very controversial, but they soon became the core of classical genetics.

The laws of inheritance were derived by Gregor Mendel, a 19th century monk conducting hybridization experiments in garden peas (*Pisum sativum*). Between 1856 and 1863, he cultivated and tested some 28,000 pea plants. From these experiments, he deduced two generalizations that later became known as Mendel's Laws of Heredity or Mendelian inheritance. He described these laws in a two part paper, "Experiments on Plant Hybridization", which was published in 1866.

Mendel's Laws

Mendel discovered that by crossing true-breeding white flower and true-breeding purple flower plants, the result was a hybrid offspring. Rather than being a mix of the two colors, the offspring was purple flowered. He then conceived the idea of heredity units, which he called "factors", one of which is a recessive characteristic and the other dominant. Mendel said that factors, later called genes, normally occur in pairs in ordinary body cells, yet segregate during the formation of sex cells. Each member of the pair becomes part of the separate sex cell. The dominant gene, such as the purple flower in Mendel's plants, will hide the recessive gene, the white flower. After Mendel self-fertilized the F1 generation and obtained an F2 generation with a 3:1 ratio, he correctly theorized that genes can be paired in three different ways for each trait: AA, aa, and Aa. The capital A represents the dominant factor while the lowercase a represents the recessive.

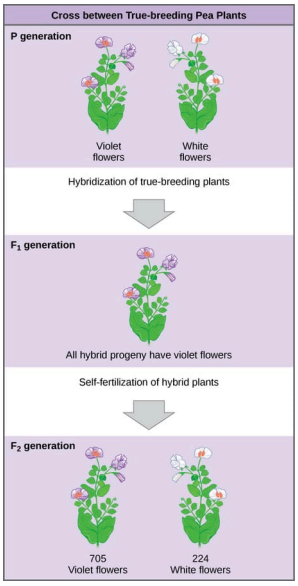


Figure 12.3A.1: Mendel's Pea Plants: In one of his experiments on inheritance patterns, Mendel crossed plants that were true-breeding for violet flower color with plants true-breeding for white flower color (the P generation). The resulting hybrids in the F1 generation all had violet flowers. In the F2 generation, approximately three-quarters of the plants had violet flowers, and one-quarter had white flowers.

Mendel stated that each individual has two alleles for each trait, one from each parent. Thus, he formed the "first rule", the

Law of Segregation, which states individuals possess two alleles and a parent passes only one allele to his/her offspring. One allele is given by the female parent and the other is given by the male parent. The two factors may or may not contain the same information. If the two alleles are identical, the individual is called homozygous for the trait. If the two alleles are different, the individual is called heterozygous. The presence of an allele does not promise that the trait will be expressed in the individual that possesses it. In heterozygous individuals, the only allele that is expressed is the dominant. The recessive allele is present, but its expression is hidden. The genotype of an individual is made up of the many alleles it possesses. An individual's physical appearance, or phenotype, is determined by its alleles as well as by its environment.

Mendel also analyzed the pattern of inheritance of seven pairs of contrasting traits in the domestic pea plant. He did this by cross-breeding dihybrids; that is, plants that were heterozygous for the alleles controlling two different traits. Mendel then crossed these dihybrids. If it is inevitable that round seeds must always be yellow and wrinkled seeds must be green, then he would have expected that this would produce a typical monohybrid cross: 75 percent round-yellow; 25 percent wrinkled-green. But, in fact, his mating generated seeds that showed all possible combinations of the color and texture traits. He found 9/16 of the offspring were round-yellow, 3/16 were round-green, 3/16 were wrinkled-yellow, and 1/16 were wrinkled-green. Finding in every case that each of his seven traits was inherited independently of the others, he formed his "second rule", the Law of Independent Assortment, which states the inheritance of one pair of factors (genes) is independent of the inheritance of the other pair. Today we know that this rule holds only if the genes are on separate chromosomes

Key Points

- By crossing purple and white pea plants, Mendel found the offspring were purple rather than mixed, indicating one color was dominant over the other.
- Mendel's Law of Segregation states individuals possess two alleles and a parent passes only one allele to his/her offspring.
- Mendel's Law of Independent Assortment states the inheritance of one pair of factors (genes) is independent of the inheritance of the other pair.
- If the two alleles are identical, the individual is called homozygous for the trait; if the two alleles are different, the individual is called heterozygous.
- Mendel cross-bred dihybrids and found that traits were inherited independently of each other.

Key Terms

- **homozygous**: of an organism in which both copies of a given gene have the same allele
- **heterozygous**: of an organism which has two different alleles of a given gene
- **allele**: one of a number of alternative forms of the same gene occupying a given position on a chromosome

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12.3B: Mendel's Law of Dominance

Learning Objectives

- Explain the concept of dominance versus recessiveness

Alleles Can Be Dominant or Recessive

Most familiar animals and some plants have paired chromosomes and are described as diploid. They have two versions of each chromosome: one contributed by the female parent in her ovum and one by the male parent in his sperm. These are joined at fertilization. The ovum and sperm cells (the gametes) have only one copy of each chromosome and are described as haploid.



Figure $12.3B.1$: Recessive traits are only visible if an individual inherits two copies of the recessive allele: The child in the photo expresses albinism, a recessive trait.

Mendel's law of dominance states that in a heterozygote, one trait will conceal the presence of another trait for the same characteristic. 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 by the same manner in which the dominant allele is transmitted. The recessive trait will only be expressed by offspring that have two copies of this allele; these offspring will breed true when self-crossed.

By definition, the terms dominant and recessive refer to the genotypic interaction of alleles in producing the phenotype of the heterozygote. The key concept is genetic: which of the two alleles present in the heterozygote is expressed, such that the organism is phenotypically identical to one of the two homozygotes. It is sometimes convenient to talk about the trait corresponding to the dominant allele as the dominant trait and the trait corresponding to the hidden allele as the recessive trait. However, this can easily lead to confusion in understanding the concept as phenotypic. For example, to say that "green peas" dominate "yellow peas" confuses inherited genotypes and expressed phenotypes. This will subsequently confuse discussion of the molecular basis of the phenotypic difference. Dominance is not inherent. One allele can be dominant to a second allele, recessive to a third allele, and codominant to a fourth. If a genetic trait is recessive, a person needs to inherit two copies of the gene for the trait to be expressed. Thus, both parents have to be carriers of a recessive trait in order for a child to express that trait.

Since Mendel's experiments with pea plants, other researchers have found that the law of dominance does not always hold true. Instead, several different patterns of inheritance have been found to exist.

Key Points

- Dominant alleles are expressed exclusively in a heterozygote, while recessive traits are expressed only if the organism is homozygous for the recessive allele.
- A single allele may be dominant over one allele, but recessive to another.
- Not all traits are controlled by simple dominance as a form of inheritance; more complex forms of inheritance have been found to exist.

Key Terms

- **dominant**: a relationship between alleles of a gene, in which one allele masks the expression (phenotype) of another allele at the same locus
- **recessive**: able to be covered up by a dominant trait

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12.3C: Mendel's Law of Segregation

Learning Objectives

- Apply the law of segregation to determine the chances of a particular genotype arising from a genetic cross

Equal Segregation of Alleles

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. The law of segregation states that each individual that is a diploid has a pair of alleles (copy) for a particular trait. Each parent passes an allele at random to their offspring resulting in a diploid organism. The allele that contains the dominant trait determines the phenotype of the offspring. In essence, the law states that copies of genes separate or segregate so that each gamete receives only one allele.

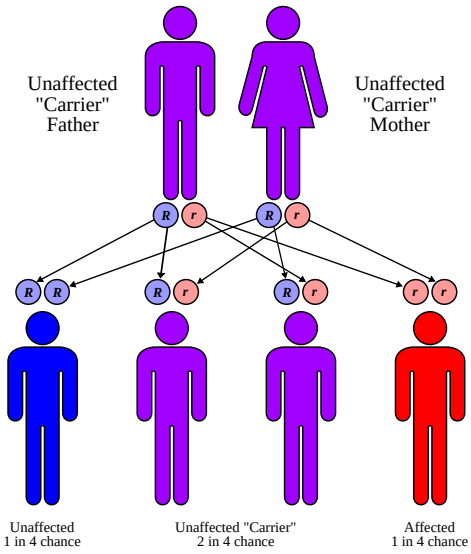


Figure $12.3C.1$: The Law of Segregation states that alleles segregate randomly into gametes: When gametes are formed, each allele of one parent segregates randomly into the gametes, such that half of the parent's gametes carry each allele.

For the F_2 generation of a monohybrid cross, the following three possible combinations of genotypes could 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. The behavior of homologous chromosomes during meiosis can account for the segregation of the alleles at each genetic locus to different gametes. As chromosomes separate into different gametes during meiosis, the two different alleles for a particular gene also segregate so that each gamete acquires one of the two alleles. In Mendel's experiments, the segregation and the independent assortment during meiosis in the F1 generation give rise to the F2 phenotypic ratios observed by Mendel. The role of the meiotic segregation of chromosomes in sexual reproduction was not understood by the scientific community during Mendel's lifetime.

Key Points

- Each gamete acquires one of the two alleles as chromosomes separate into different gametes during meiosis.
- Heterozygotes, which posess one dominant and one recessive allele, can receive each allele from either parent and will look identical to homozygous dominant individuals; the Law of Segregation supports Mendel's observed 3:1 phenotypic ratio.
- Mendel proposed the Law of Segregation after observing that pea plants with two different traits produced offspring that all expressed the dominant trait, but the following generation expressed the dominant and recessive traits in a 3:1 ratio.

Key Terms

- **law of segregation**: a diploid individual possesses a pair of alleles for any particular trait and each parent passes one of these randomly to its offspring

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12.3D: Mendel's Law of Independent Assortment

Learning Objectives

- Use the probability or forked line method to calculate the chance of any particular genotype arising from a genetic cross

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: every possible combination of alleles for every gene is equally likely to occur. The 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 green, wrinkled seeds (yyrr) and another that has yellow, round seeds (YYRR). Because each parent is homozygous, the law of segregation indicates that the gametes for the green/wrinkled plant all are yr, while the gametes for the yellow/round plant are all YR. Therefore, the F_1 generation of offspring all are YyRr.

For the F2 generation, the law of segregation requires that each gamete receive either an R allele or an r allele along with either a Y allele or a y allele. The law of independent assortment states that a gamete into which an r allele sorted would be equally likely to contain either a Y allele or a y allele. Thus, there are four equally likely gametes that can be formed when the YyRr heterozygote is self-crossed as follows: YR, Yr, yR, and yr. Arranging these gametes along the top and left of a 4 × 4 Punnett square gives us 16 equally likely genotypic combinations. From these genotypes, we infer a phenotypic ratio of 9 round/yellow:3 round/green:3 wrinkled/yellow:1 wrinkled/green. These are the offspring ratios we would expect, assuming we performed the crosses with a large enough sample size.

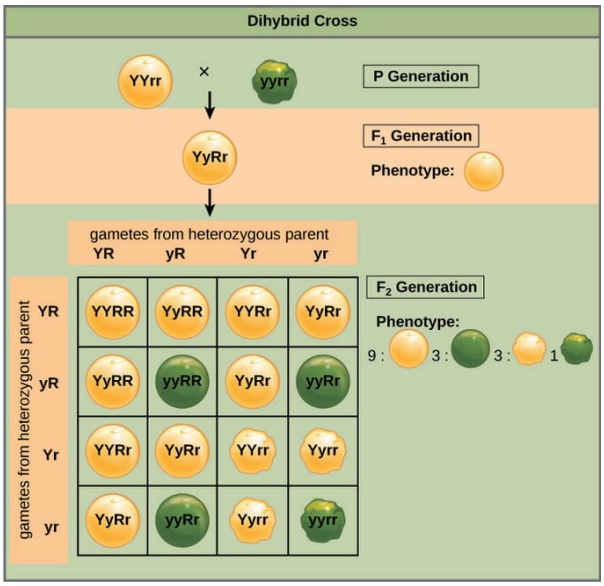


Figure $12.3D.1$: Independent assortment of 2 genes: This dihybrid cross of pea plants involves the genes for seed color and texture.

Because of independent assortment and dominance, the 9:3:3:1 dihybrid phenotypic ratio can be collapsed into two 3:1 ratios, characteristic of any monohybrid cross that follows a dominant and recessive pattern. Ignoring seed color and considering only seed texture in the above dihybrid cross, we would expect that three-quarters of the F_2 generation offspring would be round and one-quarter would be wrinkled. Similarly, isolating only seed color, we would assume that three-quarters of the F_2offspring would be yellow and one-quarter would be green. The sorting of alleles for texture and color are independent events, so we can apply the product rule. Therefore, the proportion of round and yellow F_2 offspring is expected to be (3/4) × (3/4) = 9/16, and the proportion of wrinkled and green offspring is expected to be (1/4) × (1/4) = 1/16. These proportions are identical to those obtained using a Punnett square. Round/green and wrinkled/yellow offspring can also be calculated using the product rule as each of these

genotypes includes one dominant and one recessive phenotype. Therefore, the proportion of each is calculated as (3/4) × (1/4) = 3/16.

Forked-Line Method

When more than two genes are being considered, the Punnett-square method becomes unwieldy. For instance, examining a cross involving four genes would require a 16 × 16 grid containing 256 boxes. It would be extremely cumbersome to manually enter each genotype. For more complex crosses, the forked-line and probability methods are preferred.

To prepare a forked-line diagram for a cross between F_1 heterozygotes resulting from a cross between AABBCC and aabbcc parents, we first create rows equal to the number of genes being considered and then segregate the alleles in each row on forked lines according to the probabilities for individual monohybrid crosses. We then multiply the values along each forked path to obtain the F_2 offspring probabilities. Note that this process is a diagrammatic version of the product rule. The values along each forked pathway can be multiplied because each gene assorts independently. For a trihybrid cross, the F_2phenotypic ratio is 27:9:9:9:3:3:3:1.

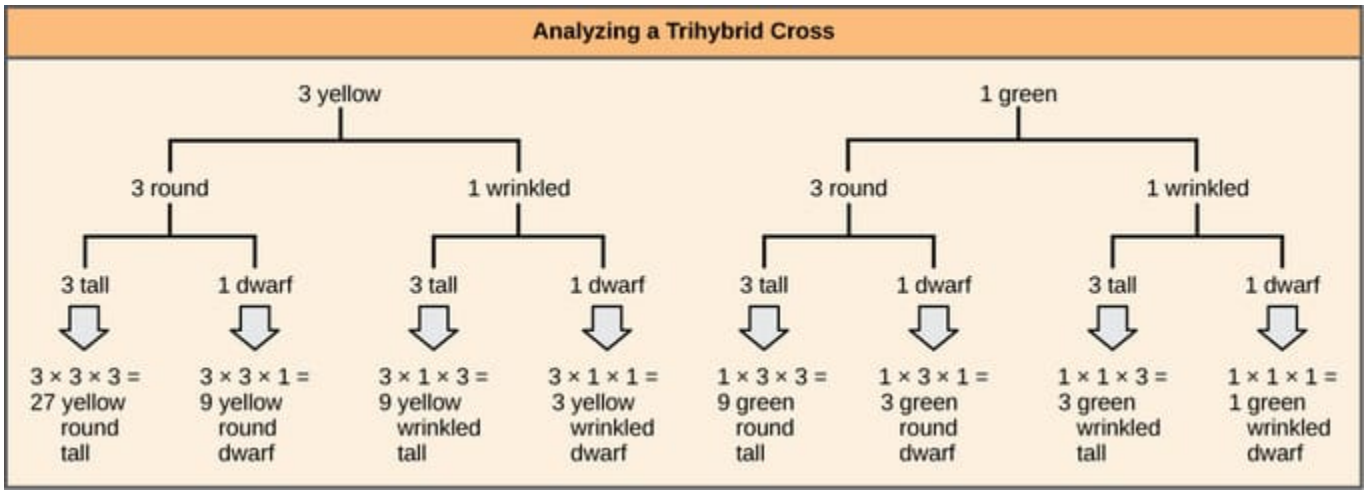


Figure $12.3D.1$: Independent assortment of 3 genes: The forked-line method can be used to analyze a trihybrid cross. Here, the probability for color in the F2 generation occupies the top row (3 yellow:1 green). The probability for shape occupies the second row (3 round:1 wrinked), and the probability for height occupies the third row (3 tall:1 dwarf). The probability for each possible combination of traits is calculated by multiplying the probability for each individual trait. Thus, the probability of F2 offspring having yellow, round, and tall traits is 3 × 3 × 3, or 27.

Probability Method

While the forked-line method is a diagrammatic approach to keeping track of probabilities in a cross, the probability method gives the proportions of offspring expected to exhibit each phenotype (or genotype) without the added visual assistance.

To fully demonstrate the power of the probability method, however, we can consider specific genetic calculations. For instance, for a tetrahybrid cross between individuals that are heterozygotes for all four genes, and in which all four genes are sorting independently in a dominant and recessive pattern, what proportion of the offspring will be expected to be homozygous recessive for all four alleles? Rather than writing out every possible genotype, we can use the probability method. We know that for each gene the fraction of homozygous recessive offspring will be 1/4. Therefore, multiplying this fraction for each of the four genes, (1/4) × (1/4) × (1/4) × (1/4), we determine that 1/256 of the offspring will be quadruply homozygous recessive.

Key Points

- Mendel's law of independent assortment states that genes do not influence each other with regard to the sorting of alleles into gametes; every possible combination of alleles for every gene is equally likely to occur.
- The calculation of any particular genotypic combination of more than one gene is, therefore, the probability of the desired genotype at the first locus multiplied by the probability of the desired genotype at the other loci.
- The forked line method can be used to calculate the chances of all possible genotypic combinations from a cross, while the

probability method can be used to calculate the chance of any one particular genotype that might result from that cross.

Key Terms

- **independent assortment**: separate genes for separate traits are passed independently of one another from parents to offspring

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12.3E: Genetic Linkage and Violation of the Law of Independent Assortment

Learning Objectives

- Describe how recombination can separate linked genes

Linked Genes Violate the Law of Independent Assortment

Although all of Mendel's pea characteristics behaved according to the law of independent assortment, we now know that some allele combinations are not inherited independently of each other. Genes that are located on separate non-homologous chromosomes will always sort independently. However, each chromosome contains hundreds or thousands of genes organized linearly on chromosomes like beads on a string. The segregation of alleles into gametes can be influenced by linkage, in which genes that are located physically close to each other on the same chromosome are more likely to be inherited as a pair. However, because of the process of recombination, or "crossover," it is possible for two genes on the same chromosome to behave independently, or as if they are not linked. To understand this, let's consider the biological basis of gene linkage and recombination.

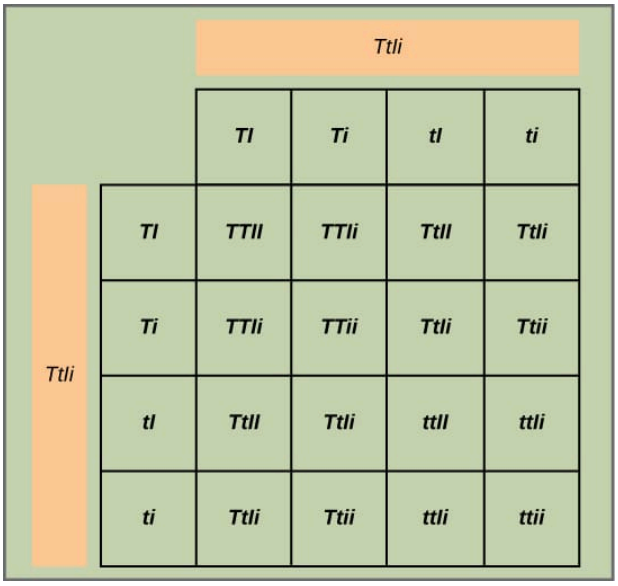


Figure $12.3E.1$: Unlinked genes assort independently: This figure shows all possible combinations of offspring resulting from a dihybrid cross of pea plants that are heterozygous for the tall/dwarf and inflated/constricted alleles.

Homologous chromosomes possess the same genes in the same linear order. The alleles may differ on homologous chromosome pairs, but the genes to which they correspond do not. In preparation for the first division of meiosis, homologous chromosomes replicate and synapse. Like genes on the homologs align with each other. At this stage, segments of homologous chromosomes exchange linear segments of genetic material. This process is called recombination, or crossover, and it is a common genetic process. Because the genes are aligned during recombination, the gene order is not altered. Instead, the result of recombination is that maternal and paternal alleles are combined onto the same chromosome. Across a given chromosome, several recombination events may occur, causing extensive shuffling of alleles.

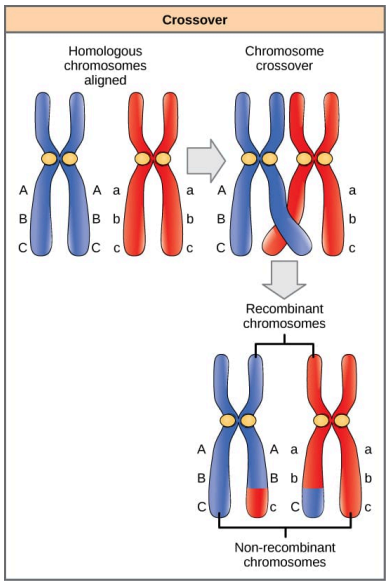


Figure $12.3E.1$: Linked genes can be separated by recombination: The process of crossover, or recombination, occurs when two homologous chromosomes align during meiosis and exchange a segment of genetic material. Here, the alleles for gene C were exchanged. The result is two recombinant and two non-recombinant chromosomes.

When two genes are located in close proximity on the same chromosome, they are considered linked, and their alleles tend to be transmitted through meiosis together. To exemplify this, imagine a dihybrid cross involving flower color and plant height in which the genes are next to each other on the chromosome. If one homologous chromosome has alleles for tall plants and red flowers, and the other chromosome has genes for short plants and yellow flowers, then when the gametes are formed, the tall and red alleles will go together into a gamete and the short and yellow alleles will go into other gametes. These are called the parental genotypes because they have been inherited intact from the parents of the individual producing gametes. But unlike if the genes were on different chromosomes, there will be no gametes with tall and yellow alleles and no gametes with short and red alleles. If you create the Punnett square with these gametes, you will see that the classical Mendelian prediction of a 9:3:3:1 outcome of a dihybrid cross would not apply. As the distance between two genes increases, the probability of one or more crossovers between them increases, and the genes behave more like they are on separate chromosomes. Geneticists have used the proportion of recombinant gametes (the ones not like the parents) as a measure of how far apart genes are on a chromosome. Using this information, they have constructed elaborate maps of genes on chromosomes for well-studied organisms, including humans.

Mendel's seminal publication makes no mention of linkage, and many researchers have questioned whether he encountered linkage, but chose not to publish those crosses out of concern that they would invalidate his independent assortment postulate. The garden pea has seven chromosomes and some have suggested that his choice of seven characteristics was not a coincidence. However, even if the genes he examined were not located on separate chromosomes, it is possible that he simply did not observe linkage because of the extensive shuffling effects of recombination.

Key Points

- Two genes close together on the same chromosome tend to be inherited together and are said to be linked.
- Linked genes can be separated by recombination in which homologous chromosomes exchange genetic information during meiosis; this results in parental, or nonrecombinant genotypes, as well as a smaller proportion of recombinant genotypes.
- Geneticists can use the amount of recombination between genes to estimate the distance between them on a chromosome.

Key Terms

- **linkage**: the property of genes of being inherited together
- **recombination**: the formation of genetic combinations in offspring that are not present in the parents

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12.3F: Epistasis

Learning Objectives

- Explain the phenotypic outcomes of epistatic effects between genes

Epistasis

Mendel's studies in pea plants implied that the sum of an individual's phenotype was controlled by genes (or as he called them, unit factors): every characteristic was distinctly and completely controlled by a single gene. In fact, single observable characteristics are almost always under the influence of multiple genes (each with two or more alleles) acting in unison. For example, at least eight genes contribute to eye color in humans.

In some cases, several genes can contribute to aspects of a common phenotype without their gene products ever directly interacting. In the case of organ development, for instance, genes may be expressed sequentially, with each gene adding to the complexity and specificity of the organ. Genes may function in complementary or synergistic fashions: two or more genes need to be expressed simultaneously to affect a phenotype. Genes may also oppose each other with one gene modifying the expression of another.

In epistasis, the interaction between genes is antagonistic: one gene masks or interferes with the expression of another. "Epistasis" is a word composed of Greek roots that mean "standing upon." The alleles that are being masked or silenced are said to be hypostatic to the epistatic alleles that are doing the masking. Often the biochemical basis of epistasis is a gene pathway in which the expression of one gene is dependent on the function of a gene that precedes or follows it in the pathway.

An example of epistasis is pigmentation in mice. The wild-type coat color, agouti (AA), is dominant to solid-colored fur (aa). However, a separate gene (C) is necessary for pigment production. A mouse with a recessive c allele at this locus is unable to produce pigment and is albino regardless of the allele present at locus A. Therefore, the genotypes AACc, Aacc, and aacc all produce the same albino phenotype. A cross between heterozygotes for both genes (AaCc x AaCc) would generate offspring with a phenotypic ratio of 9 agouti:3 solid color:4 albino. In this case, the C gene is epistatic to the A gene.

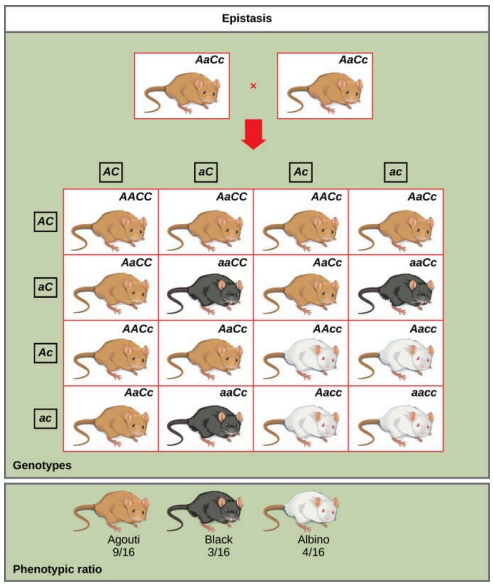


Figure $12.3F.1$: Epistasis in mouse coat color: In mice, the mottled agouti coat color (A) is dominant to a solid coloration, such as black or gray. A gene at a separate locus (C) is responsible for pigment production. The recessive c allele does not produce pigmentnand a mouse with the homozygous recessive cc genotype is albino regardless of the allele present at the A locus. Thus, the C gene is epistatic to the A gene.

Epistasis can also occur when a dominant allele masks expression at a separate gene. Fruit color in summer squash is expressed

in this way. Homozygous recessive expression of the W gene (ww) coupled with homozygous dominant or heterozygous expression of the Y gene (YY or Yy) generates yellow fruit, while the wwyy genotype produces green fruit. However, if a dominant copy of the W gene is present in the homozygous or heterozygous form, the summer squash will produce white fruit regardless of the Y alleles. A cross between white heterozygotes for both genes (WwYy × WwYy) would produce offspring with a phenotypic ratio of 12 white:3 yellow:1 green.

Finally, epistasis can be reciprocal: either gene, when present in the dominant (or recessive) form, expresses the same phenotype. In the shepherd's purse plant (*Capsella bursa-pastoris*), the characteristic of seed shape is controlled by two genes in a dominant epistatic relationship. When the genes A and B are both homozygous recessive (aabb), the seeds are ovoid. If the dominant allele for either of these genes is present, the result is triangular seeds. That is, every possible genotype other than aabb results in triangular seeds; a cross between heterozygotes for both genes (AaBb x AaBb) would yield offspring with a phenotypic ratio of 15 triangular:1 ovoid.

Keep in mind that any single characteristic that results in a phenotypic ratio that totals 16 is typical of a two-gene interaction. Recall the phenotypic inheritance pattern for Mendel's dihybrid cross, which considered two non-interacting genes: 9:3:3:1. Similarly, we would expect interacting gene pairs to also exhibit ratios expressed as 16 parts. Note that we are assuming the interacting genes are not linked; they are still assorting independently into gametes.

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Key Points

- In many cases, several genes may contribute to a particular phenotype; when the actions of one gene masks the effects of another, this gene is said to be epistatic to the second.
- Epistasis can occur when a recessive genotype masks the actions of another gene, or when a dominant allele masks the

effects of another gene.
- Epistasis can be reciprocal: either gene, when present in the dominant (or recessive) form, expresses the same phenotype.
- Any single characteristic that results in a phenotypic ratio that totals 16 (such as 12:3:1, 9:3:4, or others) is typical of a two-gene interaction.

Key Terms

- **epistasis**: the modification of the expression of a gene by another unrelated one

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13: MODERN UNDERSTANDINGS OF INHERITANCE

13.1: Chromosomal Theory and Genetic Linkage

13.1A: Chromosomal Theory of Inheritance

13.1B: Genetic Linkage and Distances

13.1C: Identification of Chromosomes and Karyotypes

13.2: Chromosomal Basis of Inherited Disorders

13.2A: Disorders in Chromosome Number

13.2B: Chromosomal Structural Rearrangements

13.2C: X-Inactivation

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13.1: CHROMOSOMAL THEORY AND GENETIC LINKAGE

- Topic hierarchy

13.1A: Chromosomal Theory of Inheritance

13.1B: Genetic Linkage and Distances

13.1C: Identification of Chromosomes and Karyotypes

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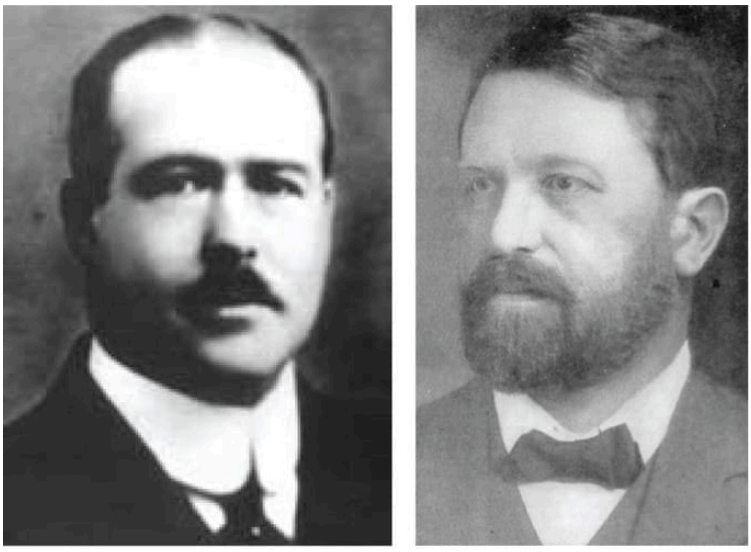
13.1A: Chromosomal Theory of Inheritance

Learning Objectives

- List the reasons that fruit flies are excellent model organisms for genetic research

Chromosomal Theory of Inheritance

The speculation that chromosomes might be the key to understanding heredity led several scientists to examine Mendel's publications and re-evaluate his model in terms of the behavior of chromosomes during mitosis and meiosis. In 1902, Theodor Boveri observed that proper embryonic development of sea urchins does not occur unless chromosomes are present. That same year, Walter Sutton observed the separation of chromosomes into daughter cells during meiosis. Together, these observations led to the development of the Chromosomal Theory of Inheritance, which identified chromosomes as the genetic material responsible for Mendelian inheritance.



(a) (b)

Figure 13.1A.1: Sutton and Boveri: (a) Walter Sutton and (b) Theodor Boveri are credited with developing the Chromosomal Theory of Inheritance, which states that chromosomes carry the unit of heredity (genes).

The Chromosomal Theory of Inheritance was consistent with Mendel's laws and was supported by the following observations:

- During meiosis, homologous chromosome pairs migrate as discrete structures that are independent of other chromosome pairs.
- The sorting of chromosomes from each homologous pair into pre-gametes appears to be random.
- Each parent synthesizes gametes that contain only half of their chromosomal complement.
- Even though male and female gametes (sperm and egg) differ in size and morphology, they have the same number of chromosomes, suggesting equal genetic contributions from each parent.
- The gametic chromosomes combine during fertilization to produce offspring with the same chromosome number as their parents.

Despite compelling correlations between the behavior of chromosomes during meiosis and Mendel's abstract laws, the Chromosomal Theory of Inheritance was proposed long before there was any direct evidence that traits were carried on chromosomes. Critics pointed out that individuals had far more independently segregating traits than they had chromosomes. It was only after several years of carrying out crosses with the fruit fly, *Drosophila melanogaster*, that Thomas Hunt Morgan provided experimental evidence to support the Chromosomal Theory of Inheritance.

In 1910, Thomas Hunt Morgan started his work with *Drosophila melanogaster*, a fruit fly. He chose fruit flies because they can be cultured easily, are present in large numbers, have a short generation time, and have only four pair of chromosomes that can be easily identified under the microscope. They have three pair of autosomes and a pair of sex chromosomes. At that time, he already knew that X and Y have to do with gender. He used normal flies with red eyes and mutated flies with white eyes and cross bred them. In flies, the wild type eye color is red (XW) and is dominant to white eye color (Xw). He was able to conclude that the gene for eye color was on the X chromosome. This trait was thus determined to be X-linked and was the first X-linked trait to be identified. Males are said to be hemizygous, in that they have only one allele for any X-linked characteristic.



Figure 13.1A.1: Eye Color in Fruit Flies: In Drosophila, the gene for eye color is located on the X chromosome. Red eye color is wild type and is dominant to white eye color.

Key Points

- Homologous chromosome pairs are independent of other chromosome pairs.
- Chromosomes from each homologous pair are sorted randomly into pre- gametes.
- Parents synthesize gametes that contain only half of their chromosomes; eggs and sperm have the same number of chromosomes.
- Gametic chromosomes combine during fertilization to produce offspring with the same chromosome number as their parents.
- Eye color in fruit flies was the first X-linked trait to be discovered; thus, Morgan's experiments with fruit flies solidified the Chromosomal Theory of Inheritance.

Key Terms

- **autosome**: any chromosome other than sex chromosomes
- **hemizygous**: having some single copies of genes in an otherwise diploid cell or organism
- **wild type**: the typical form of an organism, strain, gene or characteristic as it occurs in nature

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13.1B: Genetic Linkage and Distances

Learning Objectives

- Discuss how linked genes can be inherited separately

Genetic Linkage and Distances

Mendel's work suggested that traits are inherited independently of each other. Morgan identified a 1:1 ratio between a segregating trait and the X chromosome, suggesting that the random segregation of chromosomes was the physical basis of Mendel's model. This also demonstrated that linked genes disrupt Mendel's predicted outcomes. The fact that each chromosome can carry many linked genes explains how individuals can have many more traits than they have chromosomes. However, observations by researchers in Morgan's laboratory suggested that alleles positioned on the same chromosome were not always inherited together. During meiosis, linked genes somehow became unlinked.

Homologous Recombination

In 1909, Frans Janssen observed chiasmata (the point at which chromatids are in contact with each other and may exchange segments) prior to the first division of meiosis. He suggested that alleles become unlinked when chromosomes physically exchange segments. As chromosomes condensed and paired with their homologs, they appeared to interact at distinct points. Janssen suggested that these points corresponded to regions in which chromosome segments were exchanged. It is now known that the pairing and interaction between homologous chromosomes, known as synapsis, does more than simply organize the homologs for migration to separate daughter cells. When synapsed, homologous chromosomes undergo reciprocal physical exchanges of DNA at their arms in a process called homologous recombination, or more simply, "crossing over."

Genetic Maps

In 1913, Alfred Sturtevant, a student in Morgan's laboratory, created the first "chromosome map," a linear representation of gene order and relative distance on a chromosome.To construct a chromosome map, Sturtevant assumed that genes were ordered serially on threadlike chromosomes. He also assumed that the incidence of recombination between two homologous chromosomes could occur with equal likelihood anywhere along the length of the chromosome. Operating under these assumptions, Sturtevant hypothesized alleles that were far apart on a chromosome were more likely to dissociate during meiosis simply because there was a larger region over which recombination could occur. Conversely, alleles that were close to each other on the chromosome were likely to be inherited together. The average number of crossovers between two alleles, or their recombination frequency, correlated with their genetic distance from each other, relative to the locations of other genes on that chromosome. Sturtevant divided his genetic map into map units, or centimorgans (cM), in which a recombination frequency of 0.01 corresponds to 1 cM.

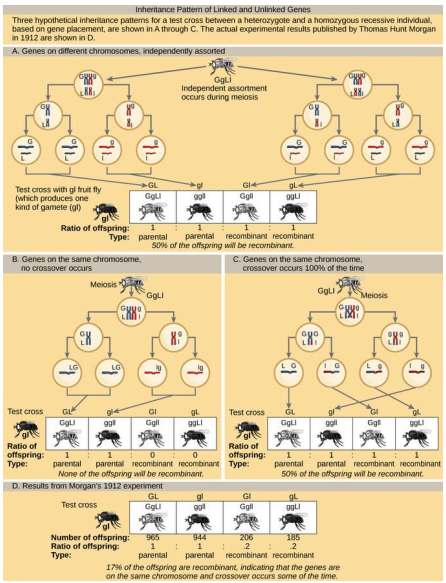


Figure $13.1B.1$: Inheritance Patterns of Unlinked and Linked Genes: In (a), two genes are located on different chromosomes so independent assortment occurs during meiosis. The offspring have an equal chance of being the parental type (inheriting the same combination of traits as the parents) or a nonparental type (inheriting a different combination of traits than the parents). In (b), two genes are very close together on the same chromosome so that no crossing over occurs between them. The genes are, therefore, always inherited together and all of the offspring are the parental type. In (c), two genes are far apart on the chromosome such that crossing over occurs during every meiotic event. The recombination frequency will be the same as if the genes were on separate chromosomes. (d) The actual recombination frequency of fruit fly wing length and body color that Thomas Morgan observed in 1912 was 17 percent. A crossover frequency between 0 percent and 50 percent indicates that the genes are on the same chromosome and crossover occurs some of the time.

Genetic Map Based on Recombination Frequencies in *Drosophila*

MUTANT		WILD TYPE
Short aristae	0	Long aristae
Black body	48.5	Gray body
Cinnabar eyes	57.5	Red eyes
Vestigial wings	65.5	Normal wings
Brown eyes	104.5	Red eyes

Values in centimorgan (cM) map units; recombination frequency of 0.01 = 1 cM

Figure $13.1B.1$: Genetic Maps: This genetic map orders Drosophila genes on the basis of recombination frequency.

By representing alleles in a linear map, Sturtevant suggested that genes can range from being perfectly linked (recombination frequency = 0) to being perfectly unlinked (recombination frequency = 0.5) when genes are on different chromosomes or genes are separated very far apart on the same chromosome. Perfectly unlinked genes correspond to the frequencies predicted by Mendel to assort independently in a dihybrid cross. A recombination frequency of 0.5 indicates that 50 percent of offspring are recombinants and the other 50 percent are parental types. That is, every type of allele combination is represented with equal frequency. This allowed Sturtevant to calculate distances between several genes on the same chromosome.

Key Points

- Alleles positioned on the same chromosome are not always inherited together because during meiosis linked genes can

became unlinked.
- Frans Janssen suggested chromosomes become unlinked during homologous recombination, a process where homologous chromosomes exchange segments of DNA.
- Alfred Sturtevant hypothesized that alleles that were closer together on a gene were more likely to be inherited together rather than alleles that were farther apart and used measurements of recombination between genes to create the first genetic map.
- When genes are perfectly linked, they have a recombination frequency of 0.
- When genes are unlinked, they have a recombination frequency of 0.5, which means 50 percent of offspring are recombinants and the other 50 percent are parental types.

Key Terms

- **homologous recombination**: a type of genetic recombination in which nucleotide sequences are exchanged between two similar or identical molecules of DNA
- **linkage**: the property of genes of being inherited together
- **synapsis**: the association of homologous maternal and paternal chromosomes during the initial part of meiosis

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13.1C: Identification of Chromosomes and Karyotypes

Learning Objectives

- Describe a normal human karyotype and discuss the various abnormalities that can be detected using this technique

Identification of Chromosomes

The isolation and microscopic observation of chromosomes forms the basis of cytogenetics and is the primary method by which clinicians detect chromosomal abnormalities in humans. A karyotype is the number and appearance of chromosomes. To obtain a view of an individual's karyotype, cytologists photograph the chromosomes and then cut and paste each chromosome into a chart, or karyogram, also known as an ideogram.

In a given species, chromosomes can be identified by their number, size, centromere position, and banding pattern. In a human karyotype, autosomes or "body chromosomes" (all of the non–sex chromosomes) are generally organized in approximate order of size from largest (chromosome 1) to smallest (chromosome 22). However, chromosome 21 is actually shorter than chromosome 22. This was discovered after the naming of Down syndrome as trisomy 21, reflecting how this disease results from possessing one extra chromosome 21 (three total). Not wanting to change the name of this important disease, chromosome 21 retained its numbering, despite describing the shortest set of chromosomes. The X and Y chromosomes are not autosomes and are referred to as the sex chromosomes.

The chromosome "arms" projecting from either end of the centromere may be designated as short or long, depending on their relative lengths. The short arm is abbreviated p (for "petite"), whereas the long arm is abbreviated q (because it follows "p" alphabetically). Each arm is further subdivided and denoted by a number. Using this naming system, locations on chromosomes can be described consistently in the scientific literature.

Although Mendel is referred to as the "father of modern genetics," he performed his experiments with none of the tools that the geneticists of today routinely employ. One such powerful cytological technique is karyotyping, a method in which traits characterized by chromosomal abnormalities can be identified from a single cell. To observe an individual's karyotype, a person's cells (like white blood cells) are first collected from a blood sample or other tissue. In the laboratory, the isolated cells are stimulated to begin actively dividing. A chemical called colchicine is then applied to cells to arrest condensed chromosomes in metaphase. Cells are then made to swell using a hypotonic solution so the chromosomes spread apart. Finally, the sample is preserved in a fixative and applied to a slide.

The geneticist then stains chromosomes with one of several dyes to better visualize the distinct and reproducible banding patterns of each chromosome pair. Following staining, the chromosomes are viewed using bright-field microscopy. A common stain choice is the Giemsa stain. Giemsa staining results in approximately 400–800 bands (of tightly coiled DNA and condensed proteins) arranged along all of the 23 chromosome pairs. An experienced geneticist can identify each chromosome based on its characteristic banding pattern. In addition to the banding patterns, chromosomes are further identified on the basis of size and centromere location. To obtain the classic depiction of the karyotype in which homologous pairs of chromosomes are aligned in numerical order from longest to shortest, the geneticist obtains a digital image, identifies each chromosome, and manually arranges the chromosomes into this pattern.



Figure 13.1C.1: A human karyotype: This karyotype is of a male human. Notice that homologous chromosomes are the same size, and have the same centromere positions and banding patterns. A human female would have an XX chromosome pair instead of the XY pair shown.

At its most basic, the karyotype may reveal genetic abnormalities in which an individual has too many or too few chromosomes per cell. Examples of this are Down Syndrome, which is identified by a third copy of chromosome 21, and Turner Syndrome, which is characterized by the presence of only one X chromosome in women instead of the normal two. Geneticists can also identify large deletions or insertions of DNA. For instance, Jacobsen Syndrome, which involves distinctive facial features as well as heart and bleeding defects, is identified by a deletion on chromosome 11. Finally, the karyotype can pinpoint translocations, which occur when a segment of genetic material breaks from one chromosome and reattaches to another chromosome or to a different part of the same chromosome. Translocations are implicated in certain cancers, including chronic myelogenous leukemia.

During Mendel's lifetime, inheritance was an abstract concept that could only be inferred by performing crosses and observing the traits expressed by offspring. By observing a karyotype, today's geneticists can actually visualize the chromosomal composition of an individual to confirm or predict genetic abnormalities in offspring, even before birth.

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Key Points

- A normal human karyotype contains 23 pairs of chromosomes: 22 pairs of autosomes and 1 pair of sex chromosomes, generally arranged in order from largest to smallest.
- The short arm of a chromosome is referred to as the p arm, while the long arm is designated the q arm.
- To observe a karyotype, cells are collected from a blood or tissue sample and stimulated to begin dividing; the chromosomes are arrested in metaphase, preserved in a fixative and applied to a slide where they are stained with a dye to visualize the distinct banding patterns of each chromosome pair.
- A karyotype can be used to visualize abnormalities in the chromosomes, such as an incorrect number of chromosomes, deletions, insertions, or translocations of DNA.

Key Terms

- **autosome**: any chromosome other than sex chromosomes
- **karyotype**: the observed characteristics (number, type, shape etc) of the chromosomes of an individual or species
- **translocation**: a transfer of a chromosomal segment to a new position, especially on a nonhomologous chromosome

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13.2: CHROMOSOMAL BASIS OF INHERITED DISORDERS



- Topic hierarchy

13.2A: Disorders in Chromosome Number

13.2B: Chromosomal Structural Rearrangements

13.2C: X-Inactivation

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13.2A: Disorders in Chromosome Number

Learning Objectives

- Define aneuploidy and explain how this condition results from nondisjunction

Disorders in Chromosome Number

Of all of the chromosomal disorders, abnormalities in chromosome number are the most obviously identifiable from a karyotype and are referred to as aneuploidy. Aneuploidy is a condition in which one or more chromosomes are present in extra copies or are deficient in number, but not a complete set. To be more specific, the loss of a single chromosome from a diploid genome is called monosomy (2n-1). The gain of one chromosome is called trisomy (2n+1).They are caused by nondisjunction, which occurs when pairs of homologous chromosomes or sister chromatids fail to separate during meiosis. Misaligned or incomplete synapsis, or a dysfunction of the spindle apparatus that facilitates chromosome migration, can cause nondisjunction. The risk of nondisjunction occurring increases with the age of the parents.

Nondisjunction can occur during either meiosis I or II, with differing results. If homologous chromosomes fail to separate during meiosis I, the result is two gametes that lack that particular chromosome and two gametes with two copies of the chromosome. If sister chromatids fail to separate during meiosis II, the result is one gamete that lacks that chromosome, two normal gametes with one copy of the chromosome, and one gamete with two copies of the chromosome. If a gamete with two copies of the chromosome combines with a normal gamete during fertilization, the result is trisomy; if a gamete with no copies of the chromosomes combines with a normal gamete during fertilization, the result is monosomy.

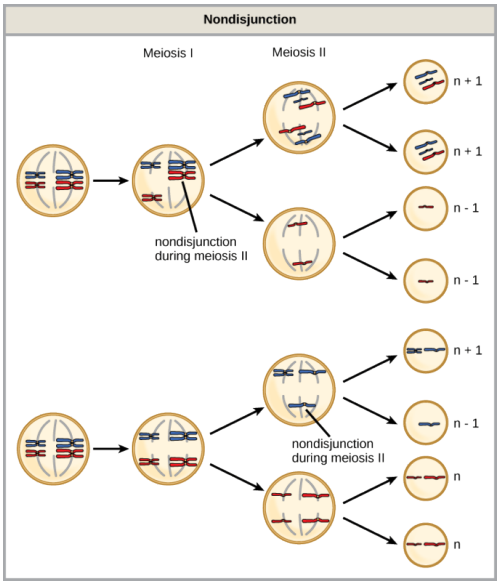


Figure 13.2A.1: Nondisjunction in Meiosis: Nondisjunction occurs when homologous chromosomes or sister chromatids fail to separate during meiosis, resulting in an abnormal chromosome number. Nondisjunction may occur during meiosis I or meiosis II.

Aneuploidy often results in serious problems such as Turner syndrome, a monosomy in which females may contain all or part of an X chromosome. Monosomy for autosomes is usually lethal in humans and other animals. Klinefelter syndrome is a trisomy genetic disorder in males caused by the presence of one or more X chromosomes. The effects of trisomy are similar to those of monosomy. Down syndrome is the only autosomal trisomy in humans that has a substantial number of survivors one year after birth. Trisomy in chromosome 21 is the cause of Down syndrome; it affects 1 infant in every 800 live births.

Key Points

- Aneuploidy is caused by nondisjunction, which occurs when pairs of homologous chromosomes or sister chromatids fail to separate during meiosis.
- The loss of a single chromosome from a diploid genome is called monosomy (2n-1), while the gain of one chromosome is called trisomy (2n+1).
- If homologous chromosomes fail to separate during meiosis I, the result is no gametes with the normal number (one) of chromosomes.
- If sister chromatids fail to separate during meiosis II, the result is two normal gametes each with one copy of the chromosome, and two abnormal gametes in which one carries two copies and the other carries none.
- Aneuploidy can be lethal or result in serious developmental disorders such as Turner Syndrome (X monosomy) or Downs Syndrome (trisomy 21).

Key Terms

- **aneuploidy**: the state of possessing a chromosome number that is not an exact multiple of the haploid number
- **nondisjunction**: the failure of chromosome pairs to separate properly during meiosis

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13.2B: Chromosomal Structural Rearrangements

Learning Objectives

- Describe the various types of structural rearrangements of chromosomes and how they can impact an organism

Chromosomal Structural Rearrangements

Cytologists have characterized numerous structural rearrangements in chromosomes, but chromosome inversions and translocations are the most common. Both are identified during meiosis by the adaptive pairing of rearranged chromosomes with their former homologs to maintain appropriate gene alignment. If the genes carried on two homologs are not oriented correctly, a recombination event could result in the loss of genes from one chromosome and the gain of genes on the other. This would produce aneuploid gametes.

Chromosome Inversions

A chromosome inversion is the detachment, 180° rotation, and reinsertion of part of a chromosome. Inversions may occur in nature as a result of mechanical shear, or from the action of transposable elements (special DNA sequences capable of facilitating the rearrangement of chromosome segments with the help of enzymes that cut and paste DNA sequences). Unless they disrupt a gene sequence, inversions only change the orientation of genes and are likely to have milder effects than aneuploid errors. However, altered gene orientation can result in functional changes because regulators of gene expression could be moved out of position with respect to their targets, causing aberrant levels of gene products.

An inversion can be pericentric and include the centromere, or paracentric and occur outside of the centromere. A pericentric inversion that is asymmetric about the centromere can change the relative lengths of the chromosome arms, making these inversions easily identifiable.

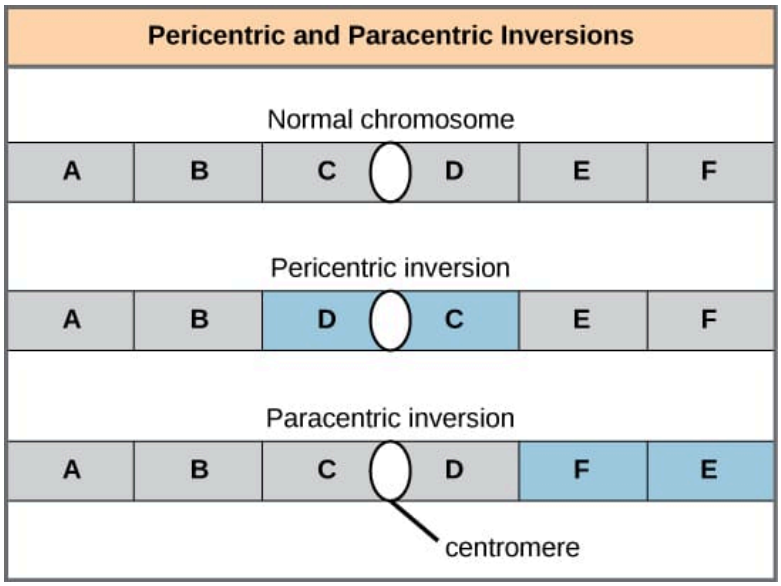


Figure 13.2B.1: Inversions can be pericentric or paracentric: Pericentric inversions include the centromere, and paracentric inversions do not. A pericentric inversion can change the relative lengths of the chromosome arms; a paracentric inversion cannot.

When one homologous chromosome undergoes an inversion, but the other does not, the individual is described as an inversion heterozygote. To maintain point-for-point synapsis during meiosis, one homolog must form a loop, and the other homolog must mold around it. Although this topology can ensure that the genes are correctly aligned, it also forces the homologs to stretch and can be associated with regions of imprecise synapsis.

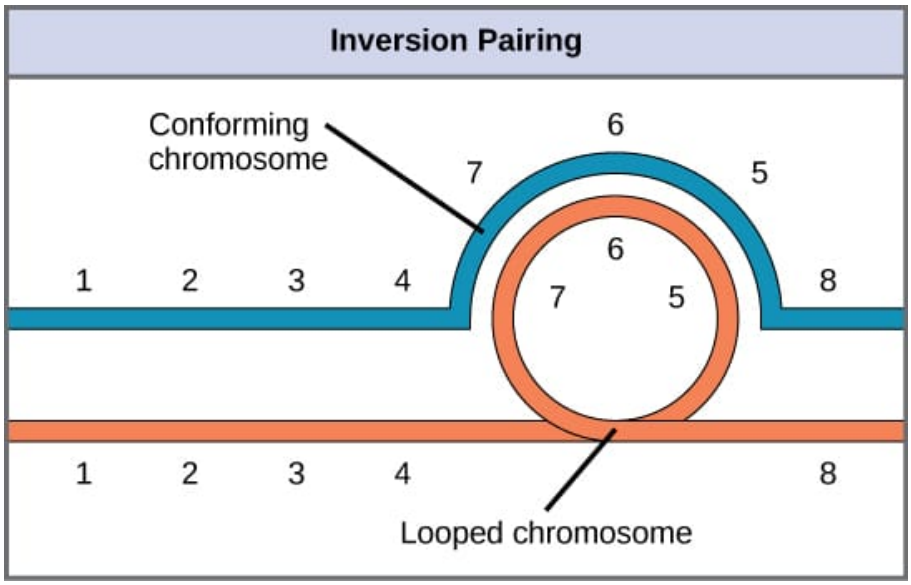


Figure 13.2B.1: Inversion heterozygotes: When one chromosome undergoes an inversion, but the other does not, one chromosome must form an inverted loop to retain point-for-point interaction during synapsis. This inversion pairing is essential to maintaining gene alignment during meiosis and to allow for recombination.

Not all structural rearrangements of chromosomes produce nonviable, impaired, or infertile individuals. In rare instances, such a change can result in the evolution of a new species. In fact, a pericentric inversion in chromosome 18 appears to have contributed to the evolution of humans. This inversion is not present in our closest genetic relatives, the chimpanzees. Humans and chimpanzees differ cytogenetically by pericentric inversions on several chromosomes and by the fusion of two separate chromosomes in chimpanzees that correspond to chromosome two in humans.

The pericentric chromosome 18 inversion is believed to have occurred in early humans following their divergence from a common ancestor with chimpanzees approximately five million years ago. Researchers characterizing this inversion have suggested that approximately 19,000 nucleotide bases were duplicated on 18p, and the duplicated region inverted and reinserted on chromosome 18 of an ancestral human.

A comparison of human and chimpanzee genes in the region of this inversion indicates that two genes—ROCK1 and USP14—that are adjacent on chimpanzee chromosome 17 (which corresponds to human chromosome 18) are more distantly positioned on human chromosome 18. This suggests that one of the inversion breakpoints occurred between these two genes. Interestingly, humans and chimpanzees express USP14 at distinct levels in specific cell types, including cortical cells and fibroblasts. Perhaps the chromosome 18 inversion in an ancestral human repositioned specific genes and reset their expression levels in a useful way. Because both ROCK1 and USP14 encode cellular enzymes, a change in their expression could alter cellular function. It is not known how this inversion contributed to hominid evolution, but it appears to be a significant factor in the divergence of humans from other primates.

Translocations

A translocation occurs when a segment of a chromosome dissociates and reattaches to a different, nonhomologous chromosome. Translocations can be benign or have devastating effects depending on how the positions of genes are altered with respect to regulatory sequences. Notably, specific translocations have been associated with several cancers and with schizophrenia. Reciprocal translocations result from the exchange of chromosome segments between two nonhomologous chromosomes such that there is no gain or loss of genetic information.

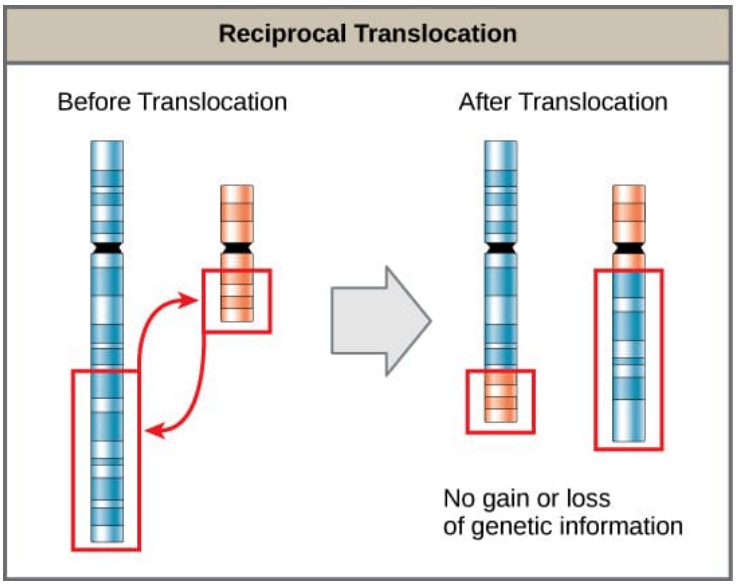


Figure 13.2B.1: Reciprocal translocations do not involve loss of genetic information: A reciprocal translocation occurs when a segment of DNA is transferred from one chromosome to another, nonhomologous chromosome.

Key Points

- A chromosome inversion is the detachment, 180° rotation, and reinsertion of part of a chromosome; this may have no effect on the organism, but if the inversion occurs within a gene or moves a gene away from its regulatory elements it can have an adverse effect.
- Pericentric inversions include the centromere, while paracentric inversions occur outside of the centromere; a pericentric inversion can change the length of the chromosome arms above and below the centromere.
- A pericentric inversion on chromsome 18 appears to have been involved in the evolution of humans.
- A translocation occurs when a segment of a chromosome dissociates and reattaches to a different, nonhomologous chromosome and can be benign or detrimental; in reciprocal translocations, there is no gain or loss of genetic information, so these are usually benign.

Key Terms

- **inversion**: a segment of DNA in the context of a chromosome that is reversed in orientation relative to a reference karyotype or genome
- **translocation**: a transfer of a chromosomal segment to a new position, especially on a nonhomologous chromosome

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13.2C: X-Inactivation

Learning Objectives

- Explain how and why X inactivation occurs in humans

Sex Chromosome Nondisjunction in Humans

Humans display dramatic deleterious effects with autosomal trisomies and monosomies. Therefore, it may seem counterintuitive that human females and males can function normally, despite carrying different numbers of the X chromosome. Rather than a gain or loss of autosomes, variations in the number of X chromosomes are associated with relatively mild effects. In part, this occurs because of a molecular process called X inactivation. Early in development, when female mammalian embryos consist of just a few thousand cells (relative to trillions in the newborn), one X chromosome in each cell inactivates by tightly condensing into a quiescent (dormant) structure called a Barr body. The chance that an X chromosome (maternally or paternally derived) is inactivated in each cell is random, but once the inactivation occurs, all cells derived from that single cell will have the same inactive X chromosome or Barr body.

By this process, a phenomenon called dosage compensation is achieved. Females possess two X chromosomes, while males have only one; therefore, if both X chromosomes remained active in the female, they would produce twice as much product from the genes on the X chromosomes as males.

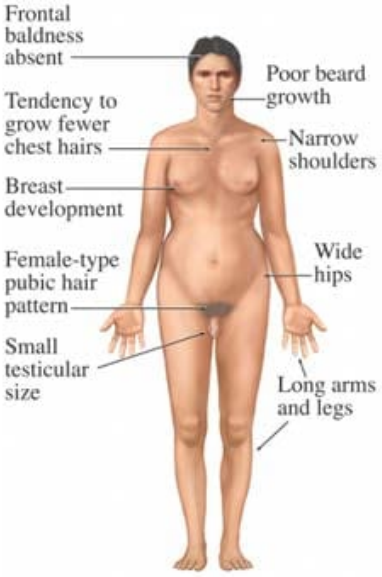


Figure $13.2C.1$: Sex Chromosome Nondisjunction: The symptoms of Klinefelter's syndrome (XXY) in a human male.

So how does X-inactivation help alleviate the effects of extra X chromosomes? An individual carrying an abnormal number of X chromosomes will inactivate all but one X chromosome in each of her cells. If three X chromosomes are present, the cell will inactivate two of them. If four X chromosomes are present, three will be inactivated, and so on. This results in an individual that is relatively phenotypically normal. However, even inactivated X chromosomes continue to express a few genes, and X chromosomes must reactivate for the proper maturation of female ovaries. As a result, X-chromosomal abnormalities are typically associated with mild mental and physical defects, as well as sterility. If the X chromosome is absent altogether, the individual will not develop in utero.

Several errors in sex chromosome number have been characterized. Individuals with three X chromosomes, called triplo-X, are phenotypically female, but express developmental delays and reduced fertility. The XXY genotype, corresponding to one type of Klinefelter syndrome, corresponds to phenotypically male individuals with small testes, enlarged breasts, and reduced body hair. More complex types of Klinefelter syndrome exist in which the individual has as many as five X chromosomes. In all types, every X

chromosome except one undergoes inactivation to compensate for the excess genetic dosage. This can be seen as several Barr bodies in each cell nucleus. Turner syndrome, characterized as an XO genotype (i.e., only a single sex chromosome), corresponds to a phenotypically female individual with short stature, webbed skin in the neck region, hearing and cardiac impairments, and sterility.

Duplications and Deletions

In addition to the loss or gain of an entire chromosome, a chromosomal segment may be duplicated or lost. Duplications and deletions often produce offspring that survive but exhibit physical and mental abnormalities. Duplicated chromosomal segments may fuse to existing chromosomes or may be free in the nucleus. Cri-du-chat (from the French for "cry of the cat") is a syndrome associated with nervous system abnormalities and identifiable physical features that result from a deletion of most of 5p (the small arm of chromosome 5). Infants with this genotype emit a characteristic high-pitched cry on which the disorder's name is based.



Figure 13.2C.1: Cri-du-chat Syndrome: This individual with cri-du-chat syndrome is shown at two, four, nine, and 12 years of age.

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Key Points

- Extra copies of the X chromosome are silenced by becoming Barr bodies.
- X chromosomal abnormalities are typically associated with mild mental and physical defects, as well as sterility.
- Conditions associated with aneuploidy of the sex chromosomes include individuals with three X chromosomes, called triplo-X; the XXY genotype, known as Klinefelter syndrome; and Turner syndrome, characterized as X monosomy.
- X-inactivation is a form of dosage compensation, in which an organism attempts to equalize the amount of X chromosome gene products in males and females.
- Since males only have one X chromosome, females inactivate one of theirs so that only one X chromosome is active in each gender.

Key Terms

- **dosage compensation**: a genetic regulatory mechanism that equalizes the phenotypic expression of characteristics determined by genes on the X chromosome so that they are equally expressed in males and females.
- **Barr body**: a sex chromosome inactivated by packing in heterochromatin
- **X inactivation**: a process by which one of the two copies of the X chromosome present in female mammals is inactivated

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14: DNA STRUCTURE AND FUNCTION



- Topic hierarchy

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14.2: DNA Structure and Sequencing

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14.4: DNA Repair

14.4A: DNA Repair

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14.1: HISTORICAL BASIS OF MODERN UNDERSTANDING

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- Topic hierarchy

14.1A: Discovery of DNA

14.1B: Modern Applications of DNA

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14.1A: Discovery of DNA

Learning Objectives

- Explain the sequence of events leading up to the discovery of the structure of DNA

What is DNA?

Deoxyribonucleic acid (DNA) is a molecule that carries most of the genetic instructions used in the development, functioning and reproduction of all known living organisms and many viruses.

DNA is a nucleic acid; alongside proteins and carbohydrates, nucleic acids are one of the three major macromolecules essential for all known forms of life. DNA stores biological information and is involved in the expression of traits in all living organisms.

The Path to Discovery

In the 1950s, Francis Crick and James Watson worked together to determine the structure of DNA at the University of Cambridge, England. At the time, other scientists like Linus Pauling and Maurice Wilkins were also actively exploring this field. Pauling had discovered the secondary structure of proteins using X-ray crystallography.

Chargaff's Rule

Erwin Chargaff met Francis Crick and James D. Watson at Cambridge in 1952, and, despite not getting along with them personally, he explained his findings to them. Chargaff's Rule showed that in natural DNA, the number of guanine units equals the number of cytosine units and the number of adenine units equals the number of thymine units. This strongly hinted towards the base pair makeup of the DNA. Chargaff's research would help the Watson and Crick laboratory team to deduce the double helical structure of DNA.

Franklin and X-Ray Diffraction

In Wilkins' lab, researcher Rosalind Franklin used X-ray diffraction methods to understand the structure of DNA. Watson and Crick were able to piece together the puzzle of the DNA molecule on the basis of Franklin's data, because Crick had also studied X-ray diffraction. In 1962, James Watson, Francis Crick, and Maurice Wilkins were awarded the Nobel Prize in Medicine.



(a) (b)

Figure 14.1A.1: A team effort: The work of pioneering scientists James Watson, Francis Crick, and Maclyn McCarty (pictured at left) led to our present day understanding of DNA. Scientist Rosalind Franklin discovered the X-ray diffraction pattern of DNA (pictured at right), which helped to elucidate its double helix structure. (credit a: modification of work by Marjorie McCarty, Public Library of Science)

Unfortunately by then, Franklin had died. Nobel prizes are not awarded posthumously, and though her work was crucial to the discovery of DNA, Franklin was never nominated for a Nobel Prize. Francis Crick, James Watson, and Maurice Wilkins were awarded a Nobel Prize for the discovery of the structure of DNA in 1962. There is still much controversy on how her image was given to Watson and Crick and why she was not given due credit.

Key Points

- DNA is one of the most basic molecules of life; it carries genetic instructions for the development, functioning and reproduction of all known living organisms.
- The discovery of DNA's double-helix structure is largely credited to the scientists Watson and Crick, for which they won a Nobel Prize.
- However, the X-ray crystallography work of Rosalind Franklin and Erwin Chargaff's work in discovering the composition of DNA were instrumental to the discovery of DNA's structure.

Key Terms

- **double helix**: The structure formed by double-stranded molecules of nucleic acids such as DNA.

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14.1B: Modern Applications of DNA

Learning Objectives

- Explain why DNA is a practical tool in various fields, such as forensics and medicine

The acronym “DNA” has become synonymous with solving crimes, testing for paternity, identifying human remains, and genetic testing. DNA can be retrieved from hair, blood, or saliva. Each person’s DNA sequences are unique, and it is possible to detect differences between individuals within a species on the basis of these unique features. DNA testing can also be used to identify pathogens, identify biological remains in archaeological digs, trace disease outbreaks, and study human migration patterns. In the medical field, DNA is used in diagnostics, new vaccine development, and cancer therapy. It is now also possible to determine predispositions to some diseases by looking at genes.

Cloning

Reproductive cloning is a method used to make a clone or an identical copy of an entire multicellular organism.
In cloning both the original organism and the clone have identical DNA. Identical twins are, in one sense, clones of each other; they have identical DNA, having developed from the same fertilized egg.
Cloning became an issue in scientific ethics when a sheep became the first mammal cloned from an adult cell in 1996.
Since then several animals such as horses, bulls, and goats have been successfully cloned, although these individuals often exhibit facial, limb, and cardiac abnormalities.



Figure $14.1B.1$: Modern understanding of DNA structure and function has led to cloning: Dolly the sheep was the first large mammal to be cloned.

There have been attempts at producing cloned human embryos as sources of embryonic stem cells, sometimes referred to as ‘cloning for therapeutic purposes’. Therapeutic cloning produces stem cells to attempt to remedy detrimental diseases or defects (unlike reproductive cloning, which aims to reproduce an organism). Still, therapeutic cloning efforts have met with resistance because of bioethical considerations.

CRISPR

CRISPR (Clustered, Regularly-Interspaced Short Palindromic Repeats) allows scientists to edit genomes, far better than older techniques for gene splicing and editing. The CRISPR technique has enormous potential application, including altering the

germline of humans, animals and other organisms, and modifying the genes of food crops.
Ethical concerns have surfaced about this biotechnology and the prospect of editing the human germline and making so-called 'designer babies'.

CRISPR Technique: This movie goes through the process of CRISPR.

Genetically Modified Organisms

A genetically modified organism (GMO) is any organism whose genetic material has been altered using genetic engineering techniques. GMOs are a source of medicines and genetically modified foods and are also widely used in scientific research, along with the production of other goods.
Genetic modification involves the mutation, insertion, or deletion of genes. Inserted genes usually come from a different species in a form of horizontal gene-transfer.



Figure 14.1B.1: Glo Fish: The GloFish is a patented and trademarked brand of genetically modified (GM) fluorescent fish. A gene that encodes the green fluorescent protein, originally extracted from a jellyfish, that naturally produced bright green fluorescence was inserted into a zebrafish embryo.

Bacteria, plants, and animals have been genetically modified since the early 1970s for academic, medical, agricultural, and industrial purposes. In the US, GMOs such as Roundup-Ready soybeans and borer-resistant corn are part of many common processed foods. As in many of these biotechnology areas there is considerable controversy in the use of GMOs.

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Key Points

- DNA is unique to each individual, and therefore can be used for identification purposes.
- The human genome consists of about 3 billion base pairs, corresponding to about 20,000 to 25,000 functional genes.
- Each person's DNA is inherited from their parents: 23 chromosomes from the mother, and 23 chromosomes from the father.

Key Terms

- **genotype**: The combination of alleles, situated on corresponding chromosomes, that determines a specific trait of an individual.
- **zygote**: The single cell that arises from the union of two gametes; in animals, the cell that arises from the union of sperm and ovum.
- **gene**: A unit of heredity; the functional units of chromosomes that determine specific characteristics by coding for specific RNAs or proteins.
- **phenotype**: The appearance of an organism based on a multifactorial combination of genetic traits and environmental factors.

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14.2: DNA STRUCTURE AND SEQUENCING

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- Topic hierarchy

14.2A: The Structure and Sequence of DNA
14.2B: DNA Sequencing Techniques

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14.2A: The Structure and Sequence of DNA

Learning Objectives

- Describe the structure of DNA and summarize the importance of DNA sequencing

The monomeric building blocks of DNA are deoxyribomononucleotides (usually referred to as just nucleotides), and DNA is formed from linear chains, or polymers, of these nucleotides. The components of the nucleotide used in DNA synthesis are a nitrogenous base, a deoxyribose, and a phosphate group. The nucleotide is named depending on which nitrogenous base is present. The nitrogenous base can be a purine such as adenine (A) and guanine (G), characterized by double-ring structures, or a pyrimidine such as cytosine (C) and thymine (T), characterized by single-ring structures. In polynucleotides (the linear polymers of nucleotides) the nucleotides are connected to each other by covalent bonds known as phosphodiester bonds or phosphodiester linkages.

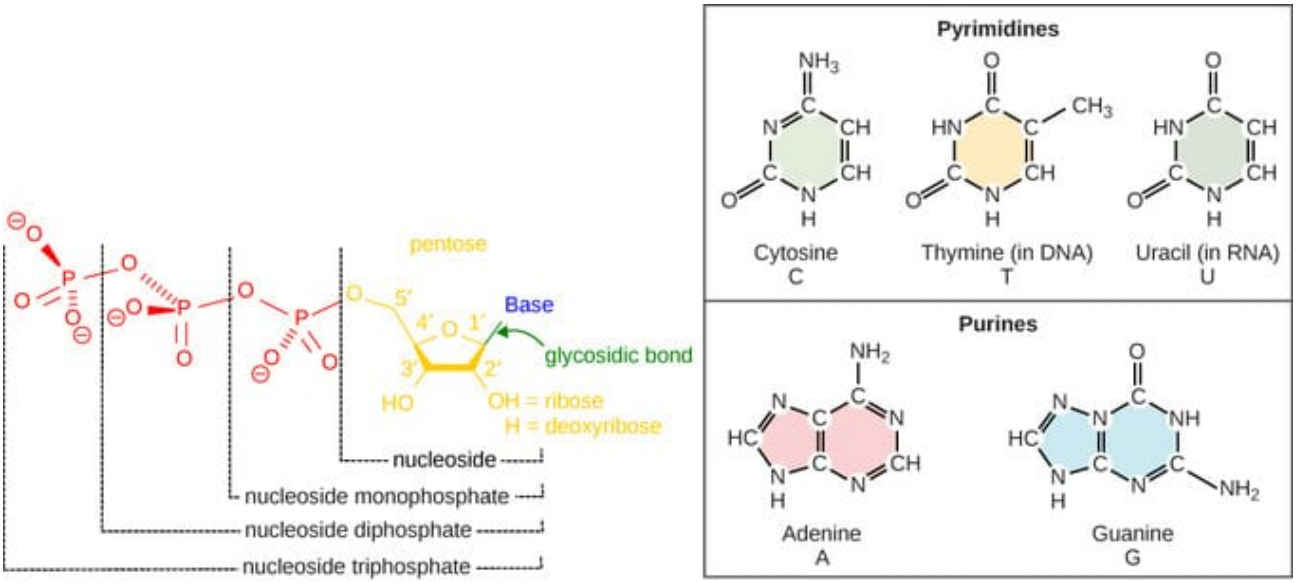


Figure 14.2A.1: Nucleotide Structure: Each nucleotide is made up of a sugar, a phosphate group, and a nitrogenous base. The sugar is deoxyribose in DNA and ribose in RNA. In their mononucleotide form, nucleotides can have one, two, or three phosphates attached to them. When linked together in polynucleotide chains, the nucleotides always have just one phosphate. A molecule with just a nitrogenous base and a sugar is known as a nucleoside. Once at least one phosphate is covalently attached, it is known as a nucleotide.

James Watson and Francis Crick, with some help from Rosalind Franklin and Maurice Wilkins, are credited with figuring out the structure of DNA. Watson and Crick proposed that DNA is made up of two polynucleotide strands that are twisted around each other to form a right-handed helix.

The two polynucleotide strands are anti-parallel in nature. That is, they run in opposite directions.

The sugars and phosphates of the nucleotides form the backbone of the structure, whereas the pairs of nitrogenous bases are pointed towards the interior of the molecule.

The twisting of the two strands around each other results in the formation of uniformly-spaced major and minor grooves bordered by the sugar-phosphate backbones of the two strands.

image

Figure 14.2A.1: Three representations of DNA's double helical structure.: A is a spacefill model of DNA, where every atom is represented as a sphere. The two anti-parallel polynucleotide strands are colored differently to illustrate how they coil around each other. B is a cartoon model of DNA, where the sugar-phosphate backbones are represented as violet strands and the nitrogenous bases are represented as color-coded rings. C is another spacefill model, with the sugar-phosphate atoms colored violet and all nitrogenous base atoms colored green. The major and minor grooves, which wrap around the entire molecule, are apparent as the spaces between the sugar-phosphate backbones.

The diameter of the DNA double helix is 2 nm and is uniform throughout. Only the pairing between a purine and pyrimidine can explain the uniform diameter. That is to say, at each point along the DNA molecule, the two sugar phosphate backbones are always separated by three rings, two from a purine and one from a pyrimidine.

The two strands are held together by base pairing between nitrogenous bases of one strand and nitrogenous bases from the other strand. Base pairing takes place between a purine and pyrimidine stabilized by hydrogen bonds: A pairs with T via two hydrogen bonds and G pairs with C via three hydrogen bonds.

The interior basepairs rotate with respect to one another, but are also stacked on top of each other when the molecule is viewed looking up or down its long axis.

Each base pair is separated from the previous base pair by a height of 0.34 nm and each 360° turn of the helix travels 3.4 nm along the long axis of the molecule. Therefore, ten base pairs are present per turn of the helix.

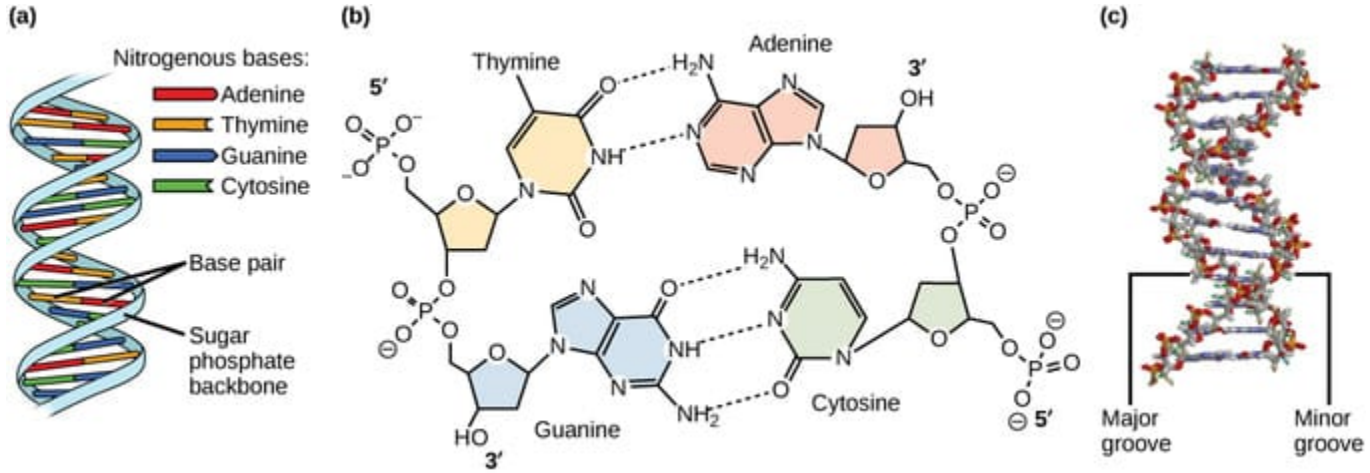


Figure 14.2A.1: DNA Structure: DNA has (a) a double helix structure and (b) phosphodiester bonds. The (c) major and minor grooves are binding sites for DNA binding proteins during processes such as transcription (the copying of RNA from DNA) and replication.

DNA sequencing is the process of determining the precise order of nucleotides within a DNA molecule. Rapid DNA sequencing methods has greatly accelerated biological and medical research and discovery. Knowledge of DNA sequences has become indispensable for basic biological research, and in numerous applied fields such as diagnostics, biotechnology, forensic biology, and biological systematics. The rapid speed of sequencing attained with modern technology has been instrumental in obtaining complete DNA sequences, or genomes, of numerous types and species of life, including the human genome and those of other animal, plant, and microbial species.

Key Points

- The two DNA strands are anti-parallel in nature; that is, the 3′ end of one strand faces the 5′ end of the other strand.
- The nucleotides that comprise DNA contain a nitrogenous base, a deoxyribose sugar, and a phosphate group which covalently link with other nucleotides to form phosphodiester bonds.
- Nucleotide bases can be classified as purines (containing a double-ring structure) or pyrimidines (containing a single-ring structure).
- Adenine (purine) and thymine (pyrimidine) are complementary base pairs as are guanine (purine) and cytosine (pyrimidine).
- DNA sequencing is the process of determining the precise order of nucleotides within a DNA molecule.

Key Terms

- **deoxyribose**: a derivative of the pentose sugar ribose in which the 2′ hydroxyl (-OH) is reduced to a hydrogen (H); a constituent of the nucleotides that comprise deoxyribonucleic acid, or DNA
- **hydrogen bond**: A weak bond in which a hydrogen atom already covalently bonded to a oxygen or nitrogen atom in one molecule is attracted to an electronegative atom (usually nitrogen or oxygen) in the same or different molecule.
- **nucleotide**: the monomer comprising DNA or RNA molecules; consists of a nitrogenous heterocyclic base that can be a purine or pyrimidine, a five-carbon pentose sugar, and a phosphate group

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14.2B: DNA Sequencing Techniques

Learning Objectives

- Differentiate among the techniques used to sequence DNA

DNA Sequencing Techniques

While techniques to sequence proteins have been around since the 1950s, techniques to sequence DNA were not developed until the mid-1970s, when two distinct sequencing methods were developed almost simultaneously, one by Walter Gilbert's group at Harvard University, the other by Frederick Sanger's group at Cambridge University. However, until the 1990s, the sequencing of DNA was a relatively expensive and long process. Using radiolabeled nucleotides also compounded the problem through safety concerns. With currently-available technology and automated machines, the process is cheaper, safer, and can be completed in a matter of hours. The Sanger sequencing method was used for the human genome sequencing project, which was finished its sequencing phase in 2003, but today both it and the Gilbert method have been largely replaced by better methods.

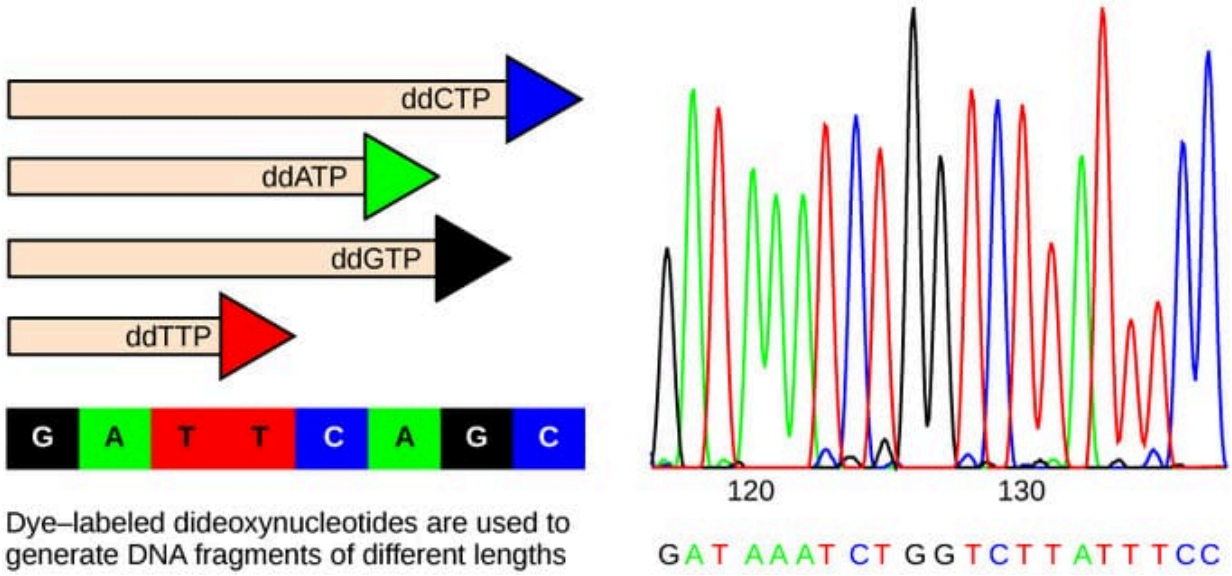


Figure 14.2B.1: Sanger Method: In Frederick Sanger's dideoxy chain termination method, fluorescent-labeled dideoxynucleotides are used to generate DNA fragments that terminate at each nucleotide along the template strand. The DNA is separated by capillary electrophoresis on the basis of size. From the order of fragments formed, the DNA sequence can be read. The smallest fragments were terminated earliest, and they come out of the column first, so the order in which different fluorescent tags exit the column is also the sequence of the strand. The DNA sequence readout is shown on an electropherogram that is generated by a laser scanner.

Sanger Sequencing

The Sanger method is also known as the dideoxy chain termination method. This sequencing method is based on the use of chain terminators, the dideoxynucleotides (ddNTPs). The dideoxynucleotides, or ddNTPSs, differ from deoxynucleotides by the lack of a free 3′ OH group on the five-carbon sugar. If a ddNTP is added to a growing DNA strand, the chain is not extended any further because the free 3′ OH group needed to add another nucleotide is not available. By using a predetermined ratio of deoxyribonucleotides to dideoxynucleotides, it is possible to generate DNA fragments of different sizes when replicating DNA in vitro.

A Sanger sequencing reaction is just a modified in vitro DNA replication reaction. As such the following components are needed: template DNA (which will the be DNA whose sequence will be determined), DNA Polymerase to catalyze the replication reactions, a primer that basepairs prior to the portion of the DNA you want to sequence, dNTPs, and ddNTPs. The ddNTPs are what

distinguish a Sanger sequencing reaction from just a replication reaction. Most of the time in a Sanger sequencing reaction, DNA Polymerase will add a proper dNTP to the growing strand it is synthesizing in vitro. But at random locations, it will instead add a ddNTP. When it does, that strand will be terminated at the ddNTP just added. If enough template DNAs are included in the reaction mix, each one will have the ddNTP inserted at a different random location, and there will be at least one DNA terminated at each different nucleotide along its length for as long as the in vitro reaction can take place (about 900 nucleotides under optimal conditions.)

The ddNTPs which terminate the strands have fluorescent labels covalently attached to them. Each of the four ddNTPs carries a different label, so each different ddNTP will fluoresce a different color.

After the reaction is over, the reaction is subject to capillary electrophoresis. All the newly synthesized fragments, each terminated at a different nucleotide and so each a different length, are separated by size. As each differently-sized fragment exits the capillary column, a laser excites the flourescent tag on its terminal nucleotide. From the color of the resulting flouresence, a computer can keep track of which nucleotide was present as the terminating nucleotide. The computer also keeps track of the order in which the terminating nucleotides appeared, which is the sequence of the DNA used in the original reaction.

Second Generation and Next-generation Sequencing

The Sanger and Gilbert methods of sequencing DNA are often called “first-generation” sequencing because they were the first to be developed. In the late 1990s, new methods, called second-generation sequencing methods, that were faster and cheaper, began to be developed. The most popular, widely-used second-generation sequencing method was one called Pyrosequencing.

Today a number of newer sequencing methods are available and others are in the process of being developed. These are often called next-generation sequencing methods. The most widely-used sequencing method currently is one called Illumina sequencing (after the name of the company which commercialized the technique), but numerous competing methods are in the developmental pipeline and may supplant Illumina sequencing.

In Illumina sequencing, up to 500,000,000 separate sequencing reactions are run simultaneously on a single slide (the size of a microscope slide) put into a single machine. Each reaction is analyzed separately and the sequences generated from all 500 million DNAs are stored in an attached computer. Each sequencing reaction is a modified replication reaction involving flourescently-tagged nucleotides, but no chain-terminating dideoxy nucleotides are needed.

When the human genome was first sequenced using Sanger sequencing, it took several years, hundreds of labs working together, and a cost of around $100 million to sequence it to almost completion. Next generation sequencing can sequence a comparably-sized genome in a matter of days, using a single machine, at a cost of under $10,000. Many researchers have set a goal of improving sequencing methods even more until a single human genome can be sequenced for under $1000.

Shotgun Sequencing

Sanger sequence can only produce several hundred nucleotides of sequence per reaction. Most next-generation sequencing techniques generate even smaller blocks of sequence. Genomes are made up of chromosomes which are tens to hundreds of millions of basepairs long. They can only be sequenced in tiny fragments and the tiny fragments have to put in the correct order to generate the uninterrupted genome sequence. Most genomic sequencing projects today make use of an approach called whole genome shotgun sequencing.

Whole genome shotgun sequencing involves isolating many copies of the chromosomal DNA of interest. The chromosomes are all fragmented into sizes small enough to be sequenced (a few hundred basepairs) at random locations. As a result, each copy of the same chromosome is fragmented at different locations and the fragments from the same part of the chromosome will overlap each other. Each fragment is sequenced and sophisticated computer algorithms compare all the different fragments to find which overlaps with which. By lining up the overlapped regions, a process called tiling, the computer can find the largest possible continuous sequences that can be generated from the fragments. Ultimately, the sequence of entire chromosomes are assembled.

image

Figure 14.2B.1: Whole genome shotgun sequencing.: In shotgun sequencing, multiple copies of the same chromosome are isolated and then fragmented in random locations. The different copies of the chromosome end up generating different length fragments. When the complete collection of fragments has been sequenced, comparing the sequences of all the fragments will reveal which fragments have ends that overlap with other fragments. The complete sequence from one end of the original DNA to the other can be assembled by following the sequence from the first overlapping fragment to the last.

Genome sequencing will greatly advance our understanding of genetic biology. It has vast potential for medical diagnosis and treatment.

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Key Points

- Genome sequencing will greatly advance our understanding of genetic biology and has vast potential for medical diagnosis and treatment.
- DNA sequencing technologies have gone through at least three “generations”: Sanger sequencing and Gilbert sequencing were first-generation, pyrosequencing was second-generation, and Illumina sequencing is next-generation.
- Sanger sequencing is based on the use of chain terminators, ddNTPs, that are added to growing DNA strands and terminate synthesis at different points.
- Illumina sequencing involves running up to 500,000,000 different sequencing reactions simultaneously on a single small slide. It makes use of a modified replication reaction and uses fluorescently-tagged nucleotides.
- Shotgun sequencing is a technique for determining the sequence of entire chromosomes and entire genomes based on producing random fragments of DNA that are then assembled by computers which order fragments by finding overlapping

ends.

Key Terms

- **DNA sequencing**: a technique used in molecular biology that determines the sequence of nucleotides (A, C, G, and T) in a particular region of DNA
- **dideoxynucleotide**: any nucleotide formed from a deoxynucleotide by loss of an a second hydroxyl group from the deoxyribose group
- **in vitro**: any biochemical process done outside of its natural biological environment, such as in a test tube, petri dish, etc. (from the Latin for “in glass”)

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14.3: DNA REPLICATION

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- Topic hierarchy

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14.3B: DNA Replication in Prokaryotes

14.3C: DNA Replication in Eukaryotes

14.3D: Telomere Replication

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14.3A: Basics of DNA Replication

Learning Objectives

- Explain how the Meselson and Stahl experiment conclusively established that DNA replication is semi-conservative.

Basics of DNA Replication

Watson and Crick's discovery that DNA was a two-stranded double helix provided a hint as to how DNA is replicated. During cell division, each DNA molecule has to be perfectly copied to ensure identical DNA molecules to move to each of the two daughter cells. The double-stranded structure of DNA suggested that the two strands might separate during replication with each strand serving as a template from which the new complementary strand for each is copied, generating two double-stranded molecules from one.

Models of Replication

There were three models of replication possible from such a scheme: conservative, semi-conservative, and dispersive. In conservative replication, the two original DNA strands, known as the parental strands, would re-basepair with each other after being used as templates to synthesize new strands; and the two newly-synthesized strands, known as the daughter strands, would also basepair with each other; one of the two DNA molecules after replication would be "all-old" and the other would be "all-new". In semi-conservative replication, each of the two parental DNA strands would act as a template for new DNA strands to be synthesized, but after replication, each parental DNA strand would basepair with the complementary newly-synthesized strand just synthesized, and both double-stranded DNAs would include one parental or "old" strand and one daughter or "new" strand. In dispersive replication, after replication both copies of the new DNAs would somehow have alternating segments of parental DNA and newly-synthesized DNA on each of their two strands.

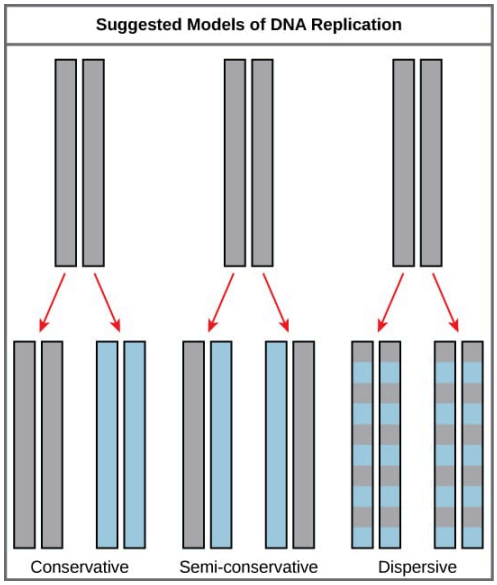


Figure 14.3A.1: Suggested Models of DNA Replication: The three suggested models of DNA replication. Grey indicates the original parental DNA strands or segments and blue indicates newly-synthesized daughter DNA strands or segments.

To determine which model of replication was accurate, a seminal experiment was performed in 1958 by two researchers: Matthew Meselson and Franklin Stahl.

Meselson and Stahl

Meselson and Stahl were interested in understanding how DNA replicates. They grew *E. coli* for several generations in a medium containing a “heavy” isotope of nitrogen (^{15}N) that is incorporated into nitrogenous bases and, eventually, into the DNA. The *E. coli* culture was then shifted into medium containing the common “light” isotope of nitrogen (^{14}N) and allowed to grow for one generation. The cells were harvested and the DNA was isolated. The DNA was centrifuged at high speeds in an ultracentrifuge in a tube in which a cesium chloride density gradient had been established. Some cells were allowed to grow for one more life cycle in ^{14}N and spun again.

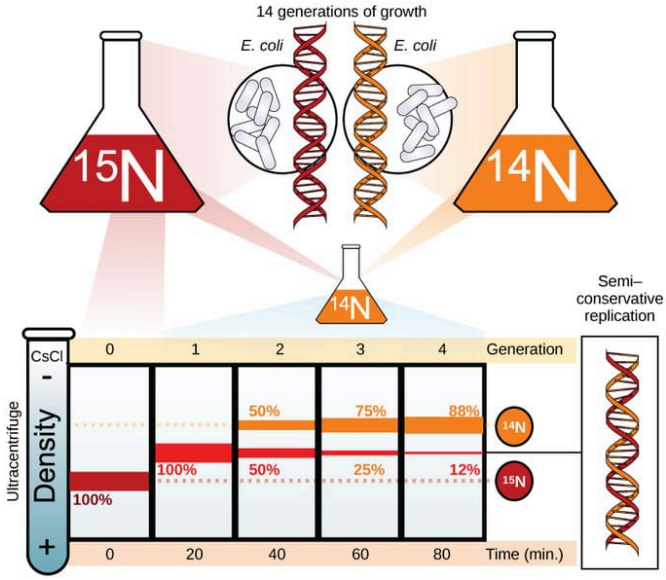


Figure 14.3A.1: Meselson and Stahl: Meselson and Stahl experimented with E. coli grown first in heavy nitrogen (^{15}N) then in ligher nitrogen (^{14}N.) DNA grown in ^{15}N (red band) is heavier than DNA grown in ^{14}N (orange band) and sediments to a lower level in the cesium chloride density gradient in an ultracentrifuge. When DNA grown in ^{15}N is switched to media containing ^{14}N, after one round of cell division the DNA sediments halfway between the ^{15}N and ^{14}N levels, indicating that it now contains fifty percent ^{14}N and fifty percent ^{15}N.. In subsequent cell divisions, an increasing amount of DNA contains ^{14}N only. These data support the semi-conservative replication model.

During the density gradient ultracentrifugation, the DNA was loaded into a gradient (Meselson and Stahl used a gradient of cesium chloride salt, although other materials such as sucrose can also be used to create a gradient) and spun at high speeds of 50,000 to 60,000 rpm. In the ultracentrifuge tube, the cesium chloride salt created a density gradient, with the cesium chloride solution being more dense the farther down the tube you went. Under these circumstances, during the spin the DNA was pulled down the ultracentrifuge tube by centrifugal force until it arrived at the spot in the salt gradient where the DNA molecules’ density matched that of the surrounding salt solution. At the point, the molecules stopped sedimenting and formed a stable band. By looking at the relative positions of bands of molecules run in the same gradients, you can determine the relative densities of different molecules. The molecules that form the lowest bands have the highest densities.

DNA from cells grown exclusively in ^{15}N produced a lower band than DNA from cells grown exclusively in ^{14}N. So DNA grown in ^{15}N had a higher density, as would be expected of a molecule with a heavier isotope of nitrogen incorporated into its nitrogenous bases. Meselson and Stahl noted that after one generation of growth in ^{14}N (after cells had been shifted from ^{15}N), the DNA molecules produced only single band intermediate in position in between DNA of cells grown exclusively in ^{15}N and DNA of cells grown exclusively in ^{14}N. This suggested either a semi-conservative or dispersive mode of replication. Conservative replication would have resulted in two bands; one representing the parental DNA still with exclusively ^{15}N in its nitrogenous bases and the other representing the daughter DNA with exclusively ^{14}N in its nitrogenous bases. The single band actually seen indicated that all the DNA molecules contained equal amounts of both ^{15}N and ^{14}N.

The DNA harvested from cells grown for two generations in ^{14}N formed two bands: one DNA band was at the intermediate position between ^{15}N and ^{14}N and the other corresponded to the band of exclusively ^{14}N DNA. These results could only be explained if

DNA replicates in a semi-conservative manner. Dispersive replication would have resulted in exclusively a single band in each new generation, with the band slowly moving up closer to the height of the ^{14}N DNA band. Therefore, dispersive replication could also be ruled out.

Meselson and Stahl's results established that during DNA replication, each of the two strands that make up the double helix serves as a template from which new strands are synthesized. The new strand will be complementary to the parental or "old" strand and the new strand will remain basepaired to the old strand. So each "daughter" DNA actually consists of one "old" DNA strand and one newly-synthesized strand. When two daughter DNA copies are formed, they have the identical sequences to one another and identical sequences to the original parental DNA, and the two daughter DNAs are divided equally into the two daughter cells, producing daughter cells that are genetically identical to one another and genetically identical to the parent cell.

Key Points

- There were three models suggested for DNA replication: conservative, semi-conservative, and dispersive.
- The conservative method of replication suggests that parental DNA remains together and newly-formed daughter strands are also together.
- The semi-conservative method of replication suggests that the two parental DNA strands serve as a template for new DNA and after replication, each double-stranded DNA contains one strand from the parental DNA and one new (daughter) strand.
- The dispersive method of replication suggests that, after replication, the two daughter DNAs have alternating segments of both parental and newly-synthesized DNA interspersed on both strands.
- Meselson and Stahl, using *E. coli* DNA made with two nitrogen istopes (^{14}N and ^{15}N) and density gradient centrifugation, determined that DNA replicated via the semi-conservative method of replication.

Key Terms

- **DNA replication**: a biological process occuring in all living organisms that is the basis for biological inheritance
- **isotope**: any of two or more forms of an element where the atoms have the same number of protons, but a different number of neutrons within their nuclei

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14.3B: DNA Replication in Prokaryotes

Learning Objectives

- Explain the functions of the enzymes involved in prokaryotic DNA replication

DNA Replication in Prokaryotes

DNA replication employs a large number of proteins and enzymes, each of which plays a critical role during the process. One of the key players is the enzyme DNA polymerase, which adds nucleotides one by one to the growing DNA chain that are complementary to the template strand. The addition of nucleotides requires energy; this energy is obtained from the nucleotides that have three phosphates attached to them, similar to ATP which has three phosphate groups attached. When the bond between the phosphates is broken, the energy released is used to form the phosphodiester bond between the incoming nucleotide and the growing chain. In prokaryotes, three main types of polymerases are known: DNA pol I, DNA pol II, and DNA pol III. DNA pol III is the enzyme required for DNA synthesis; DNA pol I and DNA pol II are primarily required for repair.

There are specific nucleotide sequences called origins of replication where replication begins. In *E. coli*, which has a single origin of replication on its one chromosome (as do most prokaryotes), it is approximately 245 base pairs long and is rich in AT sequences. The origin of replication is recognized by certain proteins that bind to this site. An enzyme called helicase unwinds the DNA by breaking the hydrogen bonds between the nitrogenous base pairs. ATP hydrolysis is required for this process. As the DNA opens up, Y-shaped structures called replication forks are formed. Two replication forks at the origin of replication are extended bi-directionally as replication proceeds. Single-strand binding proteins coat the strands of DNA near the replication fork to prevent the single-stranded DNA from winding back into a double helix. DNA polymerase is able to add nucleotides only in the 5′ to 3′ direction (a new DNA strand can be extended only in this direction). It also requires a free 3′-OH group to which it can add nucleotides by forming a phosphodiester bond between the 3′-OH end and the 5′ phosphate of the next nucleotide. This means that it cannot add nucleotides if a free 3′-OH group is not available. Another enzyme, RNA primase, synthesizes an RNA primer that is about five to ten nucleotides long and complementary to the DNA, priming DNA synthesis. A primer provides the free 3′-OH end to start replication. DNA polymerase then extends this RNA primer, adding nucleotides one by one that are complementary to the template strand.

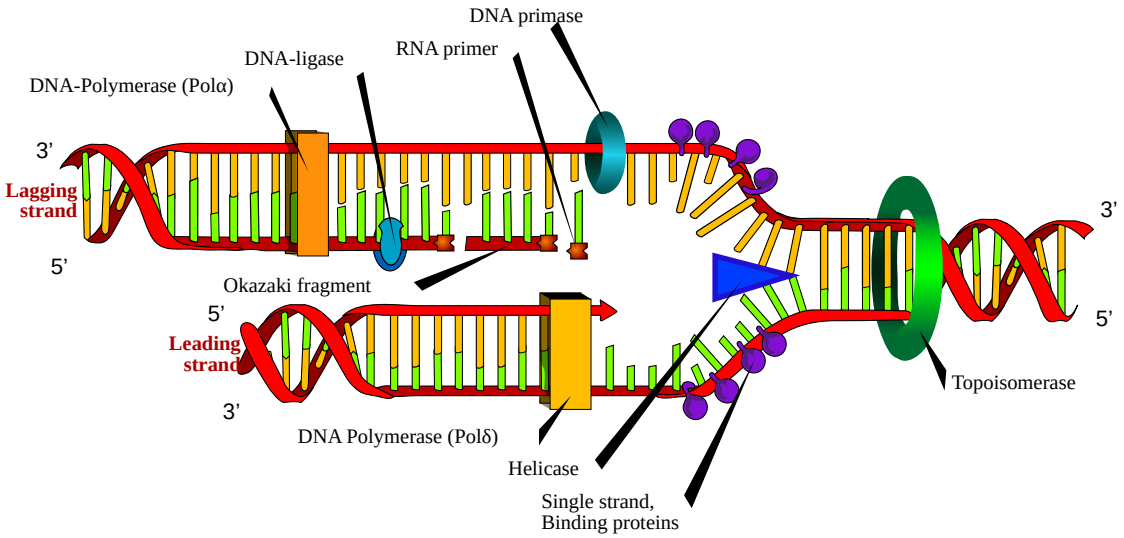


Figure 14.3B.1: DNA Replication in Prokaryotes: A replication fork is formed when helicase separates the DNA strands at the origin of replication. The DNA tends to become more highly coiled ahead of the replication fork. Topoisomerase breaks and reforms DNA's phosphate backbone ahead of the replication fork, thereby relieving the pressure that results from this supercoiling. Single-strand binding proteins bind to the single-stranded DNA to prevent the helix from re-forming. Primase synthesizes an RNA primer. DNA polymerase III uses this primer to synthesize the daughter DNA strand. On the leading strand, DNA is synthesized continuously, whereas on the lagging strand, DNA is synthesized in short stretches called Okazaki fragments. DNA polymerase I replaces the RNA primer with DNA. DNA ligase seals the gaps between the Okazaki fragments, joining the fragments into a single DNA molecule.

The replication fork moves at the rate of 1000 nucleotides per second. DNA polymerase can only extend in the 5′ to 3′ direction, which poses a slight problem at the replication fork. As we know, the DNA double helix is anti-parallel; that is, one strand is in the 5′ to 3′ direction and the other is oriented in the 3′ to 5′ direction. One strand (the leading strand), complementary to the 3′ to 5′ parental DNA strand, is synthesized continuously towards the replication fork because the polymerase can add nucleotides in this direction. The other strand (the lagging strand), complementary to the 5′ to 3′ parental DNA, is extended away from the replication fork in small fragments known as Okazaki fragments, each requiring a primer to start the synthesis. Okazaki fragments are named after the Japanese scientist who first discovered them.

The leading strand can be extended by one primer alone, whereas the lagging strand needs a new primer for each of the short Okazaki fragments. The overall direction of the lagging strand will be 3′ to 5′, while that of the leading strand will be 5′ to 3′. The sliding clamp (a ring-shaped protein that binds to the DNA) holds the DNA polymerase in place as it continues to add nucleotides. Topoisomerase prevents the over-winding of the DNA double helix ahead of the replication fork as the DNA is opening up; it does so by causing temporary nicks in the DNA helix and then resealing it. As synthesis proceeds, the RNA primers are replaced by DNA. The primers are removed by the exonuclease activity of DNA pol I, while the gaps are filled in by deoxyribonucleotides. The nicks that remain between the newly-synthesized DNA (that replaced the RNA primer) and the previously-synthesized DNA are sealed by the enzyme DNA ligase that catalyzes the formation of phosphodiester linkage between the 3′-OH end of one nucleotide and the 5′ phosphate end of the other fragment.

The table summarizes the enzymes involved in prokaryotic DNA replication and the functions of each.

Prokaryotic DNA Replication: Enzymes and Their Function	
Enzyme/protein	**Specific Function**
DNA pol I	Exonuclease activity removes RNA primer and replaces with newly synthesized DNA
DNA pol II	Repair function
DNA pol III	Main enzyme that adds nucleotides in the 5'-3' direction
Helicase	Opens the DNA helix by breaking hydrogen bonds between the nitrogenous bases
Ligase	Seals the gaps between the Okazaki fragments to create one continuous DNA strand
Primase	Synthesizes RNA primers needed to start replication
Sliding Clamp	Helps to hold the DNA polymerase in place when nucleotides are being added
Topoisomerase	Helps relieve the stress on DNA when unwinding by causing breaks and then resealing the DNA
Single-strand binding proteins (SSB)	Binds to single-stranded DNA to avoid DNA rewinding back.

Figure $14.3B.1$: Prokaryotic DNA Replication: Enzymes and Their Function: The enzymes involved in prokaryotic DNA replication and their functions are summarized on this table.

Key Points

- Helicase separates the DNA to form a replication fork at the origin of replication where DNA replication begins.
- Replication forks extend bi-directionally as replication continues.
- Okazaki fragments are formed on the lagging strand, while the leading strand is replicated continuously.
- DNA ligase seals the gaps between the Okazaki fragments.
- Primase synthesizes an RNA primer with a free 3′-OH, which DNA polymerase III uses to synthesize the daughter strands.

Key Terms

- **DNA replication**: a biological process occuring in all living organisms that is the basis for biological inheritance
- **helicase**: an enzyme that unwinds the DNA helix ahead of the replication machinery
- **origin of replication**: a particular sequence in a genome at which replication is initiated

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14.3C: DNA Replication in Eukaryotes

Learning Objectives

- Describe how DNA is replicated in eukaryotes

Because eukaryotic genomes are quite complex, DNA replication is a very complicated process that involves several enzymes and other proteins. It occurs in three main stages: initiation, elongation, and termination.

Initiation

Eukaryotic DNA is bound to proteins known as histones to form structures called nucleosomes. During initiation, the DNA is made accessible to the proteins and enzymes involved in the replication process. There are specific chromosomal locations called origins of replication where replication begins. In some eukaryotes, like yeast, these locations are defined by having a specific sequence of basepairs to which the replication initiation proteins bind. In other eukaryotes, like humans, there does not appear to be a consensus sequence for their origins of replication. Instead, the replication initiation proteins might identify and bind to specific modifications to the nucleosomes in the origin region.

Certain proteins recognize and bind to the origin of replication and then allow the other proteins necessary for DNA replication to bind the same region. The first proteins to bind the DNA are said to “recruit” the other proteins. Two copies of an enzyme called helicase are among the proteins recruited to the origin. Each helicase unwinds and separates the DNA helix into single-stranded DNA. As the DNA opens up, Y-shaped structures called replication forks are formed. Because two helicases bind, two replication forks are formed at the origin of replication; these are extended in both directions as replication proceeds creating a replication bubble. There are multiple origins of replication on the eukaryotic chromosome which allow replication to occur simultaneously in hundreds to thousands of locations along each chromosome.

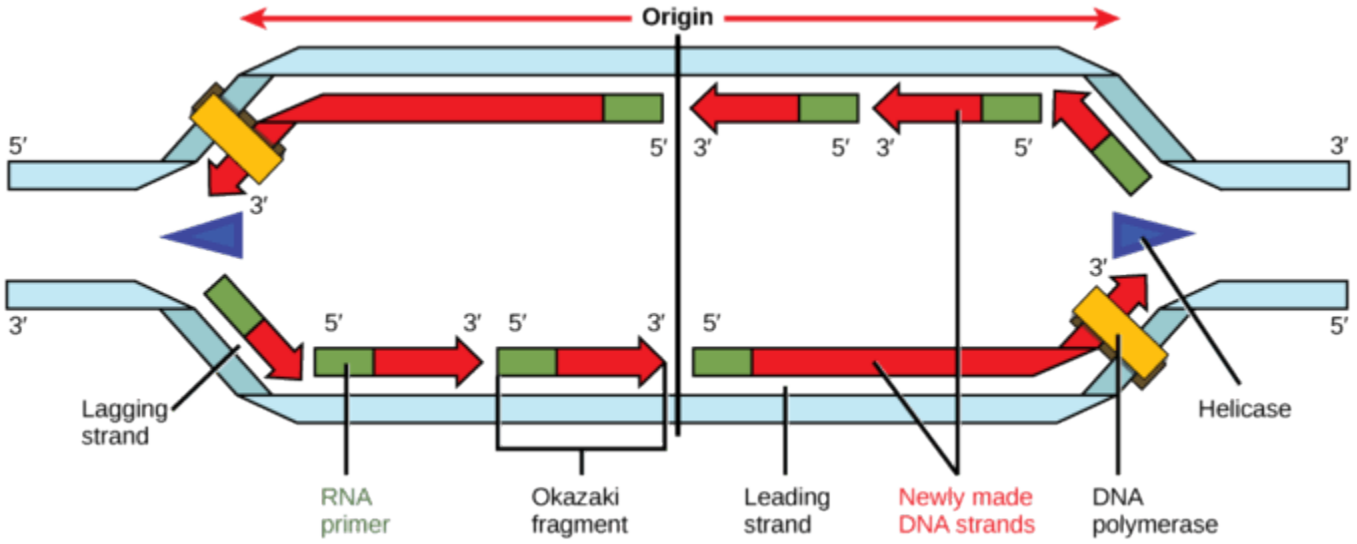


Figure $14.3C.1$: Replication Fork Formation: A replication fork is formed by the opening of the origin of replication; helicase separates the DNA strands. An RNA primer is synthesized by primase and is elongated by the DNA polymerase. On the leading strand, only a single RNA primer is needed, and DNA is synthesized continuously, whereas on the lagging strand, DNA is synthesized in short stretches, each of which must start with its own RNA primer. The DNA fragments are joined by DNA ligase (not shown).

Elongation

During elongation, an enzyme called DNA polymerase adds DNA nucleotides to the 3′ end of the newly synthesized polynucleotide

strand. The template strand specifies which of the four DNA nucleotides (A, T, C, or G) is added at each position along the new chain. Only the nucleotide complementary to the template nucleotide at that position is added to the new strand.

DNA polymerase contains a groove that allows it to bind to a single-stranded template DNA and travel one nucleotide at at time. For example, when DNA polymerase meets an adenosine nucleotide on the template strand, it adds a thymidine to the 3′ end of the newly synthesized strand, and then moves to the next nucleotide on the template strand. This process will continue until the DNA polymerase reaches the end of the template strand.

DNA polymerase cannot initiate new strand synthesis; it only adds new nucleotides at the 3′ end of an existing strand. All newly synthesized polynucleotide strands must be initiated by a specialized RNA polymerase called primase. Primase initiates polynucleotide synthesis and by creating a short RNA polynucleotide strand complementary to template DNA strand. This short stretch of RNA nucleotides is called the primer. Once RNA primer has been synthesized at the template DNA, primase exits, and DNA polymerase extends the new strand with nucleotides complementary to the template DNA.

Eventually, the RNA nucleotides in the primer are removed and replaced with DNA nucleotides. Once DNA replication is finished, the daughter molecules are made entirely of continuous DNA nucleotides, with no RNA portions.

The Leading and Lagging Strands

DNA polymerase can only synthesize new strands in the 5′ to 3′ direction. Therefore, the two newly-synthesized strands grow in opposite directions because the template strands at each replication fork are antiparallel. The “leading strand” is synthesized continuously toward the replication fork as helicase unwinds the template double-stranded DNA.

The “lagging strand” is synthesized in the direction away from the replication fork and away from the DNA helicase unwinds. This lagging strand is synthesized in pieces because the DNA polymerase can only synthesize in the 5′ to 3′ direction, and so it constantly encounters the previously-synthesized new strand. The pieces are called Okazaki fragments, and each fragment begins with its own RNA primer.

Termination

Eukaryotic chromosomes have multiple origins of replication, which initiate replication almost simultaneously. Each origin of replication forms a bubble of duplicated DNA on either side of the origin of replication. Eventually, the leading strand of one replication bubble reaches the lagging strand of another bubble, and the lagging strand will reach the 5′ end of the previous Okazaki fragment in the same bubble.

DNA polymerase halts when it reaches a section of DNA template that has already been replicated. However, DNA polymerase cannot catalyze the formation of a phosphodiester bond between the two segments of the new DNA strand, and it drops off. These unattached sections of the sugar-phosphate backbone in an otherwise full-replicated DNA strand are called nicks.

Once all the template nucleotides have been replicated, the replication process is not yet over. RNA primers need to be replaced with DNA, and nicks in the sugar-phosphate backbone need to be connected.

The group of cellular enzymes that remove RNA primers include the proteins FEN1 (flap endonulcease 1) and RNase H. The enzymes FEN1 and RNase H remove RNA primers at the start of each leading strand and at the start of each Okazaki fragment, leaving gaps of unreplicated template DNA. Once the primers are removed, a free-floating DNA polymerase lands at the 3′ end of the preceding DNA fragment and extends the DNA over the gap. However, this creates new nicks (unconnected sugar-phosphate backbone).

In the final stage of DNA replication, the enyzme ligase joins the sugar-phosphate backbones at each nick site. After ligase has connected all nicks, the new strand is one long continuous DNA strand, and the daughter DNA molecule is complete.

DNA Replication: This is a clip from a PBS production called “DNA: The Secret of Life.” It details the latest research (as of 2005) concerning the process of DNA replication.

Key Points

- During initiation, proteins bind to the origin of replication while helicase unwinds the DNA helix and two replication forks are

formed at the origin of replication.
- During elongation, a primer sequence is added with complementary RNA nucleotides, which are then replaced by DNA nucleotides.
- During elongation the leading strand is made continuously, while the lagging strand is made in pieces called Okazaki fragments.
- During termination, primers are removed and replaced with new DNA nucleotides and the backbone is sealed by DNA ligase.

Key Terms

- **origin of replication**: a particular sequence in a genome at which replication is initiated
- **leading strand**: the template strand of the DNA double helix that is oriented so that the replication fork moves along it in the 3′ to 5′ direction
- **lagging strand**: the strand of the template DNA double helix that is oriented so that the replication fork moves along it in a 5′ to 3′ manner

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14.3D: Telomere Replication

Learning Objectives

- Describe the role played by telomerase in replication of telomeres

The End Problem of Linear DNA Replication

Linear chromosomes have an end problem. After DNA replication, each newly synthesized DNA strand is shorter at its 5′ end than at the parental DNA strand's 5′ end. This produces a 3′ overhang at one end (and one end only) of each daughter DNA strand, such that the two daughter DNAs have their 3′ overhangs at opposite ends

image

Figure $14.3D.1$: The telomere end problem: A simplified schematic of DNA replication where the parental DNA (top) is replicated from three origins of replication, yielding three replication bubbles (middle) before giving rise to two daughter DNAs (bottom). Parental DNA strands are black, newly synthesized DNA strands are blue, and RNA primers are red. All RNA primers will be removed by Rnase H and FEN1, leaving gaps in the newly-synthesized DNA strands (not shown.) DNA Polymerase and Ligase will replace all the RNA primers with DNA except the RNA primer at the 5′ ends of each newly-synthesized (blue) strand. This means that each newly-synthesized DNA strand is shorter at its 5′ end than the equivalent strand in the parental DNA.

Every RNA primer synthesized during replication can be removed and replaced with DNA strands except the RNA primer at the 5′ end of the newly synthesized strand. This small section of RNA can only be removed, not replaced with DNA. Enzymes RNase H and FEN1 remove RNA primers, but DNA Polymerase will add new DNA only if the DNA Polymerase has an existing strand 5′ to it ("behind" it) to extend. However, there is no more DNA in the 5′ direction after the final RNA primer, so DNA polymerse cannot replace the RNA with DNA. Therefore, both daughter DNA strands have an incomplete 5′ strand with 3′ overhang.

In the absence of additional cellular processes, nucleases would digest these single-stranded 3′ overhangs. Each daughter DNA would become shorter than the parental DNA, and eventually entire DNA would be lost. To prevent this shortening, the ends of linear eukaryotic chromosomes have special structures called telomeres.

Telomere Replication

The ends of the linear chromosomes are known as telomeres: repetitive sequences that code for no particular gene. These telomeres protect the important genes from being deleted as cells divide and as DNA strands shorten during replication.

In humans, a six base pair sequence, TTAGGG, is repeated 100 to 1000 times. After each round of DNA replication, some telomeric sequences are lost at the 5′ end of the newly synthesized strand on each daughter DNA, but because these are noncoding sequences, their loss does not adversely affect the cell. However, even these sequences are not unlimited. After sufficient rounds of replication, all the telomeric repeats are lost, and the DNA risks losing coding sequences with subsequent rounds.

The discovery of the enzyme telomerase helped in the understanding of how chromosome ends are maintained. The telomerase enzyme attaches to the end of a chromosome and contains a catalytic part and a built-in RNA template. Telomerase adds complementary RNA bases to the 3′ end of the DNA strand. Once the 3′ end of the lagging strand template is sufficiently elongated, DNA polymerase adds the complementary nucleotides to the ends of the chromosomes; thus, the ends of the chromosomes are replicated.

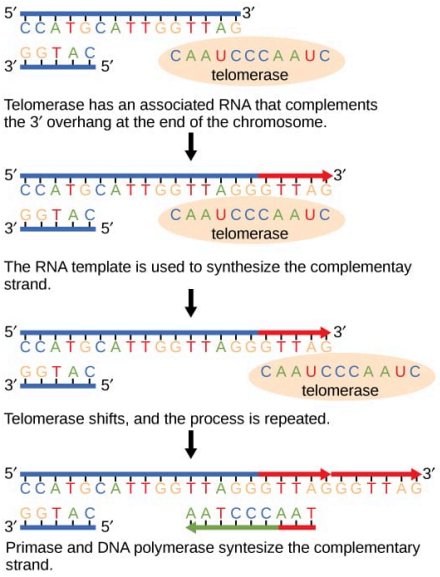


Figure 14.3D.1: Telomerase is important for maintaining chromosome integrity: The ends of linear chromosomes are maintained by the action of the telomerase enzyme.

Telomerase and Aging

Telomerase is typically active in germ cells and adult stem cells, but is not active in adult somatic cells. As a result, telomerase does not protect the DNA of adult somatic cells and their telomeres continually shorten as they undergo rounds of cell division.

In 2010, scientists found that telomerase can reverse some age-related conditions in mice. These findings may contribute to the future of regenerative medicine. In the studies, the scientists used telomerase-deficient mice with tissue atrophy, stem cell depletion, organ failure, and impaired tissue injury responses. Telomerase reactivation in these mice caused extension of telomeres, reduced DNA damage, reversed neurodegeneration, and improved the function of the testes, spleen, and intestines. Thus, telomere reactivation may have potential for treating age-related diseases in humans.

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Key Points

- DNA polymerase cannot replicate and repair DNA molecules at the ends of linear chromosomes.
- The ends of linear chromosomes, called telomeres, protect genes from getting deleted as cells continue to divide.
- The telomerase enzyme attaches to the end of the chromosome; complementary bases to the RNA template are added on the 3′ end of the DNA strand.
- Once the lagging strand is elongated by telomerase, DNA polymerase can add the complementary nucleotides to the ends of the chromosomes and the telomeres can finally be replicated.
- Cells that undergo cell division continue to have their telomeres shortened because most somatic cells do not make telomerase; telomere shortening is associated with aging.

- Telomerase reactivation in telomerase-deficient mice causes extension of telomeres; this may have potential for treating age-related diseases in humans.

Key Terms

- **telomere**: either of the repetitive nucleotide sequences at each end of a eukaryotic chromosome, which protect the chromosome from degradation
- **telomerase**: an enzyme in eukaryotic cells that adds a specific sequence of DNA to the telomeres of chromosomes after they divide, giving the chromosomes stability over time

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14.4: DNA REPAIR

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14.4A: DNA Repair

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14.4A: DNA Repair

Learning Objectives

- Explain how errors during replication are repaired

Errors during Replication

DNA replication is a highly accurate process, but mistakes can occasionally occur as when a DNA polymerase inserts a wrong base. Uncorrected mistakes may sometimes lead to serious consequences, such as cancer. Repair mechanisms can correct the mistakes, but in rare cases mistakes are not corrected, leading to mutations; in other cases, repair enzymes are themselves mutated or defective.

Mutations: In this interactive, you can "edit" a DNA strand and cause a mutation. Take a look at the effects!

Most of the mistakes during DNA replication are promptly corrected by DNA polymerase which proofreads the base that has just been added. In proofreading, the DNA pol reads the newly-added base before adding the next one so a correction can be made. The polymerase checks whether the newly-added base has paired correctly with the base in the template strand. If it is the correct base, the next nucleotide is added. If an incorrect base has been added, the enzyme makes a cut at the phosphodiester bond and releases the incorrect nucleotide. This is performed by the exonuclease action of DNA pol III. Once the incorrect nucleotide has been removed, a new one will be added again.

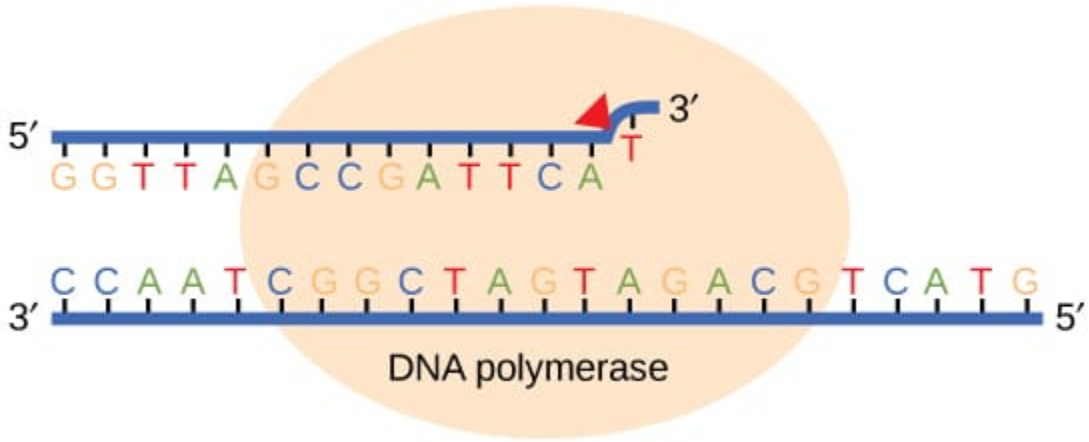


Figure 14.4A.1: DNA polymerase proofreading: Proofreading by DNA polymerase corrects errors during replication.

Some errors are not corrected during replication, but are instead corrected after replication is completed; this type of repair is known as mismatch repair. The enzymes recognize the incorrectly-added nucleotide and excise it; this is then replaced by the correct base. If this remains uncorrected, it may lead to more permanent damage. How do mismatch repair enzymes recognize which of the two bases is the incorrect one? In *E. coli*, after replication, the nitrogenous base adenine acquires a methyl group; the parental DNA strand will have methyl groups, whereas the newly-synthesized strand lacks them. Thus, DNA polymerase is able to remove the incorrectly-incorporated bases from the newly-synthesized, non-methylated strand. In eukaryotes, the mechanism is not very well understood, but it is believed to involve recognition of unsealed nicks in the new strand, as well as a short-term continuing association of some of the replication proteins with the new daughter strand after replication has been completed.

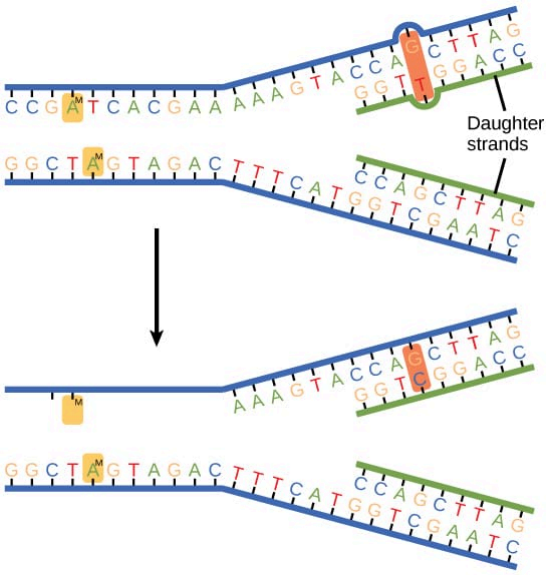


Figure 14.4A.1: Mismatch Repair: In mismatch repair, the incorrectly-added base is detected after replication. The mismatch-repair proteins detect this base and remove it from the newly-synthesized strand by nuclease action. The gap is now filled with the correctly-paired base.

In another type of repair mechanism, nucleotide excision repair, enzymes replace incorrect bases by making a cut on both the 3′ and 5′ ends of the incorrect base. The segment of DNA is removed and replaced with the correctly-paired nucleotides by the action of DNA pol. Once the bases are filled in, the remaining gap is sealed with a phosphodiester linkage catalyzed by DNA ligase. This repair mechanism is often employed when UV exposure causes the formation of pyrimidine dimers.

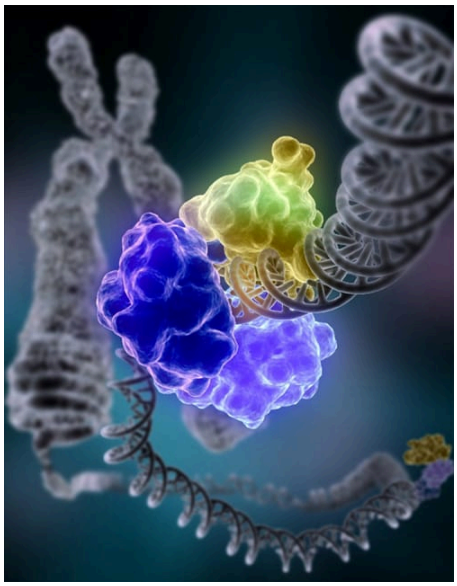


Figure 14.4A.1: DNA Ligase I Repairing Chromosomal Damage: DNA damage, due to environmental factors and normal metabolic processes inside the cell, occurs at a rate of 1,000 to 1,000,000 molecular lesions per cell per day. A special enzyme, DNA ligase (shown here in color), encircles the double helix to repair a broken strand of DNA. DNA ligase is responsible for repairing the millions of DNA breaks generated during the normal course of a cell's life. Without molecules that can mend such breaks, cells can malfunction, die, or become cancerous. DNA ligases catalyse the crucial step of joining breaks in duplex DNA during DNA repair, replication and recombination, and require either Adenosine triphosphate (ATP) or Nicotinamide adenine dinucleotide (NAD+) as a cofactor.

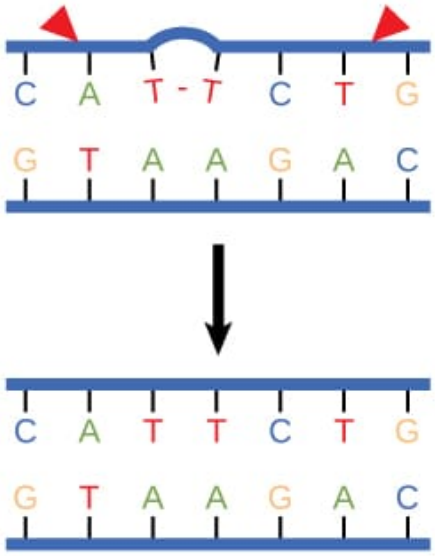


Figure 14.4A.1: Nucleotide Excision Repairs: Nucleotide excision repairs thymine dimers. When exposed to UV, thymines lying adjacent to each other can form thymine dimers. In normal cells, they are excised and replaced.

DNA Damage and Mutations

Errors during DNA replication are not the only reason why mutations arise in DNA. Mutations, variations in the nucleotide sequence of a genome, can also occur because of damage to DNA. Such mutations may be of two types: induced or spontaneous. Induced mutations are those that result from an exposure to chemicals, UV rays, X-rays, or some other environmental agent. Spontaneous mutations occur without any exposure to any environmental agent; they are a result of natural reactions taking place within the body.

Mutations may have a wide range of effects. Some mutations are not expressed; these are known as silent mutations. Point mutations are those mutations that affect a single base pair. The most common nucleotide mutations are substitutions, in which one base is replaced by another. These can be of two types: transitions or transversions. Transition substitution refers to a purine or pyrimidine being replaced by a base of the same kind; for example, a purine such as adenine may be replaced by the purine guanine. Transversion substitution refers to a purine being replaced by a pyrimidine or vice versa; for example, cytosine, a pyrimidine, is replaced by adenine, a purine. Mutations can also be the result of the addition of a base, known as an insertion, or the removal of a base, known as a deletion. Sometimes a piece of DNA from one chromosome may get translocated to another chromosome or to another region of the same chromosome.

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Key Points

- Mismatch repair enzymes recognize mis-incorporated bases, remove them from DNA, and replace them with the correct bases.
- In nucleotide excision repair, enzymes remove incorrect bases with a few surrounding bases, which are replaced with the correct bases with the help of a DNA polymerase and the template DNA.
- When replication mistakes are not corrected, they may result in mutations, which sometimes can have serious consequences.
- Point mutations, one base substituted for another, can be silent (no effect) or may have effects ranging from mild to severe.
- Mutations may also involve insertions (addition of a base), deletion (loss of a base), or translocation (movement of a DNA section to a new location on the same or another chromosome).

Key Terms

- **mismatch repair**: a system for recognizing and repairing some forms of DNA damage and erroneous insertion, deletion, or mis-incorporation of bases that can arise during DNA replication and recombination
- **nucleotide excision repair**: a DNA repair mechanism that corrects damage done by UV radiation, including thymine dimers and 6,4 photoproducts that cause bulky distortions in the DNA

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15: GENES AND PROTEINS

15.1: The Genetic Code - The Relationship Between Genes and Proteins
15.2: The Genetic Code - The Central Dogma- DNA Encodes RNA and RNA Encodes Protein
15.3: Prokaryotic Transcription - Transcription in Prokaryotes
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15.1: The Genetic Code - The Relationship Between Genes and Proteins

Learning Objectives

- Describe transcription and translation

Genes and Proteins

Since the rediscovery of Mendel's work in 1900, the definition of the gene has progressed from an abstract unit of heredity to a tangible molecular entity capable of replication, transcription, translation, and mutation. Genes are composed of DNA and are linearly arranged on chromosomes. Some genes encode structural and regulatory RNAs. There is increasing evidence from research that profiles the transcriptome of cells (the complete set all RNA transcripts present in a cell) that these may be the largest classes of RNAs produced by eukaryotic cells, far outnumbering the protein-encoding messenger RNAs (mRNAs), but the 20,000 protein-encoding genes typically found in animal cells, and the 30,000 protein-encoding genes typically found in plant cells, nonetheless have huge impacts on cellular functioning.

Protein-encoding genes specify the sequences of amino acids, which are the building blocks of proteins. In turn, proteins are responsible for orchestrating nearly every function of the cell. Both protein-encoding genes and the proteins that are their gene products are absolutely essential to life as we know it.

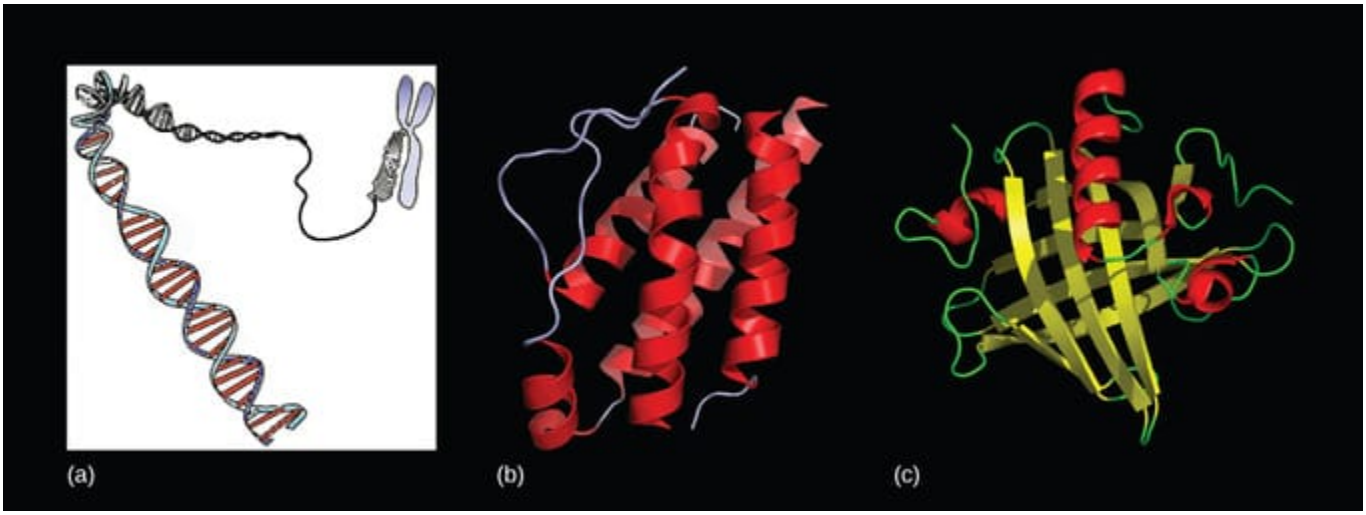


Figure 15.1.1: Genes Encode Proteins: Genes, which are carried on (a) chromosomes, are linearly-organized instructions for making the RNA and protein molecules that are necessary for all of processes of life. The (b) interleukin-2 protein and (c) alpha-2u-globulin protein are just two examples of the array of different molecular structures that are encoded by genes.

Replication, Transcription, and Translation are the three main processes used by all cells to maintain their genetic information and to convert the genetic information encoded in DNA into gene products, which are either RNAs or proteins, depending on the gene. In eukaryotic cells, or those cells that have a nucleus, replication and transcription take place within the nucleus while translation takes place outside of the nucleus in cytoplasm. In prokaryotic cells, or those cells that do not have a nucleus, all three processes occur in the cytoplasm.

Replication is the basis for biological inheritance. It copies a cell's DNA. The enzyme DNA polymerase copies a single parental double-stranded DNA molecule into two daughter double-stranded DNA molecules. Transcription makes RNA from DNA. The enzyme RNA polymerase creates an RNA molecule that is complementary to a gene-encoding stretch of DNA. Translation makes protein from mRNA. The ribosome generates a polypeptide chain of amino acids using mRNA as a template. The polypeptide chain folds up to become a protein.

Key Points

- Genes are composed of DNA arranged on chromosomes.
- Some genes encode structural or regulatory RNAs. Other genes encode proteins.
- Replication copies DNA; transcription uses DNA to make complementary RNAs; translation uses mRNAs to make proteins.
- In eukaryotic cells, replication and transcription take place within the nucleus while translation takes place in the cytoplasm.
- In prokaryotic cells, replication, transcription, and translation occur in the cytoplasm.

Key Terms

- **DNA**: a biopolymer of deoxyribonucleic acids (a type of nucleic acid) that has four different chemical groups, called bases: adenine, guanine, cytosine, and thymine
- **messenger RNA**: Messenger RNA (mRNA) is a molecule of RNA that encodes a chemical “blueprint” for a protein product.
- **protein**: any of numerous large, complex naturally-produced molecules composed of one or more long chains of amino acids, in which the amino acid groups are held together by peptide bonds

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15.2: The Genetic Code - The Central Dogma- DNA Encodes RNA and RNA Encodes Protein

Learning Objectives

- Recall the central dogma of biology

The Genetic Code Is Degenerate and Universal

The genetic code is degenerate as there are 64 possible nucleotide triplets (4^3), which is far more than the number of amino acids. These nucleotide triplets are called codons; they instruct the addition of a specific amino acid to a polypeptide chain. Sixty-one of the codons encode twenty different amino acids. Most of these amino acids can be encoded by more than one codon. Three of the 64 codons terminate protein synthesis and release the polypeptide from the translation machinery. These triplets are called stop codons. The stop codon UGA is sometimes used to encode a 21st amino acid called selenocysteine (Sec), but only if the mRNA additionally contains a specific sequence of nucleotides called a selenocysteine insertion sequence (SECIS). The stop codon UAG is sometimes used by a few species of microorganisms to encode a 22nd amino acid called pyrrolysine (Pyl). The codon AUG, also has a special function. In addition to specifying the amino acid methionine, it also serves as the start codon to initiate translation. The reading frame for translation is set by the AUG start codon.

The genetic code is universal. With a few exceptions, virtually all species use the same genetic code for protein synthesis. The universal nature of the genetic code is powerful evidence that all of life on Earth shares a common origin.

Second letter

First letter	U	C	A	G	Third letter
U	UUU Phe UUC Phe UUA Leu UUG Leu	UCU Ser UCC Ser UCA Ser UCG Ser	UAU Tyr UAC Tyr **UAA Stop** **UAG Stop**	UGU Cys UGC Cys **UGA Stop** UGG Trp	U C A G
C	CUU Leu CUC Leu CUA Leu CUG Leu	CCU Pro CCC Pro CCA Pro CCG Pro	CAU His CAC His CAA Gln CAG Gln	CGU Arg CGC Arg CGA Arg CGG Arg	U C A G
A	AUU Ile AUC Ile AUA Ile **AUG Met**	ACU Thr ACC Thr ACA Thr ACG Thr	AAU Asn AAC Asn AAA Lys AAG Lys	AGU Ser AGC Ser AGA Arg AGG Arg	U C A G
G	GUU Val GUC Val GUA Val GUG Val	GCU Ala GCC Ala GCA Ala GCG Ala	GAU Asp GAC Asp GAA Glu GAG Glu	GGU Gly GGC Gly GGA Gly GGG Gly	U C A G

Figure 15.2.1: Codons and the universal genetic code.: The genetic code for translating each nucleotide triplet (codon) in mRNA into an amino acid or a translation termination signal.

The Central Dogma: DNA Encodes RNA, RNA Encodes Protein

The central dogma of molecular biology describes the flow of genetic information in cells from DNA to messenger RNA (mRNA) to protein. It states that genes specify the sequence of mRNA molecules, which in turn specify the sequence of proteins. Because the information stored in DNA is so central to cellular function, the cell keeps the DNA protected and copies it in the form of RNA. An enzyme adds one nucleotide to the mRNA strand for every nucleotide it reads in the DNA strand. The translation of this information to a protein is more complex because three mRNA nucleotides correspond to one amino acid in the polypeptide sequence.

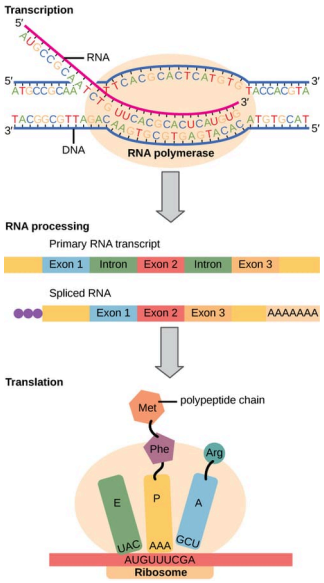


Figure 15.2.1: The central dogma: Instructions on DNA are transcribed onto messenger RNA. Ribosomes are able to read the genetic information inscribed on a strand of messenger RNA and use this information to string amino acids together into a protein.

Transcription: DNA to RNA

Transcription is the process of creating a complementary RNA copy of a sequence of DNA. Both RNA and DNA are nucleic acids, which use base pairs of nucleotides as a complementary language that enzymes can convert back and forth from DNA to RNA. During transcription, a DNA sequence is read by RNA polymerase, which produces a complementary, antiparallel RNA strand. Unlike DNA replication, transcription results in an RNA complement that substitutes the RNA uracil (U) in all instances where the DNA thymine (T) would have occurred. Transcription is the first step in gene expression. The stretch of DNA transcribed into an RNA molecule is called a transcript. Some transcripts are used as structural or regulatory RNAs, and others encode one or more proteins. If the transcribed gene encodes a protein, the result of transcription is messenger RNA (mRNA), which will then be used to create that protein in the process of translation.

Translation: RNA to Protein

Translation is the process by which mRNA is decoded and translated to produce a polypeptide sequence, otherwise known as a protein. This method of synthesizing proteins is directed by the mRNA and accomplished with the help of a ribosome, a large complex of ribosomal RNAs (rRNAs) and proteins. In translation, a cell decodes the mRNA's genetic message and assembles the brand-new polypeptide chain. Transfer RNA, or tRNA, translates the sequence of codons on the mRNA strand. The main function of tRNA is to transfer a free amino acid from the cytoplasm to a ribosome, where it is attached to the growing polypeptide chain. tRNAs continue to add amino acids to the growing end of the polypeptide chain until they reach a stop codon on the mRNA. The ribosome then releases the completed protein into the cell.

Interactive Element

DNA to protein: This interactive shows the process of DNA code being translated to a protein from start to finish!

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Key Points

- The genetic code is degenerate because 64 codons encode only 22 amino acids.
- The genetic code is universal because it is the same among all organisms.
- Replication is the process of copying a molecule of DNA.
- Transcription is the process of converting a specific sequence of DNA into RNA.
- Translation is the process where a ribosome decodes mRNA into a protein.

Key Terms

- **codon**: a sequence of three adjacent nucleotides, which encode for a specific amino acid during protein synthesis or translation
- **ribosome**: protein/mRNA complexes found in all cells that are involved in the production of proteins by translating messenger RNA
- **degenerate**: the redundancy of the genetic code (more than one codon codes for each amino acid)

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15.3: Prokaryotic Transcription - Transcription in Prokaryotes

Learning Objectives

- Describe the genetic code and how the nucleotide sequence prescribes the amino acid and the protein sequence

The Genetic Code: Nucleotide sequences prescribe the amino acids

The genetic code is the relationship between DNA base sequences and the amino acid sequence in proteins. Features of the genetic code include:

- Amino acids are encoded by three nucleotides.
- It is non-overlapping.
- It is degenerate.

There are 21 genetically-encoded amino acids universally found in the species from all three domains of life. (There is a 22nd genetically-encooded amino acid, Pyl, but so far it has only been found in a handful of Archaea and Bacteria species.) Yet there are only four different nucleotides in DNA or RNA, so a minimum of three nucleotides are needed to code each of the 21 (or 22) amino acids. The set of three nucleotides that codes for a single amino acid is known as a codon. There are 64 codons in total, 61 that encode amino acids and 3 that code for chain termination. Two of the codons for chain termination can, under certain circumstances, instead code for amino acids.

image

Figure 15.3.1: Genetic Code Table.: A codon is made of three nucleotides. Consequently there are 4^3 (=64) different codons. The 64 codons encode 22 different amino acids and three termination codons, also called stop codons.

Degeneracy is the redundancy of the genetic code. The genetic code has redundancy, but no ambiguity. For example, although codons GAA and GAG both specify glutamic acid (redundancy), neither of them specifies any other amino acid (no ambiguity). The codons encoding one amino acid may differ in any of their three positions. For example, the amino acid glutamic acid is specified by GAA and GAG codons (difference in the third position); the amino acid leucine is specified by UUA, UUG, CUU, CUC, CUA, CUG codons (difference in the first or third position); while the amino acid serine is specified by UCA, UCG, UCC, UCU, AGU, AGC (difference in the first, second or third position). These properties of the genetic code make it more fault-tolerant for point mutations.

Origin of transcription on prokaryotic organisms

Prokaryotes are mostly single-celled organisms that, by definition, lack membrane-bound nuclei and other organelles. The central region of the cell in which prokaryotic DNA resides is called the nucleoid region. Bacterial and Archaeal chromosomes are covalently-closed circles that are not as extensively compacted as eukaryotic chromosomes, but are compacted nonetheless as the diameter of a typical prokaryotic chromosome is larger than the diameter of a typical prokaryotic cell. Additionally, prokaryotes often have abundant plasmids, which are shorter, circular DNA molecules that may only contain one or a few genes and often carry traits such as antibiotic resistance.

Transcription in prokaryotes (as in eukaryotes) requires the DNA double helix to partially unwind in the region of RNA synthesis. The region of unwinding is called a transcription bubble. Transcription always proceeds from the same DNA strand for each gene, which is called the template strand. The RNA product is complementary to the template strand and is almost identical to the other (non-template) DNA strand, called the sense or coding strand. The only difference is that in RNA all of the T nucleotides are replaced with U nucleotides.

The nucleotide on the DNA template strand that corresponds to the site from which the first 5′ RNA nucleotide is transcribed is called the +1 nucleotide, or the initiation site. Nucleotides preceding, or 5′ to, the template strand initiation site are given negative numbers and are designated upstream. Conversely, nucleotides following, or 3′ to, the template strand initiation site are denoted with “+” numbering and are called downstream nucleotides.

Key Points

- The relationship between DNA base sequences and the amino acid sequence in proteins is called the genetic code.
- There are 61 codons that encode amino acids and 3 codons that code for chain termination for a total of 64 codons.
- Unlike, eukayrotes, a bacterial chromosome is a covalently-closed circle.
- The DNA double helix must partially unwind for transcription to occur; this unwound region is called a transcription bubble.

Key Terms

- **nucleotide**: the monomer comprising DNA or RNA molecules; consists of a nitrogenous heterocyclic base that can be a purine or pyrimidine, a five-carbon pentose sugar, and a phosphate group
- **amino acid**: Any of 20 naturally occurring α-amino acids (having the amino, and carboxylic acid groups on the same carbon atom), and a variety of side chains, that combine, via peptide bonds, to form proteins.
- **redundancy**: duplication of components, such as amino acid codons, to provide survival of the total system in case of failure of single components

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15.4: Prokaryotic Transcription - Initiation of Transcription in Prokaryotes

Learning Objectives

- Summarize the initial steps of transcription in prokaryotes

Prokaryotic RNA Polymerase

Prokaryotes use the same RNA polymerase to transcribe all of their genes. In *E. coli*, the polymerase is composed of five polypeptide subunits, two of which are identical. Four of these subunits, denoted α, α, β, and β', comprise the polymerase core enzyme. These subunits assemble each time a gene is transcribed; they disassemble once transcription is complete. Each subunit has a unique role: the two α-subunits are necessary to assemble the polymerase on the DNA; the β-subunit binds to the ribonucleoside triphosphate that will become part of the nascent "recently-born" mRNA molecule; and the β' binds the DNA template strand. The fifth subunit, σ, is involved only in transcription initiation. It confers transcriptional specificity such that the polymerase begins to synthesize mRNA from an appropriate initiation site. Without σ, the core enzyme would transcribe from random sites and would produce mRNA molecules that specified protein gibberish. The polymerase comprised of all five subunits is called the holoenzyme.

Prokaryotic Promoters and Initiation of Transcription

The nucleotide pair in the DNA double helix that corresponds to the site from which the first 5′ mRNA nucleotide is transcribed is called the +1 site, or the initiation site. Nucleotides preceding the initiation site are given negative numbers and are designated upstream. Conversely, nucleotides following the initiation site are denoted with "+" numbering and are called downstream nucleotides.

A promoter is a DNA sequence onto which the transcription machinery binds and initiates transcription. In most cases, promoters exist upstream of the genes they regulate. The specific sequence of a promoter is very important because it determines whether the corresponding gene is transcribed all the time, some of the time, or infrequently. Although promoters vary among prokaryotic genomes, a few elements are conserved. At the -10 and -35 regions upstream of the initiation site, there are two promoter consensus sequences, or regions that are similar across all promoters and across various bacterial species. The -10 consensus sequence, called the -10 region, is TATAAT. The -35 sequence, TTGACA, is recognized and bound by σ. Once this interaction is made, the subunits of the core enzyme bind to the site. The A–T-rich -10 region facilitates unwinding of the DNA template; several phosphodiester bonds are made. The transcription initiation phase ends with the production of abortive transcripts, which are polymers of approximately 10 nucleotides that are made and released.

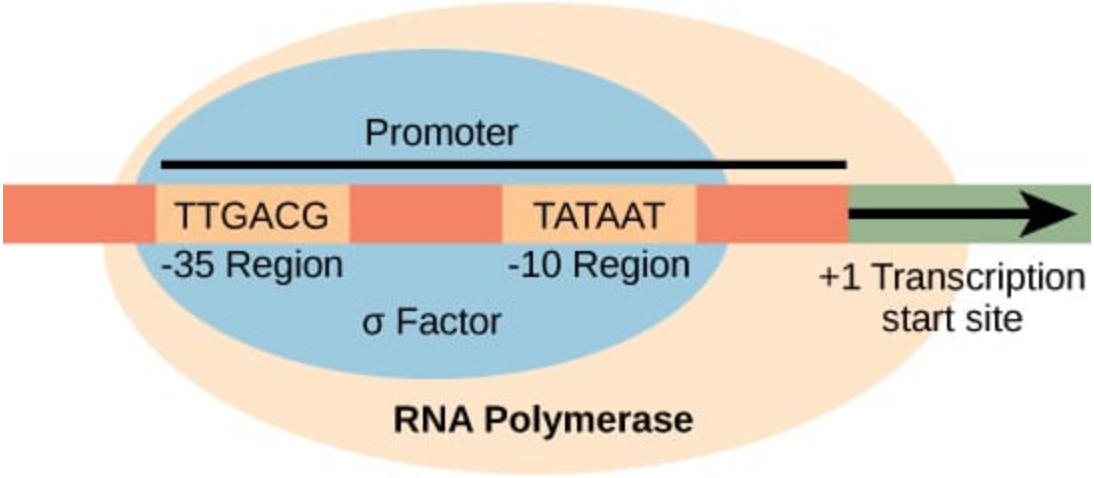


Figure 15.4.1: Promoter: The σ subunit of prokaryotic RNA polymerase recognizes consensus sequences found in the promoter region upstream of the transcription start sight. The σ subunit dissociates from the polymerase after transcription has been initiated.

Key Points

- Transcription of mRNA begins at the initiation site.
- Two promoter consensus sequences are at the -10 and -35 regions upstream of the initiation site.
- The σ subunit of RNA polymerase recognizes and binds the -35 region.
- Five subunits (α, α, β, β', and σ) make up the complete RNA polymerase holoenzyme.

Key Terms

- **holoenzyme**: a fully functioning enzyme, composed of all its subunits
- **promoter**: the section of DNA that controls the initiation of RNA transcription

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15.5: Prokaryotic Transcription - Elongation and Termination in Prokaryotes

Learning Objectives

- Explain the process of elongation and termination in prokaryotes

Elongation in Prokaryotes

The transcription elongation phase begins with the release of the σ subunit from the polymerase. The dissociation of σ allows the core RNA polymerase enzyme to proceed along the DNA template, synthesizing mRNA in the 5′ to 3′ direction at a rate of approximately 40 nucleotides per second. As elongation proceeds, the DNA is continuously unwound ahead of the core enzyme and rewound behind it. Since the base pairing between DNA and RNA is not stable enough to maintain the stability of the mRNA synthesis components, RNA polymerase acts as a stable linker between the DNA template and the nascent RNA strands to ensure that elongation is not interrupted prematurely.

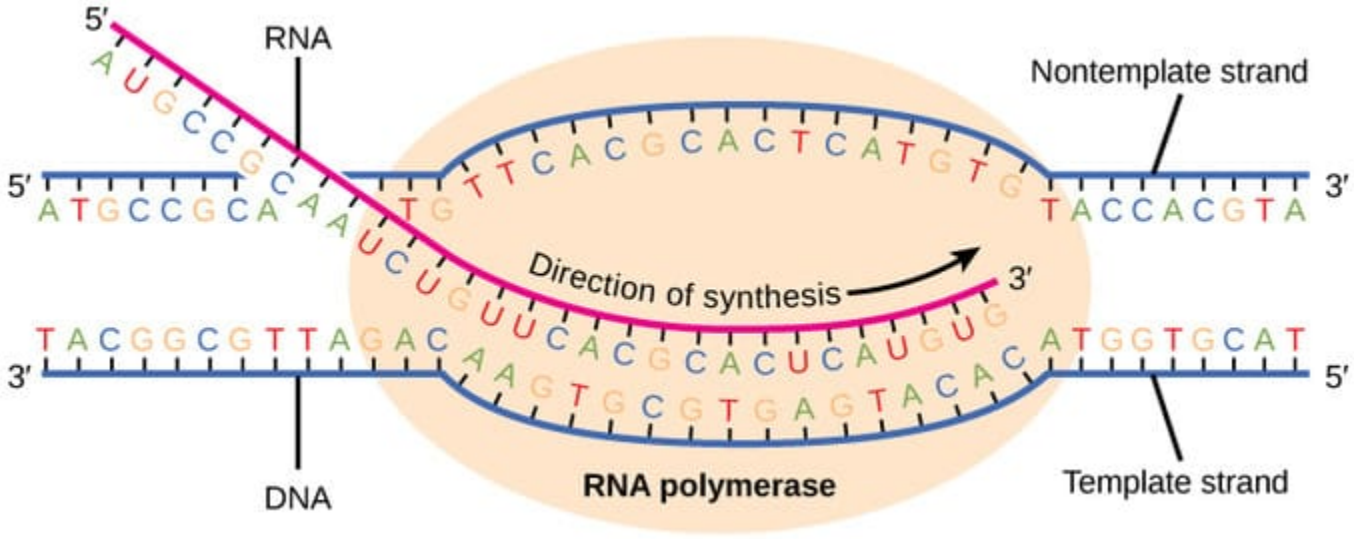


Figure 15.5.1: Elongation in prokaryotes: During elongation, the prokaryotic RNA polymerase tracks along the DNA template, synthesizes mRNA in the 5′ to 3′ direction, and unwinds and rewinds the DNA as it is read.

Termination in Prokaryotes

Once a gene is transcribed, the prokaryotic polymerase needs to be instructed to dissociate from the DNA template and liberate the newly-made mRNA. Depending on the gene being transcribed, there are two kinds of termination signals: one is protein-based and the other is RNA-based.

Rho-dependent termination is controlled by the rho protein, which tracks along behind the polymerase on the growing mRNA chain. Near the end of the gene, the polymerase encounters a run of G nucleotides on the DNA template and it stalls. As a result, the rho protein collides with the polymerase. The interaction with rho releases the mRNA from the transcription bubble.

Rho-independent termination is controlled by specific sequences in the DNA template strand. As the polymerase nears the end of the gene being transcribed, it encounters a region rich in C–G nucleotides. The mRNA folds back on itself, and the complementary C–G nucleotides bind together. The result is a stable hairpin that causes the polymerase to stall as soon as it begins to transcribe a region rich in A–T nucleotides. The complementary U–A region of the mRNA transcript forms only a weak interaction with the template DNA. This, coupled with the stalled polymerase, induces enough instability for the core enzyme to break away and

liberate the new mRNA transcript.

Upon termination, the process of transcription is complete. By the time termination occurs, the prokaryotic transcript would already have been used to begin synthesis of numerous copies of the encoded protein because these processes can occur concurrently in the cytoplasm. The unification of transcription, translation, and even mRNA degradation is possible because all of these processes occur in the same 5′ to 3′ direction and because there is no membranous compartmentalization in the prokaryotic cell. In contrast, the presence of a nucleus in eukaryotic cells prevents simultaneous transcription and translation.

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Key Points

- The transcription elongation phase begins with the dissociation of the σ subunit, which allows the core RNA polymerase enzyme to proceed along the DNA template.
- Rho-dependent termination is caused by the rho protein colliding with the stalled polymerase at a stretch of G nucleotides on the DNA template near the end of the gene.
- Rho-independent termination is caused the polymerase stalling at a stable hairpin formed by a region of complementary C–G nucleotides at the end of the mRNA.

Key Terms

- **elongation**: the addition of nucleotides to the 3′-end of a growing RNA chain during transcription

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15.6: Eukaryotic Transcription - Initiation of Transcription in Eukaryotes

Learning Objectives

- Describe how transcription is initiated and proceeds along the DNA strand

Steps in Eukaryotic Transcription

Eukaryotic transcription is carried out in the nucleus of the cell by one of three RNA polymerases, depending on the RNA being transcribed, and proceeds in three sequential stages:

1. Initiation
2. Elongation
3. Termination.

Initiation of Transcription in Eukaryotes

Unlike the prokaryotic RNA polymerase that can bind to a DNA template on its own, eukaryotes require several other proteins, called transcription factors, to first bind to the promoter region and then help recruit the appropriate polymerase. The completed assembly of transcription factors and RNA polymerase bind to the promoter, forming a transcription pre-initiation complex (PIC).

The most-extensively studied core promoter element in eukaryotes is a short DNA sequence known as a TATA box, found 25-30 base pairs upstream from the start site of transcription. Only about 10-15% of mammalian genes contain TATA boxes, while the rest contain other core promoter elements, but the mechanisms by which transcription is initiated at promoters with TATA boxes is well characterized.

The TATA box, as a core promoter element, is the binding site for a transcription factor known as TATA-binding protein (TBP), which is itself a subunit of another transcription factor: Transcription Factor II D (TFIID). After TFIID binds to the TATA box via the TBP, five more transcription factors and RNA polymerase combine around the TATA box in a series of stages to form a pre-initiation complex. One transcription factor, Transcription Factor II H (TFIIH), is involved in separating opposing strands of double-stranded DNA to provide the RNA Polymerase access to a single-stranded DNA template. However, only a low, or basal, rate of transcription is driven by the pre-initiation complex alone. Other proteins known as activators and repressors, along with any associated coactivators or corepressors, are responsible for modulating transcription rate. Activator proteins increase the transcription rate, and repressor proteins decrease the transcription rate.

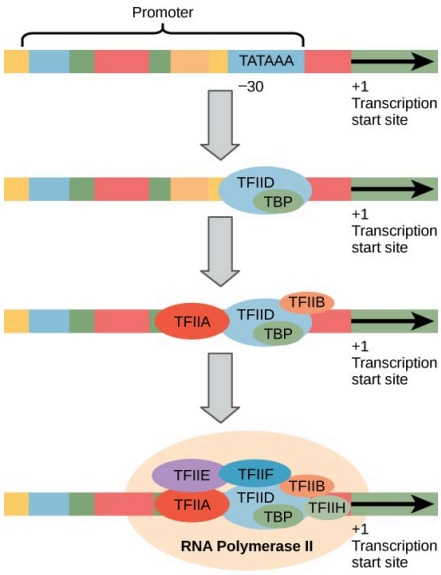


Figure 15.6.1: Eukaryotic Transcription Initiation: A generalized promoter of a gene transcribed by RNA polymerase II is shown. Transcription factors recognize the promoter, RNA polymerase II then binds and forms the transcription initiation complex.

The Three Eukaryotic RNA Polymerases (RNAPs)

The features of eukaryotic mRNA synthesis are markedly more complex those of prokaryotes. Instead of a single polymerase comprising five subunits, the eukaryotes have three polymerases that are each made up of 10 subunits or more. Each eukaryotic polymerase also requires a distinct set of transcription factors to bring it to the DNA template.

RNA polymerase I is located in the nucleolus, a specialized nuclear substructure in which ribosomal RNA (rRNA) is transcribed, processed, and assembled into ribosomes. The rRNA molecules are considered structural RNAs because they have a cellular role but are not translated into protein. The rRNAs are components of the ribosome and are essential to the process of translation. RNA polymerase I synthesizes all of the rRNAs except for the 5S rRNA molecule.

RNA polymerase II is located in the nucleus and synthesizes all protein-coding nuclear pre-mRNAs. Eukaryotic pre-mRNAs undergo extensive processing after transcription, but before translation. RNA polymerase II is responsible for transcribing the overwhelming majority of eukaryotic genes, including all of the protein-encoding genes which ultimately are translated into proteins and genes for several types of regulatory RNAs, including microRNAs (miRNAs) and long-coding RNAs (lncRNAs).

RNA polymerase III is also located in the nucleus. This polymerase transcribes a variety of structural RNAs that includes the 5S pre-rRNA, transfer pre-RNAs (pre-tRNAs), and small nuclear pre-RNAs. The tRNAs have a critical role in translation: they serve as the adaptor molecules between the mRNA template and the growing polypeptide chain. Small nuclear RNAs have a variety of functions, including “splicing” pre-mRNAs and regulating transcription factors. Not all miRNAs are transcribed by RNA Polymerase II, RNA Polymerase III transcribes some of them.

Interactive Element

Modeling transcription: This interactive models the process of DNA transcription in a eukaryotic cell.

Key Points

- Eukaryotic transcription is carried out in the nucleus of the cell and proceeds in three sequential stages: initiation, elongation, and termination.
- Eukaryotes require transcription factors to first bind to the promoter region and then help recruit the appropriate polymerase.
- RNA Polymerase II is the polymerase responsible for transcribing mRNA.

Key Terms

- **repressor**: any protein that binds to DNA and thus regulates the expression of genes by decreasing the rate of transcription
- **activator**: any chemical or agent which regulates one or more genes by increasing the rate of transcription
- **polymerase**: any of various enzymes that catalyze the formation of polymers of DNA or RNA using an existing strand of DNA or RNA as a template

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15.7: Eukaryotic Transcription - Elongation and Termination in Eukaryotes

Learning Objectives

- Describe what is happening during transcription elongation and termination

Transcription through Nucleosomes

Following the formation of the pre-initiation complex, the polymerase is released from the other transcription factors, and elongation is allowed to proceed with the polymerase synthesizing RNA in the 5′ to 3′ direction. RNA Polymerase II (RNAPII) transcribes the major share of eukaryotic genes, so this section will mainly focus on how this specific polymerase accomplishes elongation and termination.

Although the enzymatic process of elongation is essentially the same in eukaryotes and prokaryotes, the eukaryotic DNA template is more complex. When eukaryotic cells are not dividing, their genes exist as a diffuse, but still extensively packaged and compacted mass of DNA and proteins called chromatin. The DNA is tightly packaged around charged histone proteins at repeated intervals. These DNA–histone complexes, collectively called nucleosomes, are regularly spaced and include 146 nucleotides of DNA wound twice around the eight histones in a nucleosome like thread around a spool.

For polynucleotide synthesis to occur, the transcription machinery needs to move histones out of the way every time it encounters a nucleosome. This is accomplished by a special protein dimer called FACT, which stands for “facilitates chromatin transcription.” FACT partially disassembles the nucleosome immediately ahead (upstream) of a transcribing RNA Polymerase II by removing two of the eight histones (a single dimer of H2A and H2B histones is removed.) This presumably sufficiently loosens the DNA wrapped around that nucleosome so that RNA Polymerase II can transcribe through it. FACT reassembles the nucleosome behind the RNA Polymerase II by returning the missing histones to it. RNA Polymerase II will continue to elongate the newly-synthesized RNA until transcription terminates.

image

Figure 15.7.1: The FACT protein dimer allows RNA Polymerase II to transcribe through packaged DNA: DNA in eukaryotes is packaged in nucleosomes, which consist of an octomer of 4 different histone proteins. When DNA is tightly wound twice around a nucleosome, RNA Polymerase II cannot access it for transcription. FACT removes two of the histones from the nucleosome immediately ahead of RNA Polymerase, loosening the packaging so that RNA Polymerase II can continue transcription. FACT also reassembles the nucleosome immediately behindd the RNA Polymerase by returning the missing histones.

Elongation

RNA Polymerase II is a complex of 12 protein subunits. Specific subunits within the protein allow RNA Polymerase II to act as its own helicase, sliding clamp, single-stranded DNA binding protein, as well as carry out other functions. Consequently, RNA Polymerase II does not need as many accessory proteins to catalyze the synthesis of new RNA strands during transcription elongation as DNA Polymerase does to catalyze the synthesis of new DNA strands during replication elongation.

However, RNA Polymerase II does need a large collection of accessory proteins to initiate transcription at gene promoters, but once the double-stranded DNA in the transcription start region has been unwound, the RNA Polymerase II has been positioned at the +1 initiation nucleotide, and has started catalyzing new RNA strand synthesis, RNA Polymerase II clears or “escapes” the promoter region and leaves most of the transcription initiation proteins behind.

All RNA Polymerases travel along the template DNA strand in the 3′ to 5′ direction and catalyze the synthesis of new RNA strands in the 5′ to 3′ direction, adding new nucleotides to the 3′ end of the growing RNA strand.

RNA Polymerases unwind the double stranded DNA ahead of them and allow the unwound DNA behind them to rewind. As a result, RNA strand synthesis occurs in a transcription bubble of about 25 unwound DNA basebairs. Only about 8 nucleotides of

newly-synthesized RNA remain basepaired to the template DNA. The rest of the RNA molecules falls off the template to allow the DNA behind it to rewind.

RNA Polymerases use the DNA strand below them as a template to direct which nucleotide to add to the 3′ end of the growing RNA strand at each point in the sequence. The RNA Polymerase travels along the template DNA one nucleotide at at time. Whichever RNA nucleotide is capable of basepairing to the template nucleotide below the RNA Polymerase is the next nucleotide to be added. Once the addition of a new nucleotide to the 3′ end of the growing strand has been catalyzed, the RNA Polymerase moves to the next DNA nucleotide on the template below it. This process continues until transcription termination occurs.

Termination

The termination of transcription is different for the three different eukaryotic RNA polymerases.

The ribosomal rRNA genes transcribed by RNA Polymerase I contain a specific sequence of basepairs (11 bp long in humans; 18 bp in mice) that is recognized by a termination protein called TTF-1 (Transcription Termination Factor for RNA Polymerase I.) This protein binds the DNA at its recognition sequence and blocks further transcription, causing the RNA Polymerase I to disengage from the template DNA strand and to release its newly-synthesized RNA.

The protein-encoding, structural RNA, and regulatory RNA genes transcribed by RNA Polymerse II lack any specific signals or sequences that direct RNA Polymerase II to terminate at specific locations. RNA Polymerase II can continue to transcribe RNA anywhere from a few bp to thousands of bp past the actual end of the gene. However, the transcript is cleaved at an internal site before RNA Polymerase II finishes transcribing. This releases the upstream portion of the transcript, which will serve as the initial RNA prior to further processing (the pre-mRNA in the case of protein-encoding genes.) This cleavage site is considered the “end” of the gene. The remainder of the transcript is digested by a 5′-exonuclease (called Xrn2 in humans) while it is still being transcribed by the RNA Polymerase II. When the 5′-exonulease “catches up” to RNA Polymerase II by digesting away all the overhanging RNA, it helps disengage the polymerase from its DNA template strand, finally terminating that round of transcription.

In the case of protein-encoding genes, the cleavage site which determines the “end” of the emerging pre-mRNA occurs between an upstream AAUAAA sequence and a downstream GU-rich sequence separated by about 40-60 nucleotides in the emerging RNA. Once both of these sequences have been transcribed, a protein called CPSF in humans binds the AAUAAA sequence and a protein called CstF in humans binds the GU-rich sequence. These two proteins form the base of a complicated protein complex that forms in this region before CPSF cleaves the nascent pre-mRNA at a site 10-30 nucleotides downstream from the AAUAAA site. The Poly(A) Polymerase enzyme which catalyzes the addition of a 3′ poly-A tail on the pre-mRNA is part of the complex that forms with CPSF and CstF.

Figure 15.7.1: Transcription termination by RNA Polymerase II on a protein-encoding gene.: RNA Polymerase II has no specific signals that terminate its transcription. In the case of protein-encoding genes, a protein complex will bind to two locations on the growing pre-mRNA once the RNA Polymerase has transcribed past the end of the gene. CPSF in the complex will bind a AAUAAA sequence, and CstF in the complex will bind a GU-rich sequence (top figure). CPSF in the complex will cleave the pre-mRNA at a site between the two bound sequences, releasing the pre-mRNA (middle figure). Poly(A) Polymerase is a part of the same complex and will begin to add a poly-A tail to the pre-mRNA. At the same time, Xrn2 protein, which is an exonuclease, attacks the 5′ end of the RNA strand still associated with the RNA Polymerase. Xrn2 will start digesting the non-released portion of the newly synthesized RNA until Xrn2 reaches the RNA Polymerase, where it aids in displacing the RNA Polymerase from the template DNA strand. This terminates transcription at some random location downstream from the true end of the gene (bottom figure).

The tRNA, 5S rRNA, and structural RNAs genes transcribed by RNA Polymerase III have a not-entirely-understood termination signal. The RNAs transcribed by RNA Polymerase III have a short stretch of four to seven U’s at their 3′ end. This somehow triggers RNA Polymerase III to both release the nascent RNA and disengage from the template DNA strand.

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Key Points

- RNA polymerase II (RNAPII) transcribes the major share of eukaryotic genes.
- During elongation, the transcription machinery needs to move histones out of the way every time it encounters a nucleosome.
- Transcription elongation occurs in a bubble of unwound DNA, where the RNA Polymerase uses one strand of DNA as a template to catalyze the synthesis of a new RNA strand in the 5′ to 3′ direction.
- RNA Polymerase I and RNA Polymerase III terminate transcription in response to specific termination sequences in either the DNA being transcribed (RNA Polymerase I) or in the newly-synthesized RNA (RNA Polymerase III).
- RNA Polymerase II terminates transcription at random locations past the end of the gene being transcribed. The newly-synthesized RNA is cleaved at a sequence-specified location and released before transcription terminates.

Key Terms

- **nucleosome**: any of the subunits that repeat in chromatin; a coil of DNA surrounding a histone core
- **histone**: any of various simple water-soluble proteins that are rich in the basic amino acids lysine and arginine and are complexed with DNA in the nucleosomes of eukaryotic chromatin
- **chromatin**: a complex of DNA, RNA, and proteins within the cell nucleus out of which chromosomes condense during cell division

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15.8: RNA Processing in Eukaryotes - mRNA Processing

Learning Objectives

- Outline the steps of pre-mRNA processing

Pre-mRNA Processing

The eukaryotic pre-mRNA undergoes extensive processing before it is ready to be translated. The additional steps involved in eukaryotic mRNA maturation create a molecule with a much longer half-life than a prokaryotic mRNA. Eukaryotic mRNAs last for several hours, whereas the typical *E. coli* mRNA lasts no more than five seconds.

Pre-mRNAs are first coated in RNA-stabilizing proteins; these protect the pre-mRNA from degradation while it is processed and exported out of the nucleus. The three most important steps of pre-mRNA processing are the addition of stabilizing and signaling factors at the 5′ and 3′ ends of the molecule, and the removal of intervening sequences that do not specify the appropriate amino acids. In rare cases, the mRNA transcript can be “edited” after it is transcribed.

5′ Capping

While the pre-mRNA is still being synthesized, a 7-methylguanosine cap is added to the 5′ end of the growing transcript by a 5′-to-5′ phosphate linkage. This moiety protects the nascent mRNA from degradation. In addition, initiation factors involved in protein synthesis recognize the cap to help initiate translation by ribosomes.

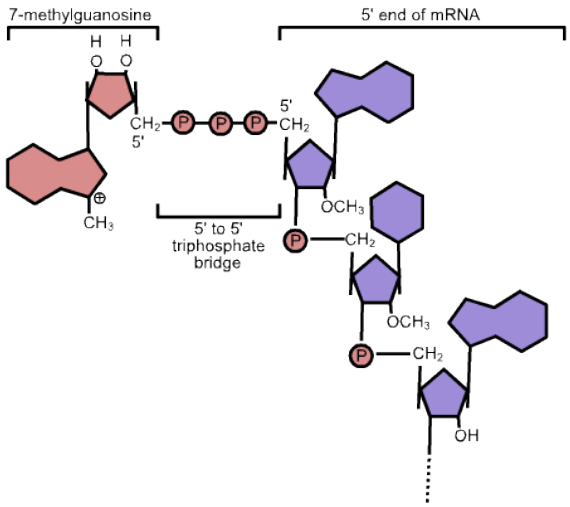


Figure 15.8.1: 5′ cap structure: Capping of the pre-mRNA involves the addition of 7-methylguanosine (m^7G) to the 5′ end. The cap protects the 5′ end of the primary RNA transcript from attack by ribonucleases and is recognized by eukaryotic initiation factors involved in assembling the ribosome on the mature mRNA prior to initiating translation.

3′ Poly-A Tail

While RNA Polymerase II is still transcribing downstream of the proper end of a gene, the pre-mRNA is cleaved by an endonuclease-containing protein complex between an AAUAAA consensus sequence and a GU-rich sequence. This releases the functional pre-mRNA from the rest of the transcript, which is still attached to the RNA Polymerase. An enzyme called poly (A) polymerase (PAP) is part of the same protein complex that cleaves the pre-mRNA and it immediately adds a string of

approximately 200 A nucleotides, called the poly (A) tail, to the 3′ end of the just-cleaved pre-mRNA. The poly (A) tail protects the mRNA from degradation, aids in the export of the mature mRNA to the cytoplasm, and is involved in binding proteins involved in initiating translation.

image

Figure 15.8.1: Poly (A) Polymerase adds a 3′ poly (A) tail to the pre-mRNA.: The pre-mRNA is cleaved off the rest of the growing transcript before RNA Polymerase II has stopped transcribing. This cleavage is done by an endonuclease-containing protein complex that binds to an AAUAAA sequence upstream of the cleavage site and to a GU-rich sequence downstream of the cut site. Immediately after the cleavage, Poly (A) Polymerase (PAP), which is also part of the protein complex, catalyzes the addition of up to 200 A nucleotides to the 3′ end of the just-cleaved pre-mRNA.

Pre-mRNA Splicing

Eukaryotic genes are composed of exons, which correspond to protein-coding sequences (*ex*-on signifies that they are *ex*pressed), and intervening sequences called introns (*int*-ron denotes their *int*ervening role), which may be involved in gene regulation, but are removed from the pre-mRNA during processing. Intron sequences in mRNA do not encode functional proteins.

Discovery of Introns

The discovery of introns came as a surprise to researchers in the 1970s who expected that pre-mRNAs would specify protein sequences without further processing, as they had observed in prokaryotes. The genes of higher eukaryotes very often contain one or more introns. While these regions may correspond to regulatory sequences, the biological significance of having many introns or having very long introns in a gene is unclear. It is possible that introns slow down gene expression because it takes longer to transcribe pre-mRNAs with lots of introns. Alternatively, introns may be nonfunctional sequence remnants left over from the fusion of ancient genes throughout evolution. This is supported by the fact that separate exons often encode separate protein subunits or domains. For the most part, the sequences of introns can be mutated without ultimately affecting the protein product.

Intron Processing

All introns in a pre-mRNA must be completely and precisely removed before protein synthesis. If the process errs by even a single nucleotide, the reading frame of the rejoined exons would shift, and the resulting protein would be dysfunctional. The process of removing introns and reconnecting exons is called splicing. Introns are removed and degraded while the pre-mRNA is still in the nucleus. Splicing occurs by a sequence-specific mechanism that ensures introns will be removed and exons rejoined with the accuracy and precision of a single nucleotide. The splicing of pre-mRNAs is conducted by complexes of proteins and RNA molecules called spliceosomes.

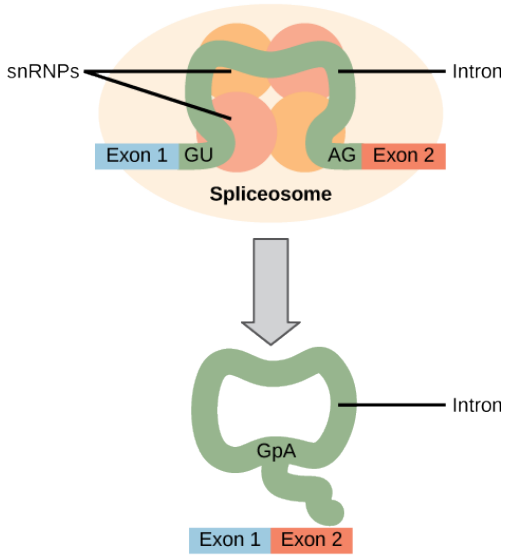


Figure 15.8.1: Pre-mRNA splicing: Pre-mRNA splicing involves the precise removal of introns from the primary RNA transcript. The splicing process is catalyzed by large complexes called spliceosomes. Each spliceosome is composed of five subunits called snRNPs. The spliceseome's actions result in the splicing together of the two exons and the release of the intron in a lariat form.

Each spliceosome is composed of five subunits called snRNPs (for small nuclear ribonucleoparticles, and pronounced "snurps".) Each snRNP is itself a complex of proteins and a special type of RNA found only in the nucleus called snRNAs (small nuclear RNAs). Spliceosomes recognize sequences at the 5′ end of the intron because introns always start with the nucleotides GU and they recognize sequences at the 3′ end of the intron because they always end with the nucleotides AG. The spliceosome cleaves the pre-mRNA's sugar phosphate backbone at the G that starts the intron and then covalently attaches that G to an internal A nucleotide within the intron. Then the spliceosme connects the 3′ end of the first exon to the 5′ end of the following exon, cleaving the 3′ end of the intron in the process. This results in the splicing together of the two exons and the release of the intron in a lariat form.

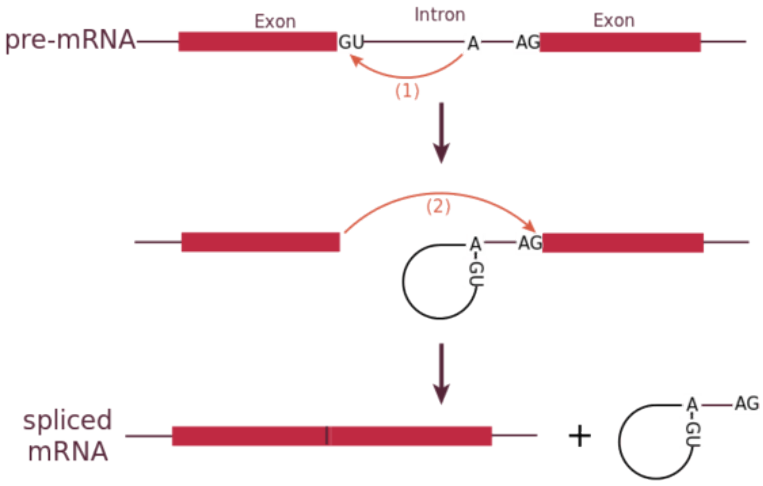


Figure 15.8.1: Mechanism of pre-mRNA splicing.: The snRNPs of the spliceosome were left out of this figure, but it shows the sites within the intron whose interactions are catalyzed by the spliceosome. Initially, the conserved G which starts an intron is cleaved from the 3′ end of the exon upstream to it and the G is covalently attached to an internal A within the intron. Then the 3′ end of the just-released exon is joined to the 5′ end of the next exon, cleaving the bond that attaches the 3′ end of the intron to its adjacent exon. This both joins the two exons and removes the intron in lariat form.

Key Points

- A 7-methylguanosine cap is added to the 5′ end of the pre-mRNA while elongation is still in progress. The 5′ cap protects the nascent mRNA from degradation and assists in ribosome binding during translation.
- A poly (A) tail is added to the 3′ end of the pre-mRNA once elongation is complete. The poly (A) tail protects the mRNA from degradation, aids in the export of the mature mRNA to the cytoplasm, and is involved in binding proteins involved in initiating translation.
- Introns are removed from the pre-mRNA before the mRNA is exported to the cytoplasm.

Key Terms

- **intron**: a portion of a split gene that is included in pre-RNA transcripts but is removed during RNA processing and rapidly degraded
- **moiety**: a specific segment of a molecule
- **spliceosome**: a dynamic complex of RNA and protein subunits that removes introns from precursor mRNA

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15.9: RNA Processing in Eukaryotes - Processing of tRNAs and rRNAs

Learning Objectives

- Describe how pre-rRNAs and pre-tRNAs are processed into mature rRNAs and tRNAs.

Processing of tRNAs and rRNAs

The tRNAs and rRNAs are structural molecules that have roles in protein synthesis; however, these RNAs are not themselves translated. In eukaryotes, pre-rRNAs are transcribed, processed, and assembled into ribosomes in the nucleolus, while pre-tRNAs are transcribed and processed in the nucleus and then released into the cytoplasm where they are linked to free amino acids for protein synthesis.

Ribosomal RNA (rRNA)

The four rRNAs in eukaryotes are first transcribed as two long precursor molecules. One contains just the pre-rRNA that will be processed into the 5S rRNA; the other spans the 28S, 5.8S, and 18S rRNAs. Enzymes then cleave the precursors into subunits corresponding to each rRNA. In bacteria, there are only three rRNAs and all are transcribed in one long precursor molecule that is cleaved into the individual rRNAs. Some of the bases of pre-rRNAs are methylated for added stability. Mature rRNAs make up 50-60% of each ribosome. Some of a ribosome's RNA molecules are purely structural, whereas others have catalytic or binding activities.

The eukaryotic ribosome is composed of two subunits: a large subunit (60S) and a small subunit (40S). The 60S subunit is composed of the 28S rRNA, 5.8S rRNA, 5S rRNA, and 50 proteins. The 40S subunit is composed of the 18S rRNA and 33 proteins. The bacterial ribosome is composed of two similar subunits, with slightly different components. The bacterial large subunit is called the 50S subunit and is composed of the 23S rRNA, 5S rRNA, and 31 proteins, while the bacterial small subunit is called the 30S subunit and is composed of the 16S rRNA and 21 proteins.

The two subunits join to constitute a functioning ribosome that is capable of creating proteins.

Transfer RNA (tRNA)

Each different tRNA binds to a specific amino acid and transfers it to the ribosome. Mature tRNAs take on a three-dimensional structure through intramolecular basepairing to position the amino acid binding site at one end and the anticodon in an unbasepaired loop of nucleotides at the other end. The anticodon is a three-nucleotide sequence, unique to each different tRNA, that interacts with a messenger RNA (mRNA) codon through complementary base pairing.

There are different tRNAs for the 21 different amino acids. Most amino acids can be carried by more than one tRNA.

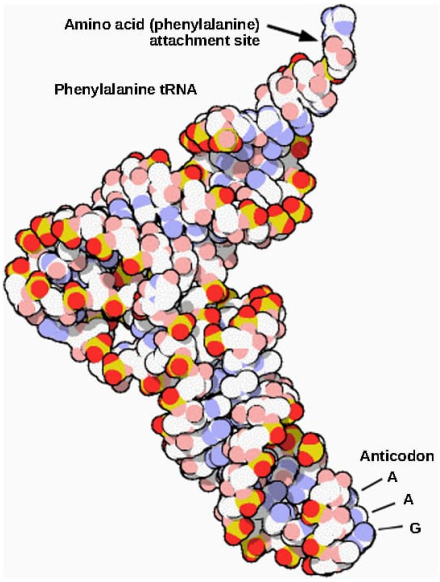


Figure 15.9.1: Structure of tRNA: This is a space-filling model of a tRNA molecule that adds the amino acid phenylalanine to a growing polypeptide chain. The anticodon AAG binds the codon UUC on the mRNA. The amino acid phenylalanine is attached to the other end of the tRNA.

In all organisms, tRNAs are transcribed in a pre-tRNA form that requires multiple processing steps before the mature tRNA is ready for use in translation. In bacteria, multiple tRNAs are often transcribed as a single RNA. The first step in their processing is the digestion of the RNA to release individual pre-tRNAs. In archaea and eukaryotes, each pre-tRNA is transcribed as a separate transcript.

The processing to convert the pre-tRNA to a mature tRNA involves five steps.

1. The 5′ end of the pre-tRNA, called the 5′ leader sequence, is cleaved off.

2. The 3′ end of the pre-tRNA is cleaved off.

3. In all eukaryote pre-tRNAs, but in only some bacterial and archaeal pre-tRNAs, a CCA sequence of nucleotides is added to the 3′ end of the pre-tRNA after the original 3′ end is trimmed off. Some bacteria and archaea pre-tRNAs already have the CCA encoded in their transcript immediately upstream of the 3′ cleavage site, so they don't need to add one. The CCA at the 3′ end of the mature tRNA will be the site at which the tRNA's amino acid will be added.

4. Multiple nucleotides in the pre-tRNA are chemically modified, altering their nitorgen bases. On average about 12 nucleotides are modified per tRNA. The most common modifications are the conversion of adenine (A) to pseudouridine (Ψ), the conversion of adenine to inosine (I), and the conversion of uridine to dihydrouridine (D). But over 100 other modifications can occur.

5. A significant number of eukaryotic and archaeal pre-tRNAs have introns that have to be spliced out. Introns are rarer in bacterial pre-tRNAs, but do occur occasionally and are spliced out.

After processing, the mature pre-tRNA is ready to have its cognate amino acid attached. The cognate amino acid for a tRNA is the one specified by its anticodon. Attaching this amino acid is called charging the tRNA. In eukaryotes, the mature tRNA is generated in the nucleus, and then exported to the cytoplasm for charging.

image

Figure 15.9.1: Processing of a pre-tRNA.: A typical pre-tRNA undergoing processing steps to generate a mature tRNA ready to have its cognate amino acid attached. Nucleotides that are cleaved away are shown in green. Chemically-modified nucleotides are in yellow, as is the CAA trinucleotide that is added to the 3′ end of the pre-tRNA during processing. The anticodon nucleotides are shown in a lighter shade of red.

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Key Points

- Ribosomal RNA (rRNA) is a structural molecule that makes up over half of the mass of a ribosome and aids in protein synthesis.
- Transfer RNA (tRNA) recognizes a codon on mRNA and brings the appropriate amino acid to that site.
- rRNAs are processed from larger pre-rRNAs by trimming the larger rRNAs down and methylating some of the nucleotides.
- tRNAs are processed from pre-tRNAs by trimming both ends of the pre-tRNA, adding a CCA trinucleotide to the 3′ end, if needed, removing any introns present, and chemically modified 12 nucleotides on average per tRNA.

Key Terms

- **anticodon**: a sequence of three nucleotides in transfer RNA that binds to the complementary triplet (codon) in messenger RNA, specifying an amino acid during protein synthesis

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15.10: Ribosomes and Protein Synthesis - The Protein Synthesis Machinery

Learning Objectives

- Explain the role played by ribosomes, tRNA, and aminoacyl tRNA synthetases in protein synthesis

The Protein Synthesis Machinery

In addition to the mRNA template, many molecules and macromolecules contribute to the process of translation. The composition of each component may vary across species. For instance, ribosomes may consist of different numbers of rRNAs and polypeptides depending on the organism. However, the general structures and functions of the protein synthesis machinery are comparable from bacteria to archaea to human cells. Translation requires the input of an mRNA template, ribosomes, tRNAs, and various enzymatic factors.

Ribosomes

A ribosome is a complex macromolecule composed of structural and catalytic rRNAs, and many distinct polypeptides. In eukaryotes, the synthesis and assembly of rRNAs occurs in the nucleolus.

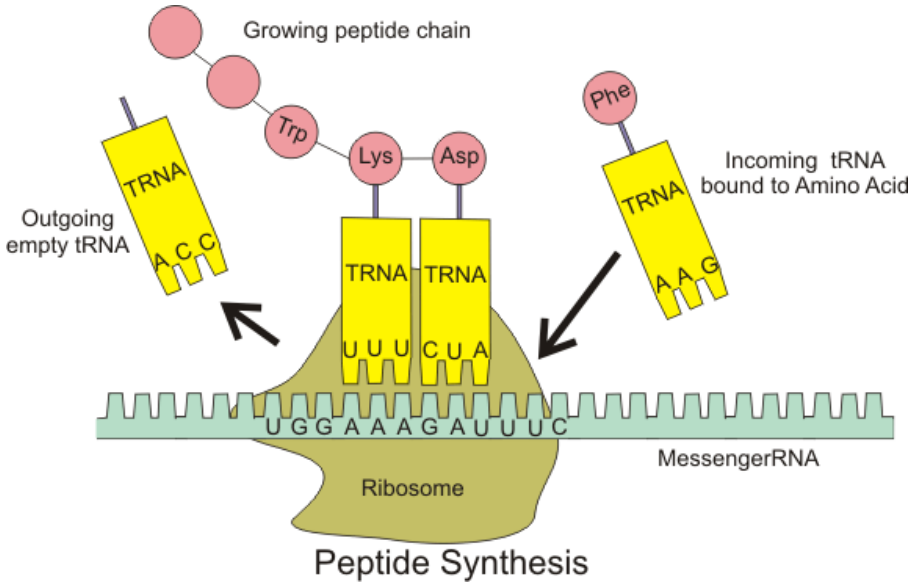


Figure 15.10.1: The ribosome in action: Structure and role of ribosomes during translation

Ribosomes exist in the cytoplasm in prokaryotes and in the cytoplasm and on rough endoplasmic reticulum membranes in eukaryotes. Mitochondria and chloroplasts also have their own ribosomes, and these look more similar to prokaryotic ribosomes (and have similar drug sensitivities) than the cytoplasmic ribosomes. Ribosomes dissociate into large and small subunits when they are not synthesizing proteins and reassociate during the initiation of translation.*E. coli* have a 30S small subunit and a 50S large subunit, for a total of 70S when assembled (recall that Svedberg units are not additive). Mammalian ribosomes have a small 40S subunit and a large 60S subunit, for a total of 80S. The small subunit is responsible for binding the mRNA template, whereas the large subunit sequentially binds tRNAs.

In bacteria, archaea, and eukaryotes, the intact ribosome has three binding sites that accomodate tRNAs: The A site, the P site, and the E site. Incoming aminoacy-tRNAs (a tRNA with an amino acid covalently attached is called an aminoacyl-tRNA) enter the ribosome at the A site. The peptidyl-tRNA carrying the growing polypeptide chain is held in the P site. The E site holds empty

tRNAs just before they exit the ribosome.

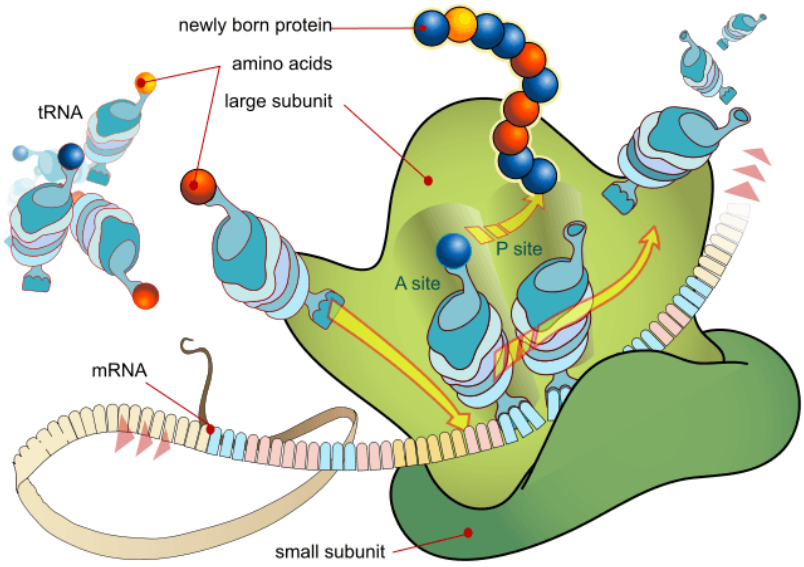


Figure 15.10.1: Ribosome structure: The large ribosomal subunit sits atop the small ribosomal subunit and the mRNA is threaded through a groove near the interface of the two subunits. The intact ribosome has three tRNA binding sites: the A site for incoming aminoacyl-tRNAs; the P site for the peptidyl-tRNA carrying the growing polypeptide chain; and the E site where empty tRNAs exit (not shown in this figure but immediately adjacent to the P site.)

Each mRNA molecule is simultaneously translated by many ribosomes, all reading the mRNA from 5′ to 3′ and synthesizing the polypeptide from the N terminus to the C terminus. The complete mRNA/poly-ribosome structure is called a polysome.

tRNAs in eukaryotes

The tRNA molecules are transcribed by RNA polymerase III. Depending on the species, 40 to 60 types of tRNAs exist in the cytoplasm. Specific tRNAs bind to codons on the mRNA template and add the corresponding amino acid to the polypeptide chain. (More accurately, the growing polypeptide chain is added to each new amino acid bound in by a tRNA.)

The transfer RNAs (tRNAs) are structural RNA molecules. In eukaryotes, tRNA mole are transcribed from tRNA genes by RNA polymerase III. Depending on the species, 40 to 60 types of tRNAs exist in the cytoplasm. Serving as adaptors, specific tRNAs bind to sequences on the mRNA template and add the corresponding amino acid to the polypeptide chain. (More accurately, the growing polypeptide chain is added to each new amino acid brought in by a tRNA.) Therefore, tRNAs are the molecules that actually “translate” the language of RNA into the language of proteins.

Of the 64 possible mRNA codons (triplet combinations of A, U, G, and C) three specify the termination of protein synthesis and 61 specify the addition of amino acids to the polypeptide chain. Of the three termination codons, one (UGA) can also be used to encode the 21st amino acid, selenocysteine, but only if the mRNA contains a specific sequence of nucleotides known as a SECIS sequence. Of the 61 non-termination codons, one codon (AUG) also encodes the initiation of translation.

Each tRNA polynucleotide chain folds up so that some internal sections basepair with other internal sections. If just diagrammed in two dimensions, the regions where basepairing occurs are called stems, and the regions where no basepairs form are called loops, and the entire pattern of stems and loops that forms for a tRNA is called the “cloverleaf” structure. All tRNAs fold into very similar cloverleaf structures of four major stems and three major loops.

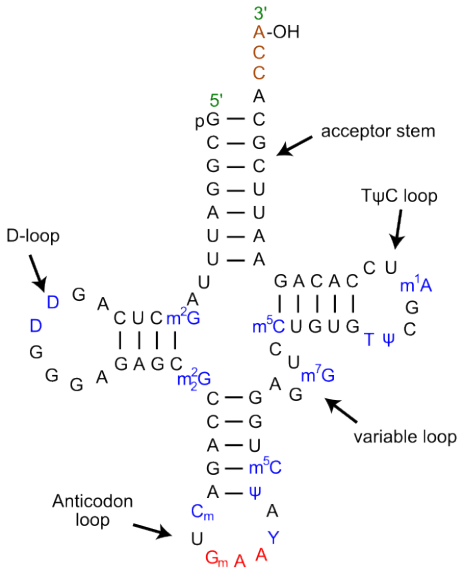


Figure 15.10.1: The two-dimensional cloverleaf structure of a typical tRNA.: All tRNAs, regardless of the species they come from or the amino acid they carry, self-basepair to produce a cloverleaf structure of four main stems and three main loops. The amino acid carried by the tRNA is covalently attached to the nucleotide at the 3′ end of the tRNA, known as the tRNA's acceptor arm. The opposite end of the folded tRNA has the anticodon loop where the tRNA will basepair to the mRNA codon.

If viewed as a three-dimensional structure, all the basepaired regions of the tRNA are helical, and the tRNA folds into a L-shaped structure.

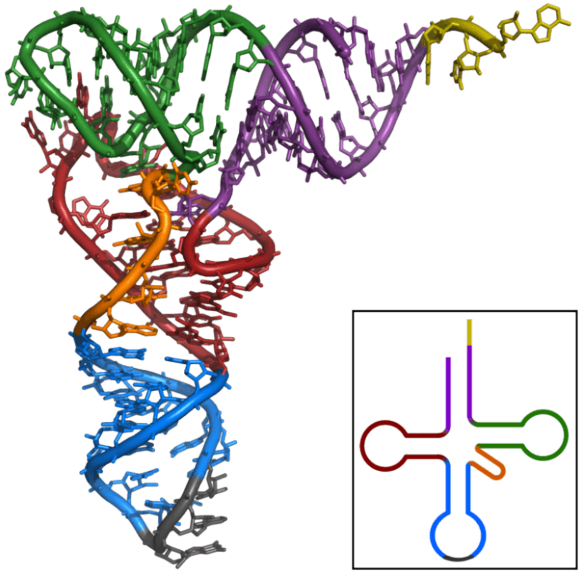


Figure 15.10.1: The three dimensional shape taken by tRNAs.: If viewed as a three-dimensional structure, all tRNAs are partially helical molecules that are vaguely L-shaped. The anticodon-containing loop is at one end of the molecule (in grey here) and the amino acid acceptor arm is at the other end of the molecule (in yellow here) past the bend of the "L".

Each tRNA has a sequence of three nucleotides located in a loop at one end of the molecule that can basepair with an mRNA codon. This is called the tRNA's anticodon. Each different tRNA has a different anticodon. When the tRNA anticodon basepairs with one of the mRNA codons, the tRNA will add an amino acid to a growing polypeptide chain or terminate translation, according to the genetic code. For instance, if the sequence CUA occurred on a mRNA template in the proper reading frame, it would bind a tRNA with an anticodon expressing the complementary sequence, GAU. The tRNA with this anticodon would be linked to the amino acid leucine.

Aminoacyl tRNA Synthetases

The process of pre-tRNA synthesis by RNA polymerase III only creates the RNA portion of the adaptor molecule. The corresponding amino acid must be added later, once the tRNA is processed and exported to the cytoplasm. Through the process of tRNA "charging," each tRNA molecule is linked to its correct amino acid by a group of enzymes called aminoacyl tRNA synthetases. When an amino acid is covalently linked to a tRNA, the resulting complex is known as an aminoacyl-tRNA. At least one type of aminoacyl tRNA synthetase exists for each of the 21 amino acids; the exact number of aminoacyl tRNA synthetases varies by species. These enzymes first bind and hydrolyze ATP to catalyze the formation of a covalent bond between an amino acid and adenosine monophosphate (AMP); a pyrophosphate molecule is expelled in this reaction. This is called "activating" the amino acid. The same enzyme then catalyzes the attachment of the activated amino acid to the tRNA and the simultaneous release of AMP. After the correct amino acid covalently attached to the tRNA, it is released by the enzyme. The tRNA is said to be charged with its cognate amino acid. (the amino acid specified by its anticodon is a tRNA's cognate amino acid.)

Key Points

- Ribosomes, macromolecular structures composed of rRNA and polypeptide chains, are formed of two subunits (in bacteria and archaea, 30S and 50S; in eukaryotes, 40S and 60S), that bring together mRNA and tRNAs to catalyze protein synthesis.
- Fully assembled ribosomes have three tRNA binding sites: an A site for incoming aminoacyl-tRNAs, a P site for peptidyl-tRNAs, and an E site where empty tRNAs exit.
- tRNAs (transfer ribonucleic acids), which serve to deliver the appropriate amino acid to the growing peptide chain, consist of a modified RNA chain with the appropriate amino acid covalently attached.
- tRNAs have a loop of unbasepaired nucleotides at one end of the molecule that contains three nucleotides that act as the anticodon that basepairs to the mRNA codon.
- Aminoacyl tRNA synthetases are enzymes that load the individual amino acids onto the tRNAs.

Key Terms

- **ribosome**: protein/mRNA complexes found in all cells that are involved in the production of proteins by translating messenger RNA

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15.11: Ribosomes and Protein Synthesis - The Mechanism of Protein Synthesis

Learning Objectives

- Describe the process of translation

As with mRNA synthesis, protein synthesis can be divided into three phases: initiation, elongation, and termination.

Initiation of Translation

Protein synthesis begins with the formation of a pre-initiation complex. In *E. coli*, this complex involves the small 30S ribosome, the mRNA template, three initiation factors (IFs; IF-1, IF-2, and IF-3), and a special initiator tRNA, called fMet-tRNA. The initiator tRNA basepairs to the start codon AUG (or rarely, GUG) and is covalently linked to a formylated methionine called fMet. Methionine is one of the 21 amino acids used in protein synthesis; formylated methionine is a methione to which a formyl group (a one-carbon aldehyde) has been covalently attached at the amino nitrogen. Formylated methionine is inserted by fMet-tRNA at the beginning of every polypeptide chain synthesized by *E. coli*, and is usually clipped off after translation is complete. When an in-frame AUG is encountered during translation elongation, a non-formylated methionine is inserted by a regular Met-tRNA. In *E. coli* mRNA, a sequence upstream of the first AUG codon, called the Shine-Dalgarno sequence (AGGAGG), interacts with the rRNA molecules that compose the ribosome. This interaction anchors the 30S ribosomal subunit at the correct location on the mRNA template.

In eukaryotes, a pre-initiation complex forms when an initiation factor called eIF2 (eukaryotic initiation factor 2) binds GTP, and the GTP-eIF2 recruits the eukaryotic initiator tRNA to the 40s small ribosomal subunit. The initiator tRNA, called Met-tRNA$_i$, carries unmodified methionine in eukaryotes, not fMet, but it is distinct from other cellular Met-tRNAs in that it can bind eIFs and it can bind at the ribosome P site. The eukaryotic pre-initiation complex then recognizes the 7-methylguanosine cap at the 5′ end of a mRNA. Several other eIFs, specifically eIF1, eIF3, and eIF4, act as cap-binding proteins and assist the recruitment of the pre-initiation complex to the 5′ cap. Poly (A)-Binding Protein (PAB) binds both the poly (A) tail of the mRNA and the complex of proteins at the cap and also assists in the process. Once at the cap, the pre-initiation complex tracks along the mRNA in the 5′ to 3′ direction, searching for the AUG start codon. Many, but not all, eukaryotic mRNAs are translated from the first AUG sequence. The nucleotides around the AUG indicate whether it is the correct start codon.

Once the appropriate AUG is identified, eIF2 hydrolyzes GTP to GDP and powers the delivery of the tRNA$_i$-Met to the start codon, where the tRNA$_i$ anticodon basepairs to the AUG codon. After this, eIF2-GDP is released from the complex, and eIF5-GTP binds. The 60S ribosomal subunit is recruited to the pre-initiation complex by eIF5-GTP, which hydrolyzes its GTP to GDP to power the assembly of the full ribosome at the translation start site with the Met-tRNAi positioned in the ribosome P site. The remaining eIFs dissociate from the ribosome and translation is ready to begins.

In archaea, translation initiation is similar to that seen in eukaryotes, except that the initiation factors involved are called aIFs (archaeal inititiaion factors), not eIFs.

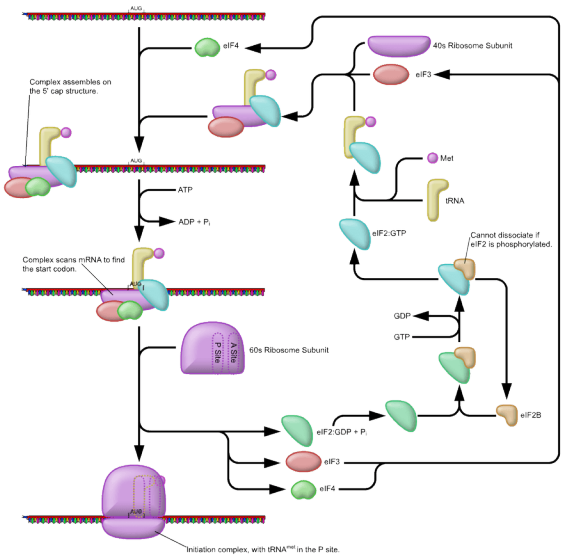


Figure 15.11.1: Translation initiation in eukaryotes.: In eukaryotes, a preinitiation complex forms made of the small 40S subunit, the initiator Met-tRNAi, and eIF2-GTP. This preinitiation complex binds to the 5′-m^7G cap of the mRNA with the help of other eIFS and PAB, which binds the poly(A) tail of the mRNA, and loops the tail to the cap. Once at the cap, the preinitiation complex slides along the mRNA until it encounters the initiator AUG codon. There, GTP is hydrolyzed by eIF2 and the Met-tRNA$_i$ is loaded onto the AUG. Next, eIF5-GTP recruits the 60S large ribosomal subunit to the 40S subunit at the AUG and hydrolyzes GTP. This allows the large ribosomal subunit to assemble on top of the small subunit, generating the intact 80S ribosome, and places the Met-tRNAi in the P site of the intact ribosome. The ribosome A site is positioned over the second codon in the mRNA reading frame, and translation elongation can begin. (CC BY-SA 3.0; Zephyris via Wikipedia)

Translation Elongation

The basics of elongation are the same in prokaryotes and eukaryotes. The intact ribosome has three compartments: the A site binds incoming aminoacyl tRNAs; the P site binds tRNAs carrying the growing polypeptide chain; the E site releases dissociated tRNAs so that they can be recharged with amino acids. The initiator tRNA, rMet-tRNA in *E. coli* and Met-tRNA$_i$ in eukaryotes and archaea, binds directly to the P site. This creates an initiation complex with a free A site ready to accept the aminoacyl-tRNA corresponding to the first codon after the AUG.

The aminoacyl-tRNA with an anticodon complementary to the A site codon lands in the A site. A peptide bond is formed between the amino group of the A site amino acid and the carboxyl group of the most-recently attached amino acid in the growing polypeptide chain attached to the P-site tRNA.The formation of the peptide bond is catalyzed by peptidyl transferase, an RNA-based enzyme that is integrated into the large ribosomal subunit. The energy for the peptide bond formation is derived from GTP hydrolysis, which is catalyzed by a separate elongation factor.

Catalyzing the formation of a peptide bond removes the bond holding the growing polypeptide chain to the P-site tRNA. The growing polypeptide chain is transferred to the amino end of the incoming amino acid, and the A-site tRNA temporarily holds the growing polypeptide chain, while the P-site tRNA is now empty or uncharged.

The ribosome moves three nucleotides down the mRNA. The tRNAs are basepaired to a codon on the mRNA, so as the ribosome moves over the mRNA, the tRNAs stay in place while the ribosome moves and each tRNA is moved into the next tRNA binding site. The E site moves over the former P-site tRNA, now empty or uncharged, the P site moves over the former A-site tRNA, now carrying the growing polypeptide chain, and the A site moves over a new codon. In the E site, the uncharged tRNA detaches from its anticodon and is expelled. A new aminoacyl-tRNA with an anticodon complementary to the new A-site codon enters the ribosome at the A site and the elongation process repeats itself. The energy for each step of the ribosome is donated by an elongation factor that hydrolyzes GTP.

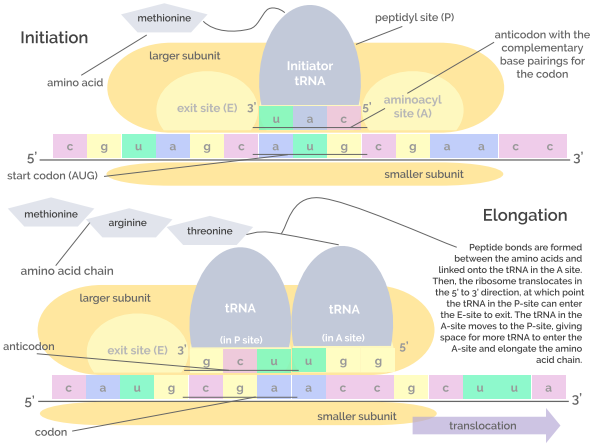


Figure 15.11.2: Translation elongation in eukaryotes.: During translation elongation, the incoming aminoacyl-tRNA enters the ribosome A site, where it binds if the tRNA anticodon is complementary to the A site mRNA codon. The elongation factor eEF1 assists in loading the aminoacyl-tRNA, powering the process through the hydrolysis of GTP. The growing polypeptide chain is attached to the tRNA in the ribosome P site. The ribosome's peptidyl transferase catalyses the transfer of the growing polypeptide chain from the P site tRNA to the amino group of the A site amino acid. This creates a peptide bond between the C terminus of the growing polypeptide chain and the A site amino acid. After the peptide bond is created, the growing polypeptide chain is attached to the A site tRNA, and the tRNA in the P site is empty. The ribosome translocates once codon on the mRNA. The elongation factor eEF2 assists in the translocation, powering the process through the hydrolysis of GTP. During translocation, the two tRNAs remain basepaired to their mRNA codons, so the ribosome moves over them, putting the empty tRNA in the E site (where it will be expelled from the ribosome) and the tRNA with the growing polypeptide chain in the P site. The A site moves over an empty codon, and the process repeats itself until a stop codon is reached. (CC BY-SA 4.0; Jordan Nguyen via Wikipedia)

Translation termination

Termination of translation occurs when the ribosome moves over a stop codon (UAA, UAG, or UGA). There are no tRNAs with anticodons complementary to stop codons, so no tRNAs enter the A site. Instead, in both prokaryotes and eukaryotes, a protein called a release factor enters the A site. The release factors cause the ribosome peptidyl transferase to add a water molecule to the carboxyl end of the most recently added amino acid in the growing polypeptide chain attached to the P-site tRNA. This causes the polypeptide chain to detach from its tRNA, and the newly-made polypeptide is released. The small and large ribosomal subunits dissociate from the mRNA and from each other; they are recruited almost immediately into another translation initiation complex. After many ribosomes have completed translation, the mRNA is degraded so the nucleotides can be reused in another transcription reaction.

Interactive Element

Modeling translation: This interactive models the process of translation in eukaryotes.

Key Points

- Protein synthesis, or translation, begins with a process known as pre-initiation, when the small ribosmal subunit, the mRNA template, initiator factors, and a special initiator tRNA, come together.
- During translocation and elongation, the ribosome moves one codon 3′ down the mRNA, brings in a charged tRNA to the A site, transfers the growing polypeptide chain from the P-site tRNA to the carboxyl group of the A-site amino acid, and ejects the uncharged tRNA at the E site.
- When a stop or nonsense codon (UAA, UAG, or UGA) is reached on the mRNA, the ribosome terminates translation.

Key Terms

- **translation**: a process occurring in the ribosome in which a strand of messenger RNA (mRNA) guides assembly of a sequence of amino acids to make a protein

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15.12: Ribosomes and Protein Synthesis - Protein Folding, Modification, and Targeting

Learning Objectives

- Discuss how post-translational events affect the proper function of a protein

Protein Folding

After being translated from mRNA, all proteins start out on a ribosome as a linear sequence of amino acids. This linear sequence must “fold” during and after the synthesis so that the protein can acquire what is known as its native conformation. The native conformation of a protein is a stable three-dimensional structure that strongly determines a protein’s biological function. When a protein loses its biological function as a result of a loss of three-dimensional structure, we say that the protein has undergone denaturation. Proteins can be denatured not only by heat, but also by extremes of pH; these two conditions affect the weak interactions and the hydrogen bonds that are responsible for a protein’s three-dimensional structure. Even if a protein is properly specified by its corresponding mRNA, it could take on a completely dysfunctional shape if abnormal temperature or pH conditions prevent it from folding correctly. The denatured state of the protein does not equate with the unfolding of the protein and randomization of conformation. Actually, denatured proteins exist in a set of partially-folded states that are currently poorly understood. Many proteins fold spontaneously, but some proteins require helper molecules, called chaperones, to prevent them from aggregating during the complicated process of folding.

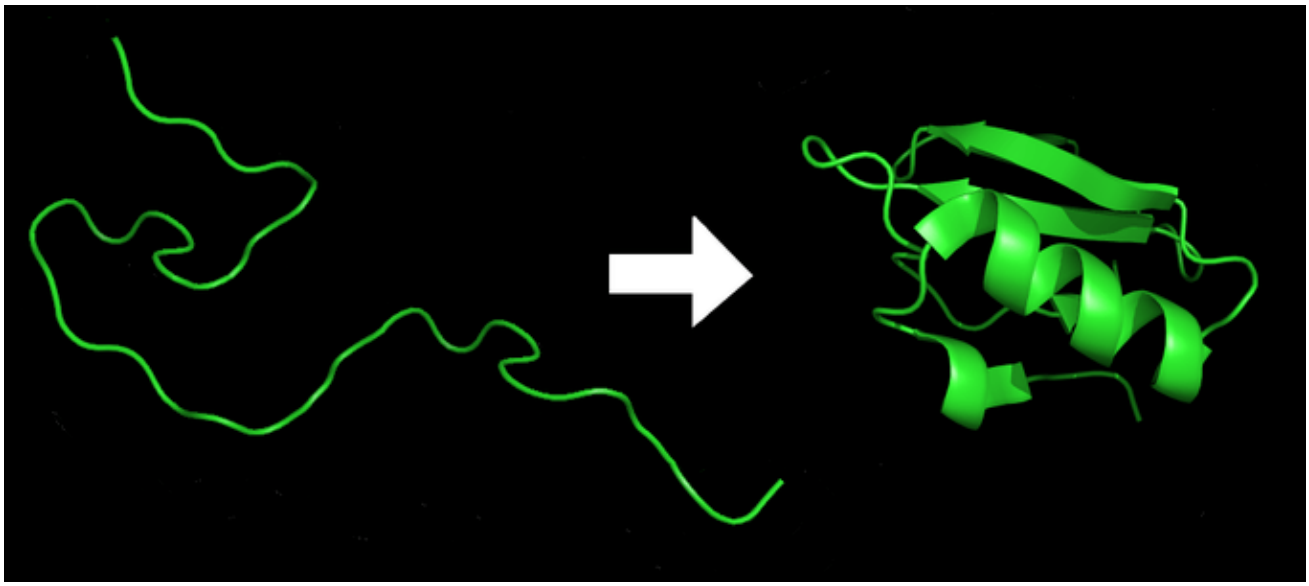


Figure 15.12.1: Protein folding: A protein starts as a linear sequence of amino acids, then folds into a 3-dimensional shape imbued with all the functional properties required inside the cell.

Protein Modification and Targeting

During and after translation, individual amino acids may be chemically modified and signal sequences may be appended to the protein. A signal sequence is a short tail of amino acids that directs a protein to a specific cellular compartment. These sequences at the amino end or the carboxyl end of the protein can be thought of as the protein’s “train ticket” to its ultimate destination. Other cellular factors recognize each signal sequence and help transport the protein from the cytoplasm to its correct compartment. For instance, a specific sequence at the amino terminus will direct a protein to the mitochondria or chloroplasts (in plants). Once the protein reaches its cellular destination, the signal sequence is usually clipped off.

Misfolding

It is very important for proteins to achieve their native conformation since failure to do so may lead to serious problems in the accomplishment of its biological function. Defects in protein folding may be the molecular cause of a range of human genetic disorders. For example, cystic fibrosis is caused by defects in a membrane-bound protein called cystic fibrosis transmembrane conductance regulator (CFTR). This protein serves as a channel for chloride ions. The most common cystic fibrosis-causing mutation is the deletion of a Phe residue at position 508 in CFTR, which causes improper folding of the protein. Many of the disease-related mutations in collagen also cause defective folding.

A misfolded protein, known as prion, appears to be the agent of a number of rare degenerative brain diseases in mammals, like the mad cow disease. Related diseases include kuru and Creutzfeldt-Jakob. The diseases are sometimes referred to as spongiform encephalopathies, so named because the brain becomes riddled with holes. Prion, the misfolded protein, is a normal constituent of brain tissue in all mammals, but its function is not yet known. Prions cannot reproduce independently and not considered living microoganisms. A complete understanding of prion diseases awaits new information about how prion protein affects brain function, as well as more detailed structural information about the protein. Therefore, improved understanding of protein folding may lead to new therapies for cystic fibrosis, Creutzfeldt-Jakob, and many other diseases.

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Key Points

- Protein folding is a process in which a linear chain of amino acids attains a defined three-dimensional structure, but there is a possibility of forming misfolded or denatured proteins, which are often inactive.
- Proteins must also be located in the correct part of the cell in order to function correctly; therefore, a signal sequence is often attached to direct the protein to its proper location, which is removed after it attains its location.
- Protein misfolding is the cause of numerous diseases, such as mad cow disease, Creutzfeldt-Jakob disease, and cystic fibrosis.

Key Terms

- **prion**: a self-propagating misfolded conformer of a protein that is responsible for a number of diseases that affect the brain and other neural tissue
- **chaperone**: a protein that assists the non-covalent folding/unfolding of other proteins

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16: GENE EXPRESSION

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16.1: Regulation of Gene Expression - The Process and Purpose of Gene Expression Regulation

Learning Objectives

- Discuss how the genome and proteome contribute to the specialization of a cell

Each somatic cell in the body generally contains the same DNA. A few exceptions include red blood cells, which contain no DNA in their mature state, and some immune system cells that rearrange their DNA while producing antibodies. In general, however, the genes that determine whether you have green eyes, brown hair, and how fast you metabolize food are the same in the cells in your eyes and your liver, even though these organs function quite differently. If each cell has the same DNA, how is it that cells or organs are different? Why do cells in the eye differ so dramatically from cells in the liver ?

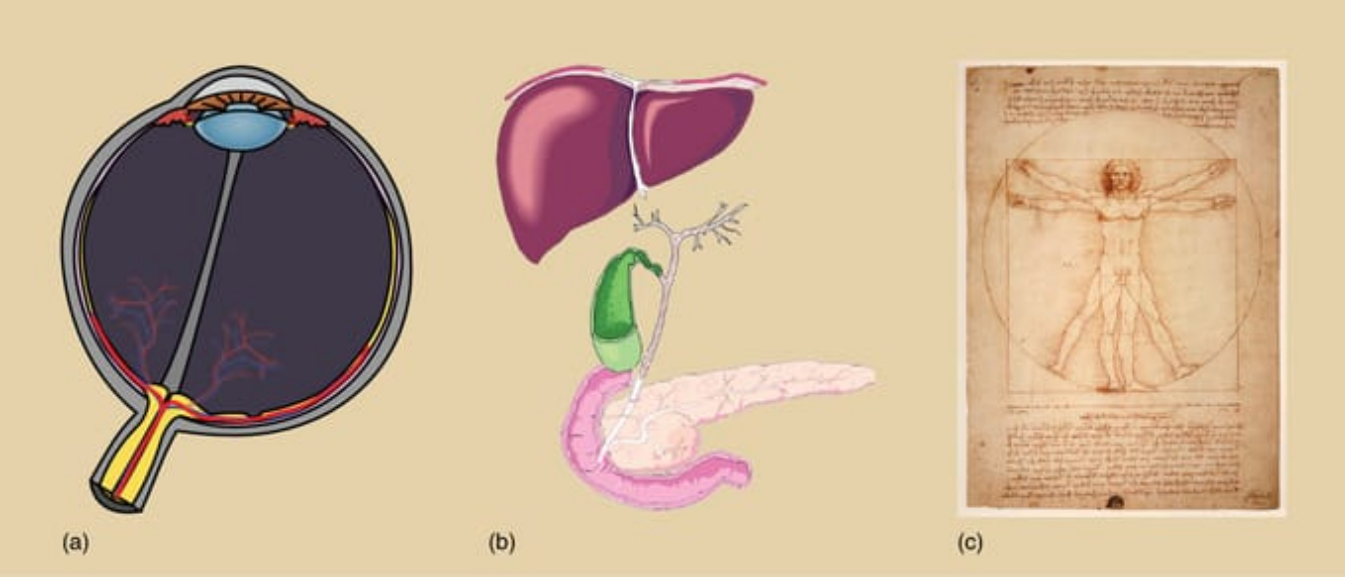


Figure 16.1.1: Gene Expression: The genetic content of each somatic cell in an organism is the same, but not all genes are expressed in every cell. The control of which genes are expressed dictates whether a cell is (a) an eye cell or (b) a liver cell. It is the differential gene expression patterns that arise in different cells that give rise to (c) a complete organism.

Whereas each cell shares the same genome and DNA sequence, each cell does not turn on, or express, the same set of genes. Each cell type needs a different set of proteins to perform its function. Therefore, only a small subset of proteins is expressed in a cell that constitutes its proteome. For the proteins to be expressed, the DNA must be transcribed into RNA and the RNA must be translated into protein. In a given cell type, not all genes encoded in the DNA are transcribed into RNA or translated into protein because specific cells in our body have specific functions. Specialized proteins that make up the eye (iris, lens, and cornea) are only expressed in the eye, whereas the specialized proteins in the heart (pacemaker cells, heart muscle, and valves) are only expressed in the heart. At any given time, only a subset of all of the genes encoded by our DNA are expressed and translated into proteins. The expression of specific genes is a highly-regulated process with many levels and stages of control. This complexity ensures the proper expression in the proper cell at the proper time.

In this section, you will learn about the various methods of gene regulation and the mechanisms used to control gene expression, such as: epigenetic, transcriptional, post-transcriptional, translational, and post-translational controls in eukaryotic gene expression, and transcriptional control in prokaryotic gene expression.

Key Points

- Every cell within an organism shares the same genome (with exceptions, i.e. mature red blood cells), but has variation

between its proteomes.
- Gene expression involves the process of transcribing DNA into RNA and then translating RNA into proteins.
- Gene expression is a highly complex and tightly-regulated process.

Key Terms

- **somatic**: part of, or relating to the body of an organism
- **genome**: the cell's complete genetic information packaged as a double-stranded DNA molecule
- **proteome**: the complete set of proteins encoded by a particular genome

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16.2: Regulation of Gene Expression - Prokaryotic versus Eukaryotic Gene Expression

Learning Objectives

- Compare and contrast prokaryotic and eukaryotic gene expression

Prokaryotic versus Eukaryotic Gene Expression

To understand how gene expression is regulated, we must first understand how a gene codes for a functional protein in a cell. The process occurs in both prokaryotic and eukaryotic cells, just in slightly different manners.

Prokaryotic organisms are single-celled organisms that lack a defined nucleus; therefore, their DNA floats freely within the cell cytoplasm. To synthesize a protein, the processes of transcription (DNA to RNA) and translation (RNA to protein) occur almost simultaneously. When the resulting protein is no longer needed, transcription stops. Thus, the regulation of transcription is the primary method to control what type of protein and how much of each protein is expressed in a prokaryotic cell. All of the subsequent steps occur automatically. When more protein is required, more transcription occurs. Therefore, in prokaryotic cells, the control of gene expression is mostly at the transcriptional level.

Eukaryotic cells, in contrast, have intracellular organelles that add to their complexity. In eukaryotic cells, the DNA is contained inside the cell's nucleus where it is transcribed into RNA. The newly-synthesized RNA is then transported out of the nucleus into the cytoplasm where ribosomes translate the RNA into protein. The processes of transcription and translation are physically separated by the nuclear membrane; transcription occurs only within the nucleus, and translation occurs only outside the nucleus within the cytoplasm. The regulation of gene expression can occur at all stages of the process. Regulation may occur when the DNA is uncoiled and loosened from nucleosomes to bind transcription factors (epigenetics), when the RNA is transcribed (transcriptional level), when the RNA is processed and exported to the cytoplasm after it is transcribed (post-transcriptional level), when the RNA is translated into protein (translational level), or after the protein has been made (post-translational level).

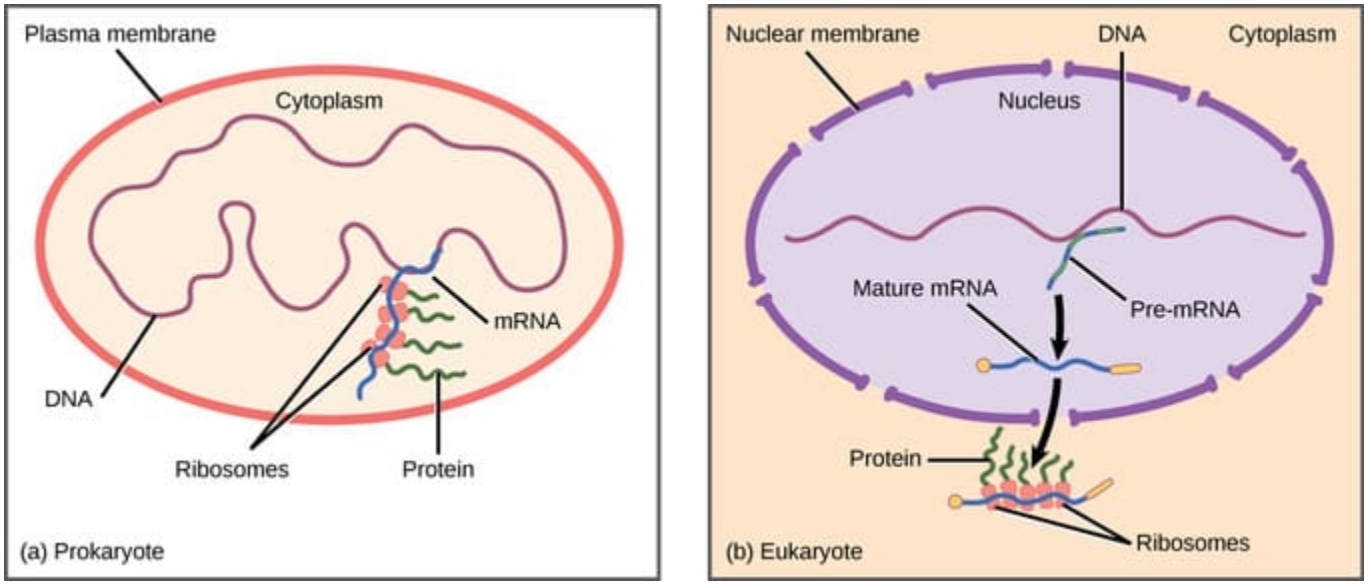


Figure 16.2.1: Prokaryotic vs Eukaryotic Gene Expression: Prokaryotic transcription and translation occur simultaneously in the cytoplasm, and regulation occurs at the transcriptional level. Eukaryotic gene expression is regulated during transcription and RNA processing, which take place in the nucleus, and during protein translation, which takes place in the cytoplasm. Further regulation may occur through post-translational modifications of proteins.

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Key Points

- Prokaryotic gene expression is primarily controlled at the level of transcription.
- Eukaryotic gene expression is controlled at the levels of epigenetics, transcription, post-transcription, translation, and post-translation.
- Prokaryotic gene expression (both transcription and translation) occurs within the cytoplasm of a cell due to the lack of a defined nucleus; thus, the DNA is freely located within the cytoplasm.
- Eukaryotic gene expression occurs in both the nucleus (transcription) and cytoplasm (translation).

Key Terms

- **epigenetics**: the study of heritable changes caused by the activation and deactivation of genes without any change in DNA sequence
- **nucleosome**: any of the subunits that repeat in chromatin; a coil of DNA surrounding a histone core

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16.3: Prokaryotic Gene Regulation - The trp Operon- A Repressor Operon

Learning Objectives

- Explain the relationship between structure and function of an operon and the ways in which repressors regulate gene expression

Bacteria such as *E. coli* need amino acids to survive. Tryptophan is one such amino acid that *E. coli* can ingest from the environment. *E. coli* can also synthesize tryptophan using enzymes that are encoded by five genes. These five genes are next to each other in what is called the tryptophan (trp) operon. If tryptophan is present in the environment, then *E. coli* does not need to synthesize it; the switch controlling the activation of the genes in the trp operon is turned off. However, when tryptophan availability is low, the switch controlling the operon is turned on, transcription is initiated, the genes are expressed, and tryptophan is synthesized.

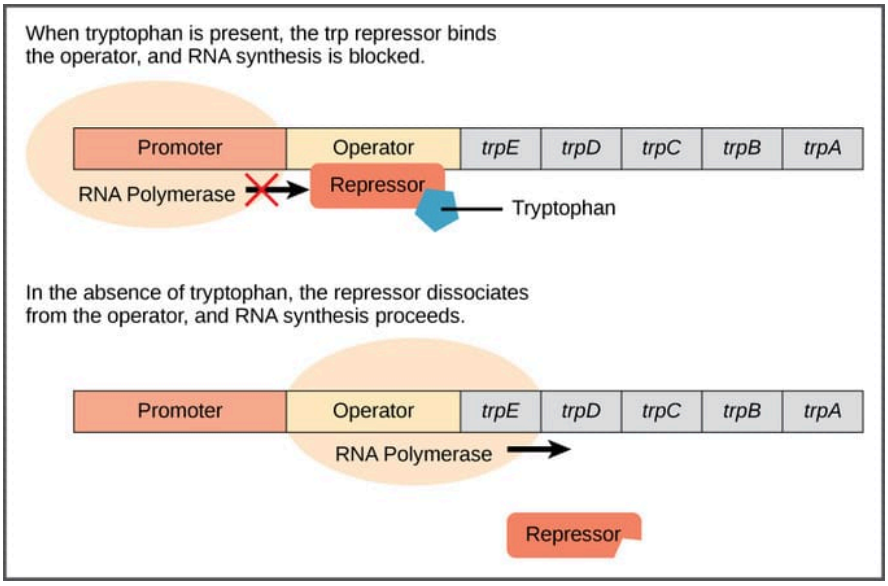


Figure 16.3.1: The trp operon: The five genes that are needed to synthesize tryptophan in E. coli are located next to each other in the trp operon. When tryptophan is plentiful, two tryptophan molecules bind the repressor protein at the operator sequence. This physically blocks the RNA polymerase from transcribing the tryptophan genes. When tryptophan is absent, the repressor protein does not bind to the operator and the genes are transcribed.

A DNA sequence that codes for proteins is referred to as the coding region. The five coding regions for the tryptophan biosynthesis enzymes are arranged sequentially on the chromosome in the operon. Just before the coding region is the transcriptional start site. This is the region of DNA to which RNA polymerase binds to initiate transcription. The promoter sequence is upstream of the transcriptional start site. Each operon has a sequence within or near the promoter to which proteins (activators or repressors) can bind and regulate transcription.

A DNA sequence called the operator sequence is encoded between the promoter region and the first trp-coding gene. This operator contains the DNA code to which the repressor protein can bind. When tryptophan is present in the cell, two tryptophan molecules bind to the trp repressor, which changes shape to bind to the trp operator. Binding of the tryptophan–repressor complex at the operator physically prevents the RNA polymerase from binding and transcribing the downstream genes.

When tryptophan is not present in the cell, the repressor by itself does not bind to the operator; therefore, the operon is active and tryptophan is synthesized. Because the repressor protein actively binds to the operator to keep the genes turned off, the trp operon is negatively regulated and the proteins that bind to the operator to silence trp expression are negative regulators.

Key Points

- The operator sequence is encoded between the promoter region and the first trp-coding gene.
- The trp operon is repressed when tryptophan levels are high by binding the repressor protein to the operator sequence via a corepressor which blocks RNA polymerase from transcribing the trp-related genes.
- The trp operon is activated when tryptophan levels are low by dissociation of the repressor protein to the operator sequence which allows RNA polymerase to transcribe the trp genes in the operon.

Key Terms

- **repressor**: any protein that binds to DNA and thus regulates the expression of genes by decreasing the rate of transcription
- **operon**: a unit of genetic material that functions in a coordinated manner by means of an operator, a promoter, and structural genes that are transcribed together

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16.4: Prokaryotic Gene Regulation - Catabolite Activator Protein (CAP)- An Activator Regulator

Learning Objectives

- Explain how an activator works to increase transcription of a gene

Just as the trp operon is negatively regulated by tryptophan molecules, there are proteins that bind to the operator sequences that act as a positive regulator to turn genes on and activate them. For example, when glucose is scarce, *E. coli* bacteria can turn to other sugar sources for fuel. To do this, new genes to process these alternate genes must be transcribed. This type of process can be seen in the lac operon which is turned on in the presence of lactose and absence of glucose.

When glucose levels drop, cyclic AMP (cAMP) begins to accumulate in the cell. The cAMP molecule is a signaling molecule that is involved in glucose and energy metabolism in *E. coli*. When glucose levels decline in the cell, accumulating cAMP binds to the positive regulator catabolite activator protein (CAP), a protein that binds to the promoters of operons that control the processing of alternative sugars, such as the lac operon. The CAP assists in production in the absence of glucose. CAP is a transcriptional activator that exists as a homodimer in solution, with each subunit comprising a ligand-binding domain at the N-terminus, which is also responsible for the dimerization of the protein and a DNA-binding domain at the C-terminus. Two cAMP molecules bind dimeric CAP with negative cooperativity and function as allosteric effectors by increasing the protein's affinity for DNA. CAP has a characteristic helix-turn-helix structure that allows it to bind to successive major grooves on DNA. This opens up the DNA molecule, allowing RNA polymerase to bind and transcribe the genes involved in lactose catabolism. When cAMP binds to CAP, the complex binds to the promoter region of the genes that are needed to use the alternate sugar sources. In these operons, a CAP-binding site is located upstream of the RNA-polymerase-binding site in the promoter. This increases the binding ability of RNA polymerase to the promoter region and the transcription of the genes. As cAMP-CAP is required for transcription of the lac operon, this requirement reflects the greater simplicity with which glucose may be metabolized in comparison to lactose.

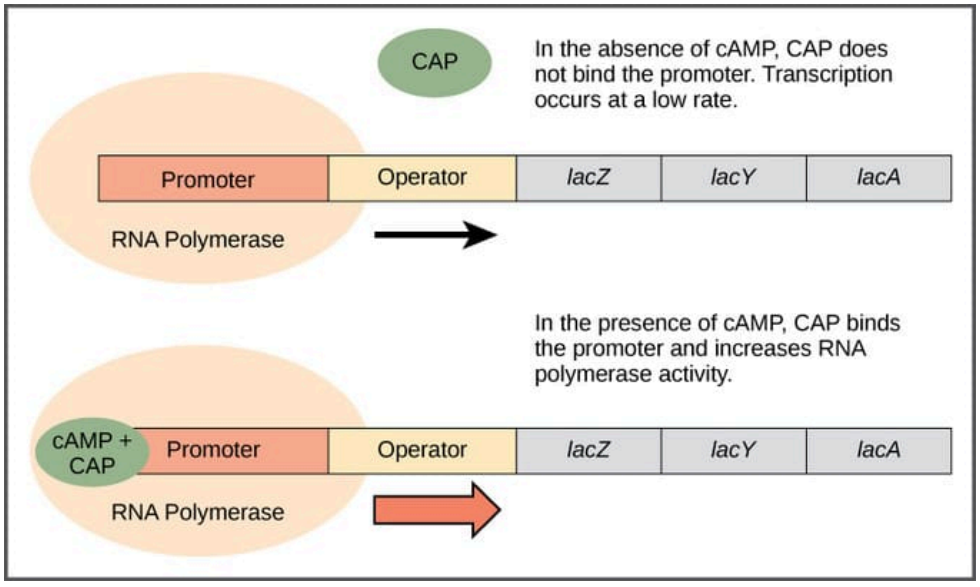


Figure 16.4.1: Catabolite Activator Protein (CAP) Regulation: When glucose levels fall, E. coli may use other sugars for fuel, but must transcribe new genes to do so. As glucose supplies become limited, cAMP levels increase. This cAMP binds to the CAP protein, a positive regulator that binds to an operator region upstream of the genes required to use other sugar sources.

Key Points

- Catabolite activator protein (CAP) must bind to cAMP to activate transcription of the lac operon by RNA polymerase.
- CAP is a transcriptional activator with a ligand-binding domain at the N-terminus and a DNA -binding domain at the C-

terminus.
- cAMP molecules bind to CAP and function as allosteric effectors by increasing CAP's affinity to DNA.

Key Terms

- **RNA polymerase**: a DNA-dependent RNA polymerase, an enzyme, that produces RNA
- **operon**: a unit of genetic material that functions in a coordinated manner by means of an operator, a promoter, and structural genes that are transcribed together
- **promoter**: the section of DNA that controls the initiation of RNA transcription

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16.5: Prokaryotic Gene Regulation - The lac Operon- An Inducer Operon

Learning Objectives

- Describe the components of the lac operon and their role in its function

A major type of gene regulation that occurs in prokaryotic cells utilizes and occurs through inducible operons. Inducible operons have proteins that can bind to either activate or repress transcription depending on the local environment and the needs of the cell. The lac operon is a typical inducible operon. As mentioned previously, *E. coli* is able to use other sugars as energy sources when glucose concentrations are low. To do so, the cAMP–CAP protein complex serves as a positive regulator to induce transcription. One such sugar source is lactose. The lac operon encodes the genes necessary to acquire and process the lactose from the local environment, which includes the structural genes lacZ, lacY, and lacA. *lacZ* encodes β-galactosidase (LacZ), an intracellular enzyme that cleaves the disaccharide lactose into glucose and galactose. *lacY* encodes β-galactoside permease (LacY), a membrane-bound transport protein that pumps lactose into the cell. *lacA* encodes β-galactoside transacetylase (LacA), an enzyme that transfers an acetyl group from acetyl-CoA to β-galactosides. Only lacZ and lacY appear to be necessary for lactose catabolism.

CAP binds to the operator sequence upstream of the promoter that initiates transcription of the lac operon. The *lac* operon uses a two-part control mechanism to ensure that the cell expends energy producing β-galactosidase, β-galactoside permease, and thiogalactoside transacetylase (also known as galactoside O-acetyltransferase) only when necessary. However, for the lac operon to be activated, two conditions must be met. First, the level of glucose must be very low or non-existent. Second, lactose must be present. If glucose is absent, then CAP can bind to the operator sequence to activate transcription. If lactose is absent, then the repressor binds to the operator to prevent transcription. If either of these requirements is met, then transcription remains off. The cell can use lactose as an energy source by producing the enzyme b-galactosidase to digest that lactose into glucose and galactose. Only when both conditions are satisfied is the lac operon transcribed, such as when glucose is absent and lactose is present. This process is beneficial and makes most sense for the cell as it would be energetically wasteful to create the proteins to process lactose if glucose were plentiful or if lactose were not available.

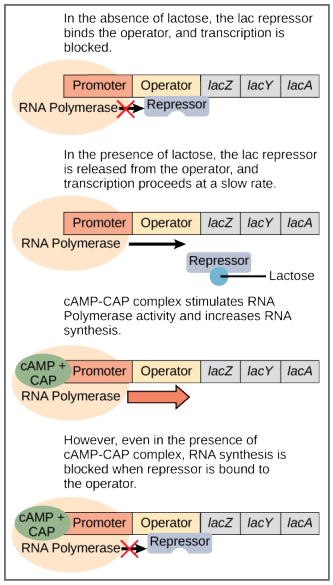


Figure 16.5.1: The lac Operon: Transcription of the lac operon is carefully regulated so that its expression only occurs when glucose is limited and lactose is present to serve as an alternative fuel source.

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Key Points

- The lac operon contains an operator, promoter, and structural genes that are transcribed together and are under the control of the catabolite activator protein (CAP) or repressor.
- The lac operon is not activated and transcription remains off when the level of glucose is low or non-existent, but lactose is absent.
- The lac operon encodes for the genes needed to utilize lactose as an energy source.

Key Terms

- **operator**: a segment of DNA to which a transcription factor protein binds
- **repressor**: any protein that binds to DNA and thus regulates the expression of genes by decreasing the rate of transcription

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16.6: Eukaryotic Gene Regulation - The Promoter and the Transcription Machinery

Learning Objectives

- Describe the role of promoters in RNA transcription

Genes are organized to make the control of gene expression easier. The promoter region is immediately upstream of the coding sequence. This region can be short (only a few nucleotides in length) or quite long (hundreds of nucleotides long). The longer the promoter, the more available space for proteins to bind. This also adds more control to the transcription process. The length of the promoter is gene-specific and can differ dramatically between genes. Consequently, the level of control of gene expression can also differ quite dramatically between genes. The purpose of the promoter is to bind transcription factors that control the initiation of transcription.

Within the promoter region, just upstream of the transcriptional start site, resides the TATA box. This box is simply a repeat of thymine and adenine dinucleotides (literally, TATA repeats). RNA polymerase binds to the transcription initiation complex, allowing transcription to occur. To initiate transcription, a transcription factor (TFIID) is the first to bind to the TATA box. Binding of TFIID recruits other transcription factors, including TFIIB, TFIIE, TFIIF, and TFIIH to the TATA box. Once this transcription initiation complex is assembled, RNA polymerase can bind to its upstream sequence. When bound along with the transcription factors, RNA polymerase is phosphorylated. This releases part of the protein from the DNA to activate the transcription initiation complex and places RNA polymerase in the correct orientation to begin transcription; DNA-bending protein brings the enhancer, which can be quite a distance from the gene, in contact with transcription factors and mediator proteins.

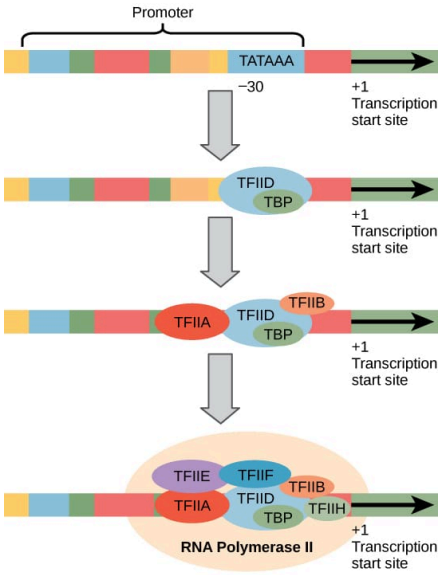


Figure 16.6.1: Promoters: A generalized promoter of a gene transcribed by RNA polymerase II is shown. Transcription factors recognize the promoter. RNA polymerase II then binds and forms the transcription initiation complex.

In addition to the general transcription factors, other transcription factors can bind to the promoter to regulate gene transcription. These transcription factors bind to the promoters of a specific set of genes. They are not general transcription factors that bind to every promoter complex, but are recruited to a specific sequence on the promoter of a specific gene. There are hundreds of transcription factors in a cell that each bind specifically to a particular DNA sequence motif. When transcription factors bind to the promoter just upstream of the encoded gene, they are referred to as cis-acting elements because they are on the same chromosome, just next to the gene. The region that a particular transcription factor binds to is called the transcription factor binding site. Transcription factors respond to environmental stimuli that cause the proteins to find their binding sites and initiate transcription of the gene that is needed.

Key Points

- The purpose of the promoter is to bind transcription factors that control the initiation of transcription.
- The promoter region can be short or quite long; the longer the promoter is, the more available space for proteins to bind.
- To initiate transcription, a transcription factor (TFIID) binds to the TATA box, which causes other transcription factors to subsequently bind to the TATA box.
- Once the transcription initiation complex is assembled, RNA polymerase can bind to its upstream sequence and is then phosphorylated.
- Phosphorylation of RNA polymerase releases part of the protein from the DNA to activate the transcription initiation complex and places RNA polymerase in the correct orientation to begin transcription.
- Transcription factors respond to environmental stimuli that cause the proteins to find their binding sites and initiate transcription of the gene that is needed.

Key Terms

- **TATA box**: a DNA sequence (cis-regulatory element) found in the promoter region of genes in archaea and eukaryotes
- **transcription factor**: a protein that binds to specific DNA sequences, thereby controlling the flow (or transcription) of genetic information from DNA to mRNA
- **promoter**: the section of DNA that controls the initiation of RNA transcription

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16.7: Eukaryotic Gene Regulation - Transcriptional Enhancers and Repressors

Learning Objectives

- Explain how enhancers and repressors regulate gene expression

Enhancers and Transcription

In some eukaryotic genes, there are regions that help increase or enhance transcription. These regions, called enhancers, are not necessarily close to the genes they enhance. They can be located upstream of a gene, within the coding region of the gene, downstream of a gene, or may be thousands of nucleotides away.

Enhancer regions are binding sequences, or sites, for transcription factors. When a DNA-bending protein binds to an enhancer, the shape of the DNA changes. This shape change allows the interaction between the activators bound to the enhancers and the transcription factors bound to the promoter region and the RNA polymerase to occur. Whereas DNA is generally depicted as a straight line in two dimensions, it is actually a three-dimensional object. Therefore, a nucleotide sequence thousands of nucleotides away can fold over and interact with a specific promoter.

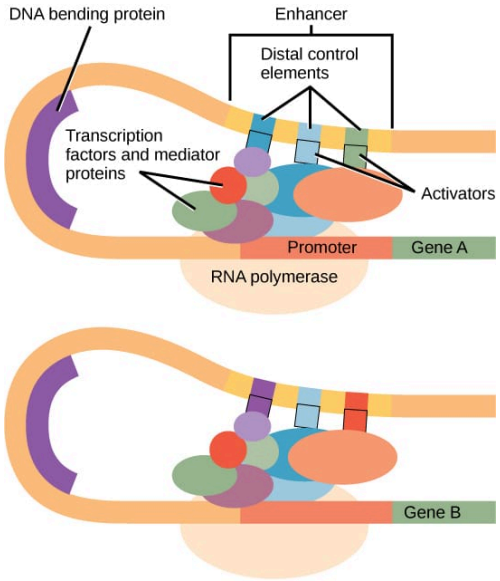


Figure 16.7.1: Enhancers: An enhancer is a DNA sequence that promotes transcription. Each enhancer is made up of short DNA sequences called distal control elements. Activators bound to the distal control elements interact with mediator proteins and transcription factors.

Turning Genes Off: Transcriptional Repressors

Like prokaryotic cells, eukaryotic cells also have mechanisms to prevent transcription. Transcriptional repressors can bind to promoter or enhancer regions and block transcription. Like the transcriptional activators, repressors respond to external stimuli to prevent the binding of activating transcription factors.

A corepressor is a protein that decreases gene expression by binding to a transcription factor that contains a DNA-binding domain. The corepressor is unable to bind DNA by itself. The corepressor can repress transcriptional initiation by recruiting histone deacetylase, which catalyzes the removal of acetyl groups from lysine residues. This increases the positive charge on histones, which strengthens the interaction between the histones and DNA, making the DNA less accessible to the process of transcription.

Key Points

- Enhancers can be located upstream of a gene, within the coding region of the gene, downstream of a gene, or thousands of nucleotides away.
- When a DNA -bending protein binds to the enhancer, the shape of the DNA changes, which allows interactions between the activators and transcription factors to occur.
- Repressors respond to external stimuli to prevent the binding of activating transcription factors.
- Corepressors can repress transcriptional initiation by recruiting histone deacetylase.
- Histone deactylation increases the positive charge on histones, which strengthens the interaction between the histones and DNA, making the DNA less accessible to transcription.

Key Terms

- **enhancer**: a short region of DNA that can increase transcription of genes
- **repressor**: any protein that binds to DNA and thus regulates the expression of genes by decreasing the rate of transcription
- **activator**: any chemical or agent which regulates one or more genes by increasing the rate of transcription

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16.8: Eukaryotic Gene Regulation - Epigenetic Control- Regulating Access to Genes within the Chromosome

Learning Objectives

- Discuss how eukaryotic gene regulation occurs at the epigenetic level and the various epigenetic changes that can be made to DNA

Epigenetic Control: Regulating Access to Genes within the Chromosome

The human genome encodes over 20,000 genes; each of the 23 pairs of human chromosomes encodes thousands of genes. The DNA in the nucleus is precisely wound, folded, and compacted into chromosomes so that it will fit into the nucleus. It is also organized so that specific segments can be accessed as needed by a specific cell type.

The first level of organization, or packing, is the winding of DNA strands around histone proteins. Histones package and order DNA into structural units called nucleosome complexes, which can control the access of proteins to the DNA regions. Under the electron microscope, this winding of DNA around histone proteins to form nucleosomes looks like small beads on a string. These beads (histone proteins) can move along the string (DNA) and change the structure of the molecule.

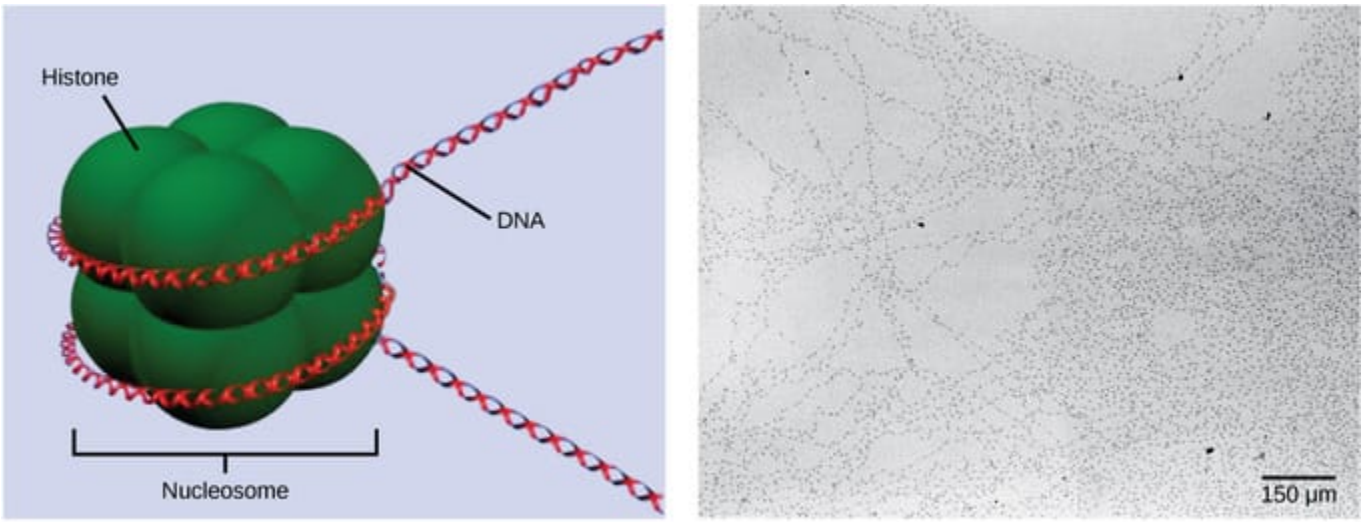


Figure 16.8.1: DNA Packaging: DNA is folded around histone proteins to create (a) nucleosome complexes. These nucleosomes control the access of proteins to the underlying DNA. When viewed through an electron microscope (b), the nucleosomes look like beads on a string.

If DNA encoding a specific gene is to be transcribed into RNA, the nucleosomes surrounding that region of DNA can slide down the DNA to open that specific chromosomal region and allow for the transcriptional machinery (RNA polymerase) to initiate transcription. Nucleosomes can move to open the chromosome structure to expose a segment of DNA, but do so in a very controlled manner.

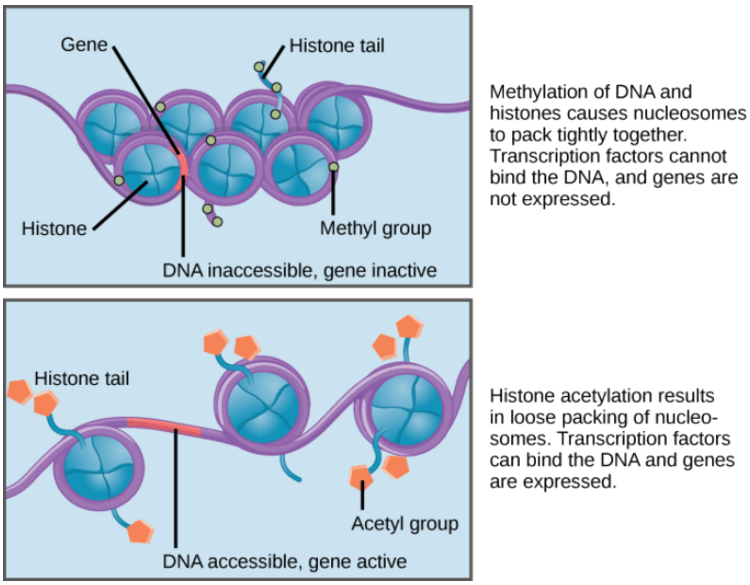


Figure 16.8.1: Nucleosomes can change position to allow transcription of genes: Nucleosomes can slide along DNA. When nucleosomes are spaced closely together (top), transcription factors cannot bind and gene expression is turned off. When the nucleosomes are spaced far apart (bottom), the DNA is exposed. Transcription factors can bind, allowing gene expression to occur. Modifications to the histones and DNA affect nucleosome spacing.

How the histone proteins move is dependent on signals found on both the histone proteins and on the DNA. These signals are tags, or modifications, added to histone proteins and DNA that tell the histones if a chromosomal region should be open or closed. These tags are not permanent, but may be added or removed as needed. They are chemical modifications (phosphate, methyl, or acetyl groups) that are attached to specific amino acids in the protein or to the nucleotides of the DNA. The tags do not alter the DNA base sequence, but they do alter how tightly wound the DNA is around the histone proteins. DNA is a negatively-charged molecule; therefore, changes in the charge of the histone will change how tightly wound the DNA molecule will be. When unmodified, the histone proteins have a large positive charge; by adding chemical modifications, such as acetyl groups, the charge becomes less positive.

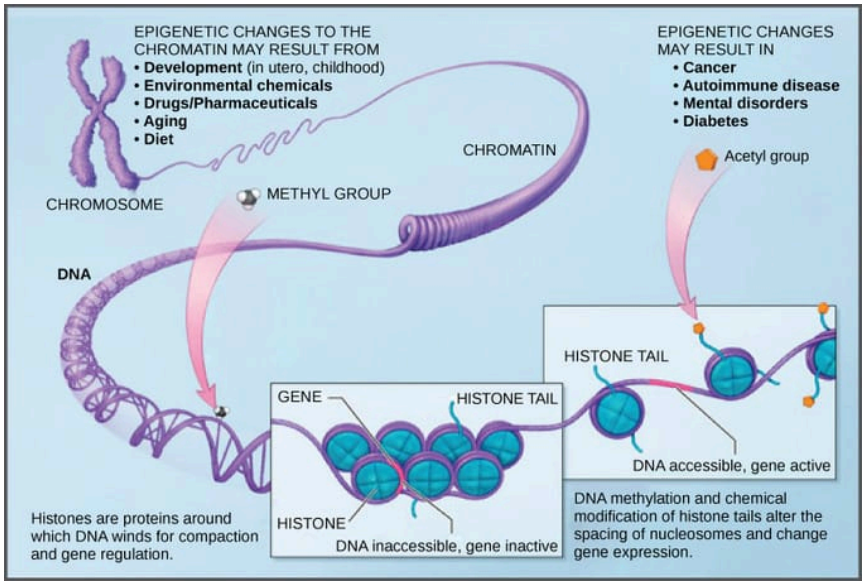


Figure 16.8.1: Modifications to histones and DNA can alter gene expression: Histone proteins and DNA nucleotides can be modified chemically. Modifications affect nucleosome spacing and gene expression.

The DNA molecule itself can also be modified. This occurs within very specific regions called CpG islands. These are stretches with a high frequency of cytosine and guanine dinucleotide DNA pairs (CG) found in the promoter regions of genes. When this configuration exists, the cytosine member of the pair can be methylated (a methyl group is added). This modification changes how the DNA interacts with proteins, including the histone proteins that control access to the region. Highly-methylated

(hypermethylated) DNA regions with deacetylated histones are tightly coiled and transcriptionally inactive. These changes to DNA are inherited from parent to offspring, such that while the DNA sequence is not altered, the pattern of gene expression is passed to the next generation.

This type of gene regulation is called epigenetic regulation. Epigenetics means “above genetics.” The changes that occur to the histone proteins and DNA do not alter the nucleotide sequence and are not permanent. Instead, these changes are temporary (although they often persist through multiple rounds of cell division) and alter the chromosomal structure (open or closed) as needed. A gene can be turned on or off depending upon the location and modifications to the histone proteins and DNA. If a gene is to be transcribed, the histone proteins and DNA are modified surrounding the chromosomal region encoding that gene. This opens the chromosomal region to allow access for RNA polymerase and other proteins, called transcription factors, to bind to the promoter region, located just upstream of the gene, and initiate transcription. If a gene is to remain turned off, or silenced, the histone proteins and DNA have different modifications that signal a closed chromosomal configuration. In this closed configuration, the RNA polymerase and transcription factors do not have access to the DNA and transcription cannot occur.

Key Points

- DNA is packaged by wrapping around histone proteins into structures called nucleosomes, which resemble beads on a string.
- When DNA is to be transcribed, the nucleosomes can slide away from that region of DNA, opening it up to the transcription machinery of the cell.
- Chemical modifications to either the histone proteins or the DNA itself signals whether or not a particular region of the genome should be “open” or “closed” to the transcription machinery.
- Modifications such as acetylation or methylation of the histones can alter how tightly DNA is wrapped around them, while methylation of DNA changes how the DNA interacts with proteins, including the histone proteins that control access to the region.
- This type of genetic regulation is called epigenetic regulation (“above genetics”) as it does not change the nucleotide sequence of the DNA.

Key Terms

- **nucleosome**: any of the subunits that repeat in chromatin; a coil of DNA surrounding a histone core
- **epigenetics**: the study of heritable changes caused by the activation and deactivation of genes without any change in DNA sequence
- **histone**: any of various simple water-soluble proteins that are rich in the basic amino acids lysine and arginine and are complexed with DNA in the nucleosomes of eukaryotic chromatin

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16.9: Eukaryotic Gene Regulation - RNA Splicing

Learning Objectives

- Explain the role of RNA splicing in regulating gene expression

RNA splicing, the first stage of post-transcriptional control

Gene expression is the process that transfers genetic information from a gene made of DNA to a functional gene product made of RNA or protein. Genetic Information flows from DNA to RNA by the process of transcription and then from RNA to protein by the process of translation. In order to ensure that the proper products are produced, gene expression is regulated at many different stages during and in between transcription and translation. In eukaryotes, the gene contains extra sequences that do not code for protein. In these organisms, transcription of DNA produces pre-mRNA. These pre-mRNA transcripts often contain regions, called introns, that are intervening sequences which must be removed prior to translation by the process of splicing. The regions of RNA that code for protein are called exons. Splicing can be regulated so that different mRNAs can contain or lack exons, in a process called alternative splicing. Alternative splicing allows more than one protein to be produced from a gene and is an important regulatory step in determining which functional proteins are produced from gene expression. Thus, splicing is the first stage of post-transcriptional control.

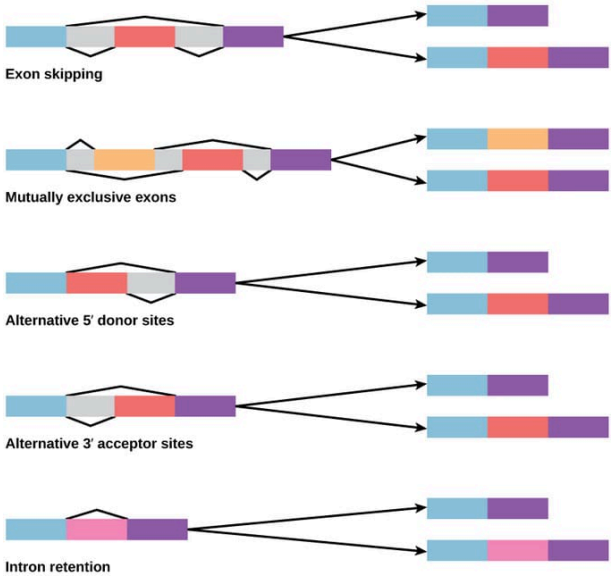


Figure 16.9.1: Alternative Splicing: There are five basic modes of alternative splicing.

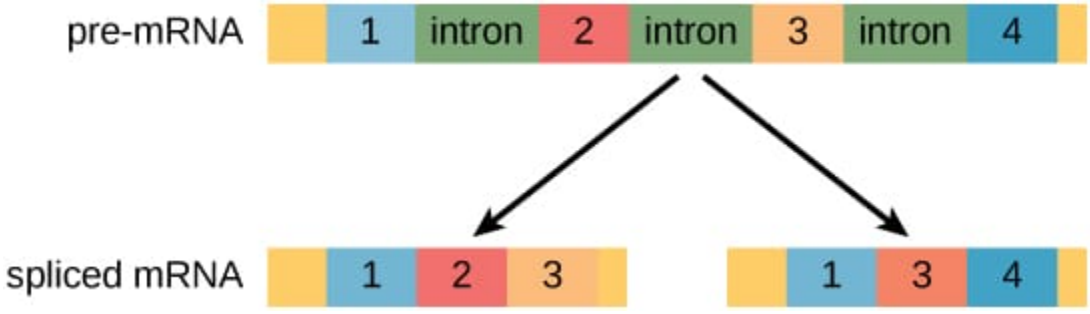


Figure 16.9.1: Alternative Splicing: Pre-mRNA can be alternatively spliced to create different proteins.

Alternative Splicing

Alternative splicing is a process that occurs during gene expression and allows for the production of multiple proteins (protein isoforms) from a single gene coding. Alternative splicing can occur due to the different ways in which an exon can be excluded from or included in the messenger RNA. It can also occur if portions on an exon are excluded/included or if there is an inclusion of introns. For example, if a pre-mRNA has four exons (A, B, C, and D), these can be spliced and translated in a number of different combinations. Exons A, B, and C can be translated together or Exons A, C, and D can be translated. This results in what is called alternative splicing. The pattern of splicing and production of alternatively-spliced messenger RNA is controlled by the binding of regulatory proteins (trans-acting proteins that contain the genes) to cis-acting sites that are found on the pre-RNA. Some of these regulatory proteins include splicing activators (proteins that promote certain splicing sites) and splicing repressors (proteins that reduce the use of certain sites). Some common splicing repressors include: heterogeneous nuclear ribonucleoprotein (hnRNP) and polypyrimidine tract binding protein (PTB). Proteins that are translated from alternatively-spliced messenger RNAs differ in the sequence of their amino acids which results in altered function of the protein. This is one reason why the human genome can encode a wide diversity of proteins. Alternative splicing is a common process that occurs in eukaryotes; most of the multi-exonic genes in humans are spliced alternatively. Unfortunately, abnormal variations in splicing are also the reason why there are many genetic diseases and disorders.

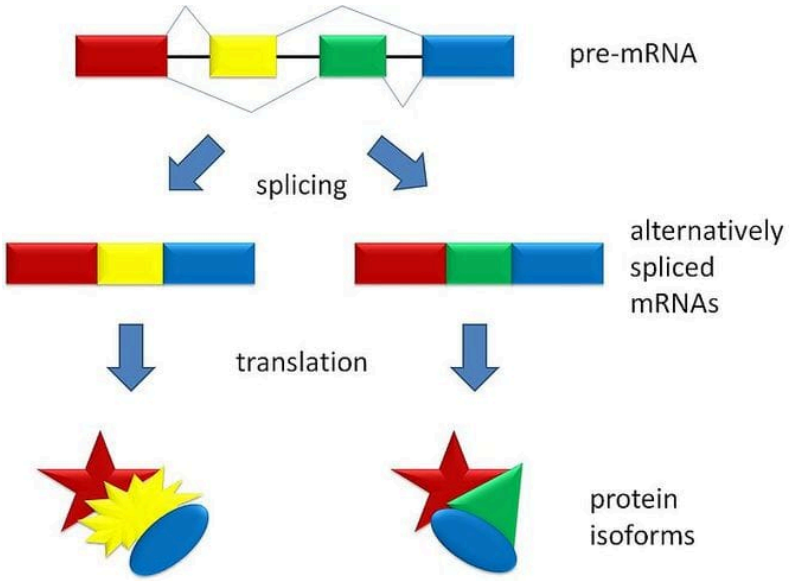


Figure 16.9.1: Mechanism of Splicing: Alternative splicing can result in protein isoforms.

Spliceosome

The splicing of messenger RNA is accomplished and catalyzed by a macro-molecule complex known as the spliceosome. The areas for ligation and cleavage are determined by the many sub-units of the spliceosome which include the branch site (A) and the 5′ and 3′ splice sites. Interactions between these sub-units and the small nuclear ribonucleoproteins (snRNP) found in the spliceosome create a spliceosome A complex which helps determine which introns to leave out and which exons to keep and bind together. Once the introns are cleaved and removed, the exons are joined together by a phosphodiester bond.

Regulatory Proteins

As noted above, splicing is regulated by repressor proteins and activator proteins, which are are also known as trans-acting proteins. Equally as important are the silencers and enhancers that are found on the messenger RNAs, also known as cis-acting sites. These regulatory functions work together in order to create splicing code that determines alternative splicing.

Key Points

- Introns are intervening sequences within a pre-mRNA molecule that do not code for proteins and are removed during RNA

processing by a spliceosome.
- Exons are expressing sequences within a pre-mRNA molecule that are spliced together once introns are removed to form mature mRNA molecules that are translated into proteins.
- Alternative splicing allows for the production of various protein isoforms from one single gene coding.
- A spliceosome is a complex comprised of both RNA molecules and proteins which determine which introns to leave out and which exons to keep and bind together.

Key Terms

- **intron**: a portion of a split gene that is included in pre-RNA transcripts but is removed during RNA processing and rapidly degraded
- **exon**: a region of a transcribed gene present in the final functional RNA molecule
- **spliceosome**: a dynamic complex of RNA and protein subunits that removes introns from precursor mRNA

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16.10: Eukaryotic Gene Regulation - The Initiation Complex and Translation Rate

Learning Objectives

- Discuss how eukaryotes assemble ribosomes on the mRNA to begin translation

Ribosome Assembly and Translation Rate

Like transcription, translation is controlled by proteins that bind and initiate the process. In translation, before protein synthesis can begin, ribosome assembly has to be completed. This is a multi-step process.

In ribosome assembly, the large and small ribosomal subunits and an initiator tRNA ($tRNA_i$) containing the first amino acid of the final polypeptide chain all come together at the translation start codon on an mRNA to allow translation to begin. First, the small ribosomal subunit binds to the $tRNA_i$ which carries methionine in eukaryotes and archaea and carries N-formyl-methionine in bacteria. (Because the $tRNA_i$ is carrying an amino acid, it is said to be charged.) Next, the small ribosomal subunit with the charged $tRNA_i$ still bound scans along the mRNA strand until it reaches the start codon AUG, which indicates where translation will begin. The start codon also establishes the reading frame for the mRNA strand, which is crucial to synthesizing the correct sequence of amino acids. A shift in the reading frame results in mistranslation of the mRNA. The anticodon on the $tRNA_i$ then binds to the start codon via basepairing. The complex consisting of mRNA, charged $tRNA_i$, and the small ribosomal subunit attaches to the large ribosomal subunit, which completes ribosome assembly. These components are brought together by the help of proteins called initiation factors which bind to the small ribosomal subunit during initiation and are found in all three domains of life. In addition, the cell spends GTP energy to help form the initiation complex. Once ribosome assembly is complete, the charged $tRNA_i$ is positioned in the P site of the ribosome and the empty A site is ready for the next aminoacyl-tRNA. The polypeptide synthesis begins and always proceeds from the N-terminus to the C-terminus, called the N-to-C direction.

In eukaryotes, several eukaryotic initiation factor proteins (eIFs) assist in ribosome assembly. The eukaryotic initiation factor-2 (eIF-2) is active when it binds to guanosine triphosphate (GTP). With GTP bound to it, eIF-2 protein binds to the small 40S ribosomal subunit. Next, the initiatior tRNA charged with methionine (Met-$tRNA_i$) associates with the GTP-eIF-2/40S ribosome complex, and once all these components are bound to each other, they are collectively called the 43S complex.

Eukaryotic initiation factors eIF1, eIF3, eIF4, and eIF5 help bring the 43S complex to the 5′-m^7G cap of an mRNA be translated. Once bound to the mRNA's 5′ m^7G cap, the 43S complex starts travelling down the mRNA until it reaches the initiation AUG codon at the start of the mRNA's reading frame. Sequences around the AUG may help ensure the correct AUG is used as the initiation codon in the mRNA.

Once the 43S complex is at the initiation AUG, the tRNAi-Met is positioned over the AUG. The anticodon on $tRNA_i$-Met basepairs with the AUG codon. At this point, the GTP bound to eIF2 in the 43S complexx is hydrolyzed to GDP + phosphate, and energy is released. This energy is used to release the eIF2 (with GDP bound to it) from the 43S complex, leaving the 40S ribosomal subunit and the $tRNA_i$-Met at the translation start site of the mRNA.

Next, eIF5 with GTP bound binds to the 40S ribosomal subunit complexed to the mRNA and the $tRNA_i$-Met. The eIF5-GTP allows the 60S large ribosomal subunit to bind. Once the 60S ribosomal subunit arrives, eIF5 hydrolyzes its bound GTP to GDP + phosphate, and energy is released. This energy powers assembly of the two ribosomal subunits into the intact 80S ribosome, with tRNAi-Met in its P site while also basepaired to the initiation AUG codon on the mRNA. Translation is ready to begin.

The binding of eIF-2 to the 40S ribosomal subunit is controlled by phosphorylation. If eIF-2 is phosphorylated, it undergoes a conformational change and cannot bind to GTP. Therefore, the 43S complex cannot form properly and translation is impeded. When eIF-2 remains unphosphorylated, it binds the 40S ribosomal subunit and actively translates the protein.

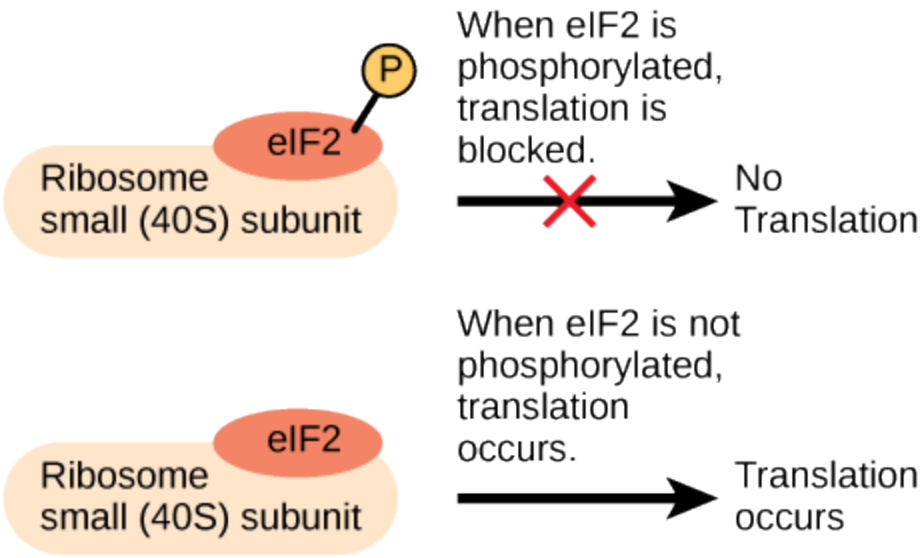


Figure 16.10.1: Translation Initiation Complex: Gene expression can be controlled by factors that bind the translation initiation complex.

The ability to fully assemble the ribosome directly affects the rate at which translation occurs. But protein synthesis is regulated at various other levels as well, including mRNA synthesis, tRNA synthesis, rRNA synthesis, and eukaryotic initiation factor synthesis. Alteration in any of these components affects the rate at which translation can occur.

Key Points

- The components involved in ribosome assembly are brought together by the help of proteins called initiation factors which bind to the small ribosomal subunit.
- Initiator tRNA is used to locate the start codon AUG (the amino acid methionine) which establishes the reading frame for the mRNA strand.
- GTP carried by eIF2 is the energy source used for loading the initiator tRNA carried by the small ribosomal subunit on the correct start codon in the mRNA.
- GTP carried by eIF5 is the energy source for assembling the large and small ribosomal subunits together.

Key Terms

- **reading frame**: either of three possible triplets of codons in which a DNA sequence could be transcribed
- **phosphorylation**: the addition of a phosphate group to a compound; often catalyzed by enzymes

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16.11: Eukaryotic Gene Regulation - Regulating Protein Activity and Longevity

Learning Objectives

- Explain how chemical modifications affect protein activity and longevity

Chemical Modifications, Protein Activity, and Longevity

Proteins can be chemically modified with the addition of methyl, phosphate, acetyl, and ubiquitin groups. The addition or removal of these groups from proteins regulates their activity or the length of time they exist in the cell. Sometimes these modifications can regulate where a protein is found in the cell; for example, in the nucleus, the cytoplasm, or attached to the plasma membrane.

Chemical modifications occur in response to external stimuli such as stress, the lack of nutrients, heat, or ultraviolet light exposure. These changes can alter protein function, epigenetic accessibility, transcription, mRNA stability, or translation; all resulting in changes in expression of various genes. This is an efficient way for the cell to rapidly change the abundance levels of specific proteins in response to the environment. Because proteins are involved in every stage of gene regulation, the phosphorylation of a protein (depending on the protein that is modified) can alter accessibility to the chromosome, can alter translation (by altering transcription factor binding or function), can change nuclear shuttling (by influencing modifications to the nuclear pore complex), can alter RNA stability (by binding or not binding to the RNA to regulate its stability), can modify translation (increase or decrease), or can change post-translational modifications (add or remove phosphates or other chemical modifications). All of these protein activities are affected by the phosphorylation process. The enzymes which are responsible for phosphorylation are known as protein kinases. The addition of a phosphate group to a protein can result in either activation or deactivation; it is protein dependent.

Another example of chemical modifications affecting protein activity include the addition or removal of methyl groups. Methyl groups are added to proteins via the process of methylation; this is the most common form of post-translational modification. The addition of methyl groups to a protein can result in protein-protein interactions that allows for transcriptional regulation, response to stress, protein repair, nuclear transport, and even differentiation processes. Methylation on side chain nitrogens is considered largely irreversible while methylation of the carboxyl groups is potentially reversible. Methylation in the proteins negates the negative charge on it and increases the hydrophobicity of the protein. Methylation on carboxylate side chains covers up a negative charge and adds hydrophobicity. The addition of this chemical group changes the property of the protein and, thus, affects it activity.

The addition of an ubiquitin group to a protein marks that protein for degradation. Ubiquitin acts like a flag indicating that the protein lifespan is complete. These proteins are moved to the proteasome, an organelle that functions to remove proteins to be degraded. One way to control gene expression is to alter the longevity of the protein: ubiquitination shortens a protein's lifespan.

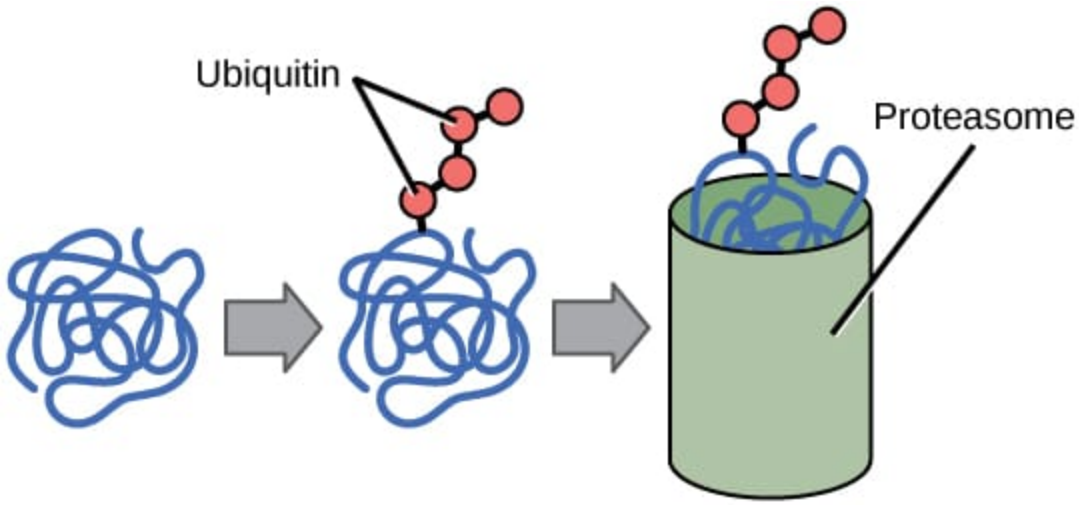


Figure 16.11.1: Ubiquitin Tags: Proteins with ubiquitin tags are marked for degradation within the proteasome.

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Key Points

- Proteins can be chemically modified by adding methyl, phosphate, acetyl, and ubiquitin groups.
- Protein longevity can be affected by altering stages of gene regulation, including but not limited to altering: accessibility to chromosomal DNA for transcription, rate of translation, nuclear shuttling, RNA stability, and post-translational modifications.
- Ubiquitin is added to a protein to mark it for degradation by the proteasome.

Key Terms

- **ubiquitin**: a small polypeptide present in the cells of all eukaryotes; it plays a part in modifying and degrading proteins
- **proteasome**: a complex protein, found in bacterial, archaeal and eukaryotic cells, that breaks down other proteins via proteolysis

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16.12: Regulating Gene Expression in Cell Development - Gene Expression in Stem Cells

Learning Objectives

- Discuss the types of cell division that can occur to add cells during development

Adding cells through cellular division

Stem cells are undifferentiated biological cells found in multicellular organisms, that can differentiate into specialized cells (asymmetric division) or can divide to produce more stem cells (symmetric division). In mammals, there are two broad types of stem cells: embryonic stem cells, which are isolated from the inner cell mass of blastocysts, and adult stem cells, which are found in various tissues. In adult organisms, stem cells and progenitor cells act as a repair system for the body by replenishing adult tissues. In a developing embryo, stem cells can differentiate into all of the specialized cells (including ectoderm, endoderm and mesoderm cells) but also maintain the normal turnover of regenerative organs, such as blood, skin, or intestinal tissues. The pathway that is taken to produced specialized cells included: the embryonic cells develop from totipotent cells, to pluripotent cells which undergo differentiation and become more specialized. The key component however, in the ability to maintain tissues is the ability to maintain a key of stem cells.

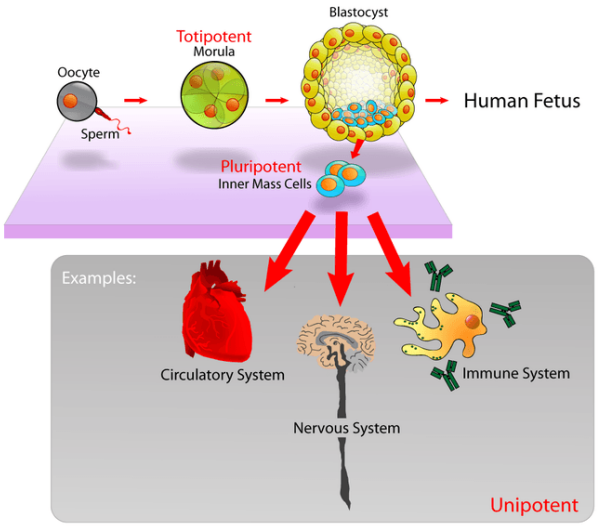


Figure 16.12.1: Stem Cells: Pluripotent, embryonic stem cells originate as inner cell mass (ICM) cells within a blastocyst. These stem cells can become any tissue in the body, excluding a placenta. Only cells from an earlier stage of the embryo, known as the morula, are totipotent, able to become all tissues in the body and the extraembryonic placenta.

There are three accessible sources of autologous adult stem cells in humans: (1) bone marrow, which requires extraction by harvesting (i.e., drilling into bone); (2) adipose tissue (lipid cells), which requires extraction by liposuction; and (3) blood, which requires extraction through apheresis (wherein blood is drawn from the donor, passed through a machine that extracts the stem cells, and returned to the donor). Stem cells can also be taken from umbilical cord blood just after birth. Of all the stem cell types, autologous harvesting involves the least risk. By definition, autologous cells are obtained from one's own body, just as one may bank his or her own blood for elective surgical procedures. Highly plastic adult stem cells are routinely used in medical therapies, for example in bone marrow transplantation. Stem cells can now be artificially grown and differentiated into specialized cell types with characteristics consistent with muscle or nerve cells through cell culture. Embryonic cell lines and autologous embryonic stem cells generated through therapeutic cloning have also been proposed as promising candidates for future therapies.

Symmetric and asymmetric cell division

To ensure self-renewal, stem cells undergo two types of cell division: symmetric and asymmetric. Symmetric division gives rise to two identical daughter cells both endowed with stem cell properties. Asymmetric division, on the other hand, produces only one stem cell and a progenitor cell with limited self-renewal potential. Progenitors can go through several rounds of cell division themselves before terminally differentiating into a mature cell.. It is possible that the molecular distinction between symmetric and asymmetric division lies in differential segregation of cell membrane proteins between the daughter cells. An alternative theory is that stem cells remain undifferentiated due to environmental cues in their particular niche. Stem cells differentiate when they leave that niche or no longer receive those signals.

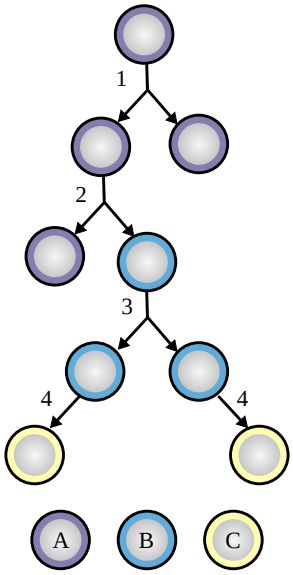


Figure 16.12.1: Symmetric and Asymmetric Division: This diagram illustrates stem cell division and differentiation, through the processes of (1) symmetric stem cell division, (2) asymmetric stem cell division, (3) progenitor division, and (4) terminal differentiation. Stem cells are indicated by (A), progenitor cells by (B), and differentiated cells by (C).

An asymmetric cell division produces two daughter cells with different cellular fates. This is in contrast to normal symmetric cell divisions, which give rise to daughter cells of equivalent fates. Notably, stem cells divide asymmetrically to give rise to two distinct daughter cells: one copy of the original stem cell as well as a second daughter programmed to differentiate into a non-stem cell fate.

In principle, there are two mechanisms by which distinct properties may be conferred on the daughters of a dividing cell. In one, the daughter cells are initially equivalent but a difference is induced by signaling between the cells, from surrounding cells, or from the precursor cell. This mechanism is known as extrinsic asymmetric cell division. Extrinsic factors involve interactions with neighboring cells and the micro and macro environment of the precursor cell.

In the second mechanism, the prospective daughter cells are inherently different at the time of division of the mother cell. Because this latter mechanism does not depend on interactions of cells with each other or with their environment, it must rely on intrinsic asymmetry. The term asymmetric cell division usually refers to such intrinsic asymmetric divisions. Intrinsic factors generally involve differing amounts of cell-fate determinants being distributed into each daughter cell.

Animals are made up of a vast number of distinct cell types. During development, the zygote undergoes many cell divisions that give rise to various cell types, including embryonic stem cells. Asymmetric divisions of these embryonic cells gives rise to one cell of the same potency (self-renewal), and another that may be of the same potency or stimulated to further differentiate into specialized cell types such as neurons. Asymmetric division of stem cells plays a key role in development by allowing for the differentiation of a subset of daughter cells while maintaining stem cell pluripotency. Since it can be controlled by both intrinsic and extrinsic factors, upon delineating these particular factors it may be possible to use this knowledge in applications of tissue and whole organ generation.

Key Points

- Symmetric cell division of stem cells ensures that a constant pool of stem cells is available by giving rise to two identical daughter cells both endowed with stem cell properties.
- Asymmetric division of stem cells results in the production of only one stem cell and a progenitor cell with limited self-renewal potential.
- Progenitor cells that are produced via asymmetric cell division will go through additional rounds of cell division until they are terminally differentiated into a mature, specialized cell.
- Asymmetric division can be controlled by both intrinsic and extrinsic factors.
- Intrinsic factors involve differing amounts of cell-fate determinants being distributed into each daughter cell, while extrinsic factors involve interactions with neighboring cells and the micro and macro environment of the precursor cell.

Key Terms

- **totipotency**: the ability of a cell to produce differentiated cells upon division
- **progenitor cell**: a biological cell that, like a stem cell, has a tendency to differentiate into a specific type of cell, but is already more specific than a stem cell and is pushed to differentiate into its “target” cell.
- **autologous**: derived from part of the same individual (i.e. from the recipient rather than the donor)
- **morula**: a spherical mass of blastomeres that forms following the splitting of a zygote; it becomes the blastula
- **pluripotent**: able to develop into more than one mature cell or tissue type, but not all

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16.13: Regulating Gene Expression in Cell Development - Cellular Differentiation

Learning Objectives

- Discuss how differentiated cells can serve different functions

To develop a multicellular organisms, cells must differentiate to specialize for different functions. Three basic categories of cells make up the mammalian body: germ cells, somatic cells, and stem cells. Each of the approximately 100 trillion cells in an adult human has its own copy or copies of the genome except certain cell types, such as red blood cells, that lack nuclei in their fully differentiated state. Most cells are diploid; they have two copies of each chromosome. The process of cellular differentiation is regulated by transcription factors and growth factors, and results in expression or inhibition of various genes between the cell types, thereby resulting in varying proteomes between cell types. The variation in proteomes between cell types is what drives differentiation and thus, specialization of cells. The ability of transcription factors to control whether a gene will be transcribed or not that contributes to specialization and growth factors to aid in the division process are key components of cell differentiation.

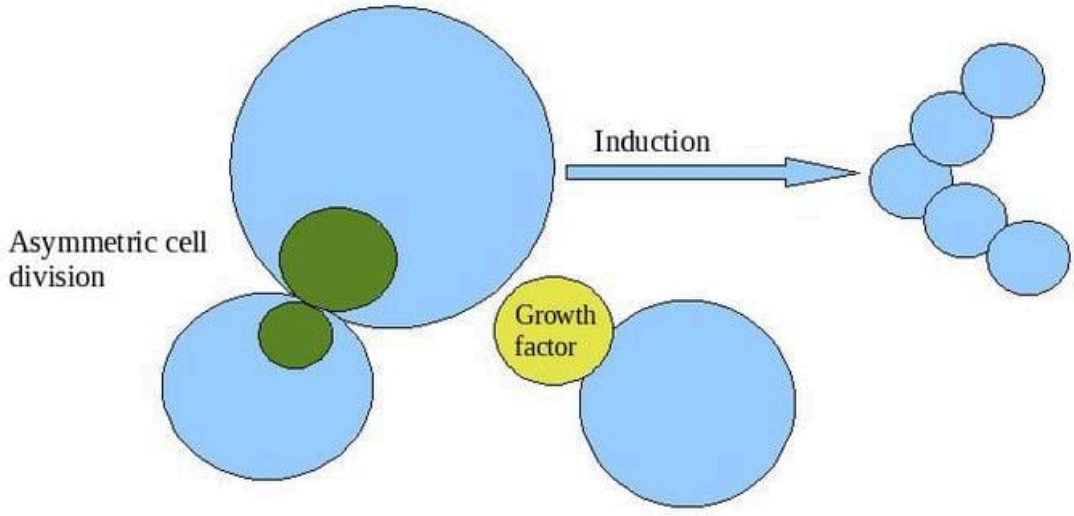


Figure 16.13.1: Cell Differentiation: Mechanics of cellular differentiation can be controlled by growth factors which can induce cell division. In asymetric cell division the cell will be induced to differentiate into a specialized cell and the growth factors will work in tandem.

Somatic cells are diploid cells that make up most of the human body, such as the skin and muscle. Germ cells are any line of cells that give rise to gametes—eggs and sperm—and thus are continuous through the generations. Stem cells, on the other hand, have the ability to divide for indefinite periods and to give rise to specialized cells. They are best described in the context of normal human development.

Embryonic Development

Development begins when a sperm fertilizes an egg and creates a single cell that has the potential to form an entire organism. In the first hours after fertilization, this cell divides into identical cells. In humans, approximately four days after fertilization and after several cycles of cell division, these cells begin to specialize, forming a hollow sphere of cells, called a blastocyst. The blastocyst has an outer layer of cells, and inside this hollow sphere, there is a cluster of cells called the inner cell mass. The cells of the inner cell mass go on to form virtually all of the tissues of the human body. Although the cells of the inner cell mass can form virtually every type of cell found in the human body, they cannot form an organism. These cells are referred to as pluripotent.

Pluripotent stem cells undergo further specialization into multipotent progenitor cells that then give rise to functional cells.

Examples of stem and progenitor cells include:

1. Hematopoietic stem cells (adult stem cells) from the bone marrow that give rise to red blood cells, white blood cells, and platelets
2. Mesenchymal stem cells (adult stem cells) from the bone marrow that give rise to stromal cells, fat cells, and types of bone cells;
3. Epithelial stem cells (progenitor cells) that give rise to the various types of skin cells
4. Muscle satellite cells (progenitor cells) that contribute to differentiated muscle tissue

A pathway that is guided by the cell adhesion molecules is created as the cellular blastomere differentiates from the single-layered blastula to the three primary layers of germ cells in mammals, namely the ectoderm, mesoderm and endoderm (listed from most distal, or exterior, to the most proximal, or interior). The ectoderm ends up forming the skin and the nervous system, the mesoderm forms the bones and muscular tissue, and the endoderm forms the internal organ tissues.

Key Points

- The three major cell types in the mammalian body include germ cells (which develop into gametes), somatic cells (diploid cells that develop into a majority of the human body) and stem cells (cells that can divide indefinitely).
- In human development, the inner cell mass exhibits the ability to differentiate and form all tissues of the body; however, they cannot form an organism.
- The various types of stem and progenitor cells included in the body that will differentiate to develop more specialized cells includes: hematopoietic stem cells, mesenchymal stem cells, epithelial stem cells and muscle satellite cells.
- To develop a multicellular oragnisms, cells must differentiate to specialize for different functions.

Key Terms

- **blastocyst**: the mammalian blastula formed during development where the inner cell mass can be found which forms the embryo
- **inner cell mass**: a mass of cells within a primordial embryo that will eventually develop into the distinct form of a fetus in most eutherian mammals
- **proteome**: the complete set of proteins encoded by a particular genome
- **pluripotent**: able to develop into more than one mature cell or tissue type, but not all

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16.14: Regulating Gene Expression in Cell Development - Mechanics of Cellular Differentation

Learning Objectives

- Summarize how a cell can differentiate into a specialized cell

Cellular differentiation

How does a complex organism such as a human develop from a single cell—a fertilized egg—into the vast array of cell types such as nerve cells, muscle cells, and epithelial cells that characterize the adult? Throughout development and adulthood, the process of cellular differentiation leads cells to assume their final morphology and physiology. Differentiation is the process by which unspecialized cells become specialized to carry out distinct functions.

Stem Cells

A stem cell is an unspecialized cell that can divide without limit as needed and can, under specific conditions, differentiate into specialized cells. Stem cells are divided into several categories according to their potential to differentiate. The first embryonic cells that arise from the division of the zygote are the ultimate stem cells; these stems cells are described as totipotent because they have the potential to differentiate into any of the cells needed to enable an organism to grow and develop. The embryonic cells that develop from totipotent stem cells and are precursors to the fundamental tissue layers of the embryo are classified as pluripotent. A pluripotent stem cell is one that has the potential to differentiate into any type of human tissue but cannot support the full development of an organism. These cells then become slightly more specialized, and are referred to as multipotent cells. A multipotent stem cell has the potential to differentiate into different types of cells within a given cell lineage or small number of lineages, such as a red blood cell or white blood cell.

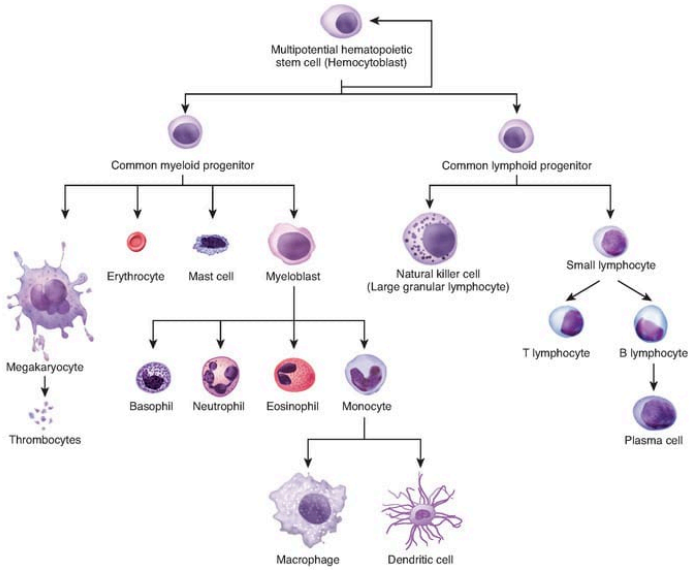


Figure 16.14.1: Hematopoiesis: the differentiation of multipotent cells: The process of hematopoiesis involves the differentiation of multipotent cells into blood and immune cells. The multipotent hematopoietic stem cells give rise to many different cell types, including the cells of the immune system and red blood cells.

Finally, multipotent cells can become further specialized oligopotent cells. An oligopotent stem cell is limited to becoming one of a few different cell types. In contrast, a unipotent cell is fully specialized and can only reproduce to generate more of its own specific cell type. Stem cells are unique in that they can also continually divide and regenerate new stem cells instead of further

specializing.

There are different stem cells present at different stages of a human's life, including the embryonic stem cells of the embryo, fetal stem cells of the fetus, and adult stem cells in the adult. One type of adult stem cell is the epithelial stem cell, which gives rise to the keratinocytes (cells that produce keratin, the primary protein in nails and hair) in the multiple layers of epithelial cells in the epidermis of skin. Adult bone marrow has three distinct types of stem cells: hematopoietic stem cells, which give rise to red blood cells, white blood cells, and platelets; endothelial stem cells, which give rise to the endothelial cell types that line blood and lymph vessels; and mesenchymal stem cells, which give rise to the different types of muscle cells.

Differentiation

When a cell differentiates (i.e., becomes more specialized), it may undertake major changes in its size, shape, metabolic activity, and overall function. Because all cells in the body, beginning with the fertilized egg, contain the same DNA, how do the different cell types come to be so different? The answer is analogous to a movie script. Different actors in a movie all read from the same script, but each one only reads their own part of the script. Similarly, all cells contain the same full complement of DNA, but each type of cell only "reads" the portions of DNA that are relevant to its own functioning. In other terms, each cell has the genome but will only express specific genes, thereby having unique proteomes. In biology, this is referred to as the unique genetic expression of each cell. In order for a cell to differentiate into its specialized form and function, it need only manipulate those genes (and thus those proteins) that will be expressed, and not those that will remain silent.

Mechanism

The primary mechanism by which genes are turned "on" or "off" is through transcription factors. A transcription factor is one of a class of proteins that bind to specific genes on the DNA molecule and either promote or inhibit their transcription. The primary mechanism that determines which genes will be expressed and which ones will not is through the use of different transcription factor proteins, which bind to DNA and promote or hinder the transcription of different genes. Through the action of these transcription factors, cells specialize into one of hundreds of different cell types in the human body.

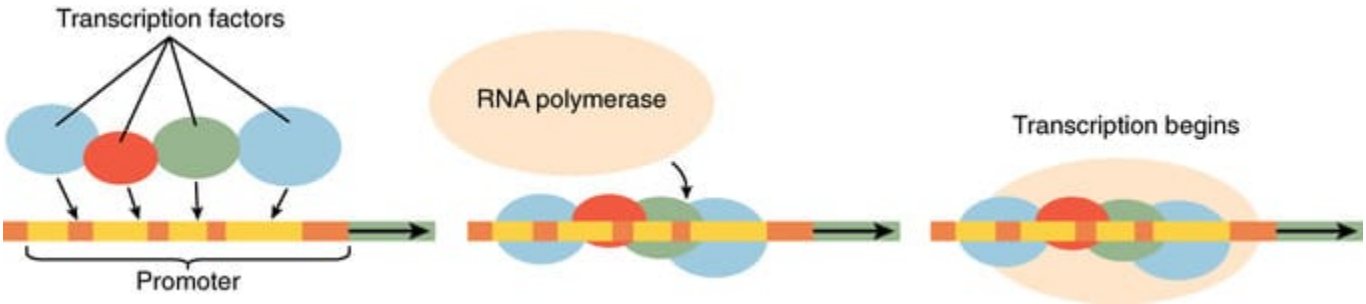


Figure 16.14.1: Transcription Factors Regulate Gene Expression: While each body cell contains the organism's entire genome, different cells regulate gene expression with the use of various transcription factors. Transcription factors are proteins that affect the binding of RNA polymerase to a particular gene on the DNA molecule.

Key Points

- Different types of stem cells exhibit varying abilities to differentiate into specialized cells (from the most unlimited stem cell to the most restricted): totipotent, pluripotent, multipotent to oligopotent.
- Totipotent cells have the potential to differentiate into any of the cells needed to enable an organism to grow and develop; pluripotent cells have the potential to differentiate into any type of human tissue but cannot support the full development of an organism.
- A multipotent stem cell has the potential to differentiate into different types of cells within a given cell lineage or small number of lineages, while an oligopotent stem cell is limited to becoming one of a few different cell types.
- The process of cellular differentiation is under strict regulation by transcription factors which can either activate or repress expression of genes that will affect the proteome of the cell and thus, provide the necessary components it needs to become a specialized cell.
- All cells contain the same complement of DNA, or genome, but once differentiation occurs, it is the changes in the proteome that will distinguish one cell type from another.

Key Terms

- **differentiate**: to produce distinct cells, organs or to achieve specific functions by a process of development
- **proteome**: the complete set of proteins encoded by a particular genome
- **transcription**: the synthesis of RNA under the direction of DNA

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16.15: Regulating Gene Expression in Cell Development - Establishing Body Axes during Development

Learning Objectives

- Summarize the mechanisms and cell types that establish the body axes

Vertebrate axis formation

During development, as the germ layers form, the ball of cells still retains its spherical shape. However, animal bodies have lateral-medial (left-right), dorsal-ventral (back-belly), and anterior-posterior (head-feet) axes. How are these established? In one of the most seminal experiments ever to be carried out in developmental biology, Spemann and Mangold took dorsal cells from one embryo and transplanted them into the belly region of another embryo. They found that the transplanted embryo now had two notochords: one at the dorsal site from the original cells and another at the transplanted site. This suggested that the dorsal cells were genetically programmed to form the notochord and define the axis. Since then, researchers have identified many genes that are responsible for axis formation. Mutations in these genes leads to the loss of symmetry required for organism development. Animal bodies have externally visible symmetry. However, the internal organs are not symmetric. For example, the heart is on the left side and the liver on the right. The formation of the central left-right axis is an important process during development. This internal asymmetry is established very early during development and involves many genes. Research is still ongoing to fully understand the developmental implications of these genes.

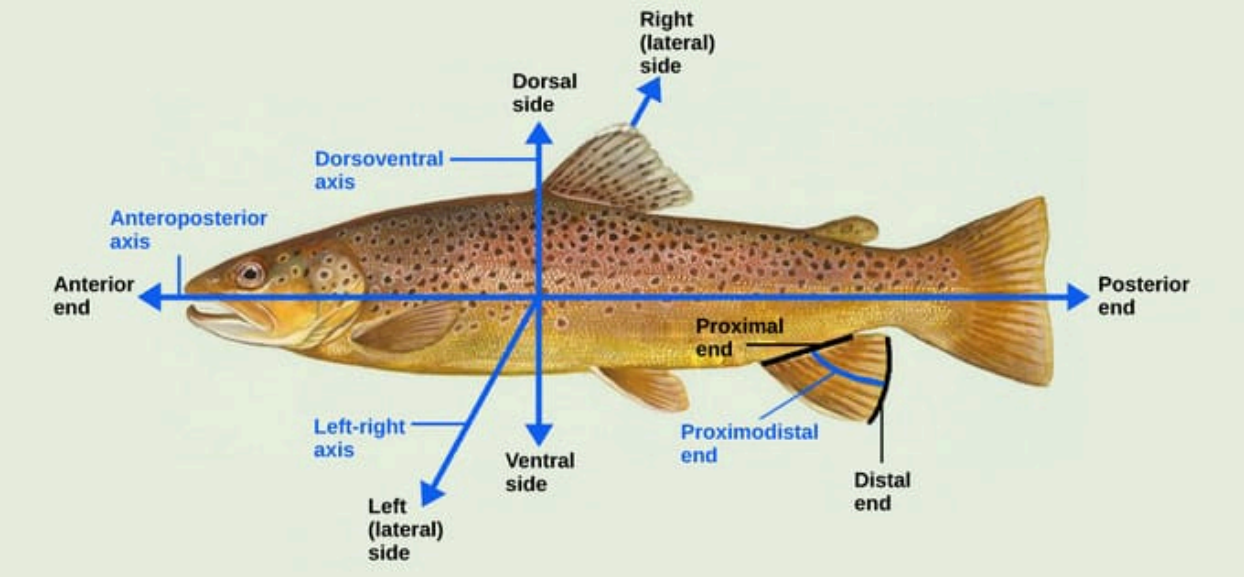


Figure 16.15.1: Vertebrate Axis Formation: Animal bodies have three axes for symmetry:lateral-medial (left-right), dorsal-ventral (back-belly), and anterior-posterior (head-feet).

Neural tube

In the developing chordate (including vertebrates), the neural tube is the embryo's precursor to the central nervous system, which comprises the brain and spinal cord. The neural groove gradually deepens as the neural folds become elevated, and ultimately the folds meet and coalesce in the middle line and convert the groove into a closed tube, the neural tube or neural canal, the ectodermal wall of which forms the rudiment of the nervous system.

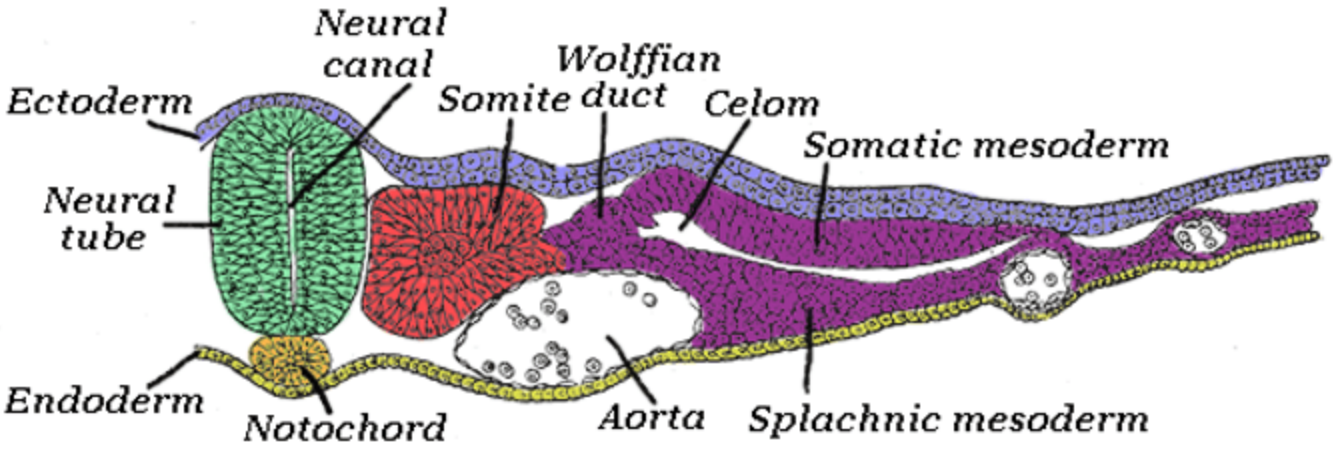


Figure 16.15.1: Neural Tube: Transverse section of half of a chick embryo of forty-five hours' incubation. The dorsal (back) surface of the embryo is toward the top of this page, while the ventral (front) surface is toward the bottom. (Neural tube is in green.)

Primary and secondary neurulation

The neural tube develops in two ways: primary neurulation and secondary neurulation. Primary neurulation divides the ectoderm into three cell types: the internally located neural tube, the externally located epidermis, and the neural crest cells, which develop in the region between the neural tube and epidermis but then migrate to new locations. Primary neurulation begins after the neural plate forms. The edges of the neural plate start to thicken and lift upward, forming the neural folds. The center of the neural plate remains grounded, allowing a U-shaped neural groove to form. This neural groove sets the boundary between the right and left sides of the embryo. The neural folds pinch in towards the midline of the embryo and fuse together to form the neural tube. In secondary neurulation, the cells of the neural plate form a cord-like structure that migrates inside the embryo and hollows to form the tube.

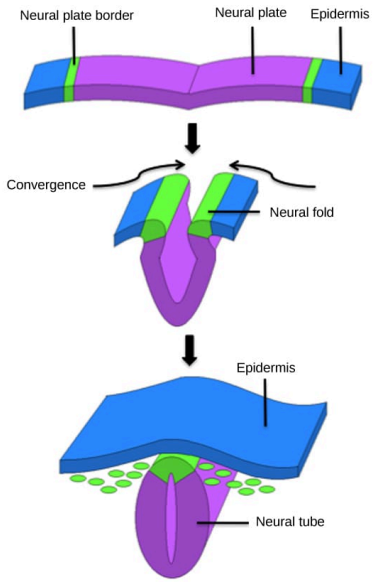


Figure 16.15.1: Neural Tube Formation: The central region of the ectoderm forms the neural tube, which gives rise to the brain and the spinal cord.

Each organism uses primary and secondary neurulation to varying degrees. Neurulation in fish proceeds only via the secondary form. In avian species the posterior regions of the tube develop using secondary neurulation and the anterior regions develop by primary neurulation. In mammals, secondary neurulation begins around the 35th somite. Mammalian neural tubes close in the head in the opposite order that they close in the trunk. In the head, neural crest cells migrate, the neural tube closes, and the overlying ectoderm closes. In the trunk, overlying ectoderm closes, the neural tube closes and neural crest cells migrate.

Neural tube subdivisions

Four neural tube subdivisions eventually develop into distinct regions of the central nervous system by the division of neuroepithelial cells: the prosencephalon, the mesencephalon, the rhombencephalon and the spinal cord. The prosencephalon further goes on to develop into the telencephalon (the forebrain or cerebrum) and the diencephalon (the optic vesicles and hypothalamus). The mesencephalon develops into the midbrain. The rhombencephalon develops into the metencephalon (the pons and cerebellum) and the myelencephalon (the medulla oblongata).

For a short time, the neural tube is open both cranially and caudally. These openings, called neuropores, close during the fourth week in the human. Improper closure of the neuropores can result in neural tube defects such as anencephaly or spina bifida. The dorsal part of the neural tube contains the alar plate, which is primarily associated with sensation. The ventral part of the neural tube contains the basal plate, which is primarily associated with motor (i.e., muscle) control.

Signaling molecules and other factors

The neural tube patterns along the dorsal-ventral axis establish defined compartments of neural progenitor cells that lead to distinct classes of neurons. This patterning occurs early in development and results from the activity of several secreted signaling molecules. Sonic hedgehog (Shh) is a key player in patterning the ventral axis, while Bone morphogenic proteins (Bmp) and Wnt family members play an important role in patterning the dorsal axis. Other factors shown to provide positional information to the neural progenitor cells include Fibroblast growth factors (FGF) and Retinoic Acid. Retinoic acid is required ventrally along with Shh to induce Pax6 and Olig2 during differentiation of motor neurons. Three main ventral cell types are established during early neural tube development: the floor plate cells, which form at the ventral midline during the neural fold stage; as well as the more dorsally located motor neurons and interneurons. These cell types are specified by the secretion of Shh from the notochord (located ventrally to the neural tube), and later from the floor plate cells. Shh acts as a morphogen, meaning that it acts in a concentration-dependent manner to specify cell types as it moves further from its source. The different combinations of expression of transcription factors along the dorsal-ventral axis of the neural tube are responsible for creating the identity of the neuronal progenitor cells.

Key Points

- The three axes of the animal body are established in development via the expression of specific sets of genes that regulate which cells will develop into specific structures.
- During development, the dorsal cells are genetically programmed to develop into the notochord and define the axis.
- The neural tube can develop in two ways: primary or secondary neurulation, which are used by organisms in varying degrees to establish the neural tube that will develop into the central nervous system (brain and spinal cord).
- Specific patterns along the neural tube that are established via secretion and production of specific signaling molecules (such as Wnt, Shh, BMP and retinoic acid) play a key role in patterning the dorsal and ventral axes.

Key Terms

- **neural tube**: hollow longitudinal dorsal tube formed in the folding and subsequent fusion of the opposite ectodermal folds in the embryo that gives rise to the brain and spinal cord
- **neurulation**: the process by which the beginnings of the vertebrate nervous system is formed in embryos
- **anencephaly**: a lethal birth defect in which most of the brain and parts of the skull are missing; absence of the encephalon
- **notochord**: a flexible rodlike structure that forms the main support of the body in the lowest chordates; a primitive spine

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16.16: Regulating Gene Expression in Cell Development - Gene Expression for Spatial Positioning

Learning Objectives

- Describe the role genes play in development and ensuring proper spatial positioning

Genes provide positional information

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, known as organogenesis, is characterized by rapid and precise movements of the cells within the embryo.

Organogenesis

Organs form from the germ layers through the process of differentiation. During differentiation, the embryonic stem cells express specific sets of genes which will determine their ultimate cell type. For example, some cells in the ectoderm (the outer tissue layer of the embryo) will express the genes specific to skin cells. As a result, these cells will differentiate into epidermal cells. The process of differentiation is regulated by cellular signaling cascades. Scientists study organogenesis extensively in the lab in fruit flies (Drosophila) and the nematode Caenorhabditis elegans. Drosophila have segments along their bodies, and the patterning associated with the segment formation has allowed scientists to study which genes play important roles in organogenesis along the length of the embryo at different time points. The nematode C.elegans has roughly 1000 somatic cells and scientists have studied the fate of each of these cells during their development in the nematode life cycle. There is little variation in patterns of cell lineage between individuals, unlike in mammals where cell development from the embryo is dependent on cellular cues.

In vertebrates, one of the primary steps during organogenesis is the formation of the neural system. The ectoderm forms epithelial cells and tissues, as well as neuronal tissues. During the formation of the neural system, special signaling molecules called growth factors signal some cells at the edge of the ectoderm to become epidermis cells. The remaining cells in the center form the neural plate. If the signaling by growth factors were disrupted, then the entire ectoderm would differentiate into neural tissue. The neural plate undergoes a series of cell movements where it rolls up and forms a tube called the neural tube. In further development, the neural tube will give rise to the brain and the spinal cord. The mesoderm that lies on either side of the vertebrate neural tube will develop into the various connective tissues of the animal body. A spatial pattern of gene expression reorganizes the mesoderm into groups of cells called somites with spaces between them. The somites will further develop into the ribs, lungs, and segmental (spine) muscle. The mesoderm also forms a structure called the notochord, which is rod-shaped and forms the central axis of the animal body.



Figure 16.16.1: Somites: In this five-week old human embryo, somites are segments along the length of the body.

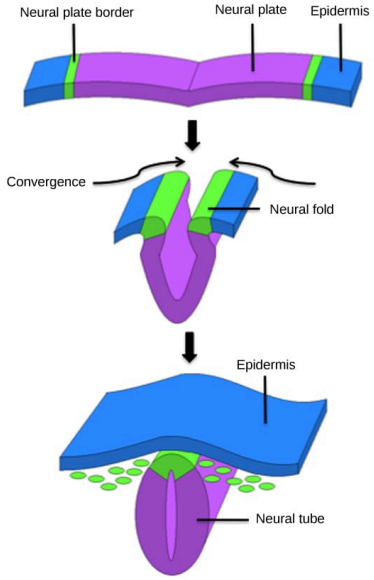


Figure 16.16.1: Neural Tube Formation: The central region of the ectoderm forms the neural tube, which gives rise to the brain and the spinal cord.

Key Points

- Organogenesis results in the formation of the various organs in the body; however it will only occur if specific sets of genes are expressed to determine ultimate cell type.
- The ability of specific cells to migrate to the the edge of the ectoderm is highly regulated by specific gene expression and allows for differentiation into epidermal cells; in contrast, the cells which remain in the center will develop into the neural plate.
- The expression of specific sets of genes will also regulate the reorganization of the mesoderm into distinct groups of cells, called somites, which develop into the ribs, lungs, spine muscle and notochord.

Key Terms

- **gastrulation**: the stage of embryo development at which a gastrula is formed from the blastula by the inward migration of cells
- **organogenesis**: the formation and development of the organs of an organism from embryonic cells

- **somite**: one of the paired masses of mesoderm distributed along the sides of the neural tube that will eventually become dermis, skeletal muscle, or vertebrae

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16.17: Regulating Gene Expression in Cell Development - Cell Migration in Multicellular Organisms

Learning Objectives

- Describe how cells can migrate within an organism

Cell migration

Cell migration is a central process in the development and maintenance of multicellular organisms. Processes such as tissue formation during embryonic development, wound healing, and immune responses, all require the orchestrated movement of cells in particular directions to specific locations. Errors during this process have serious consequences, including intellectual disability, vascular disease, tumor formation and metastasis. An understanding of the mechanism by which cells migrate may lead to the development of novel therapeutic strategies for controlling, for example, invasive tumor cells.

Cells often migrate in response to specific external signals, including chemical signals and mechanical signals. Due to a highly viscous environment, cells need to permanently produce forces in order to move. Cells achieve active movement by very different mechanisms. Many less complex prokaryotic organisms (and sperm cells) use flagella or cilia to propel themselves. Eukaryotic cell migration typically is far more complex and can consist of combinations of different migration mechanisms. It generally involves drastic changes in cell shape which are driven by the cytoskeleton, for instance a series of contractions and expansions due to cytoplasmic displacement. Two very distinct migration scenarios are crawling motion (most commonly studied) and blebbing motility.

The migration of cultured cells attached to a surface is commonly studied using microscopy. As cell movement is very slow (only a few µm/minute), time-lapse microscopy videos are recorded of the migrating cells to speed up the movement. Such videos reveal that the leading cell front is very active with a characteristic behavior of successive contractions and expansions. It is generally accepted that the leading front is the main motor that pulls the cell forward.

YouTube Video

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

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Cell Migration: Phase images of BSC 1 cells migrating in a scratch assay in the absence of serum over a period of 15 hours.

Common features of cell migration

The processes underlying mammalian cell migration are believed to be consistent with those of (non-spermatozoic) locomotion. Observations in common include cytoplasmic displacement at the leading front and laminar removal of dorsally-accumulated debris toward trailing end. The latter feature is most easily observed when aggregates of a surface molecule are cross-linked with a fluorescent antibody or when small beads become artificially bound to the front of the cell. Other eukaryotic cells are observed to migrate similarly. The amoeba *Dictyostelium discoideum* is useful to researchers because they consistently exhibit chemotaxis in response to cyclic AMP; they move more quickly than cultured mammalian cells; and they have a haploid genome that simplifies the process of connecting a particular gene product with its effect on cellular behavior.

Key Points

- The disruption or dysfunction of cell migration processes can lead to formation of various diseases such as metastasis, tumor formation and vascular disease.
- In prokaryotic organisms, and some eukaryotic cells such as sperm cells, cell migration occurs via the use of a cilia or flagella to propel forward.
- In eukaryotic organisms, cell migration is a much more complex process and can include, but is not excluded to, changes in the cytoskeleton, motor proteins, blebbing, and cytoplasmic displacement; it involves both external and internal signals that mediate these processes.

Key Terms

- **bleb**: an irregular bulge in the plasma membrane of a cell
- **chemotaxis**: the movement of a cell or an organism in response to a chemical stimulant
- **laminar**: of fluid motion, smooth and regular, flowing as though in different layers
- **metastasis**: the transference of a bodily function or disease to another part of the body; specifically the development of a secondary area of disease remote from the original site, as with some cancers

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16.18: Regulating Gene Expression in Cell Development - Programmed Cell Death

Learning Objectives

- Explain the importance of programmed cell death, including apoptosis and autophagy

Programmed cell death

Programmed cell-death (or PCD) is death of a cell in any form, mediated by an intracellular program. PCD is carried out in a regulated process, which usually confers advantage during an organism's life-cycle. For example, the differentiation of fingers and toes in a developing human embryo occurs because cells between the fingers apoptose, or die; the result is that the digits are separate. PCD serves fundamental functions during both plant and metazoa (multicellular animal) tissue development. Apoptosis and autophagy are both forms of PCD, but necrosis is a non-physiological process that occurs as a result of infection or injury.

Apoptosis

Apoptosis is the process of PCD that may occur in multicellular organisms. Biochemical events lead to characteristic cell changes (morphology) and death. These changes include blebbing, cell shrinkage, nuclear fragmentation, chromatin condensation, and chromosomal DNA fragmentation. There appears to be some variation in the morphology and indeed the biochemistry of these "suicide" pathways. Some tread the path of apoptosis, while others follow a more generalized pathway to deletion; however both are usually genetically and synthetically motivated. There is some evidence that certain symptoms of apoptosis, such as endonuclease activation, can be spuriously induced without engaging a genetic cascade; however, it is presumed that true apoptosis and PCD must be genetically mediated. It is also becoming clear that mitosis (the division of the cell nucleus) and apoptosis are linked in some way, and that the balance achieved depends on signals received from appropriate growth or survival factors.

When a cell is damaged, superfluous, or potentially dangerous to an organism, a cell can initiate a mechanism to trigger apoptosis. Apoptosis allows a cell to die in a controlled manner that prevents the release of potentially damaging molecules from inside the cell. There are many internal checkpoints that monitor a cell's health; if abnormalities are observed, a cell can spontaneously initiate the process of apoptosis. However, in some cases, such as a viral infection or uncontrolled cell division due to cancer, the cell's normal checks and balances fail.

Apoptosis can also be initiated via external signaling. For example, most normal animal cells have receptors that interact with the extracellular matrix, a network of glycoproteins that provides structural support for cells in an organism. The binding of cellular receptors to the extracellular matrix initiates a signaling cascade within the cell. However, if the cell moves away from the extracellular matrix, the signaling ceases, and the cell undergoes apoptosis. This system keeps cells from traveling through the body and proliferating out of control, as happens with tumor cells that metastasize.



Figure 16.18.1: Programmed Cell Death: This histological section of a foot of a 15-day-old mouse embryo, visualized using light microscopy, reveals areas of tissue between the toes, which apoptosis will eliminate before the mouse reaches its full gestational age at 27 days.

Another example of external signaling that leads to apoptosis occurs in T-cell development. T-cells are immune cells that bind to foreign macromolecules and particles, and target them for destruction by the immune system. Normally, T-cells do not target "self" proteins (those of their own organism), a process that can lead to autoimmune diseases. In order to develop the ability to discriminate between self and non-self, immature T-cells undergo screening to determine whether they bind to so-called self proteins. If the T-cell receptor binds to self proteins, the cell initiates apoptosis to remove the potentially dangerous cell.

Apoptosis is also essential for normal embryological development. In vertebrates, for example, early stages of development include the formation of web-like tissue between individual fingers and toes. During the course of normal development, these unneeded cells must be eliminated, enabling fully separated fingers and toes to form. A cell signaling mechanism triggers apoptosis, which destroys the cells between the developing digits.

Autophagy

Macroautophagy, often referred to as autophagy, is a type of programmed cell death accomplished through self-digestion. It is a catabolic process that results in the autophagosomic-lysosomal degradation of bulk cytoplasmic contents, abnormal protein aggregates, and excess or damaged organelles. Autophagy is generally activated by conditions of nutrient deprivation but has also been associated with physiological as well as pathological processes such as development, differentiation, neurodegenerative diseases, stress (physiology), infection and cancer.

Necrosis

Necrosis is the death of a cell caused by external factors such as trauma or infection and occurs in several different forms. Recently a form of programmed necrosis, called necroptosis, has been recognized as an alternate form of PCD. It is hypothesized that necroptosis can serve as a cell-death backup to apoptosis when the apoptosis signaling is blocked by endogenous or exogenous factors, such as viruses or mutations.

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Key Points

- Programmed cell death can provide an advantage to an organism during development, for instance by maintaining homeostasis and protection against potentially disruptive issues which may arise during the life of a cell.
- Apoptosis is a process of programmed cell death that is regulated by numerous biochemical events and appears to be genetically mediated.
- Autophagy is a process of programmed cell death that is characterized as a catabolic process via formation of an

autophagolysosome which degrades damaged cellular contents.
- Necrosis occurs when cellular death is caused by external factors and is characterized as an alternate form of programmed cell death, called necroptosis.

Key Terms

- **apoptosis**: a process of programmed cell death
- **extracellular matrix**: All the connective tissues and fibres that are not part of a cell, but rather provide support.
- **autophagy**: a type of programmed cell death accomplished through self-digestion

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16.19: Cancer and Gene Regulation - Altered Gene Expression in Cancer

Learning Objectives

- Describe how cancer is caused by uncontrolled cell growth

Cancer: Disease of Altered Gene Expression

Cancer can be described as a disease of altered gene expression. There are many proteins that are turned on or off (gene activation or gene silencing) that dramatically alter the overall activity of the cell. A gene that is not normally expressed in that cell can be switched on and expressed at high levels. This can be the result of gene mutation or changes in gene regulation (epigenetic, transcription, post-transcription, translation, or post-translation).

Changes in epigenetic regulation, transcription, RNA stability, protein translation, and post-translational control can be detected in cancer. While these changes do not occur simultaneously in one cancer, changes at each of these levels can be detected when observing cancer at different sites in different individuals. Therefore, changes in histone acetylation (epigenetic modification that leads to gene silencing), activation of transcription factors by phosphorylation, increased RNA stability, increased translational control, and protein modification can all be detected at some point in various cancer cells. Scientists are working to understand the common changes that give rise to certain types of cancer or how a modification might be exploited to destroy a tumor cell.

Tumor Suppressor Genes, Oncogenes, and Cancer

In normal cells, some genes function to prevent excess, inappropriate cell growth. These are tumor suppressor genes, which are active in normal cells to prevent uncontrolled cell growth. There are many tumor suppressor genes in cells, but the one most studied is p53, which is mutated in over 50 percent of all cancer types. The p53 protein itself functions as a transcription factor. It can bind to sites in the promoters of genes to initiate transcription. Therefore, the mutation of p53 in cancer will dramatically alter the transcriptional activity of its target genes.

Another type of gene often deregulated in cancers are proto-oncogenes which are positive cell-cycle regulators. When mutated, proto-oncogenes can become oncogenes and cause cancer. Overexpression of the oncogene can lead to uncontrolled cell growth because oncogenes can alter transcriptional activity, stability, or protein translation of another gene that directly or indirectly controls cell growth. An example of an oncogene involved in cancer is a protein called myc. Myc is a transcription factor that is aberrantly activated in Burkett's Lymphoma, a cancer of the lymph system. Overexpression of myc transforms normal B cells into cancerous cells that continue to grow uncontrollably. High B-cell numbers can result in tumors that can interfere with normal bodily function. Patients with Burkett's lymphoma can develop tumors on their jaw or in their mouth that interfere with the ability to eat.

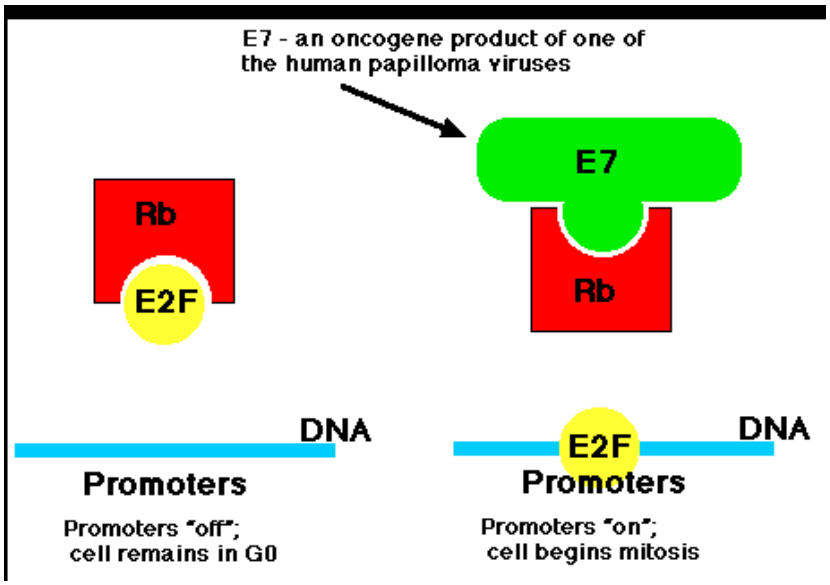


Figure 16.19.1: Proto-oncogenes Can Become Oncogenes: When mutated, proto-oncogenes can become oncogenes and cause cancer due to uncontrolled cell growth.

Key Points

- Cancer results from a gene that is not normally expressed in a cell, but is switched on and expressed at high levels due to mutations or alterations in gene regulation.
- Alterations in histone acetylation, activation of transcription factors, increased RNA stability, increased translational control, and protein modification are all observed in cancer cells.
- Tumor suppressor genes, active in normal cells, work to prevent uncontrolled cell growth.
- Proto- oncogenes, which are positive cell-cycle regulators, can become oncogenes and cause cancer when mutated.

Key Terms

- **oncogene**: any gene that contributes to the conversion of a normal cell into a cancerous cell when mutated or expressed at high levels
- **proto-oncogene**: a gene that promotes the specialization and division of normal cells that becomes an oncogene following mutation
- **cancer**: a disease in which the cells of a tissue undergo uncontrolled (and often rapid) proliferation

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16.20: Cancer and Gene Regulation - Epigenetic Alterations in Cancer

Learning Objectives

- Describe the role played by epigenetic alterations to gene expression in the development of cancer

Cancer and Epigenetic Alterations

Cancer epigenetics is the study of epigenetic modifications to the genome of cancer cells that do not involve a change in the nucleotide sequence. Epigenetic alterations are as important as genetic mutations in a cell's transformation to cancer. Mechanisms of epigenetic silencing of tumor suppressor genes and activation of oncogenes include: alteration in CpG island methylation patterns, histone modifications, and dysregulation of DNA binding proteins.

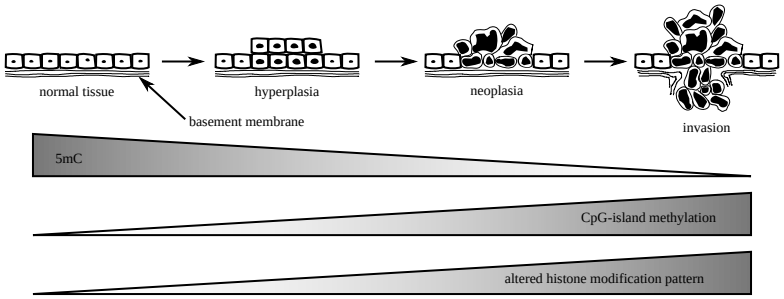


Figure 16.20.1: Epigenetic Alterations in Cancer Cells: In cancer cells, silencing genes through epigenetic mechanisms is a common occurrence. Mechanisms can include modifications to histone proteins and DNA associated with these silencing genes.

Silencing genes through epigenetic mechanisms is very common in cancer cells and include modifications to histone proteins and DNA that are associated with silenced genes. In cancer cells, the DNA in the promoter region of silenced genes is methylated on cytosine DNA residues in CpG islands, genomic regions that contain a high frequency of CpG sites, where a cytosine nucleotide occurs next to a guanine nucleotide. Histone proteins that surround that region lack the acetylation modification (the addition of an acetyl group) that is present when the genes are expressed in normal cells. This combination of DNA methylation and histone deacetylation (epigenetic modifications that lead to gene silencing) is commonly found in cancer. When these modifications occur, the gene present in that chromosomal region is silenced. Increasingly, scientists are understanding how these epigenetic changes are altered in cancer. Because these changes are temporary and can be reversed (for example, by preventing the action of the histone deacetylase protein that removes acetyl groups, or by DNA methyl transferase enzymes that add methyl groups to cytosines in DNA) it is possible to design new drugs and new therapies to take advantage of the reversible nature of these processes. Indeed, many researchers are testing how a silenced gene can be switched back on in a cancer cell to help re-establish normal growth patterns.

Genes involved in the development of many other illnesses, ranging from allergies to inflammation to autism, are also thought to be regulated by epigenetic mechanisms. As our knowledge deepens of how genes are controlled, new ways to treat these diseases and cancer will emerge.

Key Points

- The DNA in the promoter region of silenced genes in cancer cells is methylated on cytosine DNA residues in CpG islands.
- Histone proteins that surround the promoter region of silenced genes lack the acetylation modification that is present when the genes are expressed in normal cells.
- When the combination of DNA methylation and histone deacetylation occur within cancer cells, the gene present in that chromosomal region is silenced.
- Epigenetic changes that are altered in cancer can be reversed and may, therefore, be helpful in new drug and therapy design.

Key Terms

- **epigenetic**: the study of heritable changes in gene expression or cellular phenotype caused by mechanisms other than changes in the underlying DNA sequence
- **methylation**: the addition of a methyl group to cytosine and adenine residues in DNA that leads to the epigenetic modification of DNA and the reduction of gene expression and protein production
- **acetylation**: the reaction of a substance with acetic acid or one of its derivatives; the introduction of one or more acetyl groups into a substance

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16.21: Cancer and Gene Regulation - Cancer and Transcriptional Control

Learning Objectives

- Explain the role of transcription factors in cancer

Cancer and Transcriptional Control

Many transcription factors, especially some that are proto-oncogenes or tumor suppressors, help regulate the cell cycle and, as such, determine how large a cell will get and when it can divide into two daughter cells. Alterations in cells that give rise to cancer can affect the transcriptional control of gene expression. Mutations that activate transcription factors, such as increased phosphorylation, can increase the binding of a transcription factor to its binding site in a promoter. This could lead to increased transcriptional activation of that gene that results in modified cell growth. Alternatively, a mutation in the DNA of a promoter or enhancer region can increase the binding ability of a transcription factor. This could also lead to the increased transcription and aberrant gene expression that is seen in cancer cells.

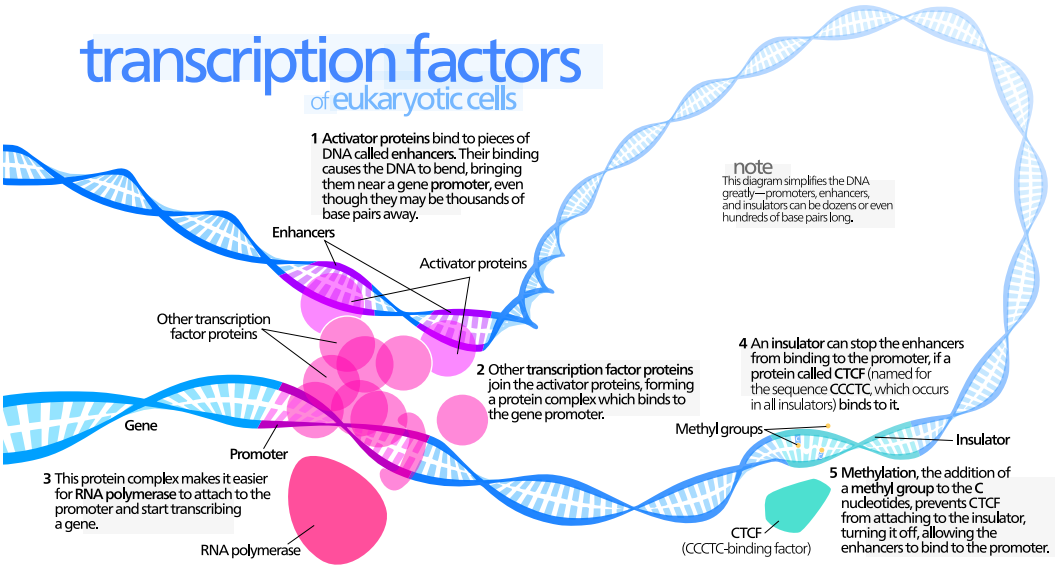


Figure 16.21.1: Transcription Factors: Transcription factors, especially some that are proto-oncogenes or tumor suppressors, help regulate the cell cycle; however, when regulation gives rise to cancer cells, then transcriptional control of gene expression is affected.

Researchers have been investigating how to control the transcriptional activation of gene expression in cancer. Identifying how a transcription factor binds, or a pathway that activates where a gene can be turned off, has led to new drugs and new ways to treat cancer. In breast cancer, for example, many proteins are overexpressed. This can lead to increased phosphorylation of key transcription factors that increase transcription. One such example is the overexpression of the epidermal growth factor receptor (EGFR) in a subset of breast cancers. The EGFR pathway activates many protein kinases that, in turn, activate many transcription factors that control genes involved in cell growth. New drugs that prevent the activation of EGFR have been developed and are used to treat these cancers.

Key Points

- The mutations that activate transcription factors can increase the binding of a transcription factor to its binding site in a promoter leading to increased transcriptional activation of that gene and resulting in altered cell growth.
- A mutation in the DNA of a promoter or enhancer region may increase the binding ability of a transcription factor, which may

then lead to the increased transcription and anomalous gene expression that is seen in cancer cells.
- Studying how to control the transcriptional activation of gene expression in cancer cells along with identifying how a transcription factor binds or a pathway activates where a gene can be turned off has led researchers to new drugs and novel ways of treating cancer.

Key Terms

- **transcription factor**: a protein that binds to specific DNA sequences, thereby controlling the flow (or transcription) of genetic information from DNA to mRNA

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16.22: Cancer and Gene Regulation - Cancer and Post-Transcriptional Control

Learning Objectives

- Explain how post-transcriptional control can result in cancer

Cancer and Post-transcriptional Control

Post-transcriptional regulation is the control of gene expression at the RNA level; therefore, between the transcription and the translation of the gene. After being produced, the stability and distribution of the different transcripts is regulated (post-transcriptional regulation) by means of RNA-binding proteins (RBP) that control the various steps and rates of the transcripts: events such as alternative splicing, nuclear degradation (exosome), processing, nuclear export (three alternative pathways), sequestration in DCP2-bodies for storage or degradation, and, ultimately, translation.

Changes in the post-transcriptional control of a gene can result in cancer. Recently, several groups of researchers have shown that specific cancers have altered expression of microRNAs (miRNAs). miRNAs bind to the 3′ UTR or 5′ UTR of RNA molecules to degrade them. Overexpression of these miRNAs could be detrimental to normal cellular activity. An increase in many miRNAs could dramatically decrease the RNA population leading to a decrease in protein expression. Several studies have demonstrated a change in the miRNA population in specific cancer types. It appears that the subset of miRNAs expressed in breast cancer cells is quite different from the subset expressed in lung cancer cells or even from normal breast cells. This suggests that alterations in miRNA activity can contribute to the growth of breast cancer cells. These types of studies also suggest that if some miRNAs are specifically expressed only in cancer cells, they could be potential drug targets. It would, therefore, be conceivable that new drugs that turn off miRNA expression in cancer could be an effective method to treat cancer.

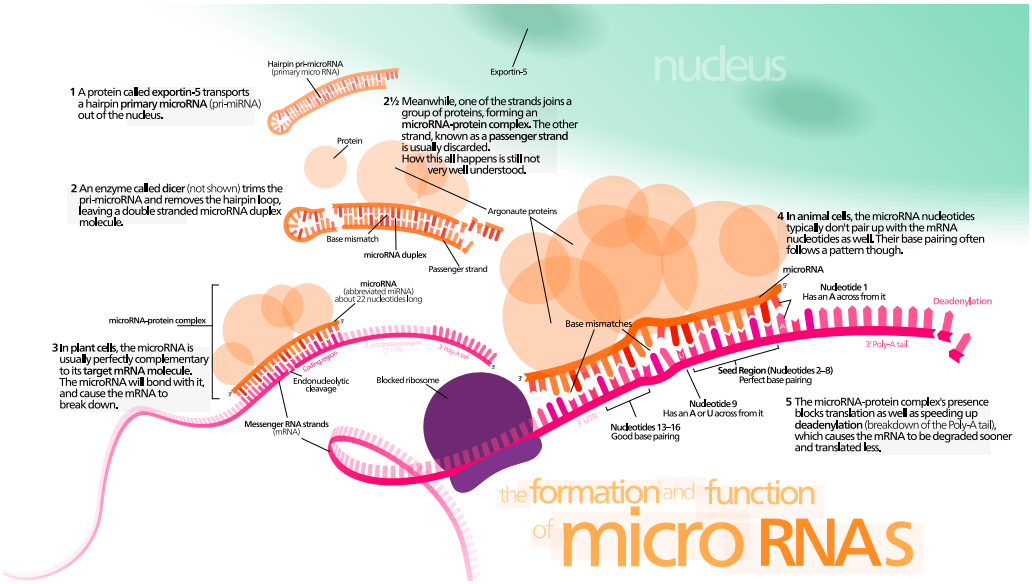


Figure 16.22.1: MicroRNA: Overexpression of miRNAs could be detrimental to normal cellular activity because miRNAs bind to the 3′ UTR of RNA molecules to degrade them. Specific types of miRNAs are only found in cancer cells.

Key Points

- Specific cancers have altered expression of miRNAs; changes in the miRNA population of particular cancers varies depending on the type of cancer.
- Having too many miRNAs can dramatically decrease the RNA population leading to a decrease in protein expression.

- Studies have found that some miRNAs are specifically expressed only in cancer cells.

Key Terms

- **microRNA**: a single-stranded, non-coding form of RNA, having only about 20-30 nucleotides, that has a number of functions including the regulation of gene expression
- **exosome**: a vesicle responsible for the selective removal of plasma membrane proteins

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16.23: Cancer and Gene Regulation - Cancer and Translational Control

Learning Objectives

- Determine how translational or post-translational modifications can lead to cancer

There are many examples of translational or post-translational modifications of proteins that arise in cancer. Modifications are found in cancer cells from the increased translation of a protein to changes in protein phosphorylation to alternative splice variants of a protein. An example of how the expression of an alternative form of a protein can have dramatically different outcomes is seen in colon cancer cells. The c-Flip protein, a protein involved in mediating the cell death pathway, comes in two forms: long (c-FLIPL) and short (c-FLIPS). Both forms appear to be involved in initiating controlled cell death mechanisms in normal cells. However, in colon cancer cells, expression of the long form results in increased cell growth instead of cell death. Clearly, the expression of the wrong protein dramatically alters cell function and contributes to the development of cancer.

New Drugs to Combat Cancer: Targeted Therapy

Scientists are using what is known about the regulation of gene expression in disease states, including cancer, to develop new ways to treat and prevent disease development. Many scientists are designing drugs on the basis of the gene expression patterns within individual tumors. This idea, that therapy and medicines can be tailored to an individual, has given rise to the field of personalized medicine. With an increased understanding of gene regulation and gene function, medicines can be designed to specifically target diseased cells without harming healthy cells. Some new medicines, called targeted therapies, have exploited the overexpression of a specific protein or the mutation of a gene to develop a new medication to treat disease. One such example is the use of anti-EGF receptor medications to treat the subset of breast cancer tumors that have very high levels of the EGF protein. Undoubtedly, more targeted therapies will be developed as scientists learn more about how gene expression changes can cause cancer.

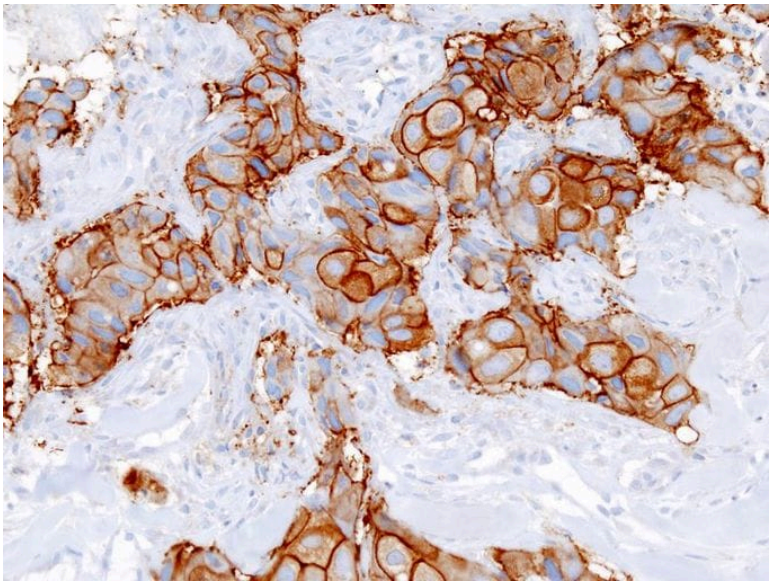


Figure 16.23.1: Using Gene Expression in Targeted Therapy: Scientists are using knowledge of the regulation of gene expression in individual cancers to develop new ways to treat target diseased cells and prevent the disease from occurring. Target therapies exploit the overexpression of a specific protein or gene mutation to develop new medications against the specific cancer.

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Key Points

- Protein modifications from the increased translation of a protein to changes in protein phosphorylation to alternative splice variants of a protein are found in cancer cells.
- The expression of the wrong protein dramatically alters cell function and contributes to the progression of cancer.
- Gene regulation and gene function provide scientists with the opportunity to design medicines and therapies that specifically target diseased cells or exploit the overexpression of specific proteins as cancer treatment.

Key Terms

- **targeted therapy**: a type of medication that blocks the growth of cancer cells by interfering with specific targeted molecules rather than by interfering with rapidly dividing cells
- **cancer**: a disease in which the cells of a tissue undergo uncontrolled (and often rapid) proliferation
- **post-translational modification**: the chemical modification of a protein after its translation; one of the later steps in protein biosynthesis, and thus gene expression, for many proteins

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17: BIOTECHNOLOGY AND GENOMICS

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17.1: BIOTECHNOLOGY

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17.1A: Biotechnology

Learning Objectives

- Justify an overview of the field of biotechnology

The study of nucleic acids began with the discovery of DNA, progressed to the study of genes and small fragments, and has now exploded to the field of genomics. Genomics is the study of entire genomes, including the complete set of genes, their nucleotide sequence and organization, and their interactions within a species and with other species. The advances in genomics have been made possible by DNA sequencing technology. Just as information technology has led to Google maps that enable people to get detailed information about locations around the globe, genomic information is used to create similar maps of the DNA of different organisms. These findings have helped anthropologists to better understand human migration and have aided the field of medicine through the mapping of human genetic diseases. The ways in which genomic information can contribute to scientific understanding are varied and quickly growing.

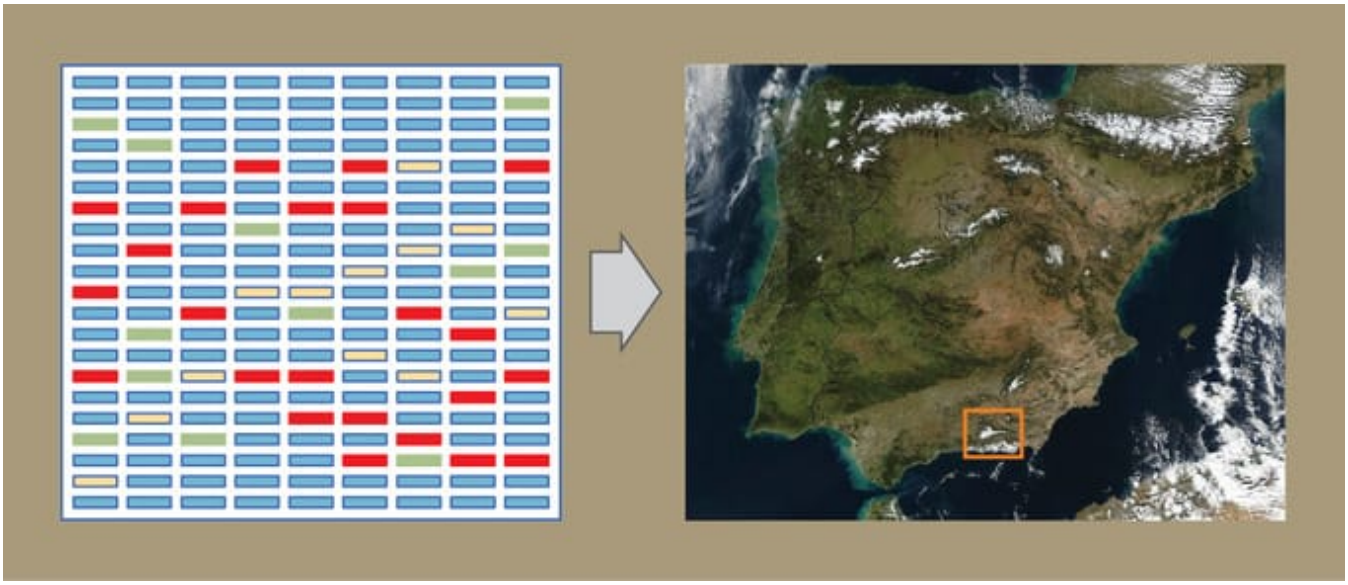


Figure 17.1A.1: Genomics: In genomics, the DNA of different organisms is compared, enabling scientists to create maps with which to navigate the DNA of different organisms.

Another rapidly-advancing field that utilizes DNA is biotechnology. This field involves the use of biological agents for technological advancement. Biotechnology was used for breeding livestock and crops long before the scientific basis of these techniques was understood. Since the discovery of the structure of DNA in 1953, the field of biotechnology has grown rapidly through both academic research and private companies. The primary applications of this technology are in medicine (production of vaccines and antibiotics) and agriculture (genetic modification of crops, such as to increase yields). Biotechnology also has many industrial applications, such as fermentation, the treatment of oil spills, and the production of biofuels.

Key Points

- Genomics includes the study of a complete set of genes, their nucleotide sequence and organization, and their interactions within a species and with other species.
- Through DNA sequencing, genomic information is used to create maps of the DNA of different organisms.
- Biotechnology, or the use of biological agents for technological progression, has applications in medicine, agriculture, and in industry, which include processes such as fermentation and the production of biofuels.

Key Terms

- **genomics**: the study of the complete genome of an organism
- **sequencing**: the procedure of determining the order of amino acids in the polypeptide chain of a protein (protein sequencing) or of nucleotides in a DNA section comprising a gene (gene sequencing)
- **biotechnology**: the use of living organisms (especially microorganisms) in industrial, agricultural, medical, and other technological applications

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17.1B: Basic Techniques to Manipulate Genetic Material (DNA and RNA)

Learning Objectives

- Distinguish among the basic techniques used to manipulate DNA and RNA

Basic Techniques to Manipulate Genetic Material (DNA and RNA)

To understand the basic techniques used to work with nucleic acids, remember that nucleic acids are macromolecules made of nucleotides (a sugar, a phosphate, and a nitrogenous base) linked by phosphodiester bonds. The phosphate groups on these molecules each have a net negative charge. An entire set of DNA molecules in the nucleus is called the genome. DNA has two complementary strands linked by hydrogen bonds between the paired bases. The two strands can be separated by exposure to high temperatures (DNA denaturation) and can be reannealed by cooling. The DNA can be replicated by the DNA polymerase enzyme. Unlike DNA, which is located in the nucleus of eukaryotic cells, RNA molecules leave the nucleus. The most common type of RNA that is analyzed is the messenger RNA (mRNA) because it represents the protein -coding genes that are actively expressed.

DNA and RNA Extraction

To study or manipulate nucleic acids, the DNA or RNA must first be isolated or extracted from the cells. This can be done through various techniques. Most nucleic acid extraction techniques involve steps to break open the cell and use enzymatic reactions to destroy all macromolecules that are not desired (such as degradation of unwanted molecules and separation from the DNA sample). Cells are broken using a lysis buffer (a solution that is mostly a detergent); lysis means “to split.” These enzymes break apart lipid molecules in the membranes of the cell and the nucleus. Macromolecules are inactivated using enzymes such as proteases that break down proteins, and ribonucleases (RNAses) that break down RNA. The DNA is then precipitated using alcohol. Human genomic DNA is usually visible as a gelatinous, white mass. Samples can be stored at –80°C for years.

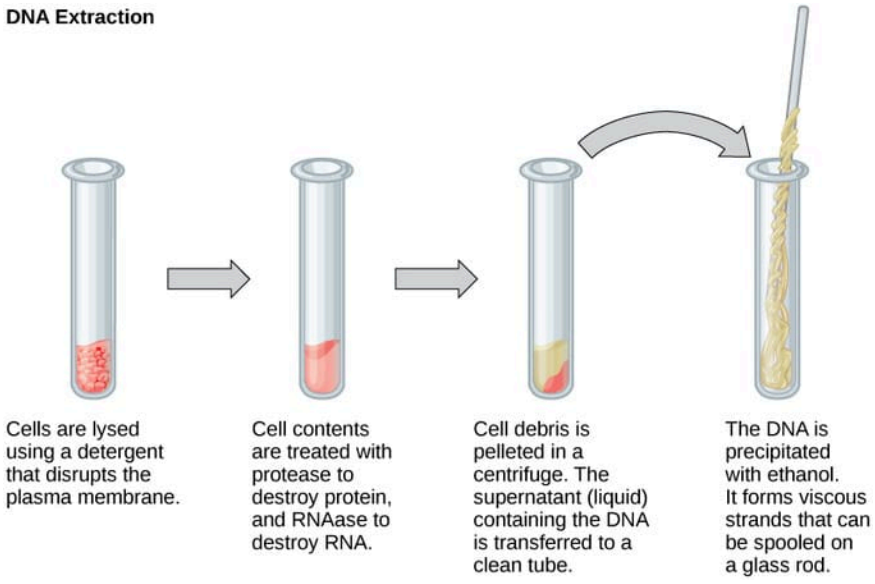


Figure 17.1B.1: DNA Extraction: This diagram shows the basic method used for extraction of DNA.

RNA analysis is performed to study gene expression patterns in cells. RNA is naturally very unstable because RNAses are commonly present in nature and very difficult to inactivate. Similar to DNA, RNA extraction involves the use of various buffers and enzymes to inactivate macromolecules and preserve the RNA.

Gel Electrophoresis

Because nucleic acids are negatively-charged ions at neutral or basic pH in an aqueous environment, they can be mobilized by an electric field. Gel electrophoresis is a technique used to separate molecules on the basis of size using this charge and may be separated as whole chromosomes or fragments. The nucleic acids are loaded into a slot near the negative electrode of a porous gel matrix and pulled toward the positive electrode at the opposite end of the gel. Smaller molecules move through the pores in the gel faster than larger molecules; this difference in the rate of migration separates the fragments on the basis of size. There are molecular-weight standard samples that can be run alongside the molecules to provide a size comparison. Nucleic acids in a gel matrix can be observed using various fluorescent or colored dyes. Distinct nucleic acid fragments appear as bands at specific distances from the top of the gel (the negative electrode end) on the basis of their size.

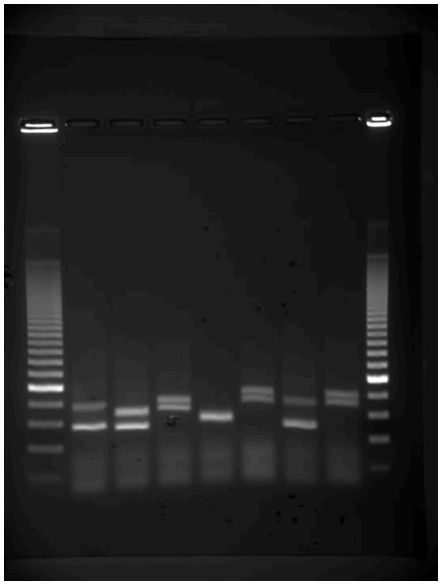


Figure 17.1B.1: Gel Electrophoresis: Shown are DNA fragments from seven samples run on a gel, stained with a fluorescent dye, and viewed under UV light.

Amplification of Nucleic Acid Fragments by Polymerase Chain Reaction

Polymerase chain reaction (PCR) is a technique used to amplify specific regions of DNA for further analysis. PCR is used for many purposes in laboratories, such as the cloning of gene fragments to analyze genetic diseases, identification of contaminant foreign DNA in a sample, and the amplification of DNA for sequencing. More practical applications include the determination of paternity and detection of genetic diseases.

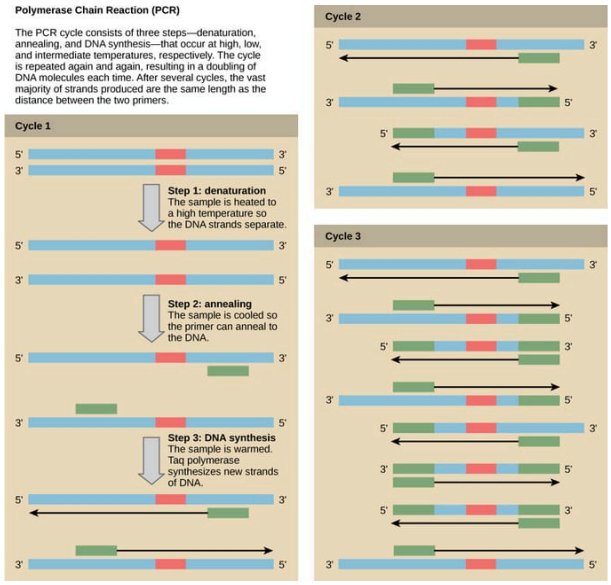


Figure 17.1B.1: PCR Amplification: Polymerase chain reaction, or PCR, is used to amplify a specific sequence of DNA. Primers—short pieces of DNA complementary to each end of the target sequence—are combined with genomic DNA, Taq polymerase, and deoxynucleotides. Taq polymerase is a DNA polymerase isolated from the thermostable bacterium Thermus aquaticus that is able to withstand the high temperatures used in PCR. Thermus aquaticus grows in the Lower Geyser Basin of Yellowstone National Park. Reverse transcriptase PCR (RT-PCR) is similar to PCR, but cDNA is made from an RNA template before PCR begins.

DNA fragments can also be amplified from an RNA template in a process called reverse transcriptase PCR (RT-PCR). The first step is to recreate the original DNA template strand (called cDNA) by applying DNA nucleotides to the mRNA. This process is called reverse transcription. This requires the presence of an enzyme called reverse transcriptase. After the cDNA is made, regular PCR can be used to amplify it.

Hybridization, Southern Blotting, and Northern Blotting

Nucleic acid samples, such as fragmented genomic DNA and RNA extracts, can be probed for the presence of certain sequences. Short DNA fragments called probes are designed and labeled with radioactive or fluorescent dyes to aid detection. Gel electrophoresis separates the nucleic acid fragments according to their size. The fragments in the gel are then transferred onto a nylon membrane in a procedure called blotting. The nucleic acid fragments that are bound to the surface of the membrane can then be probed with specific radioactively- or fluorescently-labeled probe sequences. When DNA is transferred to a nylon membrane, the technique is called Southern blotting; when RNA is transferred to a nylon membrane, it is called northern blotting. Southern blots are used to detect the presence of certain DNA sequences in a given genome, and northern blots are used to detect gene expression.

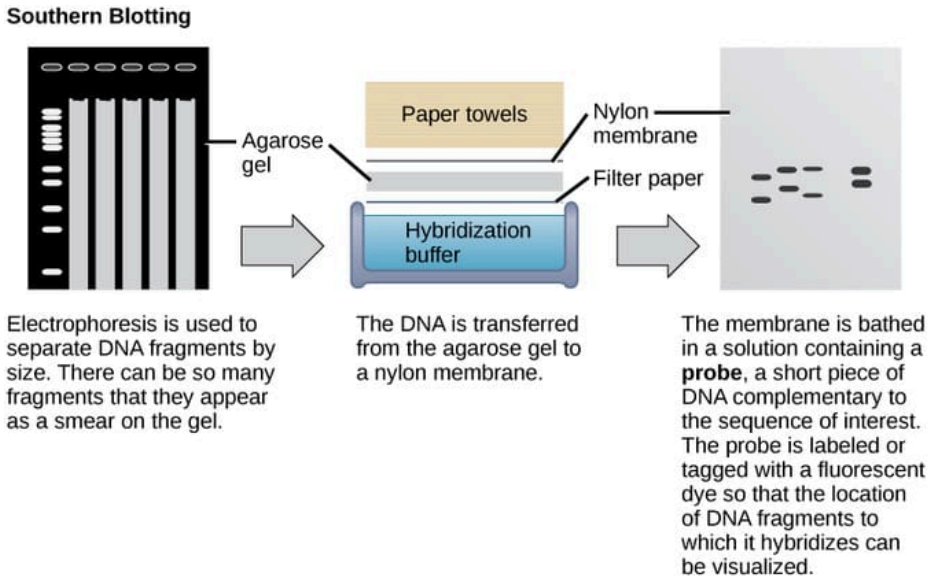


Figure 17.1B.1: Blotting Techniques: Southern blotting is used to find a particular sequence in a sample of DNA. DNA fragments are separated on a gel, transferred to a nylon membrane, and incubated with a DNA probe complementary to the sequence of interest. Northern blotting is similar to Southern blotting, but RNA is run on the gel instead of DNA. In western blotting, proteins are run on a gel and detected using antibodies.

Key Points

- The first step to study or work with nucleic acids includes the isolation or extraction of DNA or RNA from cells.
- Gel electrophoresis depends on the negatively-charged ions present on nucleic acids at neutral or basic pH to separate molecules on the basis of size.
- Specific regions of DNA can be amplified through the use of polymerase chain reaction for further analysis.
- Southern blotting involves the transfer of DNA to a nylon membrane, while northern blotting is the transfer of RNA to a nylon membrane; these techniques allow samples to be probed for the presence of certain sequences.

Key Terms

- **denaturation**: the change of folding structure of a protein (and thus of physical properties) caused by heating, changes in pH, or exposure to certain chemicals
- **electrophoresis**: a method for the separation and analysis of large molecules, such as proteins or nucleic acids, by migrating a colloidal solution of them through a gel under the influence of an electric field
- **polymerase chain reaction**: a technique in molecular biology for creating multiple copies of DNA from a sample

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17.1C: Molecular and Cellular Cloning

Learning Objectives

- Describe the process of molecular cloning

Molecular Cloning

In general, the word “cloning” means the creation of a perfect replica; however, in biology, the re-creation of a whole organism is referred to as “reproductive cloning.” Long before attempts were made to clone an entire organism, researchers learned how to reproduce desired regions or fragments of the genome, a process that is referred to as molecular cloning.

Cloning small fragments of the genome allows for the manipulation and study of specific genes (and their protein products) or noncoding regions in isolation. A plasmid (also called a vector) is a small circular DNA molecule that replicates independently of the chromosomal DNA. In cloning, the plasmid molecules can be used to provide a “folder” in which to insert a desired DNA fragment. Plasmids are usually introduced into a bacterial host for proliferation. In the bacterial context, the fragment of DNA from the human genome (or the genome of another organism that is being studied) is referred to as foreign DNA (or a transgene) to differentiate it from the DNA of the bacterium, which is called the host DNA.

Plasmids occur naturally in bacterial populations (such as *Escherichia coli*) and have genes that can contribute favorable traits to the organism such as antibiotic resistance (the ability to be unaffected by antibiotics). Plasmids have been repurposed and engineered as vectors for molecular cloning and the large-scale production of important reagents such as insulin and human growth hormone. An important feature of plasmid vectors is the ease with which a foreign DNA fragment can be introduced via the multiple cloning site (MCS). The MCS is a short DNA sequence containing multiple sites that can be cut with different commonly-available restriction endonucleases. Restriction endonucleases recognize specific DNA sequences and cut them in a predictable manner; they are naturally produced by bacteria as a defense mechanism against foreign DNA. Many restriction endonucleases make staggered cuts in the two strands of DNA, such that the cut ends have a 2- or 4-base single-stranded overhang. Because these overhangs are capable of annealing with complementary overhangs, these are called “sticky ends.” Addition of an enzyme called DNA ligase permanently joins the DNA fragments via phosphodiester bonds. In this way, any DNA fragment generated by restriction endonuclease cleavage can be spliced between the two ends of a plasmid DNA that has been cut with the same restriction endonuclease.

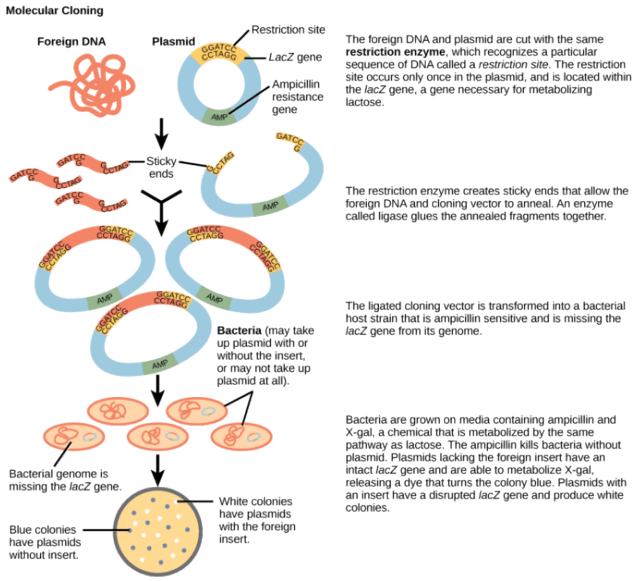


Figure $17.1C.1$: Molecular Cloning: This diagram shows the steps involved in molecular cloning, where regions or fragments of a genome are reproduced to allow the study or manipulation of genes and their protein products.

Recombinant DNA Molecules

Plasmids with foreign DNA inserted into them are called recombinant DNA molecules because they are created artificially and do not occur in nature. They are also called chimeric molecules because the origin of different parts of the molecules can be traced back to different species of biological organisms or even to chemical synthesis. Proteins that are expressed from recombinant DNA molecules are called recombinant proteins. Not all recombinant plasmids are capable of expressing genes. The recombinant DNA may need to be moved into a different vector (or host) that is better designed for gene expression. Plasmids may also be engineered to express proteins only when stimulated by certain environmental factors so that scientists can control the expression of the recombinant proteins.

Cellular Cloning

Unicellular organisms, such as bacteria and yeast, naturally produce clones of themselves when they replicate asexually by binary fission; this is known as cellular cloning. The nuclear DNA duplicates by the process of mitosis, which creates an exact replica of the genetic material.

Key Points

- Cloning small fragments of a genome allows specific genes, their protein products, and non-coding regions to be studied in isolation.
- A plasmid, also known as a vector, is a small circular DNA molecule that replicates independently of the chromosomal DNA; it can be used to provide a “folder” in which to insert a desired DNA fragment.
- Recombinant DNA molecules are plasmids with foreign DNA inserted into them; they are created artificially as they do not occur in nature.
- Bacteria and yeast naturally produce clones of themselves when they replicate asexually through cellular cloning.

Key Terms

- **recombinant DNA**: DNA that has been engineered by splicing together fragments of DNA from multiple species and introduced into the cells of a host
- **molecular cloning**: a biological method that creates many identical DNA molecules and directs their replication within a host organism
- **plasmid**: a circle of double-stranded DNA that is separate from the chromosomes, which is found in bacteria and protozoa

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17.1D: Reproductive Cloning

Learning Objectives

- Differentiate reproductive cloning from cellular and molecular cloning

Reproductive Cloning

Reproductive cloning is a method used to make a clone or an identical copy of an entire multicellular organism. Most multicellular organisms undergo reproduction by sexual means, which involves genetic hybridization of two individuals (parents), making it impossible to generate an identical copy or clone of either parent. Recent advances in biotechnology have made it possible to artificially induce asexual reproduction of mammals in the laboratory.

Parthenogenesis, or “virgin birth,” occurs when an embryo grows and develops without the fertilization of the egg occurring; this is a form of asexual reproduction. An example of parthenogenesis occurs in species in which the female lays an egg. If the egg is fertilized, it is a diploid egg and the individual develops into a female; if the egg is not fertilized, it remains a haploid egg and develops into a male. The unfertilized egg is called a parthenogenic, or virgin, egg. Some insects and reptiles lay parthenogenic eggs that can develop into adults.

Sexual reproduction requires two cells; when the haploid egg and sperm cells fuse, a diploid zygote results. The zygote nucleus contains the genetic information to produce a new individual. However, early embryonic development requires the cytoplasmic material contained in the egg cell. This idea forms the basis for reproductive cloning. If the haploid nucleus of an egg cell is replaced with a diploid nucleus from the cell of any individual of the same species (called a donor), it will become a zygote that is genetically identical to the donor. Somatic cell nuclear transfer is the technique of transferring a diploid nucleus into an enucleated egg. It can be used for either therapeutic cloning or reproductive cloning.

The first cloned animal was Dolly, a sheep who was born in 1996. The success rate of reproductive cloning at the time was very low. Dolly lived for seven years and died of respiratory complications. There is speculation that because the cell DNA belongs to an older individual, the age of the DNA may affect the life expectancy of a cloned individual. Since Dolly, several animals (e.g. horses, bulls, and goats) have been successfully cloned, although these individuals often exhibit facial, limb, and cardiac abnormalities. There have been attempts at producing cloned human embryos as sources of embryonic stem cells. Sometimes referred to as cloning for therapeutic purposes, the technique produces stem cells that attempt to remedy detrimental diseases or defects (unlike reproductive cloning, which aims to reproduce an organism). Still, therapeutic cloning efforts have met with resistance because of bioethical considerations.

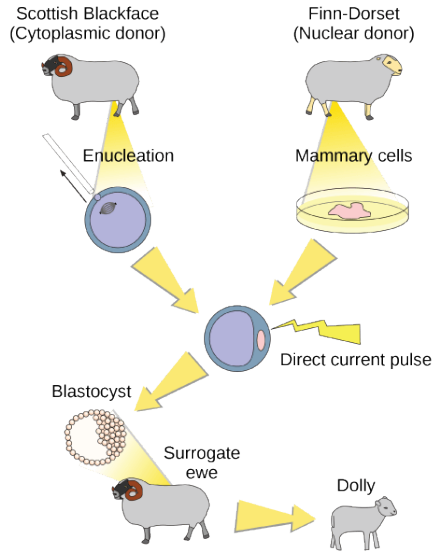


Figure 17.1D.1: Reproductive Cloning of Dolly, the Sheep: Dolly the sheep was the first mammal to be cloned. To create Dolly, the nucleus was removed from a donor egg cell. The nucleus from a second sheep was then introduced into the cell, which was allowed to divide to the blastocyst stage before being implanted in a surrogate mother.

Key Points

- A form of asexual reproduction, parthenogenesis, occurs when an embryo grows and develops without the fertilization of the egg.
- In reproductive cloning, if the haploid nucleus of an egg cell is replaced with a diploid nucleus from the cell of an individual of the same species, it will become a zygote that is genetically identical to the donor.
- Reproductive cloning has become successful, but still has limitations as cloned individuals often exhibit facial, limb, and cardiac abnormalities.
- Therapeutic cloning, the cloning of human embryos as a source of embryonic stem cells, has been attempted in order to produce cells that can be used to treat detrimental diseases or defects.

Key Terms

- **clone**: a living organism produced asexually from a single ancestor, to which it is genetically identical
- **stem cell**: a primal undifferentiated cell from which a variety of other cells can develop through the process of cellular differentiation
- **parthenogenesis**: a form of asexual reproduction where growth and development of embryos occur without fertilization

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17.1E: Genetic Engineering

Learning Objectives

- Discuss how genetic engineering leads to DNA modification.

Genetic Engineering

Genetic engineering is the alteration of an organism's genotype using recombinant DNA technology to modify an organism's DNA to achieve desirable traits. Recombinant DNA technology, or DNA cloning, is the process of transferring a DNA fragment of interest from one organism to a self-replicating genetic element, such as a bacteria plasmid, which is called a vector. The DNA of interest can then be propagated in another organism. The addition of foreign DNA in the form of recombinant DNA vectors generated by molecular cloning is the most common method of genetic engineering. The organism that receives the recombinant DNA is called a genetically-modified organism (GMO). If the foreign DNA that is introduced comes from a different species, the host organism is called transgenic. Bacteria, plants, and animals have been genetically modified since the early 1970s for academic, medical, agricultural, and industrial purposes. In the US, GMOs such as Roundup-ready soybeans and borer-resistant corn are part of many common processed foods.

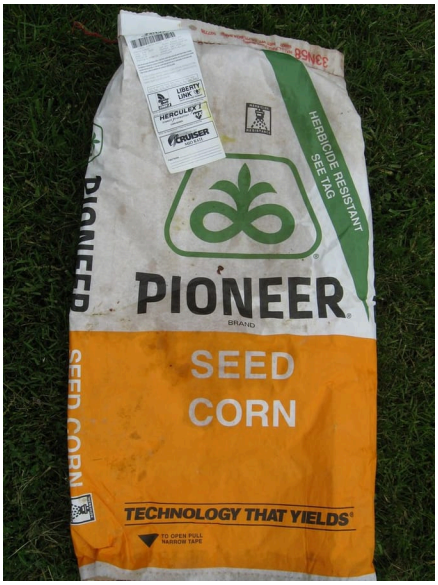


Figure $17.1E.1$: GMO Corn: Borer-resistant corn is an example of a genetically- modified organism made possible through genetic engineering methods that allow scientists to alter an organism's DNA to achieve specific traits, such as herbicide resistance.

Gene Targeting

Although classical methods of studying the function of genes began with a given phenotype and determined the genetic basis of that phenotype, modern techniques allow researchers to start at the DNA sequence level and ask: "What does this gene or DNA element do? " This technique, called reverse genetics, has resulted in reversing the classic genetic methodology. This method would be similar to damaging a body part to determine its function. An insect that loses a wing cannot fly, which means that the function of the wing is flight. The classical genetic method would compare insects that cannot fly with insects that can fly, and observe that the non-flying insects have lost wings. Similarly, mutating or deleting genes provides researchers with clues about gene function. The methods used to disable gene function are collectively called gene targeting. Gene targeting is the use of recombinant DNA vectors to alter the expression of a particular gene, either by introducing mutations in a gene, or by eliminating the expression of a certain gene by deleting a part or all of the gene sequence from the genome of an organism.

Key Points

- A genetically modified organism receives recombinant DNA generated through molecular cloning.
- Transgenic host organisms receive their foreign DNA from a different species.
- The use of recombinant DNA vectors to alter the expression of a particular gene is known as gene targeting, which is done through the addition of mutations in a gene or the exclusion of the expression of a certain gene.
- Recombinant DNA technology involves transferring a DNA fragment of interest from one organism to another by inserting it into a vector.

Key Terms

- **recombinant DNA**: DNA that has been engineered by splicing together fragments of DNA from multiple species and introduced into the cells of a host
- **genetic engineering**: the deliberate modification of the genetic structure of an organism
- **genetically modified organism**: an organism whose genetic material has been altered using genetic engineering techniques

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17.1F: Genetically Modified Organisms (GMOs)

Learning Objectives

- Describe how research on transgenic plants and animals aids humans.

Transgenic Animals

Although several recombinant proteins used in medicine are successfully produced in bacteria, some proteins require a eukaryotic animal host for proper processing. For this reason, the desired genes are cloned and expressed in animals, such as sheep, goats, chickens, and mice. Animals that have been modified to express recombinant DNA are called transgenic animals. Several human proteins are expressed in the milk of transgenic sheep and goats, while others are expressed in the eggs of chickens. Mice have been used extensively for expressing and studying the effects of recombinant genes and mutations.

Transgenic Plants

Manipulating the DNA of plants (or creating genetically modified organisms called GMOs) has helped to create desirable traits, such as disease resistance, herbicide and pesticide resistance, better nutritional value, and better shelf-life. Plants are the most important source of food for the human population. Farmers developed ways to select for plant varieties with desirable traits long before modern-day biotechnology practices were established. Plants that have received recombinant DNA from other species are called transgenic plants. Because foreign genes can spread to other species in the environment, extensive testing is required to ensure ecological stability. Staples like corn, potatoes, and tomatoes were the first crop plants to be genetically engineered.



Figure $17.1F.1$: Transgenic Plants: Corn, a major agricultural crop used to create products for a variety of industries, is often modified through plant biotechnology.

Transformation of Plants Using *Agrobacterium tumefaciens*

Gene transfer occurs naturally between species in microbial populations. Many viruses that cause human diseases, such as cancer, act by incorporating their DNA into the human genome. In plants, tumors caused by the bacterium *Agrobacterium tumefaciens* occur by transfer of DNA from the bacterium to the plant. Although the tumors do not kill the plants, they stunt the plants, which become more susceptible to harsh environmental conditions. Many plants, such as walnuts, grapes, nut trees, and beets, are affected by *A. tumefaciens*. The artificial introduction of DNA into plant cells is more challenging than in animal cells

because of the thick plant cell wall.

Researchers used the natural transfer of DNA from *Agrobacterium* to a plant host to introduce DNA fragments of their choice into plant hosts. In nature, the disease-causing *A. tumefaciens* have a set of plasmids, called the Ti plasmids (tumor-inducing plasmids), that contain genes for the production of tumors in plants. DNA from the Ti plasmid integrates into the infected plant cell's genome. Researchers manipulate the Ti plasmids to remove the tumor-causing genes and insert the desired DNA fragment for transfer into the plant genome. The Ti plasmids carry antibiotic resistance genes to aid selection and can be propagated in *E. coli* cells as well.

The Organic Insecticide *Bacillus thuringiensis*

Bacillus thuringiensis (Bt) is a bacterium that produces protein crystals during sporulation that are toxic to many insect species that affect plants. Bt toxin has to be ingested by insects for the toxin to be activated. Insects that have eaten Bt toxin stop feeding on the plants within a few hours. After the toxin is activated in the intestines of the insects, death occurs within a couple of days. Modern biotechnology has allowed plants to encode their own crystal Bt toxin that acts against insects. The crystal toxin genes have been cloned from Bt and introduced into plants. Bt toxin has been found to be safe for the environment, non-toxic to humans and other mammals, and is approved for use by organic farmers as a natural insecticide.

Flavr Savr Tomato

The first GM crop to be introduced into the market was the Flavr Savr Tomato, produced in 1994. Antisense RNA technology was used to slow down the process of softening and rotting caused by fungal infections, which led to increased shelf life of the GM tomatoes. Additional genetic modification improved the flavor of this tomato. The Flavr Savr tomato did not successfully stay in the market because of problems maintaining and shipping the crop.

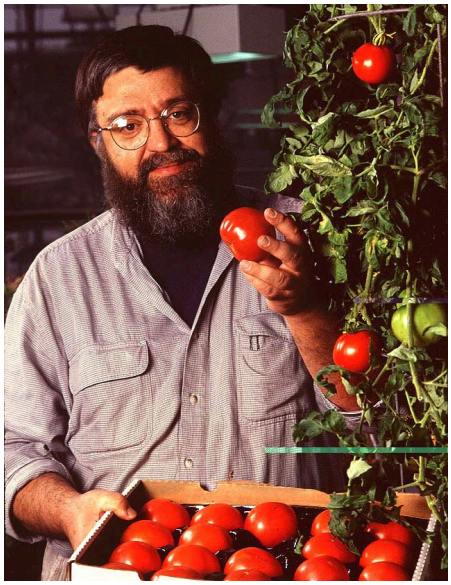


Figure $17.1F.1$: The Flavr Savr Tomato: Plant physiologist Athanasios Theologis with tomatoes that contain the bioengineered ACC synthase gene (the Flavr Savr Tomato).

Key Points

- Transgenic animals are those that have been modified to express recombinant DNA from another species.
- Manipulation of transgenic plants, those that have received recombinant DNA from other species, has led to the creation of species that display disease resistance, herbicide and pesticide resistance, better nutritional value, and better shelf-life.
- The thickness of a plant's cell wall makes the artificial introduction of DNA into plant cells much more challenging than in animal cells.

Key Terms

- **transgenic**: of or pertaining to an organism whose genome has been changed by the addition of a gene from another species; genetically modified
- **genetically modified organism**: an organism whose genetic material has been altered using genetic engineering techniques

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17.1G: Biotechnology in Medicine

Learning Objectives

- Give examples of how biotechnology is used in medicine.

Biotechnology in Medicine

It is easy to see how biotechnology can be used for medicinal purposes. Knowledge of the genetic makeup of our species, the genetic basis of heritable diseases, and the invention of technology to manipulate and fix mutant genes provides methods to treat the disease.

Pharmacogenomics is the study of how the genetic inheritance of an individual affects his/her body's response to drugs. It is a coined word derived from the words "pharmacology" and " genomics ". It is, therefore, the study of the relationship between pharmaceuticals and genetics. The vision of pharmacogenomics is to be able to design and produce drugs that are adapted to each person's genetic makeup. Pharmacogenomics results in the following benefits:

1. Development of tailor-made medicines. Using pharmacogenomics, pharmaceutical companies can create drugs based on the proteins, enzymes, and RNA molecules that are associated with specific genes and diseases. These tailor-made drugs promise not only to maximize therapeutic effects, but also to decrease damage to nearby healthy cells.

2. More accurate methods of determining appropriate drug dosages. Knowing a patient's genetics will enable doctors to determine how well the patient's body can process and metabolize a medicine. This will maximize the value of the medicine and decrease the likelihood of overdose.

3. Improvements in the drug discovery and approval process. The discovery of potential therapies will be made easier using genome targets. Genes have been associated with numerous diseases and disorders. With modern biotechnology, these genes can be used as targets for the development of effective new therapies, which could significantly shorten the drug discovery process.

4. Better vaccines. Safer vaccines can be designed and produced by organisms transformed by means of genetic engineering. These vaccines will elicit the immune response without the attendant risks of infection. They will be inexpensive, stable, easy to store, and capable of being engineered to carry several strains of pathogen at once.

Modern biotechnology can be used to manufacture existing drugs more easily and cheaply. The first genetically-engineered products were medicines designed to combat human diseases. In 1978, Genentech joined a gene for insulin with a plasmid vector and put the resulting gene into a bacterium called *Escherichia coli*. Insulin, widely used for the treatment of diabetes, was previously extracted from sheep and pigs. It was very expensive and often elicited unwanted allergic responses. The resulting genetically-engineered bacterium enabled the production of vast quantities of human insulin at low cost. Since then, modern biotechnology has made it possible to produce more easily and cheaply the human growth hormone, clotting factors for hemophiliacs, fertility drugs, erythropoietin, and other drugs. Genomic knowledge of the genes involved in diseases, disease pathways, and drug-response sites are expected to lead to the discovery of thousands more new targets.

Genetic Diagnosis and Gene Therapy

The process of testing for suspected genetic defects before administering treatment is called genetic diagnosis by genetic testing. Depending on the inheritance patterns of a disease-causing gene, family members are advised to undergo genetic testing. Treatment plans are based on the findings of genetic tests that determine the type of cancer. If the cancer is caused by inherited gene mutations, other female relatives are also advised to undergo genetic testing and periodic screening for breast cancer. Genetic testing is also offered for fetuses to determine the presence or absence of disease-causing genes in families with specific, debilitating diseases.

Genetic testing involves the direct examination of the DNA molecule itself. A scientist scans a patient's DNA sample for mutated

sequences. There are two major types of gene tests. In the first type, a researcher may design short pieces of DNA whose sequences are complementary to the mutated sequences. These probes will seek their complement among the base pairs of an individual's genome. If the mutated sequence is present in the patient's genome, the probe will bind to it and flag the mutation. In the second type, a researcher may conduct the gene test by comparing the sequence of DNA bases in a patient's gene to a normal version of the gene.

Gene therapy is a genetic engineering technique used to cure disease. In its simplest form, it involves the introduction of a good gene at a random location in the genome to aid the cure of a disease that is caused by a mutated gene. The good gene is usually introduced into diseased cells as part of a vector transmitted by a virus that can infect the host cell and deliver the foreign DNA. More advanced forms of gene therapy try to correct the mutation at the original site in the genome, such as is the case with treatment of severe combined immunodeficiency (SCID).

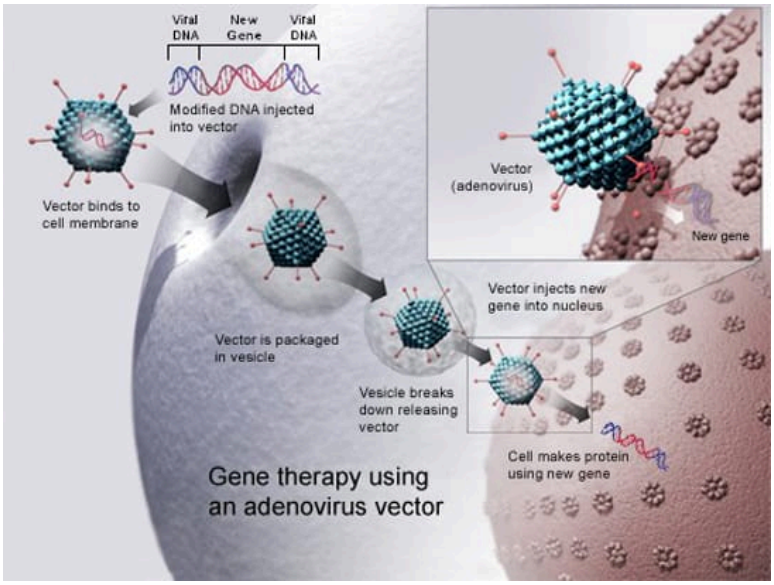


Figure 17.1G.1: Gene Therapy: Gene therapy using an adenovirus vector can be used to cure certain genetic diseases in which a person has a defective gene.

Key Points

- The study of pharmacogenomics can result in the development of tailor-made vaccines for people, more accurate means of determining drug dosages, improvements in drug discovery and approval, and the development of safer vaccines.
- Modern biotechnology can be used to manufacture drugs more easily and cheaply, as they can be produced in larger quantities from existing genetic sources.
- Genetic diagnosis involves the process of testing for suspected genetic defects before administering treatment through genetic testing.
- In gene therapy, a good gene is introduced at a random location in the genome to aid the cure of a disease that is caused by a mutated gene.

Key Terms

- **gene therapy**: any of several therapies involving the insertion of genes into a patient's cells in order to replace defective ones
- **pharmacogenomics**: the study of genes that code for enzymes that metabolize drugs, and the design of tailor-made drugs adapted to an individual's genetic make-up
- **immunodeficiency**: a depletion in the body's natural immune system, or in some component of it

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17.1H: Production of Vaccines, Antibiotics, and Hormones

Learning Objectives

- Discuss the methods by which biotechnology is used to produce vaccines, antibiotics, and hormones.

Production of Vaccines, Antibiotics, and Hormones

Vaccines

Traditional vaccination strategies use weakened or inactive forms of microorganisms to mount the initial immune response. Modern techniques use the genes of microorganisms cloned into vectors to mass produce the desired antigen. The antigen is then introduced into the body to stimulate the primary immune response and trigger immune memory. Genes cloned from the influenza virus have been used to combat the constantly-changing strains of this virus.

Antibiotics

Antibiotics are biotechnological products that inhibit bacterial growth or kill bacteria. They are naturally produced by microorganisms, such as fungi, to attain an advantage over bacterial populations. Antibiotics are produced on a large scale by cultivating and manipulating fungal cells. Many antibacterial compounds are classified on the basis of their chemical or biosynthetic origin into natural, semisynthetic, and synthetic. Another classification system is based on biological activity. In this classification, antibiotics are divided into two broad groups according to their biological effect on microorganisms: bactericidal agents kill bacteria, and bacteriostatic agents slow down or stall bacterial growth.

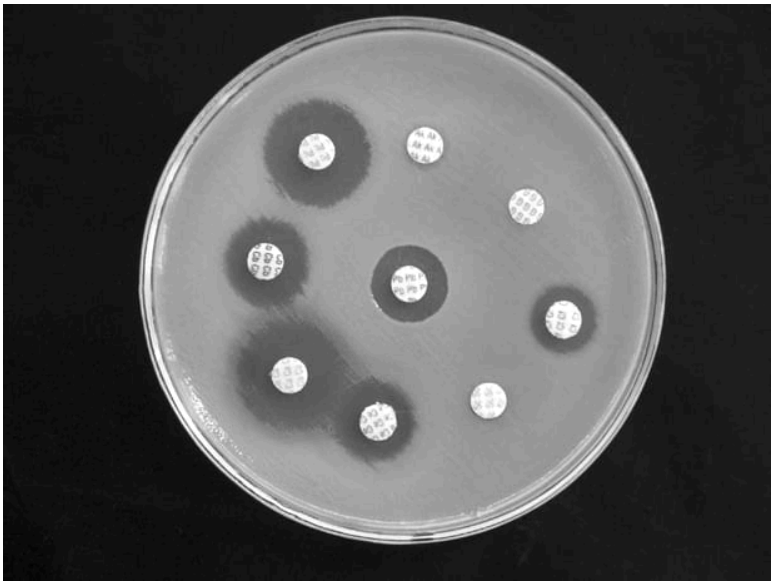


Figure $17.1H.1$: Antibiotic Treatment: Assays such as the one shown help scientists understand the effects of antibiotics on bacterial species. Clear rings around the round inserts, which contain antibiotic, mean that bacteria on the plate are inhibited or killed by the compound.

Hormones

Recombinant DNA technology was used to produce large-scale quantities of human insulin (a hormone) in *E. coli* as early as 1978. Previously, it was only possible to treat diabetes with pig insulin, which caused allergic reactions in humans because of differences in the gene product. In recent times, human growth hormone (HGH) has been used to treat growth disorders in

children. The HGH gene was cloned from a cDNA library and inserted into *E. coli* cells by cloning it into a bacterial vector. The bacteria was then grown and the hormone isolated, enabling large scale commercial production.

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Key Points

- Vaccines use weakened or inactive forms of microorganisms to mount the initial immune response through the use of antigens, which are produced through use the genes of microbes that are cloned into vectors.
- Antibiotics, agents that inhibit bacterial growth or kill bacteria, are produced by cultivating and manipulating fungal cells.
- Hormones, such as the human growth hormone (HGH), can be formulated through recombinant DNA technology; for example, HGH can be cloned from a cDNA library and inserted into *E. coli* cells by cloning it into a bacterial vector.

Key Terms

- **bactericidal**: that which kills bacteria
- **bacteriostatic**: that which slows down or stalls bacterial growth
- **antigen**: a substance that binds to a specific antibody; may cause an immune response

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17.2: MAPPING GENOMES

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- Topic hierarchy

17.2A: Genetic Maps

17.2B: Physical Maps and Integration with Genetic Maps

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17.2A: Genetic Maps

Learning Objectives

- Describe the different types of genetic markers that are used in generating genetic maps of DNA

Genetic Maps

The study of genetic maps begins with linkage analysis, a procedure that analyzes the recombination frequency between genes to determine if they are linked or show independent assortment. The term linkage was used before the discovery of DNA. Early geneticists relied on the observation of phenotypic changes to understand the genotype of an organism. Shortly after Gregor Mendel (the father of modern genetics) proposed that traits were determined by what are now known as genes, other researchers observed that different traits were often inherited together and, thereby, deduced that the genes were physically linked by being located on the same chromosome. The mapping of genes relative to each other based on linkage analysis led to the development of the first genetic maps.

Observations that certain traits were always linked and certain others were not linked came from studying the offspring of crosses between parents with different traits. For example, in experiments performed on the garden pea, it was discovered that the color of the flower and shape of the plant's pollen were linked traits; therefore, the genes encoding these traits were in close proximity on the same chromosome. The exchange of DNA between homologous pairs of chromosomes is called genetic recombination, which occurs by the crossing over of DNA between homologous strands of DNA, such as nonsister chromatids. Linkage analysis involves studying the recombination frequency between any two genes. The greater the distance between two genes, the higher the chance that a recombination event will occur between them, and the higher the recombination frequency between them. If the recombination frequency between two genes is less than 50 percent, they are said to be linked.

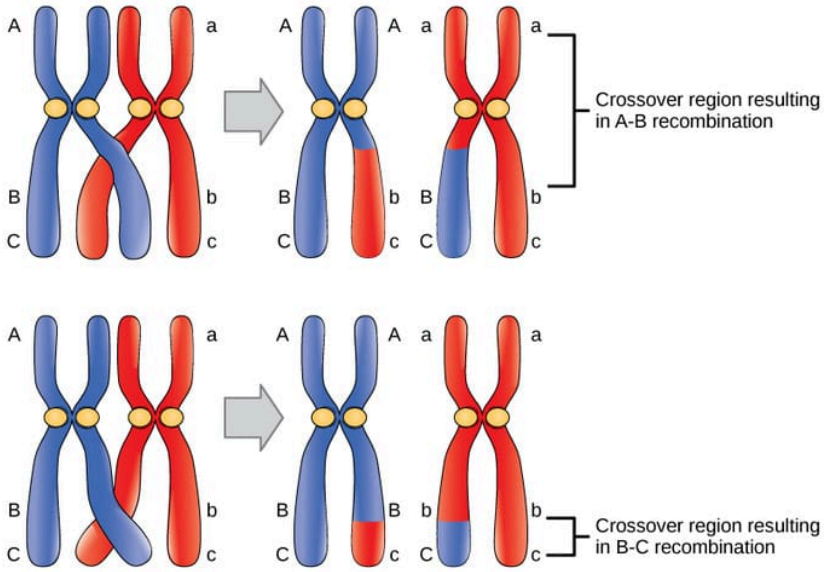


Figure 17.2A.1: Crossovers and Recombination: Crossover may occur at different locations on the chromosome. Recombination between genes A and B is more frequent than recombination between genes B and C because genes A and B are farther apart; a crossover is, therefore, more likely to occur between them.

The generation of genetic maps requires markers, just as a road map requires landmarks (such as rivers and mountains). Early genetic maps were based on the use of known genes as markers. More sophisticated markers, including those based on non-coding DNA, are now used to compare the genomes of individuals in a population. Although individuals of a given species are genetically similar, they are not identical; every individual has a unique set of traits. These minor differences in the genome between individuals in a population are useful for the purposes of genetic mapping. In general, a good genetic marker is a region on the chromosome that shows variability or polymorphism (multiple forms) in the population.

Some genetic markers used in generating genetic maps are restriction fragment length polymorphisms (RFLP), variable number of tandem repeats (VNTRs), microsatellite polymorphisms, and the single nucleotide polymorphisms (SNPs). RFLPs (sometimes pronounced “rif-lips”) are detected when the DNA of an individual is cut with a restriction endonuclease that recognizes specific sequences in the DNA to generate a series of DNA fragments, which are then analyzed by gel electrophoresis. The DNA of every individual will give rise to a unique pattern of bands when cut with a particular set of restriction endonucleases; this is sometimes referred to as an individual’s DNA “fingerprint.” Certain regions of the chromosome that are subject to polymorphism will lead to the generation of the unique banding pattern. VNTRs are repeated sets of nucleotides present in the non-coding regions of DNA. Non-coding DNA has no known biological function; however, research shows that much of this DNA is actually transcribed. While its function is uncertain, it is certainly active; it may be involved in the regulation of coding genes. The number of repeats may vary in individual organisms of a population. Microsatellite polymorphisms are similar to VNTRs, but the repeat unit is very small; thus, it is often referred to as short tandem repeats(STRs). SNPs are variations in a single nucleotide.

Because genetic maps rely completely on the natural process of recombination, mapping is affected by natural increases or decreases in the level of recombination in any given area of the genome. Some parts of the genome are recombination hotspots, whereas others do not show a propensity for recombination. For this reason, it is important to look at mapping information developed by multiple methods.

Key Points

- Genetic mapping, often called linkage mapping, provides information about the location of a specific gene along a chromosome.
- Gene linkage describes the phenomenon that certain genes are physically linked by being located on the same chromosome and have a tendency to be inherited together.
- Genetic recombination involves the production of a novel set of genetic information by breaking and rejoining DNA fragments that have a great distance between them along the chromosome.
- The construction of genetic maps is reliant on the natural process of recombination which results in the ability to identify genetic markers with variability within a population.
- Genetic markers that can be used in generating genetic maps include restriction length polymorphisms (RFLP); variable number of tandem repeats (VNTRs); microsatellite polymorphisms; and single nucleotide polymorphisms (SNPs).

Key Terms

- **polymorphism**: the regular existence of two or more different genotypes within a given species or population
- **SNP**: single nucleotide polymorphism is single base pair of DNA which is polymorphic with respect to a population
- **microsatellite**: any of a group of polymorphic loci in DNA that consist of repeat units of just a few base pairs
- **RFLP**: restriction fragment length polymorphism is a section of DNA whose length varies among individuals and which is delimited by a base which does not occur within it

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17.2B: Physical Maps and Integration with Genetic Maps

Learning Objectives

- Describe the methods used to physically map genes: cytogenetic mapping, radiation hybrid mapping, and sequence mapping

Physical Maps

A physical map provides detail of the actual physical distance between genetic markers, as well as the number of nucleotides. There are three methods used to create a physical map: cytogenetic mapping, radiation hybrid mapping, and sequence mapping. Cytogenetic mapping uses information obtained by microscopic analysis of stained sections of the chromosome. It is possible to determine the approximate distance between genetic markers using cytogenetic mapping, but not the exact distance (number of base pairs). Radiation hybrid mapping uses radiation, such as x-rays, to break the DNA into fragments. The amount of radiation can be adjusted to create smaller or larger fragments. This technique overcomes the limitation of genetic mapping and is not affected by increased or decreased recombination frequency. Sequence mapping resulted from DNA sequencing technology that allowed for the creation of detailed physical maps with distances measured in terms of the number of base pairs. The creation of genomic libraries and complementary DNA (cDNA) libraries (collections of cloned sequences or all DNA from a genome) has sped up the process of physical mapping. A genetic site used to generate a physical map with sequencing technology (a sequence-tagged site, or STS) is a unique sequence in the genome with a known exact chromosomal location. An expressed sequence tag (EST) and a single sequence length polymorphism (SSLP) are common STSs. An EST is a short STS that is identified with cDNA libraries, while SSLPs are obtained from known genetic markers and provide a link between genetic maps and physical maps.

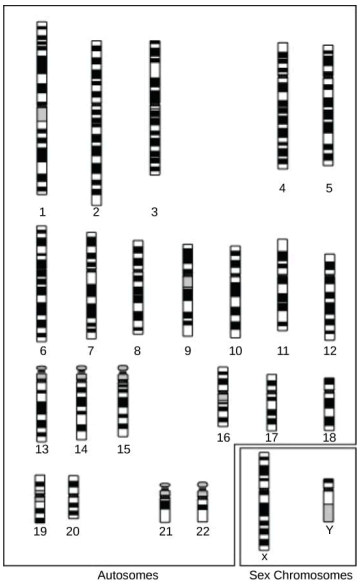


Figure $17.2B.1$: Cytogenetic Map: A cytogenetic map shows the appearance of a chromosome after it is stained and examined under a microscope.

Integration of Genetic and Physical Maps

Genetic maps provide the outline and physical maps provide the details. It is easy to understand why both types of genome mapping techniques are important to show the big picture. Information obtained from each technique is used in combination to study the genome. Genomic mapping is being used with different model research organisms. Genome mapping is an ongoing process; as better techniques are developed, more advances are expected. Genome mapping is similar to completing a complicated puzzle using every piece of available data. Mapping information generated in laboratories worldwide is entered into central databases, such as GenBank at the National Center for Biotechnology Information (NCBI). Efforts are being made to make

the information more easily accessible to researchers and the general public. Just as we use global positioning systems instead of paper maps to navigate through roadways, NCBI has created a genome viewer tool to simplify the data-mining process.

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Key Points

- Physical maps provide specified detail about the number of bases and physical distance that exists between genetic markers.
- Cytogenetic mapping is a method used to construct physical maps that uses stained sections of chromosomes to approximate the distance between genetic markers.
- Radiation hybrid mapping is a method used to construct physical maps that uses radiation or x-rays to break DNA into fragments to determine the distance between genetic markers and their order on the chromosome.
- Sequence mapping is a method used to construct physical maps that uses already-known locations of genetic markers to determine distances in number of base pairs.

Key Terms

- **cytogenetic**: of or pertaining to the origin and development of cells
- **physical map**: a map showing how much DNA separates two genes and is measured in base pairs
- **expressed sequence tag**: a short sub-sequence of a cDNA sequence that may be used to identify gene transcripts

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17.3: WHOLE-GENOME SEQUENCING

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- Topic hierarchy

17.3A: Strategies Used in Sequencing Projects
17.3B: Use of Whole-Genome Sequences of Model Organisms
17.3C: Uses of Genome Sequences

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17.3A: Strategies Used in Sequencing Projects

Learning Objectives

- Compare the different strategies used for whole-genome sequencing: Sanger method, shotgun sequencing, pairwise-end sequencing, and next-generation sequencing

Strategies Used in Sequencing Projects

The basic sequencing technique used in all modern day sequencing projects is the chain termination method (also known as the dideoxy method), which was developed by Fred Sanger in the 1970s. The chain termination method involves DNA replication of a single-stranded template with the use of a primer and a regular deoxynucleotide (dNTP), which is a monomer, or a single unit, of DNA. The primer and dNTP are mixed with a small proportion of fluorescently-labeled dideoxynucleotides (ddNTPs). The ddNTPs are monomers that are missing a hydroxyl group (–OH) at the site at which another nucleotide usually attaches to form a chain. Each ddNTP is labeled with a different color of fluorophore. Every time a ddNTP is incorporated in the growing complementary strand, it terminates the process of DNA replication, which results in multiple short strands of replicated DNA that are each terminated at a different point during replication. When the reaction mixture is processed by gel electrophoresis after being separated into single strands, the multiple, newly-replicated DNA strands form a ladder due to their differing sizes. Because the ddNTPs are fluorescently labeled, each band on the gel reflects the size of the DNA strand and the ddNTP that terminated the reaction. The different colors of the fluorophore-labeled ddNTPs help identify the ddNTP incorporated at that position. Reading the gel on the basis of the color of each band on the ladder produces the sequence of the template strand.

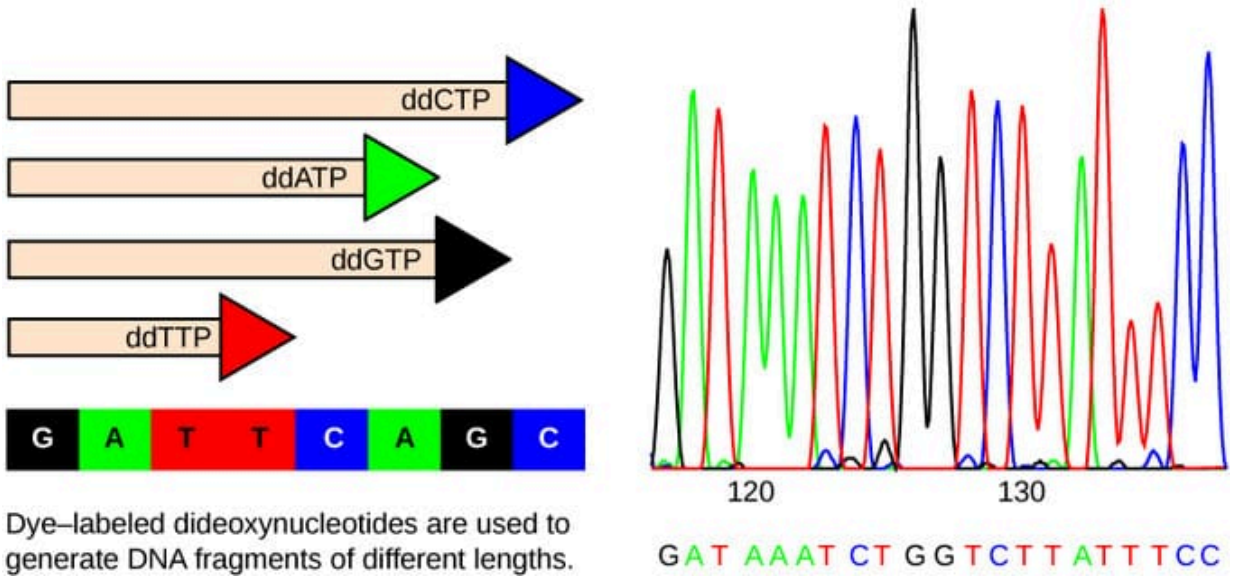


Figure 17.3A.1: Sanger's Method: Frederick Sanger's dideoxy chain termination method uses dideoxynucleotides, in which the DNA fragment can be terminated at different points. The DNA is separated on the basis of size, and these bands, based on the size of the fragments, can be read.

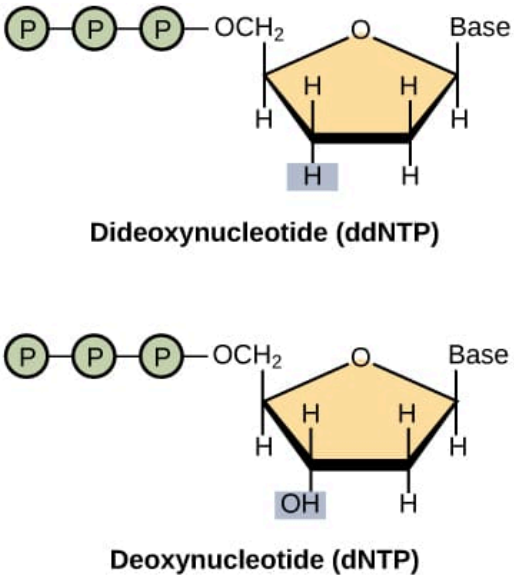


Figure 17.3A.1: Structure of a Dideoxynucleotide: A dideoxynucleotide is similar in structure to a deoxynucleotide, but is missing the 3′ hydroxyl group (indicated by the box). When a dideoxynucleotide is incorporated into a DNA strand, DNA synthesis stops.

Early Strategies: Shotgun Sequencing and Pair-Wise End Sequencing

In the shotgun sequencing method, several copies of a DNA fragment are cut randomly into many smaller pieces (somewhat like what happens to a round shot cartridge when fired from a shotgun). All of the segments are then sequenced using the chain-sequencing method. Then, with the help of a computer, the fragments are analyzed to see where their sequences overlap. By matching overlapping sequences at the end of each fragment, the entire DNA sequence can be reformed. A larger sequence that is assembled from overlapping shorter sequences is called a contig. As an analogy, consider that someone has four copies of a landscape photograph that you have never seen before and know nothing about how it should appear. The person then rips up each photograph with their hands, so that different size pieces are present from each copy. The person then mixes all of the pieces together and asks you to reconstruct the photograph. In one of the smaller pieces you see a mountain. In a larger piece, you see that the same mountain is behind a lake. A third fragment shows only the lake, but it reveals that there is a cabin on the shore of the lake. Therefore, from looking at the overlapping information in these three fragments, you know that the picture contains a mountain behind a lake that has a cabin on its shore. This is the principle behind reconstructing entire DNA sequences using shotgun sequencing.

Originally, shotgun sequencing only analyzed one end of each fragment for overlaps. This was sufficient for sequencing small genomes. However, the desire to sequence larger genomes, such as that of a human, led to the development of double-barrel shotgun sequencing, more formally known as pairwise-end sequencing. In pairwise-end sequencing, both ends of each fragment are analyzed for overlap. Pairwise-end sequencing is, therefore, more cumbersome than shotgun sequencing, but it is easier to reconstruct the sequence because there is more available information.

Next-generation Sequencing

Since 2005, automated sequencing techniques used by laboratories are under the umbrella of next-generation sequencing, which is a group of automated techniques used for rapid DNA sequencing. These automated, low-cost sequencers can generate sequences of hundreds of thousands or millions of short fragments (25 to 500 base pairs) in the span of one day. Sophisticated software is used to manage the cumbersome process of putting all the fragments in order.

Key Points

- The Sanger method is a basic sequencing technique that uses fluorescently-labeled dideoxynucleotides (ddNTPs) during DNA replication which results in multiple short strands of replicated DNA that terminate at different points, based on where the ddNTP was incorporated.
- Shotgun sequencing is a method that randomly cuts DNA fragments into smaller pieces and then, with the help of a computer,

takes the DNA fragments, analyzes them for overlapping sequences, and reassembles the entire DNA sequence.
- Pairwise-end sequencing is a type of shotgun sequencing which is used for larger genomes and analyzes both ends of the DNA fragments for overlap.
- Next-generation sequencing is a type of sequencing which is automated and relies on sophisticated software for rapid DNA sequencing.

Key Terms

- **fluorophore**: a molecule or functional group which is capable of fluorescence
- **contig**: a set of overlapping DNA segments, derived from a single source of genetic material, from which the complete sequence may be deduced
- **dideoxynucleotide**: any nucleotide formed from a deoxynucleotide by loss of an a second hydroxyl group from the deoxyribose group

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17.3B: Use of Whole-Genome Sequences of Model Organisms

Learning Objectives

- Describe the model organisms used in whole-genome sequencing

Use of Whole-Genome Sequences of Model Organisms

The first genome to be completely sequenced was of a bacterial virus, the bacteriophage fx174 (5368 base pairs). This was accomplished by Fred Sanger using shotgun sequencing. Several other organelle and viral genomes were later sequenced. The first organism whose genome was sequenced was the bacterium *Haemophilus influenzae*, which was accomplished by Craig Venter in the 1980s. Approximately 74 different laboratories collaborated on the sequencing of the genome of the yeast *Saccharomyces cerevisiae*, which began in 1989 and was completed in 1996. It took this long because it was 60 times bigger than any other genome that had been sequenced at that point. By 1997, the genome sequences of two important model organisms were available: the bacterium *Escherichia coli* K12 and the yeast *Saccharomyces cerevisiae*. Genomes of other model organisms, such as the mouse *Mus musculus*, the fruit fly *Drosophila melanogaster*, the nematode *Caenorhabditis elegans*, and the human *Homo sapiens* are now known. Much basic research is performed using model organisms because the information can be applied to the biological processes of genetically-similar organisms. Having entire genomes sequenced aids these research efforts.

The process of attaching biological information to gene sequences is called genome annotation. Annotation aids researchers doing basic experiments in molecular biology, such as designing PCR primers and RNA targets.

Sequencing genomes allows scientists to identify homologous proteins and establish evolutionary relationships. Furthermore, if a newly-discovered protein is homologous to a known protein, through homology, scientists can make an educated guess as to how the new protein functions.

Eukaryotes are organisms containing cells that enclose complex organelles within a well-defined cell membrane. The defining characteristic that sets eukaryotes and prokaryotes apart is the eukaryotes' nucleus, or nuclear envelope, in which an organism's genetic information is contained. The first eukaryotic genome to be sequenced was that of *S. cerevisiae*, which is the yeast used in baking and brewing. It is the most-studied eukaryotic model organism in molecular and cell biology, similar to *E. coli*'s role in the study of prokaryotic organisms. Research on many proteins that are important to humans is done by examining their homologs in yeasts. For example, signaling proteins and protein-processing enzymes were discovered through the help of yeast genome.

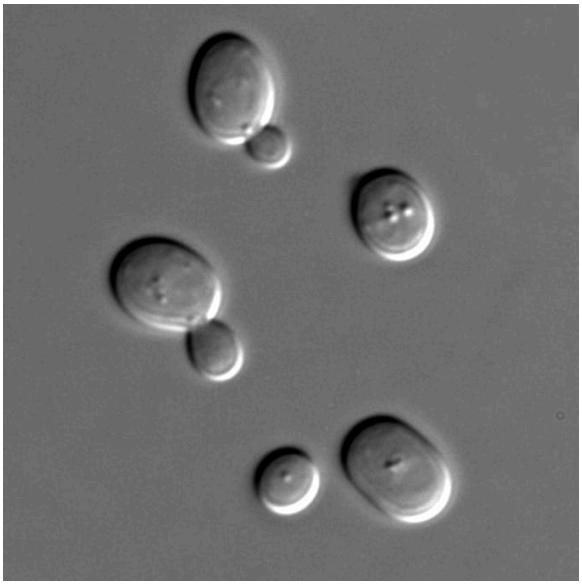


Figure $17.3B.1$: S. cerevisiae: A Model Organism for Eukaryotes: Saccharomyces cerevisiae, a yeast, is used as a model organism for studying signaling proteins and protein-processing enzymes which have homologs in humans.

Key Points

- The first genome to be completely sequenced was the bacterial virus, bacteriophage fx174, which is 5368 base pairs.
- Scientists utilize genome sequencing from model organisms to study homologous proteins and establish evolutionary relationships.
- Genome annotation is the process of attaching biological information to gene sequences identified using whole-genome sequencing.
- Model organisms include the fruit fly (*Drosophila melanogaster*), brewers yeast (*Saccharomyces cerevisiae*), the nematode, *Caenorhabditis elegans,* and the mouse (*Mus musculus*).

Key Terms

- **genome annotation**: the process of attaching biological information to gene sequences.
- **model organism**: any organism (e.g. the fruit fly) that has been extensively studied as an example of many others and from which general principles may be established

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17.3C: Uses of Genome Sequences

Learning Objectives

- Describe the various uses of genome sequences

Uses of Genome Sequences

DNA microarrays are methods used to detect gene expression by analyzing an array of DNA fragments that are fixed to a glass slide or a silicon chip to identify active genes and identify sequences. Almost one million genotypic abnormalities can be discovered using microarrays, whereas whole- genome sequencing can provide information about all six billion base pairs in the human genome. Although the study of medical applications of genome sequencing is interesting, this discipline tends to dwell on abnormal gene function. Knowledge of the entire genome will allow future onset diseases and other genetic disorders to be discovered early, which will allow for more informed decisions to be made about lifestyle, medication, and having children. Genomics is still in its infancy, although someday it may become routine to use whole-genome sequencing to screen every newborn to detect genetic abnormalities.

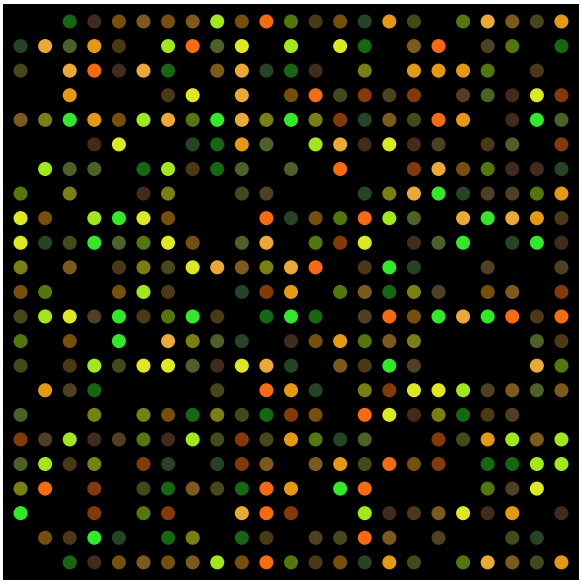


Figure $17.3C.1$: DNA Microarray: DNA microarrays can be used to analyze gene expression within the genome.

In addition to disease and medicine, genomics can contribute to the development of novel enzymes that convert biomass to biofuel, which results in higher crop and fuel production, and lower cost to the consumer. This knowledge should allow better methods of control over the microbes that are used in the production of biofuels. Genomics could also improve the methods used to monitor the impact of pollutants on ecosystems and help clean up environmental contaminants. In addition, genomics has allowed for the development of agrochemicals and pharmaceuticals that could benefit medical science and agriculture.

It sounds great to have all the knowledge we can get from whole-genome sequencing; however, humans have a responsibility to use this knowledge wisely. Otherwise, it could be easy to misuse the power of such knowledge, leading to discrimination based on a person's genetics, human genetic engineering, and other ethical concerns. This information could also lead to legal issues regarding health and privacy.

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Key Points

- DNA microarrays can be used to detect gene expression within specific samples by analyzing active genes and sequences using an array of DNA fragments fixed to a slide.
- Genome sequences can be used to discover the possibility of disease and genetic disorders prior to onset.
- Genome sequences can also be used to develop agrochemicals and pharmaceuticals.

Key Terms

- **microarray**: any of several devices containing a two-dimensional array of small quantities of biological material used for various types of assays
- **genomics**: the study of the complete genome of an organism

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17.4: APPLYING GENOMICS

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- Topic hierarchy

17.4A: Predicting Disease Risk at the Individual Level
17.4B: Pharmacogenomics, Toxicogenomics, and Metagenomics
17.4C: Genomics and Biofuels

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17.4A: Predicting Disease Risk at the Individual Level

Learning Objectives

- Explain how analysis of an individual's genome can aid in predicting disease risk

Predicting Disease Risk at the Individual Level

The introduction of DNA sequencing and whole genome sequencing projects, particularly the Human Genome project, has expanded the applicability of DNA sequence information. Genomics is now being used in a wide variety of fields, such as metagenomics, pharmacogenomics, and mitochondrial genomics. The most commonly-known application of genomics is to understand and find cures for diseases.

Predicting the risk of disease involves screening currently-healthy individuals by genome analysis at the individual level. Intervention with lifestyle changes and drugs can be recommended before disease onset. However, this approach is most applicable when the problem resides within a single gene defect. Such defects only account for approximately five percent of diseases in developed countries. Most of the common diseases, such as heart disease, are multi-factored or polygenic, which is a phenotypic characteristic that involves two or more genes interacting with environmental factors such as diet. In April 2010, scientists at Stanford University published the genome analysis of a healthy individual (Stephen Quake, a scientist at Stanford University, who had his genome sequenced); the analysis predicted his propensity to acquire various diseases. A risk assessment was performed to analyze Quake's percentage of risk for 55 different medical conditions. A rare genetic mutation was found, which showed him to be at risk for sudden heart attack. He was also predicted to have a 23 percent risk of developing prostate cancer and a 1.4 percent risk of developing Alzheimer's. The scientists used databases and several publications to analyze the genomic data. Even though genomic sequencing is becoming more affordable and analytical tools are becoming more reliable, ethical issues surrounding genomic analysis at a population level remain to be addressed.

In 2011, the United States Preventative Services Task Force recommended against using the PSA test to screen healthy men for prostate cancer. Their recommendation was based on evidence that screening does not reduce the risk of death from prostate cancer. Prostate cancer often develops very slowly and does not cause problems, while the cancer treatment can have severe side effects. The PCA3 test is considered to be more accurate, but screening may still result in men suffering side effects from treatment who would not have been harmed by the cancer itself.

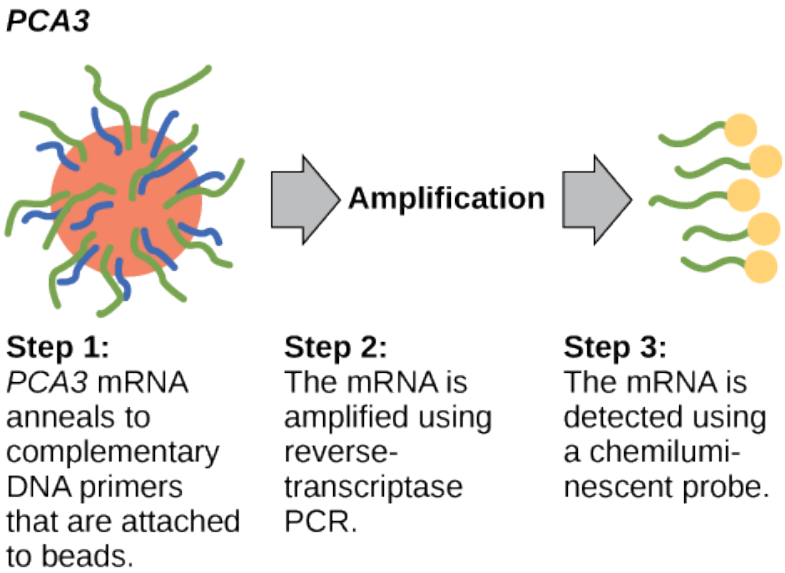


Figure 17.4A.1: PCA3: PCA3 is a gene that is expressed in prostate epithelial cells and overexpressed in cancerous cells. A high concentration of PCA3 in urine is indicative of prostate cancer.

Key Points

- Genome sequencing can predict the risk of developing diseases brought on by a single gene defect, but these defects only account for five percent of common diseases.
- Most diseases are polygenic or are brought on by environmental factors; genome sequencing cannot predict the risk of acquiring these diseases.
- Genome sequencing is becoming more reliable, but many scientists still question if it reduces the risk of death from certain diseases such as prostate cancer.

Key Terms

- **Human Genome Project**: an organized international scientific endeavor to determine the complete structure of human genetic material (DNA) to identify all the genes and understand their function
- **genome sequencing**: a laboratory process that determines the complete DNA sequence of an organism's genome at a single time
- **polygenic**: a phenotypic characteristic controlled by the interaction of two or more genes with the environment

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17.4B: Pharmacogenomics, Toxicogenomics, and Metagenomics

Learning Objectives

- Explain how microbial metagenomics can give researchers a more complete picture of a particular environment

Pharmacogenomics, also called toxicogenomics, involves evaluating the effectiveness and safety of drugs on the basis of information from an individual's genomic sequence. Genomic responses to drugs can be studied using experimental animals (such as laboratory rats or mice) or live cells in the laboratory before embarking on studies with humans. Studying changes in gene expression could provide information about the transcription profile in the presence of the drug, which can be used as an early indicator of the potential for toxic effects. For example, genes involved in cellular growth and controlled cell death, when disturbed, could lead to the growth of cancerous cells. Genome-wide studies can also help to find new genes involved in drug toxicity. Personal genome sequence information can be used to prescribe medications that will be most effective and least toxic on the basis of the individual patient's genotype. The gene signatures may not be completely accurate, but can be tested further before pathologic symptoms arise.

Microbial Genomics: Metagenomics

Traditionally, microbiology has been taught with the view that microorganisms are best studied under pure culture conditions, which involves isolating a single type of cell and culturing it in the laboratory. Because microorganisms can go through several generations in a matter of hours, their gene expression profiles adapt to the new laboratory environment very quickly. In addition, the vast majority of bacterial species resist being cultured in isolation. Most microorganisms do not live as isolated entities, but in microbial communities known as biofilms. For all of these reasons, pure culture is not always the best way to study microorganisms. Metagenomics is the study of the collective genomes of multiple species that grow and interact in an environmental niche. Metagenomics can be used to identify new species more rapidly and to analyze the effect of pollutants on the environment.

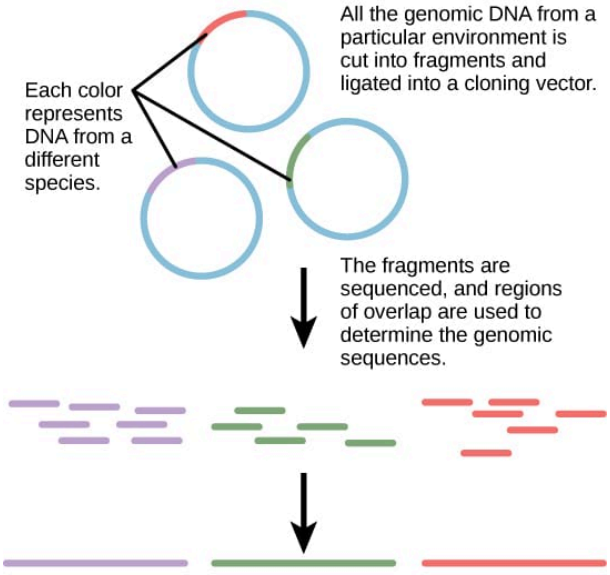


Figure 17.4B.1: Metagenomics: Metagenomics involves isolating DNA from multiple species within an environmental niche.

Key Points

- Pharmacogenomics involves evaluating the effectiveness and safety of drugs on the basis of information from an individual's

genomic sequence.
- Genomic responses to drugs can be studied using experimental animals or live cells in the laboratory, which help indicate the potentially toxic effects of a drug.
- Personal genome sequence information can be used to prescribe medications that will be most effective and least toxic on an individual level.
- Metagenomics, the study of the collective genomes of multiple species that grow and interact in an environmental niche, is often a better way to study microrganisms rather than pure culture.

Key Terms

- **pharmacogenomics**: the study of genes that code for enzymes that metabolize drugs, and the design of tailor-made drugs adapted to an individual's genetic make-up
- **metagenomics**: the study of the collective genomes of multiple species that grow and interact in an environmental niche

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17.4C: Genomics and Biofuels

Learning Objectives

- Explain the process of creating new biofuels by using microbial genomics

Knowledge of the genomics of microorganisms is being used to find better ways to harness biofuels from algae and cyanobacteria. The primary sources of fuel today are coal, oil, wood, and other plant products, such as ethanol. Although plants are renewable resources, there is still a need to find more alternative renewable sources of energy to meet our population ‘s energy demands. The microbial world is one of the largest resources for genes that encode new enzymes and produce new organic compounds, and it remains largely untapped.

For microbial biomass breakdown, many candidates have already been identified. These include Clostridia species for their ability to degrade cellulose, and fungi that express genes associated with the decomposition of the most recalcitrant features of the plant cell wall, lignin, the phenolic “glue” that imbues the plant with structural integrity and pest resistance. The white rot fungus *Phanerochaete chrysosporium* produces unique extracellular oxidative enzymes that effectively degrade lignin by gaining access through the protective matrix surrounding the cellulose microfibrils of plant cell walls.

Another fungus, the yeast *Pichia stipitis*, ferments the five-carbon “wood sugar” xylose abundant in hardwoods and agricultural harvest residue. *Pichia*‘s recently-sequenced genome has revealed insights into the metabolic pathways responsible for this process, guiding efforts to optimize this capability in commercial production strains. Pathway engineering promises to produce a wider variety of organisms able to ferment the full repertoire of sugars derived from cellulose and hemicellulose and tolerate higher ethanol concentrations to optimize fuel yields. For instance, the hindgut contents of nature’s own bioreactor, the termite, has yielded more than 500 genes related to the enzymatic deconstruction of cellulose and hemicellulose.



Figure 17.4C.1: Termites: Nature’s Bioreactors: The hindgut of the termite has yielded more than 500 genes of microbes related to the enzymatic deconstruction of cellulose.

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Key Points

- Microorganisms can encode new enzymes and produce new organic compounds that can be used as biofuels.
- Genomic analysis of the fungus *Pichia* will allow optimization of its use in fermenting ethanol fuels.
- Analysis of the microbes in the hindgut of termites have found 500 genes that may be useful in enzymatic destruction of cellulose.
- Genetic markers have been used in forensic analysis, like in 2001 when the FBI used microbial genomics to determine a specific strain of anthrax that was found in several pieces of mail.
- Genomics is used in agriculture to develop plants with more desirable traits, such as drought and disease resistance.

Key Terms

- **renewable resource**: a natural resource such that it is replenished by natural processes at a rate comparable to its rate of consumption by humans or other users
- **biofuel**: any fuel that is obtained from a renewable biological resource

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17.5: GENOMICS AND PROTEOMICS



- Topic hierarchy

17.5A: Genomics and Proteomics

17.5B: Basic Techniques in Protein Analysis

17.5C: Cancer Proteomics

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17.5A: Genomics and Proteomics

Learning Objectives

- Explain how the field of genomics led to the development of proteomics

Proteomics is a relatively-recent field; the term was coined in 1994 while the science itself had its origins in electrophoresis techniques of the 1970's and 1980's. The study of proteins, however, has been a scientific focus for a much longer time. Studying proteins generates insight into how they affect cell processes. Conversely, this study also investigates how proteins themselves are affected by cell processes or the external environment. Proteins provide intricate control of cellular machinery; they are, in many cases, components of that same machinery. They serve a variety of functions within the cell; there are thousands of distinct proteins and peptides in almost every organism. The goal of proteomics is to analyze the varying proteomes of an organism at different times in order to highlight differences between them. Put more simply, proteomics analyzes the structure and function of biological systems. For example, the protein content of a cancerous cell is often different from that of a healthy cell. Certain proteins in the cancerous cell may not be present in the healthy cell, making these unique proteins good targets for anti-cancer drugs. The realization of this goal is difficult; both purification and identification of proteins in any organism can be hindered by a multitude of biological and environmental factors.

The study of the function of proteomes is called proteomics. A proteome is the entire set of proteins produced by a cell type. Genomics led to proteomics (via transcriptomics) as a logical step. Proteomes can be studied using the knowledge of genomes because genes code for mRNAs and the mRNAs encode proteins. Although mRNA analysis is a step in the right direction, not all mRNAs are translated into proteins. Proteomics complements genomics and is useful when scientists want to test their hypotheses that were based on genes. Even though all cells of a multicellular organism have the same set of genes, the set of proteins produced in different tissues is different and dependent on gene expression. Thus, the genome is constant, but the proteome varies and is dynamic within an organism. In addition, RNAs can be alternately spliced (cut and pasted to create novel combinations and novel proteins) and many proteins are modified after translation by processes such as proteolytic cleavage, phosphorylation, glycosylation, and ubiquitination. There are also protein-protein interactions, which complicate the study of proteomes. Although the genome provides a blueprint, the final architecture depends on several factors that can change the progression of events that generate the proteome.



Figure 17.5A.1: Large-scale proteomics machinery: This machine is preparing to do a proteomic pattern analysis to identify specific cancers so that an accurate cancer prognosis can be made.

Key Points

- Proteomics investigates how proteins affect and are affected by cell processes or the external environment.
- Within an individual organism, the genome is constant, but the proteome varies and is dynamic.
- Every cell in an individual organism has the same set of genes, but the set of proteins produced in different tissues differ from one another and are dependent on gene expression.

Key Terms

- **proteomics**: the branch of molecular biology that studies the set of proteins expressed by the genome of an organism
- **proteome**: the complete set of proteins encoded by a particular genome
- **genomics**: the study of the complete genome of an organism

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17.5B: Basic Techniques in Protein Analysis

Learning Objectives

- Describe the techniques used in proteomics to analyze proteins

Basic Techniques in Protein Analysis

The ultimate goal of proteomics is to identify or compare the proteins expressed in a given genome under specific conditions, study the interactions between the proteins, and use the information to predict cell behavior or develop drug targets. Just as the genome is analyzed using the basic technique of DNA sequencing, proteomics requires techniques for protein analysis. The basic technique for protein analysis, analogous to DNA sequencing, is mass spectrometry.



Figure $17.5B.1$: Mass Spectrometer: Matrix-Assisted Laser Desorbtion Ionisation – Time Of Flight (MALDI-TOF) Mass Spectrometer. Mass spectrometry can be used in protein analysis.

Mass Spectrometry

Mass spectrometry is used to identify and determine the characteristics of a molecule. It is a technique in which gas phase molecules are ionized and their mass-to-charge ratio is measured by observing acceleration differences of ions when an electric field is applied. Lighter ions will accelerate faster and be detected first. If the mass is measured with precision, then the composition of the molecule can be identified. In the case of proteins, the sequence can be identified. The challenge of techniques used for proteomic analyses is the difficulty in detecting small quantities of proteins, but advances in spectrometry have allowed researchers to analyze very small samples of protein. Variations in protein expression in diseased states, however, can be difficult to discern. Proteins are naturally-unstable molecules, which makes proteomic analysis much more difficult than genomic analysis.

X-ray crystallography and Nuclear Magnetic Resonance

X-ray crystallography enables scientists to determine the three-dimensional structure of a protein crystal at atomic resolution. Crystallographers aim high-powered X-rays at a tiny crystal containing trillions of identical molecules. The crystal scatters the X-rays onto an electronic detector that is the same type used to capture images in a digital camera. After each blast of X-rays, lasting from a few seconds to several hours, the researchers precisely rotate the crystal by entering its desired orientation into the

computer that controls the X-ray apparatus. This enables the scientists to capture in three dimensions how the crystal scatters, or diffracts, X-rays. The intensity of each diffracted ray is fed into a computer, which uses a mathematical equation to calculate the position of every atom in the crystallized molecule. The result is a three-dimensional digital image of the molecule.

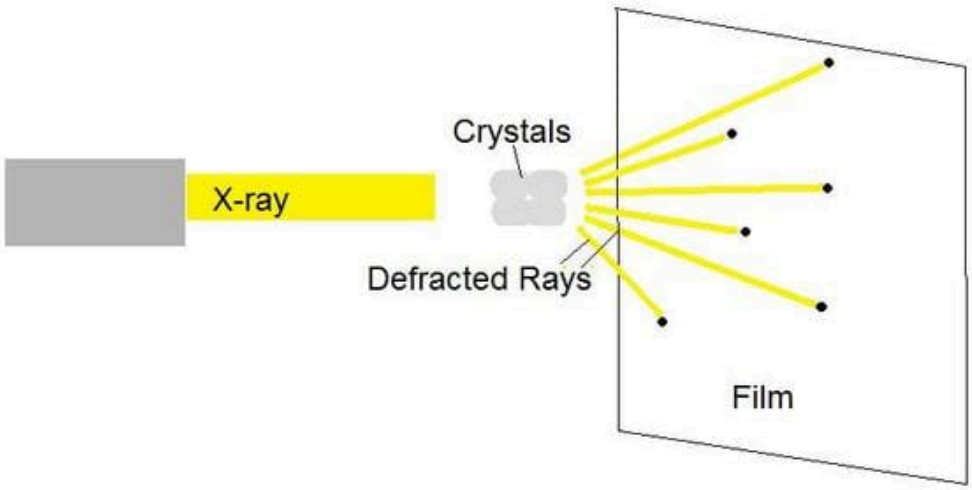


Figure $17.5B.1$: X-ray crystallography: X-rays that hit atomic nuclei are diffracted onto a detector.

Another protein imaging technique, nuclear magnetic resonance (NMR), uses the magnetic properties of atoms to determine the three-dimensional structure of proteins. NMR spectroscopy is unique in being able to reveal the atomic structure of macromolecules in solution, provided that highly-concentrated solution can be obtained. This technique depends on the fact that certain atomic nuclei are intrinsically magnetic. The chemical shift of nuclei depends on their local environment. The spins of neighboring nuclei interact with each other in ways that provide definitive structural information that can be used to determine complete three-dimensional structures of proteins.

Protein Microarrays and Two- Hybrid Screening

Protein microarrays have also been used to study interactions between proteins. These are large-scale adaptations of the basic two-hybrid screen. The premise behind the two-hybrid screen is that most eukaryotic transcription factors have modular activating and binding domains that can still activate transcription even when split into two separate fragments, as long as the fragments are brought within close proximity to each other. Generally, the transcription factor is split into a DNA-binding domain (BD) and an activation domain (AD). One protein of interest is genetically fused to the BD and another protein is fused to the AD. If the two proteins of interest bind each other, then the BD and AD will also come together and activate a reporter gene that signals interaction of the two hybrid proteins.

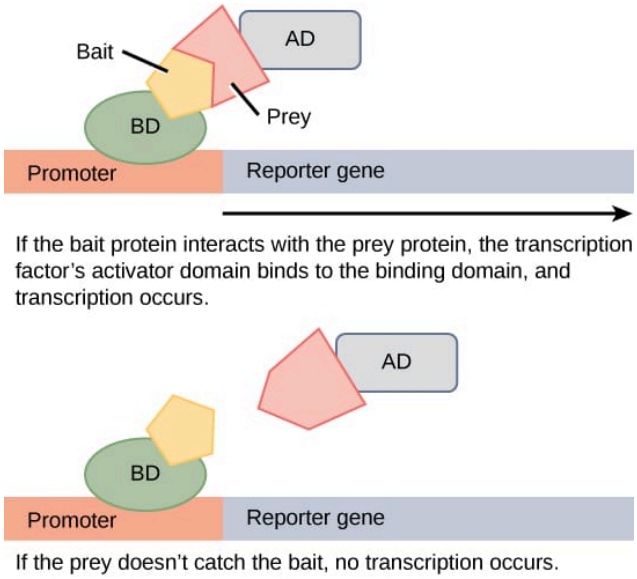


Figure $17.5B.1$: Two-hybrid screening: Two-hybrid screening is used to determine whether two proteins interact. In this method, a transcription factor is split into a DNA-binding domain (BD) and an activation domain (AD). The binding domain is able to bind the promoter in the absence of the activator domain, but it does not turn on transcription. A protein called the bait is attached to the BD, and a protein called the prey is attached to the AD. Transcription occurs only if the prey "catches" the bait.

Western Blot

The western blot, or protein immunoblot, is a technique that combines protein electrophoresis and antibodies to detect proteins in a sample. A western blot is fairly quick and simple compared to the above techniques and, thus, can serve as an assay to validate results from other experiments. The protein sample is first separated by gel electrophoresis, then transferred to a nitrocellulose or other type of membrane, and finally stained with a primary antibody that specifically binds the protein of interest. A fluorescent or radioactive-labeled secondary antibody binds to the primary antibody and provides a means of detection via either photography or x-ray film, respectively.

Key Points

- Mass Spectrometry is a technique that is useful for determining the size of a protein or protein complex.
- X-ray crystallography and NMR are techniques useful for determining the 3-D structure of a protein or protein complex.
- Protein microarrays are useful for determining protein-protein interactions.

Key Terms

- **microarray**: any of several devices containing a two-dimensional array of small quantities of biological material used for various types of assays
- **reporter gene**: a gene that researchers attach to a regulatory sequence of another gene of interest and whose product is easily identifiable in assays

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17.5C: Cancer Proteomics

Learning Objectives

- Explain the ways in which cancer proteomics may lead to better treatments

Genomes and proteomes of patients suffering from specific diseases are being studied to understand the genetic basis of diseases. The most prominent set of diseases being studied with proteomic approaches is cancer. Proteomic approaches are being used to improve screening and early detection of cancer, which is achieved by identifying proteins whose expression is affected by the disease process.

An individual protein that indicates disease is called a biomarker, whereas a set of proteins with altered expression levels is called a protein signature. For a biomarker or protein signature to be useful as a candidate for early screening and detection of a cancer, it must be secreted in body fluids (e.g. sweat, blood, or urine) such that large-scale screenings can be performed in a non-invasive fashion. The current problem with using biomarkers for the early detection of cancer is the high rate of false-negative results. A false-negative is an incorrect test result that should have been positive. In other words, many cases of cancer go undetected, which makes biomarkers unreliable. Some examples of protein biomarkers used in cancer detection are CA-125 for ovarian cancer and PSA for prostate cancer. Protein signatures may be more reliable than biomarkers to detect cancer cells.

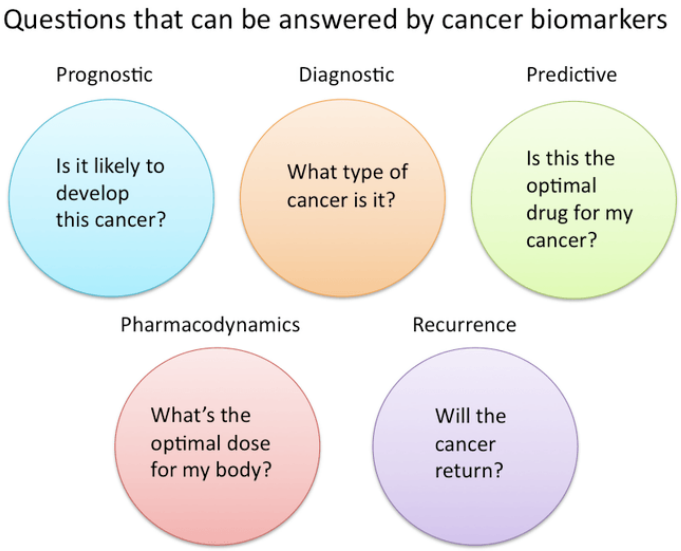


Figure $17.5C.1$: Questions that can be answered by biomarkers: In cancer research and medicine, biomarkers are used in three primary ways: (A) Diagnostic – To help diagnose conditions, as in the case of identifying early stage cancers. (B) Prognostic – To forecast how aggressive a condition is, as in the case of determining a patient's ability to fare in the absence of treatment. (C) Predictive – To predict how well a patient will respond to treatment.

Proteomics is also being used to develop individualized treatment plans, which involves the prediction of whether or not an individual will respond to specific drugs and the side effects that the individual may experience. In addition, proteomics can be used to predict the possibility of disease recurrence. The National Cancer Institute has developed programs to improve the detection and treatment of cancer. The Clinical Proteomic Technologies for Cancer and the Early Detection Research Network are efforts to identify protein signatures specific to different types of cancers. The Biomedical Proteomics Program is designed to identify protein signatures and design effective therapies for cancer patients.

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Key Points

- Identifying those proteins whose expression is affected by disease processes can be used to improve screening and early detection of cancer.
- Different biomarkers and protein signatures are being used to analyze each type of cancer.
- A future goal of cancer proteomics is to have a personalized treatment plan for each individual.

Key Terms

- **biomarker**: a substance used as an indicator of a biological state, most commonly disease

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18: EVOLUTION AND THE ORIGIN OF SPECIES



- Topic hierarchy

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18.1B: Charles Darwin and Natural Selection

18.1C: The Galapagos Finches and Natural Selection

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18.1: UNDERSTANDING EVOLUTION



- Topic hierarchy

18.1A: What is Evolution?

18.1B: Charles Darwin and Natural Selection

18.1C: The Galapagos Finches and Natural Selection

18.1D: Processes and Patterns of Evolution

18.1E: Evidence of Evolution

18.1F: Misconceptions of Evolution

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18.1A: What is Evolution?

Learning Objectives

- Describe the historical influences on Darwin's theory of evolution

Introduction: Evolution

All species of living organisms, including bacteria and chimpanzees, evolved at some point from a different species. Although it may seem that living things today stay the same, this is not the case: evolution is a gradual and ongoing process.

The theory of evolution is the unifying theory of biology, meaning it is the framework within which biologists ask questions about the living world. The Ukrainian-born American geneticist Theodosius Dobzhansky famously wrote that "nothing makes sense in biology except in the light of evolution." The tenet that all species have evolved and diversified from a common ancestor is the foundation from which we approach all questions in biology. It provides a direction for predictions about living things, which has been validated through extensive scientific experimentation.

Evolution by natural selection describes a mechanism for the change of species over time. Well before Darwin began to explore the concept of evolution, the idea that species change over time had already been suggested and debated. The view that species are static and unchanging was grounded in the writings of Plato, yet there were also ancient Greeks who expressed ideas about evolution. During the eighteenth century, ideas about the evolution of animals were reintroduced by the naturalist Georges-Louis Leclerc Comte de Buffon who observed that various geographic regions have different plant and animal populations, even when the environments are similar. It was also accepted that there are extinct species.



Figure 18.1A.1: Evolution by Natural Selection: All organisms are products of evolution adapted to their environment. (a) Saguaro (Carnegiea gigantea) can soak up 750 liters of water in a single rain storm, enabling these cacti to survive the dry conditions of the Sonoran desert in Mexico and the Southwestern United States. (b) The Andean semiaquatic lizard (Potamites montanicola), discovered in Peru in 2010, lives between 1,570 to 2,100 meters in elevation and, unlike most lizards, is nocturnal and swims. Scientists still do not know how these cold-blood animals are able to move in the cold (10 to 15°C) temperatures of the Andean night.

During this time, a Scottish naturalist named James Hutton proposed that geological change occurs gradually by the accumulation of small changes over long periods of time. This theory contrasted with the predominant view of the time: that the geology of the planet is a consequence of catastrophic events that occurred during a relatively brief past. During the nineteenth century, Hutton's views were popularized by the geologist Charles Lyell, who was a friend of Charles Darwin. Lyell's ideas, in turn, influenced Darwin's concept of evolution. The greater age of the earth proposed by Lyell supported the gradual evolution that Darwin proposed, and the slow process of geological change provided an analogy for the gradual change in species.

In the early nineteenth century, Jean-Baptiste Lamarck published a book that detailed a different mechanism for evolutionary change. This mechanism is now referred to as an inheritance of acquired characteristics. This idea states that modifications in

an individual are caused by its environment, or the use or disuse of a structure during its lifetime, and that these changes can be inherited by its offspring, bringing about change in a species. While this mechanism for evolutionary change was discredited, Lamarck's ideas were an important influence on the concept of evolution.

Key Points

- Ancient Greeks expressed ideas about evolution, which were reintroduced in the eighteenth century by Georges-Louis Leclerc Comte de Buffon who observed different environments had different plant and animal populations.
- James Hutton proposed that geological changes occur gradually over time via the accumulation of small changes rather than through large catastrophic events.
- Charles Lyell popularized James Hutton's theory; this theory of incremental change influenced Darwin's theory of evolution.
- Jean-Baptiste Lamarck proposed the theory of the inheritance of acquired characterstics; this theory has now been discredited, but it served as an important influence on the theory of evolution.

Key Terms

- **evolution**: the change in the genetic composition of a population over successive generations
- **inheritance of acquired characteristics**: hypothesis that physiological changes acquired over the life of an organism may be transmitted to its offspring

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18.1B: Charles Darwin and Natural Selection

Learning Objectives

- Explain how natural selection can lead to evolution

Charles Darwin and Natural Selection

In the mid-nineteenth century, the mechanism for evolution was independently conceived of and described by two naturalists: Charles Darwin and Alfred Russel Wallace. Importantly, each naturalist spent time exploring the natural world on expeditions to the tropics. From 1831 to 1836, Darwin traveled around the world to places like 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, as with Wallace's later journeys to the Malay Archipelago, included stops at several island chains, the last being the Galápagos Islands west of Ecuador. On these islands, Darwin observed that species of organisms on different islands were clearly similar, yet had distinct differences. For example, the ground finches inhabiting the Galápagos Islands comprised several species with a unique beak shape. The species on the islands had a graded series of beak sizes and shapes with very small differences between the most similar. He observed that these finches closely resembled another finch species on the mainland of South America. Darwin imagined that the island species might be modified from one of the original mainland species. Upon further study, he realized that the varied beaks of each finch helped the birds acquire a specific type of food. For example, seed-eating finches had stronger, thicker beaks for breaking seeds, while insect-eating finches had spear-like beaks for stabbing their prey.

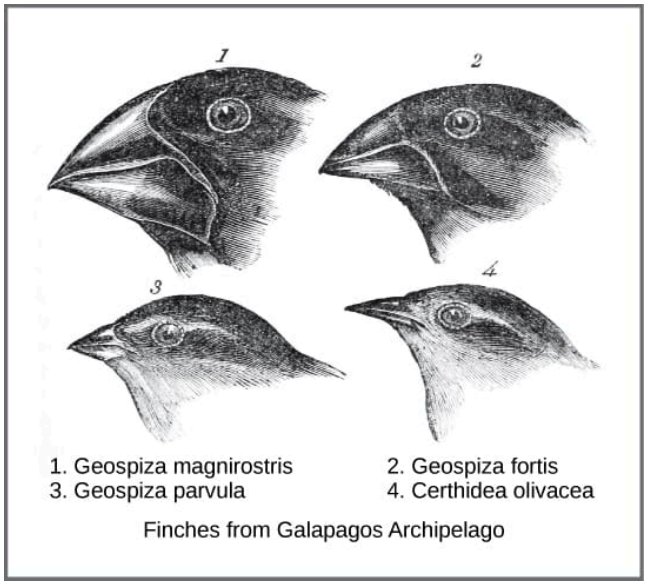


Figure 18.1B.1: Beak Shape Among Finch Species: Darwin observed that beak shape varies among finch species. He postulated that the beak of an ancestral species had adapted over time to equip the finches to acquire different food sources.

Natural Selection

Wallace and Darwin observed similar patterns in other organisms and independently developed the same explanation for how and why such changes could take place. Darwin called this mechanism natural selection. Natural selection, also known as "survival of the fittest," is the more prolific reproduction of individuals with favorable traits that survive environmental change because of those traits. This leads to evolutionary change, the trait becoming predominant within a population. For example, Darwin observed that a population of giant tortoises found in the Galapagos Archipelago have longer necks than those that lived on other islands with dry lowlands. These tortoises were "selected" because they could reach more leaves and access more food than those with short necks. In times of drought, when fewer leaves would be available, those that could reach more leaves had a better chance

to eat and survive than those that could not reach the food source. Consequently, long-necked tortoises would more probably be reproductively successful and pass the long-necked trait to their offspring. Over time, only long-necked tortoises would be present in the population.

Natural selection, Darwin argued, was an inevitable outcome of three principles that operated in nature. First, most characteristics of organisms are inherited, or passed from parent to offspring, although *how* traits were inherited was unknown. Second, more offspring are produced than are able to survive. The capacity for reproduction in all organisms outstrips the availability of resources to support their numbers. Thus, there is competition for those resources in each generation. Both Darwin and Wallace were influenced by an essay written by economist Thomas Malthus who discussed this principle in relation to human populations. Third, Darwin and Wallace reasoned that offspring with the 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 successive generations in a process that Darwin called descent with modification. Ultimately, natural selection leads to greater adaptation of the population to its local environment; it is the only mechanism known for adaptive evolution.

Papers by Darwin and Wallace presenting the idea of natural selection were read together in 1858 before the Linnean Society in London. The following year, Darwin's book, *On the Origin of Species*, was published. His book outlined his arguments for evolution by natural selection.

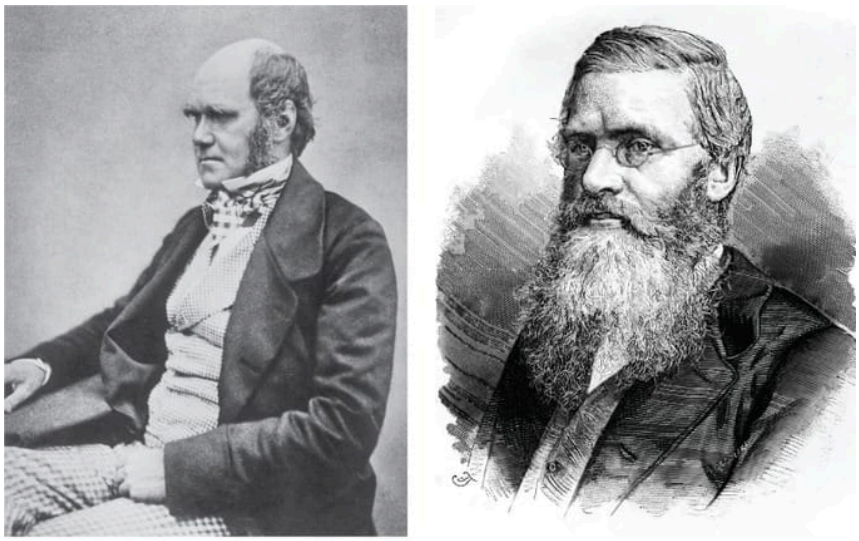


Figure $18.1B.1$: Charles Darwin and Alfred Wallace: Both (a) Charles Darwin and (b) Alfred Wallace wrote scientific papers on natural selection that were presented together before the Linnean Society in 1858.

Key Points

- Wallace traveled to Brazil to collect and observe insects from the Amazon rainforest.
- Darwin observed that finches in the Galápagos Islands had different beaks than finches in South America; these adaptations equiped the birds to acquire specific food sources.
- Wallace and Darwin observed similar patterns in the variation of organisms and independently developed the same explanation for how such variations could occur over time, a mechanism Darwin called natural selection.
- According to natural selection, also known as "survival of the fittest," individuals with traits that enable them to survive are more reproductively successful; this leads to those traits becoming predominant within a population.
- Natural selection is an inevitable outcome of three principles: most characteristics are inherited, more offspring are produced than are able to survive, and offspring with more favorable characteristics will survive and have more offspring than those individuals with less favorable traits.

Key Terms

- **natural selection**: a process in which individual organisms or phenotypes that possess favorable traits are more likely to

survive and reproduce
- **descent with modification**: change in populations over generations

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18.1C: The Galapagos Finches and Natural Selection

Learning Objectives

- Describe how finches provide visible evidence of evolution

Visible Evidence of Ongoing Evolution: Darwin's Finches

From 1831 to 1836, Darwin traveled around the world, observing animals on different continents and islands. On the Galapagos Islands, Darwin observed several species of finches with unique beak shapes. He observed 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."

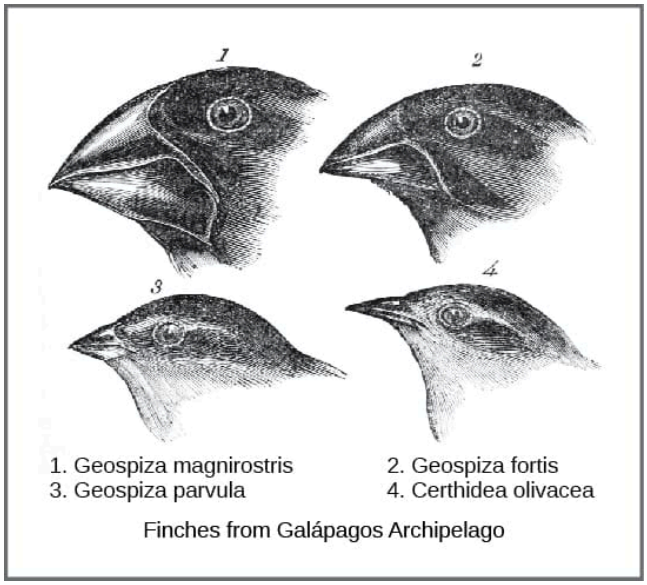


Figure 18.1C.1: Darwin's Finches: Darwin observed that beak shape varies among finch species. He postulated that the beak of an ancestral species had adapted over time to equip the finches to acquire different food sources. This illustration shows the beak shapes for four species of ground finch: 1. *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).

Natural Selection

Darwin called this mechanism of change 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 exceeds the availability of resources to support their numbers. Thus, there is a competition for those resources in each generation. Third, offspring vary among each other in regard to their characteristics and those variations are inherited. Out of these three principles, Darwin 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," or evolution.

Studies of Natural Selection After Darwin

Demonstrations of evolution by natural selection can be time consuming. 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. This was clear evidence for natural selection 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 other 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.

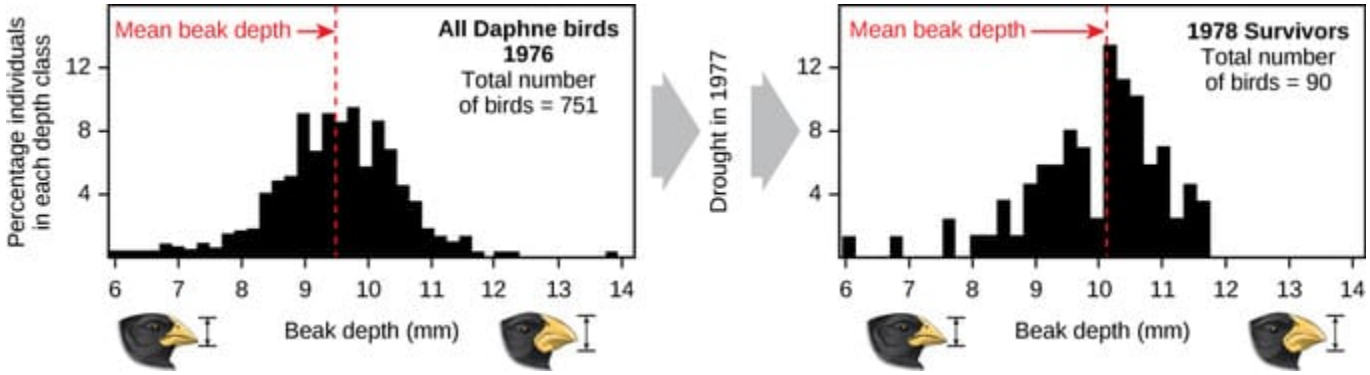


Figure 18.1C.1: Finches of Daphne Major: A drought on the Galápagos island of Daphne Major in 1977 reduced the number of small seeds available to finches, causing many of the small-beaked finches to die. This caused an increase in the finches' average beak size between 1976 and 1978.

Key Points

- Darwin observed the Galapagos finches had a graded series of beak sizes and shapes and predicted these species were modified from one original mainland species.
- Darwin called differences among species natural selection, which is caused by the inheritance of traits, competition between individuals, and the variation of traits.
- Offspring with inherited characteristics that allow them to best compete will survive and have more offspring than those individuals with variations that are less able to compete.
- Large-billed finches feed more efficiently on large, hard seeds, whereas smaller billed finches feed more efficiently on small, soft seeds.
- When small, soft seeds become rare, large-billed finches will survive better, and there will be more larger-billed birds in the following generation; when large, hard seeds become rare, the opposite will occur.

Key Terms

- **natural selection**: a process in which individual organisms or phenotypes that possess favorable traits are more likely to survive and reproduce
- **evolution**: the change in the genetic composition of a population over successive generations

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18.1D: Processes and Patterns of Evolution

Learning Objectives

- Explain why only heritable variation can be acted upon by natural selection

Processes and Patterns of Evolution

Variation

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, the 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 due to better nutrition rather than different genes.

Genetic diversity within a population comes from two main mechanisms: mutation and sexual reproduction. Mutation, a change in the DNA sequence, is the ultimate source of new alleles, or new genetic variation in any population. The genetic changes caused by mutation can have one of three outcomes:

- Many mutations will have no effect on the fitness of the phenotype; these are called neutral mutations.
- A mutation may affect the phenotype of the organism in a way that gives it reduced fitness (a lower likelihood of survival or fewer offspring).
- A mutation may produce a phenotype with a beneficial effect on fitness. Different mutations will have a range of effects on the fitness of an organism that expresses them in their phenotype, from a small effect to a great effect.

Sexual reproduction also leads to genetic diversity: when two parents reproduce, unique combinations of alleles assemble to produce the unique genotypes and thus phenotypes in each of the offspring. However, sexual reproduction can not lead to new genes, but rather provides a new combination of genes in a given individual.

Adaptations

A heritable trait that aids the survival and reproduction of an organism in its present environment is called an adaptation. Scientists describe groups of organisms becoming adapted to their environment when a change in the range of genetic variation occurs over time that increases or maintains the “fitness” of the population to its environment. The webbed feet of platypuses are an adaptation for swimming. The snow leopards’ thick fur is an adaptation for living in the cold. The cheetahs’ fast speed is an adaptation for catching prey.

Whether or not a trait is favorable depends on the environmental conditions at the time. The same traits are not always selected because environmental conditions can change. For example, consider a species of plant that grew in a moist climate and did not need to conserve water. Large leaves were selected because they allowed the plant to obtain more energy from the sun. Large leaves require more water to maintain than small leaves, and the moist environment provided favorable conditions to support large leaves. After thousands of years, the climate changed and the area no longer had excess water. The direction of natural selection shifted so that plants with small leaves were selected because those populations were able to conserve water to survive the new environmental conditions.

The evolution of species has resulted in enormous variation in form and function. Sometimes, evolution gives rise to groups of organisms that become tremendously different from each other. When two species evolve in diverse 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 18.1D.1: Flowering Plants: Flowering plants evolved from a common ancestor. Notice that the (a) dense blazing star (Liatrus spicata) and the (b) purple coneflower (Echinacea purpurea) vary in appearance, yet both share a similar basic morphology.

In other cases, similar phenotypes evolve independently in distantly-related species. For example, flight has evolved in both bats and insects; they both have structures we refer to as wings, which are adaptations to flight. However, the wings of bats and insects have evolved from very different original structures. This phenomenon is called convergent evolution, where similar traits evolve independently in species that do not share a recent common ancestry. The two species came to the same function, flying, but did so separately from each other.

These physical changes occur over enormous spans of time and help explain how evolution occurs. Natural selection acts on individual organisms, which in turn can shape an entire species. Although natural selection may work in a single generation on an individual, it can take thousands or even millions of years for the genotype of an entire species to evolve. It is over these large time spans that life on earth has changed and continues to change.

Key Points

- Genetic variation within a population is a result of mutations and sexual reproduction.
- A mutation may be neutral, reduce an organism's fitness, or increase an organism's fitness.
- An adaptation is a heritable trait that increases the survival and rate of reproduction of an organism in its present environment.
- Divergent evolution describes the process in which two species evolve in diverse directions from a common point.
- Convergent evolution is the process in which similar traits evolve independently in species that do not share a recent common ancestry.

Key Terms

- **adaptation**: modification of something or its parts that makes it more fit for existence under the conditions of its current environment
- **divergent evolution**: the process by which a species with similar traits become groups that are tremendously different from each other over many generations
- **convergent evolution**: a trait of evolution in which species not of similar recent origin acquire similar properties due to natural selection

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18.1E: Evidence of Evolution

Learning Objectives

- Explain the development of the theory of evolution

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*, to identifying patterns in nature that were consistent with evolution. Since Darwin, our understanding has become clearer and broader.

Fossils, Anatomy, and Embryology

Fossils provide solid evidence that organisms from the past are not the same as those found today; they show a progression of evolution. Scientists calculate the age of fossils and categorize them 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. For example, scientists have recovered highly-detailed records showing the evolution of humans and horses. The whale flipper shares a similar morphology to appendages of birds and mammals, indicating that these species share 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. Scientists call these synonymous parts homologous structures.

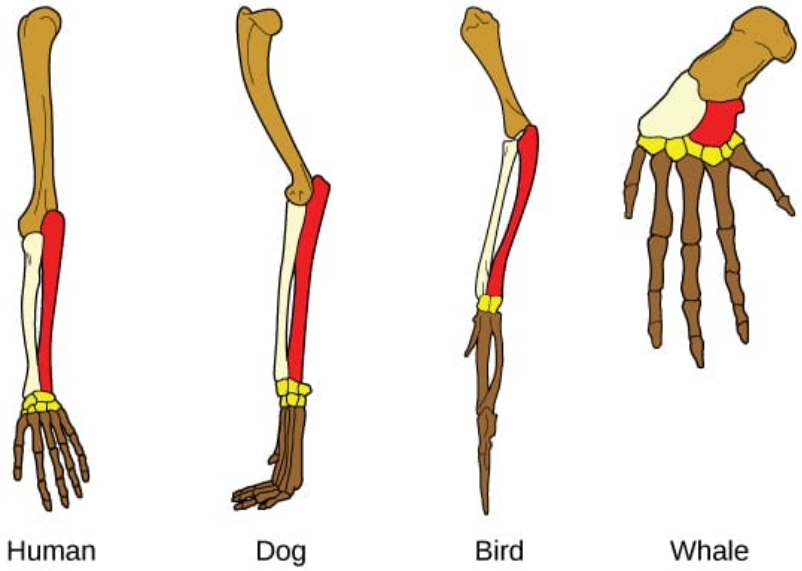


Figure $18.1E.1$: Common Ancestors: The similar construction of these appendages indicates that these organisms share a common ancestor.



(a) (b)

Figure 18.1E.1: Evolution of Humans and Horses: (a) In this display, fossil hominids are arranged from oldest (bottom) to newest (top). As hominids evolved, the shape of the skull changed. (b) An artist's rendition of extinct species of the genus Equus reveals that these ancient species resembled the modern horse (Equus ferus), but varied in size.

Some structures exist in organisms that have no apparent function at all, appearing to be residual parts from a common ancestor. These unused structures (such as wings on flightless birds, leaves on some cacti, and hind leg bones in whales) are vestigial.

Embryology, the study of the development of the anatomy of an organism to its adult form, provides evidence for evolution as embryo formation in widely-divergent groups of organisms tends to be conserved. Structures that are absent in the adults of some groups often appear in their embryonic forms, disappearing by the time the adult or juvenile form is reached. For example, all vertebrate embryos, including humans, exhibit gill slits and tails at some point in their early development. These disappear in the adults of terrestrial groups, but are maintained in adults 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 birth.

Another form of 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 living in the arctic region, have been selected for seasonal white phenotypes during winter to blend with the snow and ice. These similarities occur not because of common ancestry, but because of similar selection pressures: the benefits of not being seen by predators.



(a) (b)

Figure 18.1E.1: Adaptations: Winter Coats: The white winter coat of the (a) arctic fox and the (b) ptarmigan's plumage are adaptations to their environments.

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, such as the unique flora and fauna of northern continents that formed from the supercontinent Laurasia compared to that of the southern continents that formed from the supercontinent Gondwana.

The great diversification of marsupials in Australia and the absence of other mammals reflect Australia's long isolation. Australia has an abundance of endemic species (those found nowhere else) which is typical of islands whose isolation by expanses of water prevents species from migrating. 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 unique to their one point of origin, yet they 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, in the near universality of the genetic code, and in the machinery of DNA replication and expression. In general, the relatedness of groups of organisms is reflected in the similarity of their DNA sequences. This is 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 duplications that allow the free modification of one copy by mutation, selection, or drift (changes in a population 's gene pool resulting from chance), while the second copy continues to produce a functional protein.

Key Points

- Fossils serve to highlight the differences and similarities between current and extinct species, showing the evolution of form over time.
- Similar anatomy across different species highlights their common origin and can be seen in homologous and vestigial structures.
- Embryology provides evidence for evolution since the embryonic forms of divergent groups are extremely similar.
- The natural distribution of species across different continents supports evolution; species that evolved before the breakup of the supercontinent are distributed worldwide, whereas species that evolved more recently are more localized.
- Molecular biology indicates that the molecular basis for life evolved very early and has been maintained with little variation across all life on the planet.

Key Terms

- **homologous structure**: the traits of organisms that result from sharing a common ancestor; such traits often have similar embryological origins and development
- **biogeography**: the study of the geographical distribution of living things
- **vestigial structure**: genetically determined structures or attributes that have apparently lost most or all of their ancestral function in a given species

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18.1F: Misconceptions of Evolution

Learning Objectives

- Discuss misconceptions about the theory of evolution

Misconceptions of Evolution

Although the theory of evolution generated controversy when it was first proposed, it was almost universally accepted by biologists within 20 years of the publication of *On the Origin of Species*. Nevertheless, the theory of evolution is a difficult concept and misconceptions about it abound.

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 body of thoroughly-tested and verified explanations for a set of observations of the natural world. Scientists have a theory of the atom, a theory of gravity, and the theory of relativity, each of which describes understood facts about the world. In the same way, the theory of evolution describes facts about the living world. A theory in science has also survived significant efforts to discredit it by scientists. In contrast, a "theory" in common vernacular is a word meaning a guess or suggested explanation; this meaning is more akin to the scientific concept of "hypothesis. " 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 mis-characterization.

Individuals Evolve

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, obviously, but this is called development and 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 that population several years later, this average value *of the population* will be different as a result of evolution.

Evolution Explains the Origin of Life

It is a common misunderstanding that evolution includes an explanation of life's origins. The theory of evolution explains how populations change over time. 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 and, presumably, it occurred just once. However, 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. Once a mechanism of inheritance was in place in the form of a molecule like DNA, either within a cell or 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.

Organisms Evolve on Purpose

Statements such as "organisms evolve in response to a change in an environment" may lead to the misunderstanding that 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 characteristics are genetically determined.

It is important to understand that the variation that natural selection works on is already present 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 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, probably at a low frequency. The antibiotic, which kills the bacterial cells without the resistance gene, strongly selects 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 antibiotics.

In a larger sense, evolution is not goal directed. Species do not become “better” over time; they track their changing environment with adaptations that maximize their reproduction. The characteristics that evolve in a species are a function of preexisting variation and the environment, both of which are constantly changing non-directionally. A trait that is fit in one environment at one time may also be fatal at some point in the future.

Evolution = Natural Selection

The terms “evolution” and “natural selection” are often conflated, as the two concepts are closely related. They are not, however, synonymous. Natural selection refers to the process by which organisms better suited for their environment are more likely to survive and produce offspring, thereby proliferating those favorable genetics in a population. Evolution is defined more broadly as any change in the genetic makeup of a population over time. As expounded by Darwin, natural selection is a major driving force of evolution, but it is not the only one.

Genetic drift, for example, is another mechanism by which evolution may occurs. Genetic drift occurs when allelic frequency is altered due to random sampling. It is evolution by chance, and the smaller the population, the more significant the effects on genetic distribution due to sampling error. For example, a population bottleneck, which occurs when an event such as a natural disaster dramatically reduces the size of a population, can result in the elimination or significant reduction of a trait within a population, regardless of how beneficial that trait may be to survival or reproduction. Thus evolution can occur without natural selection.



Figure $18.1F.1$: Misconceptions of Evolution: Lamarckian evolution and giraffes: Lamarck’s hypothesis for how evolution worked stated that organisms could pass on traits they had acquired during their lifetime to the progeny, such as giraffes gaining a long neck because their parents needed to reach high food.

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Key Points

- Attacks on the theory of evolution sometimes take issue with the word “theory”, which in the vernacular means a guess or suggested explanation. In scientific language, “theory” indicates a body of thoroughly-tested and verified explanations for a set of observations of the natural world.
- Evolution does not take place on an individual level; evolution is the average change of a characteristic within an entire population.

- Evolution does not explain the origin of life; the theory of evolution instead explains how populations change over time and how traits are selected in order to increase the fitness of a population.
- Favorable traits do not arise as a result of the environment as these traits are already present; individuals with favorable traits are more likely to survive and, thus, will have greater fitness than individuals with less desirable traits.
- Evolution and natural selection are not synonymous. Natural selection is just one mechanism by which evolution occurs.

Key Terms

- **theory**: a well-substantiated explanation of some aspect of the natural world based on knowledge that has been repeatedly confirmed through observation and experimentation

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18.2: FORMATION OF NEW SPECIES

- Topic hierarchy

18.2A: The Biological Species Concept

18.2B: Reproductive Isolation

18.2C: Speciation

18.2D: Allopatric Speciation

18.2E: Sympatric Speciation

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18.2A: The Biological Species Concept

Learning Objectives

- Explain the biological species concept

Species and the Ability to Reproduce

A species is a group of individual organisms that interbreed and produce fertile, viable offspring. According to this definition, one species is distinguished from another when, in nature, it is not possible for matings between individuals from each species to produce fertile offspring.

Members of the same species share both external and internal characteristics which develop from their DNA. The closer relationship two organisms share, the more DNA they have in common, just like people and their families. People's DNA is likely to be more like their father or mother's DNA than their cousin's or grandparent's DNA. Organisms of the same species have the highest level of DNA alignment and, therefore, share characteristics and behaviors that lead to successful reproduction.

Species' appearance can be misleading in suggesting an ability or inability to mate. For example, even though domestic dogs (*Canis lupus familiaris*) display phenotypic differences, such as size, build, and coat, most dogs can interbreed and produce viable puppies that can mature and sexually reproduce.



Figure 18.2A.1: Interbreeding in Dogs: Dogs of different breeds still have the ability to reproduce. The (a) poodle and (b) cocker spaniel can reproduce to produce a breed known as (c) the cockapoo.

In other cases, individuals may appear similar although they are not members of the same species. For example, even though bald eagles (*Haliaeetus leucocephalus*) and African fish eagles (*Haliaeetus vocifer*) are both birds and eagles, each belongs to a separate species group. If humans were to artificially intervene and fertilize the egg of a bald eagle with the sperm of an African fish eagle and a chick did hatch, that offspring, called a hybrid (a cross between two species), would probably be infertile: unable to successfully reproduce after it reached maturity. Different species may have different genes that are active in development; therefore, it may not be possible to develop a viable offspring with two different sets of directions. Thus, even though hybridization may take place, the two species still remain separate.



Figure 18.2A.1: Species Similarity & Reproduction: Species that appear similar may not be able to reproduce. The (a) African fish eagle is similar in appearance to the (b) bald eagle, but the two birds are members of different species.

Populations of species share a gene pool: a collection of all the variants of genes in the species. Again, the basis to any changes in a group or population of organisms must be genetic for this is the only way to share and pass on traits. When variations occur within a species, they can only be passed to the next generation along two main pathways: asexual reproduction or sexual reproduction. The change will be passed on asexually simply if the reproducing cell possesses the changed trait. For the changed trait to be passed on by sexual reproduction, a gamete, such as a sperm or egg cell, must possess the changed trait. In other words, sexually-reproducing organisms can experience several genetic changes in their body cells, but if these changes do not occur in a sperm or egg cell, the changed trait will never reach the next generation. Only heritable traits can evolve. Therefore, reproduction plays a paramount role for genetic change to take root in a population or species. In short, organisms must be able to reproduce with each other to pass new traits to offspring.

Key Points

- Members of the same species are similar both in their external appearance and their internal physiology; the closer the relationship between two organisms, the more similar they will be in these features.
- Some species can look very dissimilar, such as two very different breeds of dogs, but can still mate and produce viable offspring, which signifies that they belong to the same species.
- Some species may look very similar externally, but can be dissimilar enough in their genetic makeup that they cannot produce viable offspring and are, therefore, different species.
- Mutations can occur in any cell of the body, but if a change does not occur in a sperm or egg cell, it cannot be passed on to the organism's offspring.

Key Terms

- **species**: a group of organsms that, in nature, are capable of mating and producing viable, fertile offspring
- **hybrid**: offspring resulting from cross-breeding different entities, e.g. two different species or two purebred parent strains
- **gene pool**: the complete set of unique alleles that would be found by inspecting the genetic material of every living member of a species or population

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18.2B: Reproductive Isolation

Learning Objectives

- Explain how reproductive isolation can result in speciation

Reproductive Isolation

Given enough time, the genetic and phenotypic divergence between populations will affect characters that influence reproduction: if individuals of the two populations were to be brought together, mating would be improbable, but if mating did occur, offspring would be non-viable or infertile. Many types of diverging characters may affect reproductive isolation, the ability to interbreed, of the two populations. Reproductive isolation is a collection of mechanisms, behaviors, and physiological processes that prevent the members of two different species that cross or mate from producing offspring, or which ensure that any offspring that may be produced is not fertile.

Scientists classify reproductive isolation in two groups: prezygotic barriers and postzygotic barriers. Recall that a zygote is a fertilized egg: the first cell of the development of an organism that reproduces sexually. Therefore, a prezygotic barrier is a mechanism that blocks reproduction from taking place; this includes barriers that prevent fertilization when organisms attempt reproduction. A postzygotic barrier occurs after zygote formation; this includes organisms that don't survive the embryonic stage and those that are born sterile.

Some types of prezygotic barriers prevent reproduction entirely. Many organisms only reproduce at certain times of the year, often just annually. Differences in breeding schedules, called temporal isolation, can act as a form of reproductive isolation. For example, two species of frogs inhabit the same area, but one reproduces from January to March, whereas the other reproduces from March to May.



Figure $18.2B.1$: Temporal isolation: These two related frog species exhibit temporal reproductive isolation. (a) Rana aurora breeds earlier in the year than (b) Rana boylii.

In some cases, populations of a species move to a new habitat and take up residence in a place that no longer overlaps with other populations of the same species; this is called habitat isolation. Reproduction with the parent species ceases and a new group exists that is now reproductively and genetically independent. For example, a cricket population that was divided after a flood could no longer interact with each other. Over time, the forces of natural selection, mutation, and genetic drift will likely result in the divergence of the two groups.

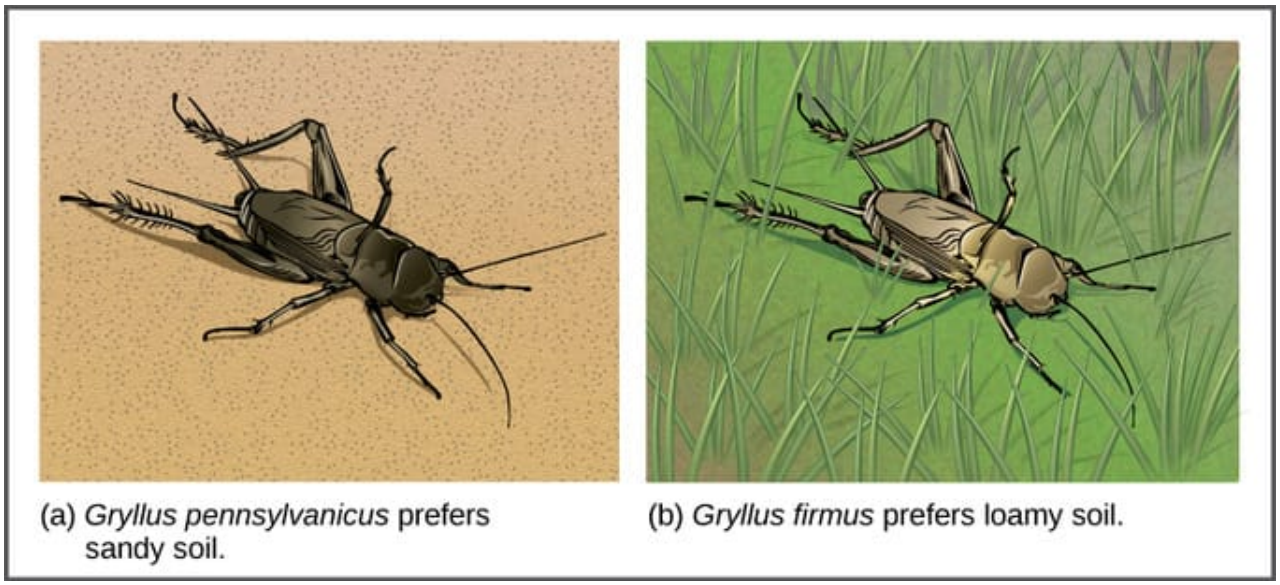


Figure $18.2B.1$: Habitat isolation: Speciation can occur when two populations occupy different habitats. The habitats need not be far apart. The cricket (a) Gryllus pennsylvanicus prefers sandy soil, while the cricket (b) Gryllus firmus prefers loamy soil. The two species can live in close proximity, but because of their different soil preferences, they became genetically isolated.

Behavioral isolation occurs when the presence or absence of a specific behavior prevents reproduction from taking place. For example, male fireflies use specific light patterns to attract females. Various species display their lights differently; if a male of one species tried to attract the female of another, she would not recognize the light pattern and would not mate with the male.

Other prezygotic barriers work when differences in their gamete cells prevent fertilization from taking place; this is called a gametic barrier. Similarly, in some cases, closely-related organisms try to mate, but their reproductive structures simply do not fit together. For example, damselfly males of different species have differently-shaped reproductive organs. If one species tries to mate with the female of another, their body parts simply do not fit together..

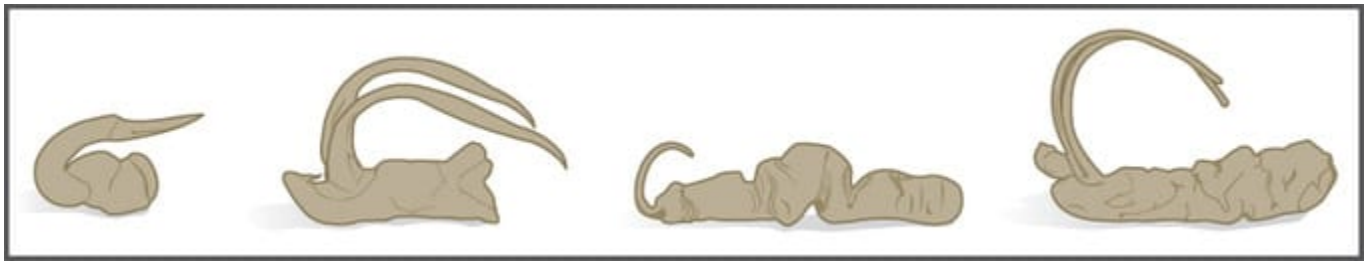


Figure $18.2B.1$: Differences in reproductive structures in male damselflies: The shape of the male reproductive organ varies among male damselfly species and is only compatible with the female of that species. Reproductive organ incompatibility keeps the species reproductively isolated.

In plants, certain structures aimed to attract one type of pollinator simultaneously prevent a different pollinator from accessing the pollen. The tunnel through which an animal must access nectar can vary in length and diameter, which prevents the plant from being cross-pollinated with a different species.

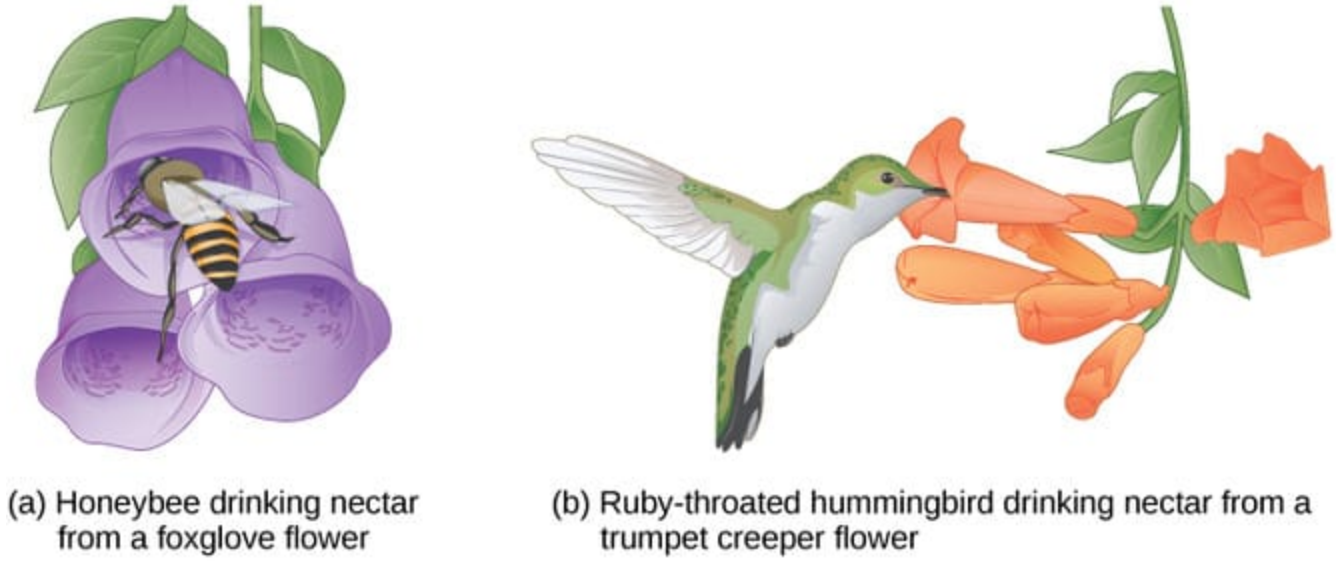


Figure $18.2B.1$: Reproductive isolation in plants: Some flowers have evolved to attract certain pollinators. The (a) wide foxglove flower is adapted for pollination by bees, while the (b) long, tube-shaped trumpet creeper flower is adapted for pollination by humming birds.

When fertilization takes place and a zygote forms, postzygotic barriers can prevent reproduction. Hybrid individuals in many cases cannot form normally in the womb and simply do not survive past the embryonic stages; this is called hybrid inviability. In another postzygotic situation, reproduction leads to the birth and growth of a hybrid that is sterile and unable to reproduce offspring of their own; this is called hybrid sterility.

Key Points

- Reproductive isolation can be either prezygotic (barriers that prevent fertilization) or postzygotic (barriers that occur after zygote formation such as organisms that die as embryos or those that are born sterile).
- Some species may be prevented from mating with each other by the incompatibility of their anatomical mating structures, or a resulting offspring may be prevented by the incompatibility of their gametes.
- Postzygotic barriers include the creation of hybrid individuals that do not survive past the embryonic stages (hybrid inviability) or the creation of a hybrid that is sterile and unable to produce offspring (hybrid sterility).
- Temporal isolation can result in species that are physically similar and may even live in the same habitat, but if their breeding schedules do not overlap then interbreeding will never occur.
- Behavioral isolation, in which the behaviors involved in mating are so unique as to prevent mating, is a prezygotic barrier that can cause two otherwise-compatible species to be uninterested in mating with each other.
- Behavioral isolation, in which the behaviors involved in mating are so unique as to prevent mating, is a prezygotic barrier that can cause two otherwise compatible species to be uninterested in mating with each other.

Key Terms

- **reproductive isolation**: a collection of mechanisms, behaviors, and physiological processes that prevent two different species that mate from producing offspring, or which ensure that any offspring produced is not fertile
- **temporal isolation**: factors that prevent potentially fertile individuals from meeting that reproductively isolate the members of distinct species
- **behavioral isolation**: the presence or absence of a specific behavior that prevents reproduction between two species from taking place
- **prezygotic barrier**: a mechanism that blocks reproduction from taking place by preventing fertilization
- **postzygotic barrier**: a mechanism that blocks reproduction after fertilization and zygote formation
- **hybrid inviability**: a situation in which a mating between two individuals creates a hybrid that does not survive past the embryonic stages
- **hybrid sterility**: a situation in which a mating between two individuals creates a hybrid that is sterile

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18.2C: Speciation

Learning Objectives

- Define speciation and discuss the ways in which it may occur

Speciation

The biological definition of species, which works for sexually-reproducing organisms, is a group of actually or potentially interbreeding individuals. 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 in nature of hybrids between similar species suggests that they may have descended from a single interbreeding species: 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*, which bears some resemblance to the more modern phylogenetic diagram of elephant evolution. The diagram shows that as one species changes over time, it branches repeatedly to form more than one new species as long as the population survives or until the organism becomes extinct.

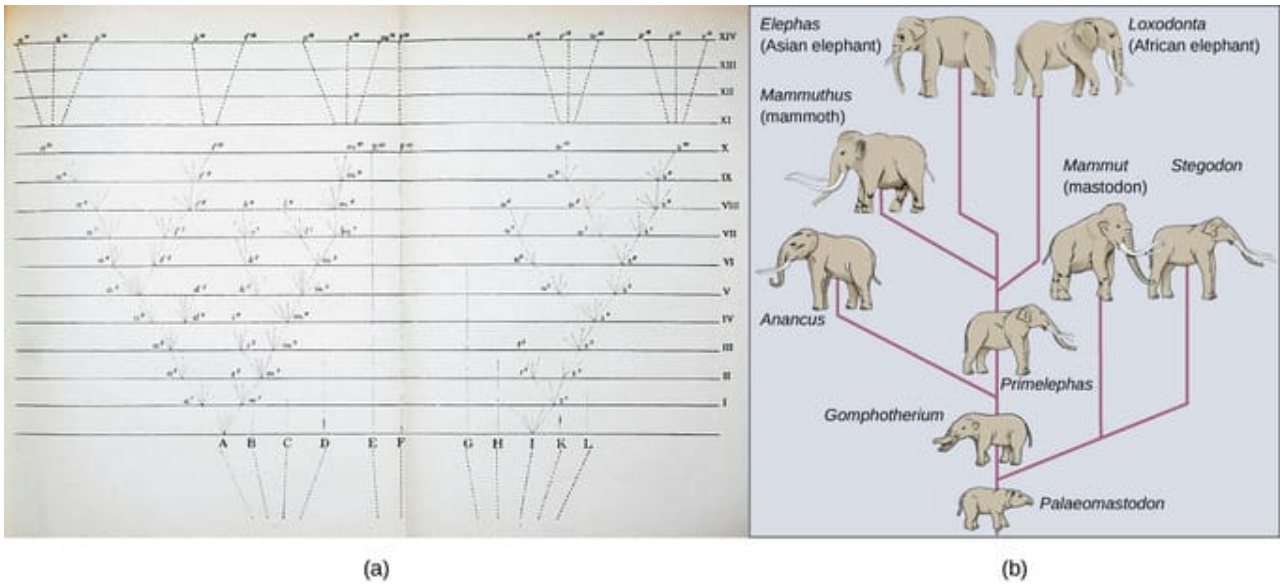


Figure 18.2C.1: The Evolution of Species: The only illustration in Darwin's On the Origin of Species is (a) a diagram showing speciation events leading to biological diversity. The diagram shows similarities to phylogenetic charts that are drawn today to illustrate the relationships of species. (b) Modern elephants evolved from the Palaeomastodon, a species that lived in Egypt 35–50 million years ago.

For speciation to occur, two new populations must be formed from one original population; 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 and sympatric speciation. Allopatric speciation (allo- = "other"; -patric = "homeland") involves geographic separation of populations from a parent species and subsequent evolution. Sympatric speciation (sym- = "same"; -patric = "homeland") involves speciation occurring within a parent species 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; multiple events can be conceptualized as single splits occurring close in time.

Key Points

- For the majority of species, the definition of a species is a group of animals that can potentially interbreed, although some different species are capable of producing hybrid offspring.
- Darwin was the first to envision speciation as the branching of two or more new species from one ancestral species; indicated by a diagram he made that bears a striking resemblance to modern-day phylogenetic diagrams.
- For a new species to be formed from an old species, certain events or changes must occur such that the new population is no longer capable of interbreeding with the old one.
- Speciation can occur either through allopatric speciation, when a population is geographically separated from one another, or through sympatric speciation, in which the two new species are not geographically separated.
- Speciation, the formation of two species from one original species, occurs as one species changes over time and branches to form more than one new species.

Key Terms

- **sympatric**: living in the same territory without interbreeding
- **allopatric**: not living in the same territory; geographically isolated and thus unable to crossbreed
- **speciation**: the process by which new distinct species evolve

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18.2D: Allopatric Speciation

Learning Objectives

- Give examples of allopatric speciation

Allopatric Speciation

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 continues for a period of time, the two populations are able to evolve along different trajectories. This is known as allopatric speciation. 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.

Isolation of populations leading to allopatric speciation can occur in a variety of ways: a river forming a new branch, erosion forming a new valley, a group of organisms traveling to a new location without the ability to return, or 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 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 improbable; therefore, speciation would be probably occur.

Biologists group allopatric processes into two categories: dispersal and vicariance. Dispersal occurs when a few members of a species move to a new geographical area, while vicariance occurs when a natural situation arises to physically divide organisms.

Scientists have documented numerous cases of allopatric speciation. For example, along the west coast of the United States, two separate sub-species 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.

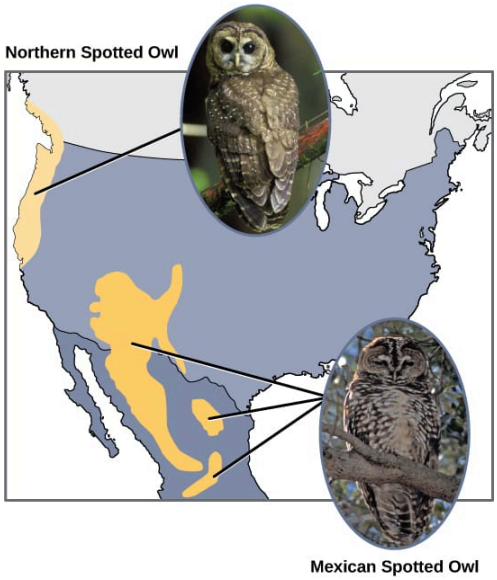


Figure $18.2D.1$: Allopatric speciation due to geographic separation: The northern spotted owl and the Mexican spotted owl inhabit geographically separate locations with different climates and ecosystems. The owl is an example of allopatric speciation.

Additionally, scientists have found that the further the distance between two groups that once were the same species, the more

probable it is that speciation will occur. This seems logical because as the distance increases, the various environmental factors would generally have less in common than locations in close proximity. Consider the two owls: in the north, the climate is cooler than in the south causing the types of organisms in each ecosystem differ, as do their behaviors and habits. Also, the hunting habits and prey choices of the southern owls vary from the northern owls. These variances can lead to evolved differences in the owls, resulting in speciation.

Adaptive Radiation

In some cases, a population of one species disperses throughout an area with each finding 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. This is called adaptive radiation because many adaptations evolve from a single point of origin, 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. The Hawaiian honeycreeper illustrates one example of adaptive radiation. From a single species, called the founder species, numerous species have evolved.

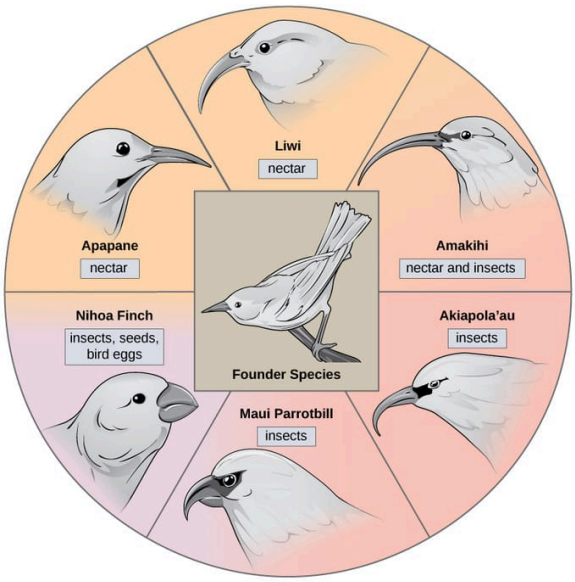


Figure $18.2D.1$: Adaptive Radiation: The honeycreeper birds illustrate adaptive radiation. From one original species of bird, multiple others evolved, each with its own distinctive characteristics.

In Hawaiian honeycreepers, the response to natural selection based on specific food sources in each new habitat led to the evolution of a different beak suited to the specific food source. The seed-eating birds have a thicker, stronger beak which is suited to break hard nuts. The nectar-eating birds have long beaks to dip into flowers to reach the nectar. The insect-eating birds have beaks like swords, appropriate for stabbing and impaling insects.

Key Points

- When a population is geographically continuous, the allele frequencies among its members are similar; however, when a population becomes separated, the allele frequencies between the two groups can begin to vary.
- If the separation between groups continues for a long period of time, the differences between their alleles can become more and more pronounced due to differences in climate, predation, food sources, and other factors, eventually leading to the formation of a new species.
- Geographic separation between populations can occur in many ways; the severity of the separation depends on the travel capabilities of the species.
- Allopatric speciation events can occur either by dispersal, when a few members of a species move to a new geographical area, or by vicariance, when a natural situation, such as the formation of a river or valley, physically divide organisms.
- When a population disperses throughout an area, into new, different and often isolated habitats, multiple speciation events can occur in which the single original species gives rise to many new species; this phenomenon is called adaptive radiation.

Key Terms

- **vicariance**: the separation of a group of organisms by a geographic barrier, resulting in differentiation of the original group into new varieties or species
- **adaptive radiation**: the diversification of species into separate forms that each adapt to occupy a specific environmental niche
- **dispersal**: the movement of a few members of a species to a new geographical area, resulting in differentiation of the original group into new varieties or species

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18.2E: Sympatric Speciation

Learning Objectives

- Give examples of sympatric speciation

Sympatric Speciation

Can divergence occur if no physical barriers are in place to separate individuals who continue to live and reproduce in the same habitat? The answer is yes. The process of speciation within the same space is called sympatric speciation. The prefix “sym” means same, so “sympatric” means “same homeland” in contrast to “allopatric” meaning “other homeland.” A number of mechanisms for sympatric speciation have been proposed and studied.

One form of sympatric speciation can begin with a serious chromosomal error during cell division. In a normal cell division event, chromosomes replicate, pair up, and then separate so that each new cell has the same number of chromosomes. However, sometimes the pairs separate and the end cell product has too many or too few individual chromosomes in a condition called aneuploidy.

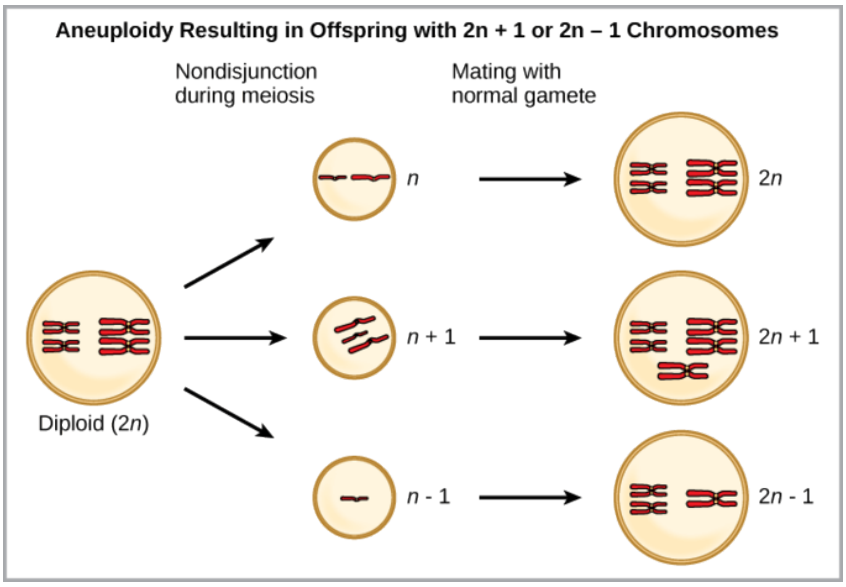


Figure $18.2E.1$: Aneuploidy of chromosomes: Aneuploidy results when the gametes have too many or too few chromosomes due to nondisjunction during meiosis. In the example shown here, the resulting offspring will have 2n+1 or 2n-1 chromosomes

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, or the inability to interbreed with normal individuals, of an individual in the polyploidy 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. 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.

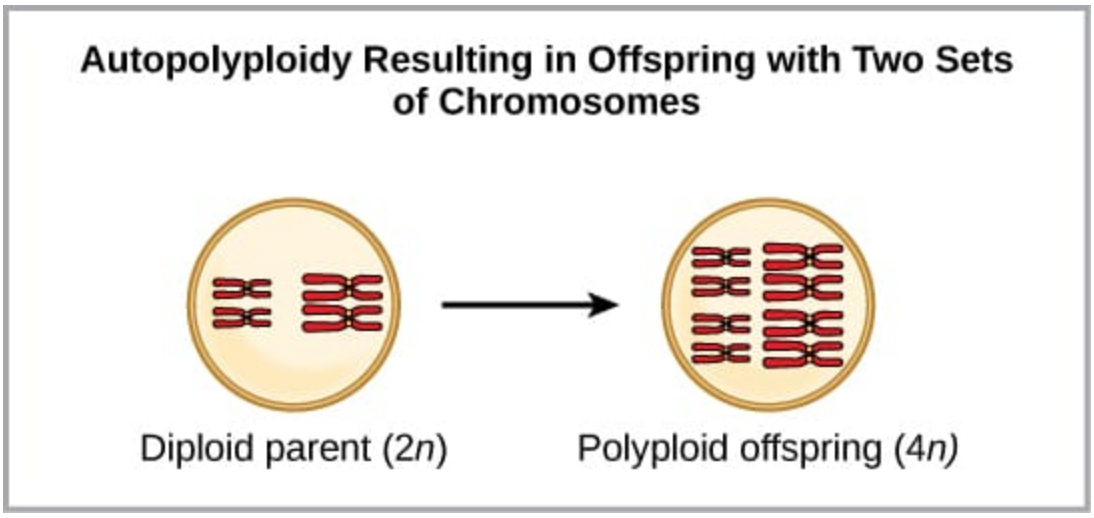


Figure $18.2E.1$: The generation of autopolyploidy: Autopolyploidy results when meiosis is not followed by cytokinesis.

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. However, 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: 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. Notice how it takes two generations, or two reproductive acts, before the viable fertile hybrid results.

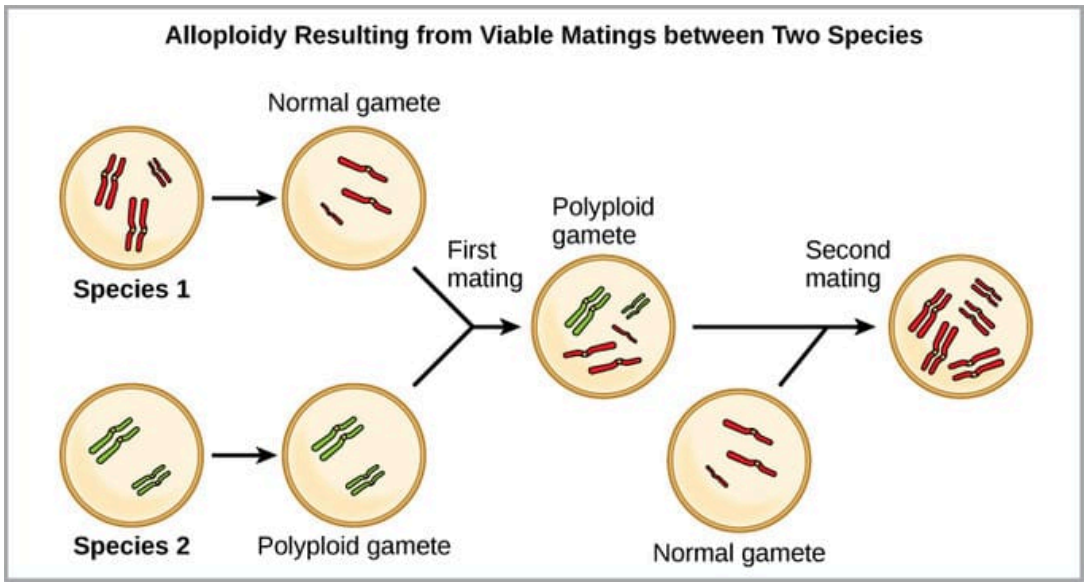


Figure $18.2E.1$: The generation of allopolyploidy: Alloploidy results when two species mate to produce viable offspring. In the example shown, a normal gamete from one species fuses with a polyploidy gamete from another. Two matings are necessary to produce viable offspring.

The cultivated forms of wheat, cotton, and tobacco plants are all allopolyploids. Although polyploidy occurs occasionally in animals, it takes place most commonly in plants. (Animals with any of the types of chromosomal aberrations described here are unlikely to survive and produce normal offspring.) Scientists have discovered more than half of all plant species studied relate back to a species evolved through polyploidy. With such a high rate of polyploidy in plants, some scientists hypothesize that this mechanism takes place more as an adaptation than as an error.

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Key Points

- Sympatric speciation can occur when one individual develops an abnormal number of chromosomes, either extra chromosomes (polyploidy) or fewer, such that viable interbreeding can no longer occur.
- When the extra sets of chromosomes in a polyploid originate with the individual because their own gametes do not undergo cytokinesis after meiosis, the result is autopolyploidy.
- When individuals of two different species reproduce to form a viable offspring, such that the extra chromosomes come from two different species, the result is an allopolyploid.
- Once a species develops an abnormal number of chromosomes, it can then only interbreed with members of the population that have the same abnormal number, which can lead to the development of a new species.

Key Terms

- **sympatric speciation**: the process through which new species evolve from a single ancestral species while inhabiting the same geographic region
- **autopolyploid**: having more than two sets of chromosomes, derived from the same species, as a result of redoubling
- **allopolyploid**: having multiple complete sets of chromosomes derived from different species

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18.3: HYBRID ZONES AND RATES OF SPECIATION

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- Topic hierarchy

18.3A: Hybrid Zones
18.3B: Varying Rates of Speciation

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18.3A: Hybrid Zones

Learning Objectives

- Discuss how the fitness of a hybrid will lead to changes in the hybrid zone over time

Reconnection After Speciation

Speciation occurs over a span of evolutionary time. When a new species arises, there is a transition period during which the closely-related species continue to interact.

After speciation, two species may recombine or even continue interacting indefinitely. Individual organisms will mate with any nearby individual with which they are capable of breeding. An area where two closely-related species continue to interact and reproduce, forming hybrids, is called a hybrid zone. Over time, the hybrid zone may change depending on the fitness strength and the reproductive barriers of the hybrids.

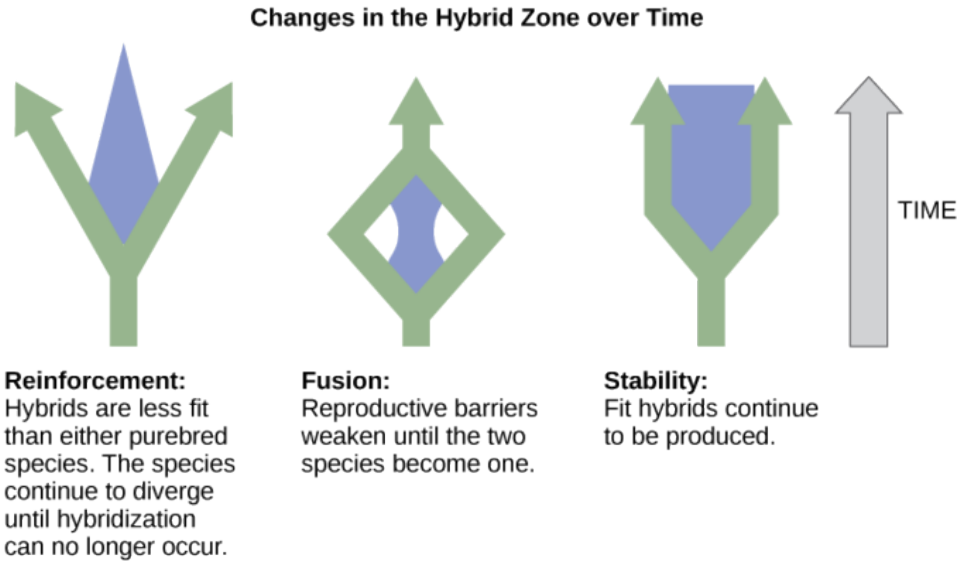


Figure 18.3A.1: Speciation and the Hybrid Zone: After speciation has occurred, the two separate-but-closely-related species may continue to produce offspring in an area called the hybrid zone. Reinforcement, fusion, or stability may result, depending on reproductive barriers and the relative fitness of the hybrids.

Hybrids can have less fitness, more fitness, or about the same fitness level as the purebred parents. Usually, hybrids tend to be less fit; therefore, reproduction to produce hybrids will diminish over time, which nudges the two species to diverge further in a process called reinforcement. This term is used because the low success of the hybrids reinforces the original speciation. If the hybrids are less fit than the parents, reinforcement of speciation occurs, and the species will continue to diverge until they can no longer mate and produce viable offspring.

If the hybrids are as fit or more fit than the parents, or the reproductive barriers weaken, the two species may fuse back into one species (reconnection). For a hybrid form to persist, it will generally have to be able to exploit the available resources better than either parent species, with which, in most cases, it will have to compete.

Over time, via a process called hybrid speciation, the hybrids themselves can become a separate species. Reproductive isolation between hybrids and their parents was once thought to be particularly difficult to achieve; thus, hybrid species were thought to be extremely rare. With DNA analysis becoming more accessible in the 1990s, hybrid speciation has been shown to be a fairly common phenomenon, particularly in plants.

Scientists have also observed that sometimes two species will remain separate, but continue to interact to produce some hybrid individuals; this is classified as stability because no real net change is taking place. For a hybrid zone to be stable, the offspring produced by the hybrids have to be less fit than members of the parent species.

Key Points

- After speciation, or sufficient evolutionary change for one species to become two distinct species, the two species may continue to co-habitate and interact.
- The area in which two closely-related species interact and reproduce is known as the hybrid zone; their offspring are known as hybrids.
- Depending on the fitness of the hybrid offspring relative to the parents, the two species may either stay as two distinct species (reinforcement), or become one species again (reconnection).

Key Terms

- **hybrid zone**: an area where the ranges of two interbreeding species meet and interbreed
- **hybrid speciation**: the formation of a new species as the direct result of mating between members of two existing species
- **reconnection**: a convergence of two species over time

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18.3B: Varying Rates of Speciation

Learning Objectives

- Explain how the interaction of an organism's population size in association with environmental changes can lead to different rates of speciation

Varying Rates of Speciation

Scientists around the world study speciation, documenting observations both of living organisms and those found in the fossil record. As their ideas take shape and as research reveals new details about how life evolves, they develop models to help explain rates of speciation. In terms of how quickly speciation occurs, two patterns are currently observed: the gradual speciation model and the punctuated equilibrium model.

In the gradual speciation model, species diverge gradually over time in small steps. In the punctuated equilibrium model, a new species changes quickly from the parent species and then remains largely unchanged for long periods of time afterward. This early change model is called punctuated equilibrium, because it begins with a punctuated or periodic change and then remains in balance afterward. While punctuated equilibrium suggests a faster tempo, it does not necessarily exclude gradualism.

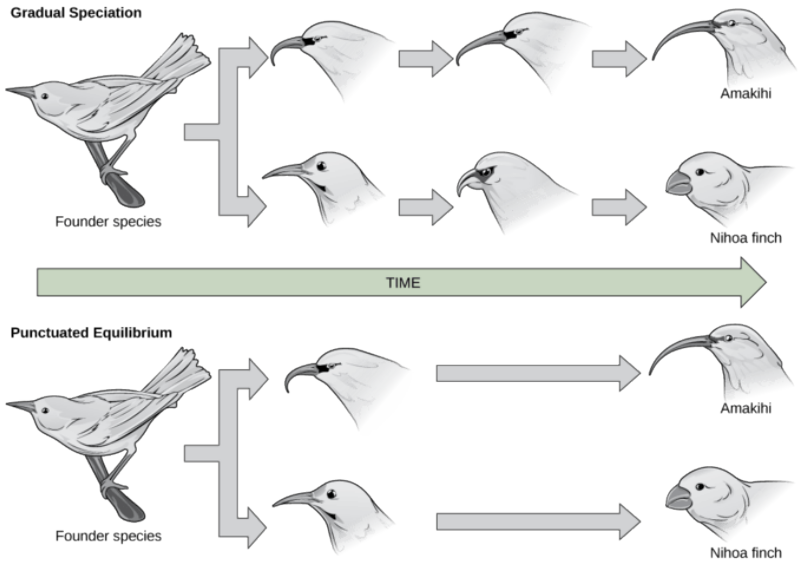


Figure $18.3B.1$: Graduated Speciation vs Punctuated Equilibrium: In (a) gradual speciation, species diverge at a slow, steady pace as traits change incrementally. In (b) punctuated equilibrium, species diverge quickly and then remain unchanged for long periods of time.

The primary influencing factor on changes in speciation rate is environmental conditions. Under some conditions, selection occurs quickly or radically. Consider a species of snails that had been living with the same basic form for many thousands of years. Layers of their fossils would appear similar for a long time. When a change in the environment takes place, such as a drop in the water level, a small number of organisms are separated from the rest in a brief period of time, essentially forming one large and one tiny population. The tiny population faces new environmental conditions. Because its gene pool quickly became so small, any variation that surfaces and that aids in surviving the new conditions becomes the predominant form.

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Key Points

- In the gradual speciation model, species diverge slowly over time in small steps while in the punctuated equilibrium model, a new species diverges rapidly from the parent species.
- The two key influencing factors on the change in speciation rate are the environmental conditions and the population size.
- Gradual speciation is most likely to occur in large populations that live in a stable environment, while the punctuation equilibrium model is more likely to occur in a small population with rapid environmental change.

Key Terms

- **punctuated equilibrium**: a theory of evolution holding that evolutionary change tends to be characterized by long periods of stability, with infrequent episodes of very fast development
- **gradualism**: in evolutionary biology, belief that evolution proceeds at a steady pace, without the sudden development of new species or biological features from one generation to the next

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18.4: EVOLUTION OF GENOMES

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- Topic hierarchy

18.4A: Genomic Similiarities between Distant Species

18.4B: Genome Evolution

18.4C: Whole-Genome Duplication

18.4D: Gene Duplications and Divergence

18.4E: Noncoding DNA

18.4F: Variations in Size and Number of Genes

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18.4A: Genomic Similiarities between Distant Species

Learning Objectives

- Discuss the evolutionary implications of observed genome similarities between distant species

Genomic Similarities Between Distant Species

Genetic distance refers to the genetic divergence between species or between populations within a species. Smaller genetic distances indicate that the populations have more similar genes, which indicates they are closely related; they have a recent common ancestor, or recent interbreeding has taken place. Genetic distance is useful in reconstructing the history of populations. For example, evidence from genetic distance suggests that humans arrived in America about 30,000 years ago. By examining the difference between allele frequencies between the populations, genetic distance can estimate how long ago the two populations were together.

Phylogenetic Relationships

Phylogeny describes the relationships of an organism, such as the relationship with its ancestors and the species it is most closely related. Phylogenetic relationships provide information on shared ancestry but not necessarily on how organisms are similar or different. The use of advanced genomic analysis has allowed us to establish phylogenetic trees, which map the relationship between species at a genetic and molecular level. The ability to use these technologies has established previously unknown relationships and has contributed to a more complex evolutionary history. These technologies have established genomic similarities between distant species by establishing genetic distances. In addition, the mechanisms by which genomic similarities between distant species occur can include horizontal gene transfer.

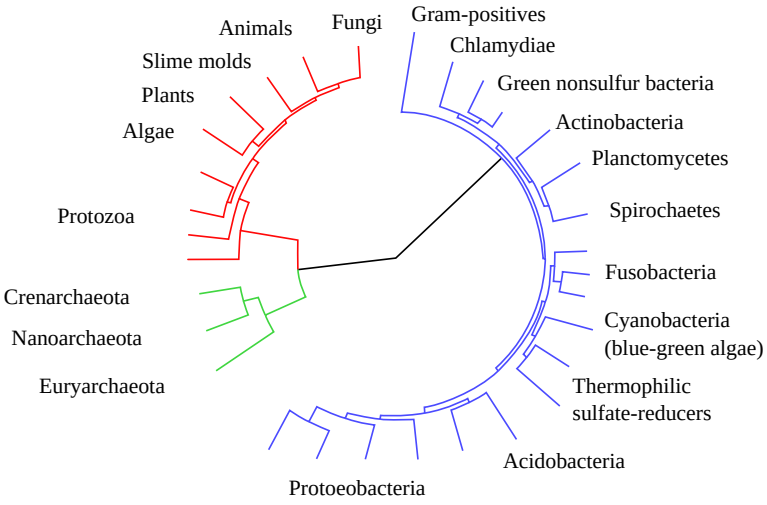


Figure 18.4A.1: Tree of Life: Diagrammatic representation of the divergence of modern taxonomic groups from their common ancestor. This shows the genomic similarities that can exist between distant species based on their relationship with this ancestor.

Horizontal Gene Transfer

Horizontal gene transfer (HGT), also known as lateral gene transfer, is the transfer of genes between unrelated species. Genes have been shown to be passed between species which are only distantly related using standard phylogeny, thus adding a layer of complexity to the understanding of phylogenetic relationships. The various ways that HGT occurs in prokaryotes is important

to understanding phylogenies. Although at present, HGT is not viewed as important to eukaryotic evolution, HGT does occur in this domain as well. Finally, as an example of the ultimate gene transfer, theories of genome fusion between symbiotic or endosymbiotic organisms have been proposed to explain an event of great importance—the evolution of the first eukaryotic cell, without which humans could not have come into existence.

The mechanism of HGT has been shown to be quite common in the prokaryotic domains of Bacteria and Archaea, significantly changing the way their evolution is viewed. The majority of evolutionary models, such as in the endosymbiont theory, propose that eukaryotes descended from multiple prokaryotes, which makes HGT all the more important to understanding the phylogenetic relationships of all extant and extinct species. These gene transfers between species are the major mechanism whereby bacteria acquire resistance to antibiotics. Classically, this type of transfer has been thought to occur by three different mechanisms: transformation, transduction and conjugation.

Although it is easy to see how prokaryotes exchange genetic material by HGT, it was initially thought that this process was absent in eukaryotes, followed by the idea that the gene transfers between multicellular eukaryotes should be more difficult. In spite of this fact, HGT between distantly related organisms has been demonstrated in several eukaryotic species.

In animals, a particularly interesting example of HGT occurs within the aphid species. Aphids are insects that vary in color based on carotenoid content. Carotenoids are pigments made by a variety of plants, fungi, and microbes, and they serve a variety of functions in animals, who obtain these chemicals from their food. Humans require carotenoids to synthesize vitamin A, and we obtain them by eating orange fruits and vegetables: carrots, apricots, mangoes, and sweet potatoes. On the other hand, aphids have acquired the ability to make the carotenoids on their own. According to DNA analysis, this ability is due to the transfer of fungal genes into the insect by HGT, presumably as the insect consumed fungi for food.



Figure 18.4A.1: Horizontal Gene Transfer in Animals: (a) Red aphids get their color from red carotenoid pigment. Genes necessary to make this pigment are present in certain fungi, and scientists speculate that aphids acquired these genes through HGT after consuming fungi for food. If genes for making carotenoids are inactivated by mutation, the aphids revert back to (b) their green color. Red coloration makes the aphids a lot more conspicuous to predators, but evidence suggests that red aphids are more resistant to insecticides than green ones. Thus, red aphids may be more fit to survive in some environments than green ones.

Key Points

- Genomic similarities between distant species can be explained by the theory that all organisms share a common ancestor.
- Genomic similarities between distant species can be analysed using genomic analysis tools to create phylogenetic trees that explain these relationships.
- Genetic distance is used to explain the genetic divergence between species or between populations within a species and can indicate how closely related they are and whether they have a recent common ancestor or recent interbreeding has taken place.
- Horizontal gene transfer (HGT) occurs when two unrelated species exchange genes, usually two prokaryotes, although HGT occurs in some eurokaryotes as well.

Key Terms

- **conjugation**: the temporary fusion of organisms, especially as part of sexual reproduction
- **phylogeny**: the evolutionary history of an organism
- **horizontal gene transfer**: the transfer of genetic material from one organism to another one that is not its offspring; especially common among bacteria
- **transformation**: the alteration of a bacterial cell caused by the transfer of DNA from another, especially if pathogenic
- **transduction**: horizontal gene transfer mechanism in prokaryotes where genes are transferred using a virus

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18.4B: Genome Evolution

Learning Objectives

- Explain the importance of genomic changes in an evolutionary context

Accumulating Changes Over Time

The evolution of the genome is characterized by the accumulation of changes. The analaysis of genomes and their changes in sequence or size over time involves various fields. There are various mechanisms that have contributed to genome evolution and these include gene and genome duplications, polyploidy, mutation rates, transposable elements, pseudogenes, exon shuffling and genomic reduction and gene loss. The concepts of gene and whole-genome duplication are discussed as their own independent concepts, thus, the focus will be on other mechanisms.

Mutation Rates

Mutation rates differ between species and even between different regions of the genome of a single species. Spontaneous mutations often occur which can cause various changes in the genome. Mutations can result in the addition or deletion of one or more nucleotide bases. A change in the code can result in a frameshift mutation which causes the entire code to be read in the wrong order and thus often results in a protein becoming non-functional. A mutation in a promoter region, enhancer region or a region coding for transcription factors can also result in either a loss of function or and upregulation or downregulation in transcription of that gene. Mutations are constantly occurring in an organism's genome and can cause either a negative effect, positive effect or no effect at all.

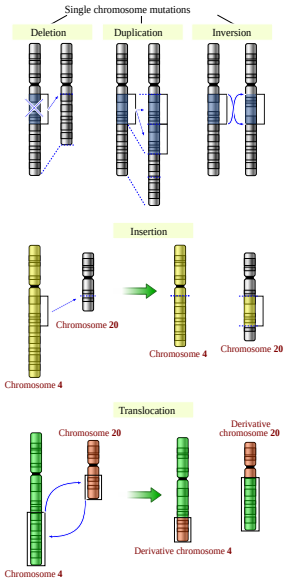


Figure $18.4B.1$: Chromosomal Mutations: Chromosomal mutations over time can accumulate and promote diversity and evolution if a produced trait is favorable.

Transposable Elements

Transposable elements are regions of DNA that can be inserted into the genetic code through one of two mechanisms. These mechanisms work similarly to "cut-and-paste" and "copy-and-paste" functionalities in word processing programs. The "cut-and-paste" mechanism works by excising DNA from one place in the genome and inserting itself into another location in the code. The "copy-and-paste" mechanism works by making a genetic copy or copies of a specific region of DNA and inserting these copies

elsewhere in the code. The most common transposable element in the human genome is the Alu sequence, which is present in the genome over one million times.

Pseudogenes

Often a result of spontaneous mutation, pseudogenes are dysfunctional genes derived from previously functional gene relatives. There are many mechanisms by which a functional gene can become a pseudogene including the deletion or insertion of one or multiple nucleotides. This can result in a shift of reading frame, causing the gene to longer code for the expected protein, a premature stop codon or a mutation in the promoter region. Often cited examples of pseudogenes within the human genome include the once functional olfactory gene families. Over time, many olfactory genes in the human genome became pseudogenes and were no longer able to produce functional proteins, explaining the poor sense of smell humans possess in comparison to their mammalian relatives.

Exon Shuffling

Exon shuffling is a mechanism by which new genes are created. This can occur when two or more exons from different genes are combined together or when exons are duplicated. Exon shuffling results in new genes by altering the current intron-exon structure. This can occur by any of the following processes: transposon mediated shuffling, sexual recombination or illegitimate recombination. Exon shuffling may introduce new genes into the genome that can be either selected against and deleted or selectively favored and conserved.

Genome Reduction and Gene Loss

Many species exhibit genome reduction when subsets of their genes are not needed anymore. This typically happens when organisms adapt to a parasitic life style, e.g. when their nutrients are supplied by a host. As a consequence, they lose the genes need to produce these nutrients. In many cases, there are both free living and parasitic species that can be compared and their lost genes identified. Good examples are the genomes of Mycobacterium tuberculosis and Mycobacterium leprae, the latter of which has a dramatically reduced genome. Another beautiful example are endosymbiont species. For instance, Polynucleobacter necessarius was first described as a cytoplasmic endosymbiont of the ciliate Euplotes aediculatus. The latter species dies soon after being cured of the endosymbiont. In the few cases in which P. necessarius is not present, a different and rarer bacterium apparently supplies the same function. No attempt to grow symbiotic P. necessarius outside their hosts has yet been successful, strongly suggesting that the relationship is obligate for both partners. Yet, closely related free-living relatives of P. necessarius have been identified. The endosymbionts have a significantly reduced genome when compared to their free-living relatives (1.56 Mbp vs. 2.16 Mbp).

Key Points

- Gene and whole genome duplications have contributed accumulations that have contributed to genome evolution.
- Mutations are constantly occurring in an organism's genome and can cause either a negative effect, positive effect or no effect at all; however, it will still result in changes to the genome.
- Transposable elements are regions of DNA that can be inserted into the genetic code and will causes changes within the genome.
- Pseudogenes are dysfunctional genes derived from previously functional gene relatives and will become a pseudogene by deletion or insertion of one or multiple nucleotides.
- Exon shuffling occurs when two or more exons from different genes are combined together or when exons are duplicated, and will result in new genes.
- Species can also exhibit genome reduction when subsets of their genes are not needed anymore.

Key Terms

- **intron**: a portion of a split gene that is included in pre-RNA transcripts but is removed during RNA processing and rapidly degraded
- **exon**: a region of a transcribed gene present in the final functional RNA molecule
- **pseudogene**: a segment of DNA that is part of the genome of an organism, and which is similar to a gene but does not code

for a gene product

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18.4C: Whole-Genome Duplication

Learning Objectives

- State the evolutionary implications of whole-genome duplication

Whole-Genome Duplication

Gene duplication is the process by which a region of DNA coding for a gene creates additional copies of the gene. Similar to gene duplication, whole-genome duplication is the process by which an organism's entire genetic information is copied, once or multiple times, which is known as polyploidy. This may provide an evolutionary benefit to the organism by supplying it with multiple copies of a gene, thus, creating a greater possibility of functional and selectively favored genes.

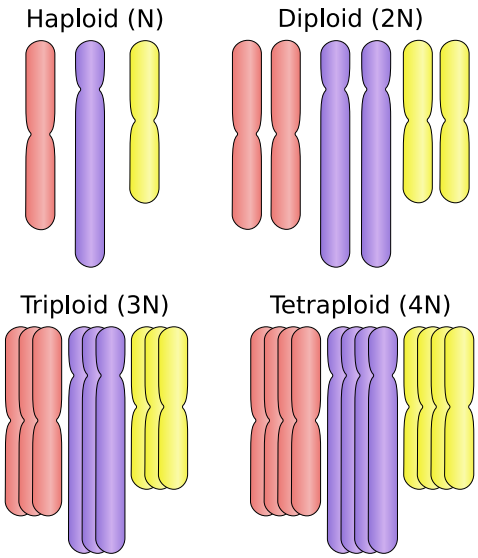


Figure $18.4C.1$: Polyploidy: This image shows haploid (single), diploid (double), triploid (triple), and tetraploid (quadruple) sets of chromosomes. Triploid and tetraploid chromosomes are examples of polyploidy.

Evolutionary importance

Paleopolyploidization events lead to massive cellular changes, including doubling of the genetic material, changes in gene expression and increased cell size. Gene loss during diploidization is not completely random, but heavily selected. Genes from large gene families are duplicated. On the other hand, individual genes are not duplicated. Overall, paleopolyploidy can have both short-term and long-term evolutionary effects on an organism's fitness in the natural environment.

Genome diversity

Genome doubling provides organisms with redundant alleles that can evolve freely with little selection pressure. The duplicated genes can undergo neofunctionalization or subfunctionalization which could help the organism adapt to the new environment or survive different stress conditions.

Speciation

Sympatric speciation can begin with a chromosomal error during meiosis or the formation of a hybrid individual with too many

chromosomes, such as polyploidy which can occur during whole-genome duplication. Scientists have identified 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. 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.

It has been suggested that many polyploidization events created new species, via a gain of adaptive traits, or by sexual incompatibility with their diploid counterparts. An example would be the recent speciation of allopolyploid Spartina — S. anglica; the polyploid plant is so successful that it is listed as an invasive species in many regions.

Evidence of Whole-Genome Duplication

In 1997, Wolfe & Shields gave evidence for an ancient duplication of the *Saccharomyces cerevisiae* (Yeast) genome. It was initially noted that this yeast genome contained many individual gene duplications. Wolfe & Shields hypothesized that this was actually the result of an entire genome duplication in the yeast’s distant evolutionary history. They found 32 pairs of homologous chromosomal regions, accounting for over half of the yeast’s genome. They also noted that although homologs were present, they were often located on different chromosomes. Based on these observations, they determined that *Saccharomyces cerevisiae* underwent a whole-genome duplication soon after its evolutionary split from *Kluyveromyces*, a genus of ascomycetous yeasts. Over time, many of the duplicate genes were deleted and rendered non-functional. A number of chromosomal rearrangements broke the original duplicate chromosomes into the current manifestation of homologous chromosomal regions.

Key Points

- Whole- genome duplication can provide an evolutionary advantage by providing the organism with multiple copies of a gene that is considered favorable.
- Whole-genome duplication can result in divergence and formation of new species over time.
- Whole-genome duplication can result in mutation and cause disease if the genes are rendered non-functional.

Key Terms

- **polyploidy**: having more than the usual two homologous sets of chromosomes
- **palaeopolyploidization**: the development of polyploid organisms in the geologic past
- **sympatric speciation**: the process through which new species evolve from a single ancestral species while inhabiting the same geographic region

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18.4D: Gene Duplications and Divergence

Learning Objectives

- Explain the mechanisms of gene duplication and divergence

Gene Duplication

Gene duplication is the process by which a region of DNA coding for a gene is copied. Gene duplication can occur as the result of an error in recombination or through a retrotransposition event. Duplicate genes are often immune to the selective pressure under which genes normally exist. This can result in a large number of mutations accumulating in the duplicate gene code. This may render the gene non-functional or in some cases confer some benefit to the organism. There are multiple mechanisms by which gene duplication can occur.

Ectopic Recombination

Duplications can arise from unequal crossing-over that occurs during meiosis between misaligned homologous chromosomes. The product of this recombination is a duplication at the site of the exchange and a reciprocal deletion. Ectopic recombination is typically mediated by sequence similarity at the duplicate breakpoints, which form direct repeats. Repetitive genetic elements, such as transposable elements, offer one source of repetitive DNA that can facilitate recombination, and they are often found at duplication breakpoints in plants and mammals.

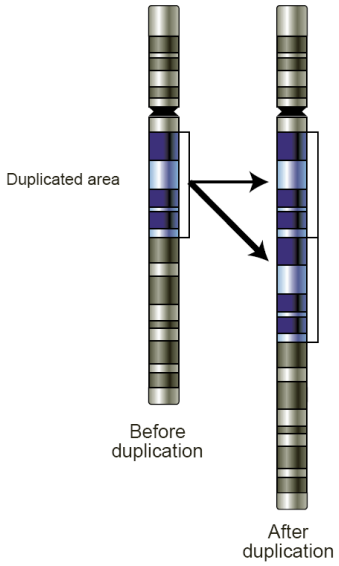


Figure $18.4D.1$: Gene Duplication: This figure indicates a schematic of a region of a chromosome before and after a duplication event. Ectopic recombination is typically mediated by sequence similarity at the duplicate breakpoints, which form direct repeats.

Replication Slippage

Replication slippage is an error in DNA replication, which can produce duplications of short genetic sequences. During replication, DNA polymerase begins to copy the DNA, and at some point during the replication process, the polymerase dissociates from the DNA and replication stalls. When the polymerase reattaches to the DNA strand, it aligns the replicating strand to an incorrect position and incidentally copies the same section more than once. Replication slippage is also often facilitated by repetitive sequence but requires only a few bases of similarity.

Retrotransposition

During cellular invasion by a replicating retroelement or retrovirus, viral proteins copy their genome by reverse transcribing RNA to DNA. If viral proteins attach irregularly to cellular mRNA, they can reverse-transcribe copies of genes to create retrogenes. Retrogenes usually lack intronic sequence and often contain poly A sequences that are also integrated into the genome. Many retrogenes display changes in gene regulation in comparison to their parental gene sequences, which sometimes results in novel functions.

Aneuploidy

Aneuploidy occurs when nondisjunction at a single chromosome results in an abnormal number of chromosomes. Aneuploidy is often harmful and in mammals regularly leads to spontaneous abortions. Some aneuploid individuals are viable. For example, trisomy 21 in humans leads to Down syndrome, but it is not fatal. Aneuploidy often alters gene dosage in ways that are detrimental to the organism and therefore, will not likely spread through populations.

Gene duplication as an evolutionary event

Gene duplications are an essential source of genetic novelty that can lead to evolutionary innovation. Duplication creates genetic redundancy and if one copy of a gene experiences a mutation that affects its original function, the second copy can serve as a 'spare part' and continue to function correctly. Thus, duplicate genes accumulate mutations faster than a functional single-copy gene, over generations of organisms, and it is possible for one of the two copies to develop a new and different function. This is an examples of neofunctionalization.

Gene duplication is believed to play a major role in evolution; this stance has been held by members of the scientific community for over 100 years. It has been argued that gene duplication is the most important evolutionary force since the emergence of the universal common ancestor.

Another possible fate for duplicate genes is that both copies are equally free to accumulate degenerative mutations, so long as any defects are complemented by the other copy. This leads to a neutral "subfunctionalization" model, in which the functionality of the original gene is distributed among the two copies. Neither gene can be lost, as both now perform important non-redundant functions, but ultimately neither is able to achieve novel functionality. Subfunctionalization can occur through neutral processes in which mutations accumulate with no detrimental or beneficial effects. However, in some cases subfunctionalization can occur with clear adaptive benefits. If an ancestral gene is pleiotropic and performs two functions, often times neither one of these two functions can be changed without affecting the other function. In this way, partitioning the ancestral functions into two separate genes can allow for adaptive specialization of subfunctions, thereby providing an adaptive benefit.

Divergence

Genetic divergence is the process in which two or more populations of an ancestral species accumulate independent genetic changes through time, often after the populations have become reproductively isolated for some period of time. In some cases, subpopulations living in ecologically distinct peripheral environments can exhibit genetic divergence from the remainder of a population, especially where the range of a population is very large. The genetic differences among divergent populations can involve silent mutations (that have no effect on the phenotype) or give rise to significant morphological and/or physiological changes. Genetic divergence will always accompany reproductive isolation, either due to novel adaptations via selection and/or due to genetic drift, and is the principal mechanism underlying speciation.

Genetic drift or allelic drift is the change in the frequency of a gene variant (allele) in a population due to random sampling. The alleles in the offspring are a sample of those in the parents, and chance has a role in determining whether a given individual survives and reproduces. A population's allele frequency is the fraction of the copies of one gene that share a particular form. Genetic drift may cause gene variants to disappear completely and thereby reduce genetic variation. When there are few copies of an allele, the effect of genetic drift is larger, and when there are many copies the effect is smaller. These changes in gene frequency can contribute to divergence.

Divergent evolution is usually a result of diffusion of the same species to different and isolated environments, which blocks the gene flow among the distinct populations allowing differentiated fixation of characteristics through genetic drift and natural selection.Divergent evolution can also be applied to molecular biology characteristics. This could apply to a pathway in two or

more organisms or cell types. This can apply to genes and proteins, such as nucleotide sequences or protein sequences that are derived from two or more homologous genes. Both orthologous genes (resulting from a speciation event) and paralogous genes (resulting from gene duplication within a population) can be said to display divergent evolution.

Key Points

- Ectopic recombination occurs when there is an unequal crossing-over and the product of this recombination are a duplication at the site of the exchange and a reciprocal deletion.
- Gene duplications do not always result in detrimental mutations; they can contribute to divergent evolution, which causes genetic differences between groups to develop and eventually form new species.
- Replication slippage can occur when there is an error during DNA replication and duplications of short genetic sequences are produced.
- Retrotranspositions occur when a retrovirus copies their genome by reverse transcribing RNA to DNA and aberrantly attach to cellular mRNA and reverse transcribe copies of genes to create retrogenes.
- Aneuploidy can occur when there is a nondisjunction even at a single chromosome thus, the result is an abnormal number of chromosomes.
- Genetic divergence can occur by mechanisms such as genetic drift which contibute to the accumulation of independent genetic changes of two or more populations derived from a common ancestor.

Key Terms

- **paralogous**: having a similar structure indicating divergence from a common ancestral gene
- **nondisjunction**: the failure of chromosome pairs to separate properly during meiosis
- **retrogene**: a DNA gene copied back from RNA by reverse transcription
- **genetic drift**: an overall shift of allele distribution in an isolated population, due to random fluctuations in the frequencies of individual alleles of the genes

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18.4E: Noncoding DNA

Learning Objectives

- Summarize the importance of noncoding DNA

Noncoding DNA

In genomics and related disciplines, noncoding DNA sequences are components of an organism's DNA that do not encode protein sequences. Some noncoding DNA is transcribed into functional noncoding RNA molecules (e.g. transfer RNA, ribosomal RNA, and regulatory RNAs), while others are not transcribed or give rise to RNA transcripts of unknown function. The amount of noncoding DNA varies greatly among species. For example, over 98% of the human genome is noncoding DNA, while only about 2% of a typical bacterial genome is noncoding DNA.

Initially, a large proportion of noncoding DNA had no known biological function and was therefore sometimes referred to as "junk DNA", particularly in the lay press. However, many types of noncoding DNA sequences do have important biological functions, including the transcriptional and translational regulation of protein-coding sequences, origins of DNA replication, centromeres, telomeres, scaffold attachment regions (SARs), genes for functional RNAs, and many others. Other noncoding sequences have likely, but as-yet undetermined, functions. Some sequences may have no biological function for the organism, such as endogenous retroviruses.

Genomic Variation between Organisms

The amount of total genomic DNA varies widely between organisms, and the proportion of coding and noncoding DNA within these genomes varies greatly as well. More than 98% of the human genome does not encode protein sequences, including most sequences within introns and most intergenic DNA. While overall genome size, and by extension the amount of noncoding DNA, are correlated to organism complexity, there are many exceptions. For example, the genome of the unicellular Polychaos dubium (formerly known as Amoeba dubia) has been reported to contain more than 200 times the amount of DNA in humans. The pufferfish Takifugu rubripes genome is only about one eighth the size of the human genome, yet seems to have a comparable number of genes; approximately 90% of the Takifugu genome is noncoding DNA.

In 2013, a new "record" for most efficient genome was discovered. Utricularia gibba, a bladderwort plant, has only 3% noncoding DNA. The extensive variation in nuclear genome size among eukaryotic species is known as the C-value enigma or C-value paradox. Most of the genome size difference appears to lie in the noncoding DNA. About 80 percent of the nucleotide bases in the human genome may be transcribed, but transcription does not necessarily imply function.



Figure $18.4E.1$: Utricularia gibba flower: Utricularia gibba has 3% noncoding DNA, which is low for flowering plants. This 3% has given this plant the title the 'most efficient' genome.

Key Points

- In the human genome, over 98% of DNA is classified as noncoding DNA and can be transcribed to regulatory noncoding RNAs (i.e. tRNAs, rRNAs), origins of DNA replication, centromeres, telomeres and scaffold attachment regions (SARs).
- Noncoding regions are most commonly referred to as 'junk DNA', however, this term is misleading as noncoding DNA does have functional importance.
- The proportion of coding and noncoding DNA within organisms varies and the amount of noncoding DNA typically correlates with organism complexity, though there are many notable exceptions.

Key Terms

- **intergenic**: describing the noncoding sections of nucleic acid between genes
- **noncoding**: DNA which does not code for protein
- **intron**: a portion of a split gene that is included in pre-RNA transcripts but is removed during RNA processing and rapidly degraded

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18.4F: Variations in Size and Number of Genes

Learning Objectives

- Describe how variations in the size and number of genes can arise through evolutionary mechanisms

Variations in Size and Number of Genes

Genetic diversity refers to any variation in the nucleotides, genes, chromosomes, or whole genomes of organisms. Genetic diversity at its most elementary level is represented by differences in the sequences of nucleotides (adenine, cytosine, guanine, and thymine) that form the DNA (deoxyribonucleic acid) within the cells of the organism. The DNA is contained in the chromosomes present within the cell; some chromosomes are contained within specific organelles in the cell (for example, the chromosomes of mitochondria and chloroplast). Nucleotide variation is measured for discrete sections of the chromosomes, called genes. Thus, each gene compromises a hereditary section of DNA that occupies a specific place of the chromosome, and controls a particular characteristic of an organism.

Chromosomes

Most organisms are diploid, having two sets of chromosomes, and therefore two copies (called alleles) of each gene. However, some organisms can be haploid, triploid, or tetraploid (having one, three, or four sets of chromosomes respectively). Within any single organism, there may be variation between the two (or more) alleles for each gene. This variation is introduced either through mutation of one of the alleles, or as a result of sexual reproduction.

During sexual reproduction, offspring inherit alleles from both parents and these alleles might be slightly different, especially if there has been migration or hybridization of organisms, so that the parents may come from different populations and gene pools. Also, when the offspring's chromosomes are copied after fertilization, genes can be exchanged in a process called sexual recombination. Harmless mutations and sexual recombination may allow the evolution of new characteristics.

Genome Size and Number

Genome size is usually measured in base pairs (or bases in single-stranded DNA or RNA). The C-value is another measure of genome size. The C-value refers to the amount, in picograms, of DNA contained within a haploid nucleus (e.g. a gamete) or one half the amount in a diploid somatic cell of a eukaryotic organism. In some cases (notably among diploid organisms), the terms C-value and genome size are used interchangeably, however in polyploids the C-value may represent two or more genomes contained within the same nucleus.

Different species can have different numbers of genes within the entire DNA or genome of the organism. However, a greater total number of genes might not correspond with a greater observable complexity in the anatomy and physiology of the organism (i.e. greater phenotypic complexity). For example, the predicted size of the human genome is not much larger than the genomes of some invertebrates and plants, and may even be smaller than the Indian rice genome. In humans, more proteins are encoded per gene than in other species. In prokaryotic genomes, research has shown that there is a significant positive correlation between the C-value of prokaryotes and the amount of genes that compose the genome. This indicates that gene number is the main factor influencing the size of the prokaryotic genome.

Genes vs Genome Size

In eukaryotic organisms, there is a paradox observed, namely that the number of genes that make up the genome does not correlate with genome size. In other words, the genome size is much larger than would be expected given the total number of protein coding genes. Genome size can increase by duplication, insertion, or polyploidization and the process of recombination can lead to both DNA loss or gain. It is also possible that genomes can shrink due to deletions.

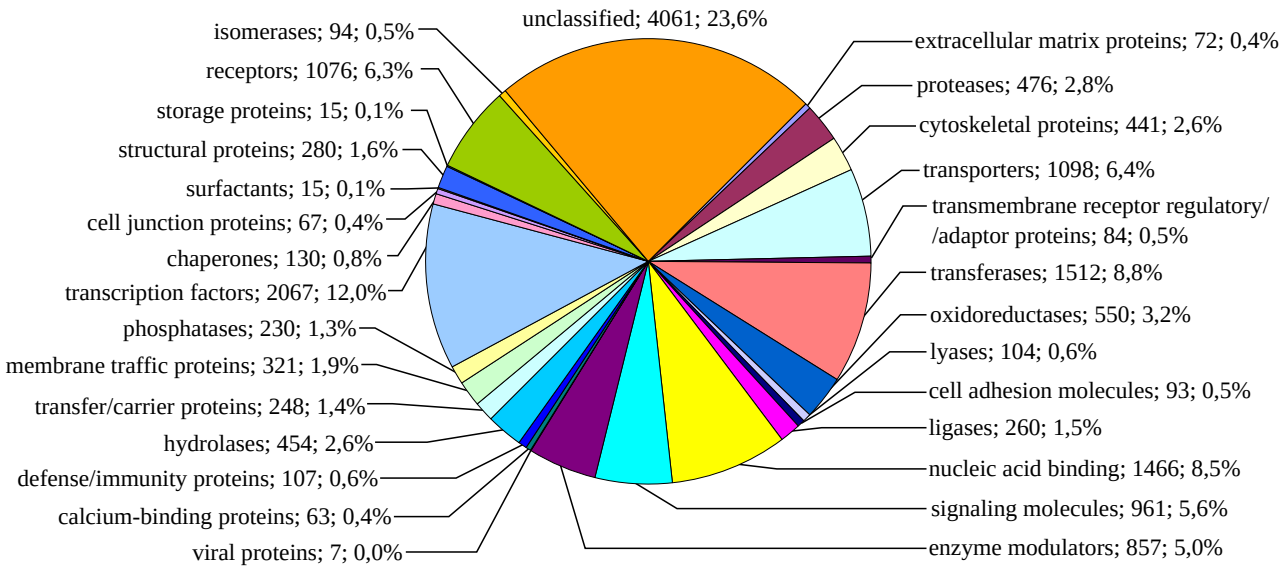


Figure $18.4F.1$: Gene variation in the Genome: This figure represents the human genome, categorized by function of each gene product, given both as number of genes and as percentage of all genes. Importantly, genome size does not necessarily correlate with complexity.

A famous example for such gene decay is the genome of Mycobacterium leprae, the causative agent of leprosy. M.leprae has lost many once-functional genes over time due to the formation of pseudogenes. This is evident in looking at its closest ancestor Mycobacterium tuberculosis. M. leprae lives inside and replicates inside of a host and due to this arrangement it does not have a need for many of the genes it once carried which allowed it to live and prosper outside of the host. Thus over time these genes have lost their function through mechanisms such as mutation causing them to become pseudogenes. It is beneficial to an organism to rid itself of non-essential genes because it makes replicating its DNA much faster and more energy-efficient.

An example of increasing genome size over time is seen in filamentous plant pathogens. These plant pathogen genomes have been growing larger over the years due to repeat-driven expansion. The repeat-rich regions contain genes coding for host interaction proteins. With the addition of more and more repeats to these regions the plants increase the possibility of developing new virulence factors through mutation and other forms of genetic recombination. In this way it is beneficial for these plant pathogens to have larger genomes.

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Key Points

- Harmless mutations and sexual recombination of chromosomes may allow the evolution of new characteristics.
- Genome size can be affected by various events, including duplication, insertion, recombination, deletion and polyploidization events.
- Genome size can be affected by evolution of an organism and result is an increased or decreased need for specific genes for survival based on behavior.
- The human genome exemplifies the concept that complexity does not always correlate with an increase in genome size; there are fewer protein coding genes present than expected relative to the genome size.

Key Terms

- **polyploidization**: hybridization that leads to polyploidy
- **pseudogene**: a segment of DNA that is part of the genome of an organism, and which is similar to a gene but does not code for a gene product
- **genome**: the cell's complete genetic information packaged as a double-stranded DNA molecule

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18.5: EVIDENCE OF EVOLUTION

- Topic hierarchy

18.5A: The Fossil Record as Evidence for Evolution

18.5B: Fossil Formation

18.5C: Gaps in the Fossil Record

18.5D: Carbon Dating and Estimating Fossil Age

18.5E: The Fossil Record and the Evolution of the Modern Horse

18.5F: Homologous Structures

18.5G: Convergent Evolution

18.5H: Vestigial Structures

18.5I: Biogeography and the Distribution of Species

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18.5A: The Fossil Record as Evidence for Evolution

Learning Objectives

- Synthesize the contributions of the fossil record to our understanding of evolution

What Fossils Tell Us

Fossils are the preserved remains or traces of animals, plants, and other organisms from the past. Fossils range in age from 10,000 to 3.48 billion years old. The observation that certain fossils were associated with certain rock strata led 19th century geologists to recognize a geological timescale. Like extant organisms, fossils vary in size from microscopic, like single-celled bacteria, to gigantic, like dinosaurs and trees.



Figure 18.5A.1: "Sue" T-rex skeleton: The bones of this Tyrannosaurus rex were preserved through the process of permineralization, which suggests that this organism was covered by sediment soon after death.

Permineralization

Permineralization is a process of fossilization that occurs when an organism is buried. The empty spaces within an organism (spaces filled with liquid or gas during life) become filled with mineral-rich groundwater. Minerals precipitate from the groundwater, occupying the empty spaces. This process can occur in very small spaces, such as within the cell wall of a plant cell. Small-scale permineralization can produce very detailed fossils. For permineralization to occur, the organism must be covered by sediment soon after death, or soon after the initial decay process.

The degree to which the remains are decayed when covered determines the later details of the fossil. Fossils usually consist of the portion of the organisms that was partially mineralized during life, such as the bones and teeth of vertebrates or the chitinous or calcareous exoskeletons of invertebrates. However, other fossils contain traces of skin, feathers or even soft tissues.

Trace Fossils

Fossils may also consist of the marks left behind by the organism while it was alive, such as footprints or feces. These types of fossils are called trace fossils, or ichnofossils, as opposed to body fossils. Past life may also leave some markers that cannot be seen but can be detected in the form of biochemical signals; these are known as chemofossils or biomarkers.



Figure 18.5A.1: Dinosaur footprints: Footprints are examples of trace fossils, which contribute to the fossil record.

The Fossil Record

The totality of fossils, both discovered and undiscovered, and their placement in fossiliferous (fossil-containing) rock formations and sedimentary layers (strata) is known as the fossil record. The fossil record was one of the early sources of data underlying the study of evolution and continues to be relevant to the history of life on Earth. The development of radiometric dating techniques in the early 20th century allowed geologists to determine the numerical or "absolute" age of various strata and their included fossils.

Evidence for Evolution

Fossils provide solid evidence that organisms from the past are not the same as those found today; fossils show a progression of evolution. Fossils, along with the comparative anatomy of present-day organisms, constitute the morphological, or anatomical, record. By comparing the anatomies of both modern and extinct species, paleontologists can infer the lineages of those species. This approach is most successful for organisms that had hard body parts, such as shells, bones or teeth. The resulting fossil record tells the story of the past and shows the evolution of form over millions of years.

Key Points

- Fossils are the preserved remains or traces of animals, plants, and other organisms from the past.
- Fossils are important evidence for evolution because they show that life on earth was once different from life found on earth today.
- Usually only a portion of an organism is preserved as a fossil, such as body fossils (bones and exoskeletons), trace fossils (feces and footprints), and chemofossils (biochemical signals).
- Paleontologists can determine the age of fossils using methods like radiometric dating and categorize them to determine the evolutionary relationships between organisms.

Key Terms

- **biomarker**: A substance used as an indicator of a biological state, most commonly disease.
- **trace fossil**: A type of fossil reflecting the reworking of sediments and hard substrates by organisms including structures like burrows, trails, and impressions.
- **fossil record**: All discovered and undiscovered fossils and their placement in rock formations and sedimentary layers.
- **strata**: Layers of sedimentary rock.
- **fossiliferous**: Containing fossils.

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18.5B: Fossil Formation

Learning Objectives

- Predict the conditions suitable to fossil formation

Fossil Formation

The process of a once living organism becoming a fossil is called fossilization. Fossilization is a very rare process, and of all the organisms that have lived on Earth, only a tiny percentage of them ever become fossils. To see why, imagine an antelope that dies on the African plain. Most of its body is quickly eaten by scavengers, and the remaining flesh is soon eaten by insects and bacteria, leaving behind only scattered bones. As the years go by, the bones are scattered and fragmented into small pieces, eventually turning into dust and returning their nutrients to the soil. As a result, it would be rare for any of the antelope's remains to actually be preserved as a fossil.

Fossilization can occur in many ways. Most fossils are preserved in one of five processes:

- preserved remains
- permineralization
- molds and casts
- replacement
- compression

Preserved Remains

The rarest form of fossilization is the preservation of original skeletal material and even soft tissue. For example, some insects have been preserved perfectly in amber, which is ancient tree sap. In addition, several mammoths and even a Neanderthal hunter have been discovered frozen in glaciers. These preserved remains allow scientists the rare opportunity to examine the skin, hair, and organs of ancient creatures. Scientists have collected DNA from these remains and compared the DNA sequences to those of modern creatures.



Figure $18.5B.1$: Amber: The image depicts a gnat preserved in amber. A lot of insects have been found to be perfectly maintained in this ancient tree sap.

Permineralization

The most common method of fossilization is permineralization. After a bone, wood fragment, or shell is buried in sediment, it may be exposed to mineral-rich water that moves through the sediment. This water will deposit minerals, typically silica, into empty spaces, producing a fossil. Fossilized dinosaur bones, petrified wood, and many marine fossils were formed by permineralization.



Figure $18.5B.1$: Permineralization: These fossils from the Road Canyon Formation (Middle Permian of Texas) have been silicified (replaced with silica), which is a form of permineralization.

Molds and Casts

In some cases, the original bone or shell dissolves away, leaving behind an empty space in the shape of the shell or bone. This depression is called a mold. Later, the space may be filled with other sediments to form a matching cast in the shape of the original organism. Many mollusks (bivalves, snails, and squid) are commonly found as molds and casts because their shells dissolve easily.

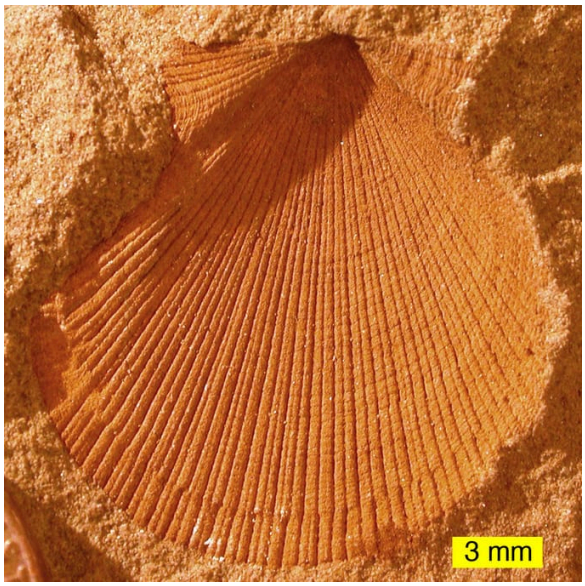


Figure $18.5B.1$: Molds: The depression in the image is an external mold of a bivalve from the Logan Formation, Lower Carboniferous, Ohio

Replacement

In some cases, the original shell or bone dissolves away and is replaced by a different mineral. For example, shells that were originally calcite may be replaced by dolomite, quartz, or pyrite. If quartz fossils are surrounded by a calcite matrix, the calcite can be dissolved away by acid, leaving behind an exquisitely preserved quartz fossil. When permineralization and replacement occur together, the organism is said to have undergone petrification, the process of turning organic material into stone. However, replacement can occur without permineralization and vice versa.

Compression

Some fossils form when their remains are compressed by high pressure. This can leave behind a dark imprint of the fossil. Compression is most common for fossils of leaves and ferns but also can occur with other organisms.

Conditions for Fossilization

Following the death of an organism, several forces contribute to the dissolution of its remains. Decay, predators, or scavengers will typically rapidly remove the flesh. The hard parts, if they are separable at all, can be dispersed by predators, scavengers, or currents. The individual hard parts are subject to chemical weathering and erosion, as well as to splintering by predators or scavengers, which will crunch up bones for marrow and shells to extract the flesh inside. Also, an animal swallowed whole by a predator, such as a mouse swallowed by a snake, will have not just its flesh but some, and perhaps all, its bones destroyed by the gastric juices of the predator.

It would not be an exaggeration to say that the typical vertebrate fossil consists of a single bone, or tooth, or fish scale. The preservation of an intact skeleton with the bones in the relative positions they had in life requires a remarkable circumstances, such as burial in volcanic ash, burial in aeolian sand due to the sudden slumping of a sand dune, burial in a mudslide, burial by a turbidity current, and so forth. The mineralization of soft parts is even less common and is seen only in exceptionally rare chemical and biological conditions.

Key Points

- Preservation of remains in amber or other substances is the rarest from of fossilization; this mechanism allows scientists to study the skin, hair, and organs of ancient creatures.
- Permineralization, where minerals like silica fill the empty spaces of shells, is the most common form of fossilization.
- Molds form when shells or bones dissolve, leaving behind an empty depression; a cast is then formed when the depression is filled by sediment.
- Replacement occurs when the original shell or bone dissolves away and is replaced by a different mineral; when this occurs with permineralization, it is called petrification.
- In compression, the most common form of fossilization of leaves and ferns, a dark imprint of the fossil remains.
- Decay, chemical weathering, erosion, and predators are factors that deter fossilization.
- Fossilization of soft body parts is rare, and hard parts are better preserved when buried.

Key Terms

- **amber**: a hard, generally yellow to brown translucent fossil resin
- **permineralization**: form of fossilization in which minerals are deposited in the pores of bone and similar hard animal parts
- **petrification**: process by which organic material is converted into stone through the replacement of the original material and the filling of the original pore spaces with minerals

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18.5C: Gaps in the Fossil Record

Learning Objectives

- Explain the gap in the fossil record

Incompleteness of the Fossil Record

Each fossil discovery represents a snapshot of the process of evolution. Because of the specialized and rare conditions required for a biological structure to fossilize, many important species or groups may never leave fossils at all. Even if they do leave fossils, humans may never find them—for example, if they are buried under hundreds of feet of ice in Antarctica. The number of species known about through the fossil record is less than 5% of the number of species alive today. Fossilized species may represent less than 1% of all the species that have ever lived.

Types of Fossils in the Fossil Record

The fossil record is very uneven and is mostly comprised of fossils of organisms with hard body parts, leaving most groups of soft-bodied organisms with little to no fossil record. Groups considered to have a good fossil record, including transitional fossils between these groups, are the vertebrates, the echinoderms, the brachiopods, and some groups of arthropods. Their hard bones and shells fossilize easily, unlike the bodies of organisms like cephalopods or jellyfish.

Romer's Gap

Romer's gap is an example of an apparent gap in the tetrapod fossil record used in the study of evolutionary biology. These gaps represent periods from which no relevant fossils have been found. Romer's gap is named after paleontologist Alfred Romer, who first recognized it. Romer's gap spanned from approximately 360 to 345 million years ago, corresponding to the first 15 million years of the Carboniferous Period.



Figure $18.5C.1$: Romer's Gap: The bank of the Whiteadder Water in Scotland is one of the few known localities bearing fossils of tetrapods from Romer's gap.

There has been much debate over why there are so few fossils from this time period. Some scientists have suggested that the geochemistry of the time period caused bad conditions for fossil formation, so few organisms were fossilized. Another theory

suggests that scientists have simply not yet discovered an excavation site for these fossils, due to inaccessibility or random chance.

Key Points

- The number of species known about through fossils is less than 1% of all species that have ever lived.
- Because hard body parts are more easily preserved than soft body parts, there are more fossils of animals with hard body parts, such as vertebrates, echinoderms, brachiopods, and some groups of arthropods.
- Very few fossils have been found in the period from 360 to 345 million years ago, known as Romer's gap. Theories to explain this include the period's geochemistry, errors in excavation, and limited vertebrate diversity.

Key Terms

- **transitional fossil**: Fossilized remains of a life form that exhibits traits common to both an ancestral group and its derived descendant group.
- **Romer's gap**: A period in the tetrapod fossil record (360 to 345 million years ago) from which excavators have not yet found relevant fossils.

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18.5D: Carbon Dating and Estimating Fossil Age

Learning Objectives

- Summarize the available methods for dating fossils

Determining Fossil Ages

Paleontology seeks to map out how life evolved across geologic time. A substantial hurdle is the difficulty of working out fossil ages. There are several different methods for estimating the ages of fossils, including:

1. stratigraphy
2. biostratigraphy
3. carbon dating

Stratigraphy

Paleontologists rely on stratigraphy to date fossils. Stratigraphy is the science of understanding the strata, or layers, that form the sedimentary record. Strata are differentiated from each other by their different colors or compositions and are exposed in cliffs, quarries, and river banks. These rocks normally form relatively horizontal, parallel layers, with younger layers forming on top.

If a fossil is found between two layers of rock whose ages are known, the fossil's age is thought to be between those two known ages. Because rock sequences are not continuous, but may be broken up by faults or periods of erosion, it is difficult to match up rock beds that are not directly adjacent.



Figure $18.5D.1$: Sedimentary layers: The layers of sedimentary rock, or strata, can be seen as horizontal bands of differently colored or differently structured materials exposed in this cliff. The deeper layers are older than the layers found at the top, which aids in determining the relative age of fossils found within the strata.

Biostratigraphy

Fossils of species that survived for a relatively short time can be used to match isolated rocks: this technique is called biostratigraphy. For instance, the extinct chordate *Eoplacognathus pseudoplanus* is thought to have existed during a short range

in the Middle Ordovician period. If rocks of unknown age have traces of *E. pseudoplanus*, they have a mid-Ordovician age. Such index fossils must be distinctive, globally distributed, and occupy a short time range to be useful. Misleading results can occur if the index fossils are incorrectly dated.

Relative Dating

Stratigraphy and biostratigraphy can in general provide only relative dating (A was before B), which is often sufficient for studying evolution. This is difficult for some time periods, however, because of the barriers involved in matching rocks of the same age across continents. Family-tree relationships can help to narrow down the date when lineages first appeared. For example, if fossils of B date to X million years ago and the calculated "family tree" says A was an ancestor of B, then A must have evolved earlier.

It is also possible to estimate how long ago two living branches of a family tree diverged by assuming that DNA mutations accumulate at a constant rate. However, these "molecular clocks" are sometimes inaccurate and provide only approximate timing. For example, they are not sufficiently precise and reliable for estimating when the groups that feature in the Cambrian explosion first evolved, and estimates produced by different approaches to this method may vary as well.

Carbon Dating

Together with stratigraphic principles, radiometric dating methods are used in geochronology to establish the geological time scale. Beds that preserve fossils typically lack the radioactive elements needed for radiometric dating (" radiocarbon dating " or simply "carbon dating"). The principle of radiocarbon dating is simple: the rates at which various radioactive elements decay are known, and the ratio of the radioactive element to its decay products shows how long the radioactive element has existed in the rock. This rate is represented by the half-life, which is the time it takes for half of a sample to decay.

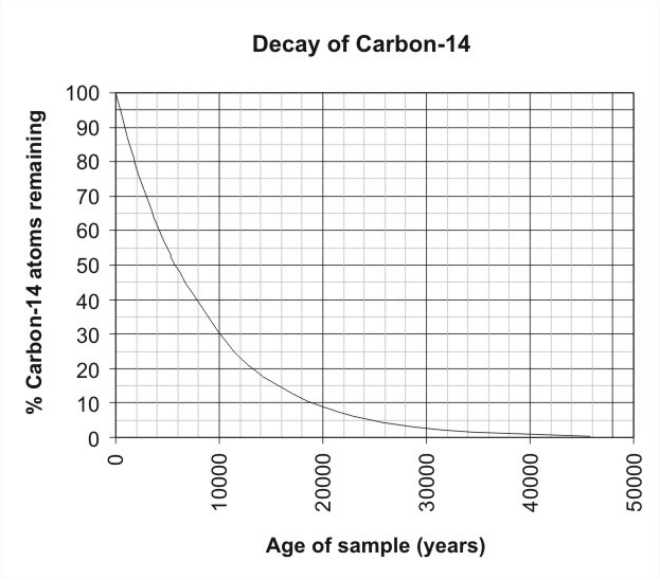


Figure $18.5D.1$: Half-life of Carbon-14: Radiometric dating is a technique used to date materials such as rocks or carbon, usually based on a comparison between the observed abundance of a naturally occurring radioactive isotope and its decay products, using known decay rates.

The half-life of carbon-14 is 5,730 years, so carbon dating is only relevant for dating fossils less than 60,000 years old. Radioactive elements are common only in rocks with a volcanic origin, so the only fossil-bearing rocks that can be dated radiometrically are volcanic ash layers. Carbon dating uses the decay of carbon-14 to estimate the age of organic materials, such as wood and leather.

Key Points

- Determining the ages of fossils is an important step in mapping out how life evolved across geologic time.
- The study of stratigraphy enables scientists to determine the age of a fossil if they know the age of layers of rock that surround it.

- Biostratigraphy enables scientists to match rocks with particular fossils to other rocks with those fossils to determine age.
- Paleontology seeks to map out how life evolved across geologic time. A substantial hurdle is the difficulty of working out fossil ages.
- Scientists use carbon dating when determining the age of fossils that are less than 60,000 years old, and that are composed of organic materials such as wood or leather.

Key Terms

- **half-life**: The time required for half of the nuclei in a sample of a specific isotope to undergo radioactive decay.
- **stratigraphy**: The study of rock layers and the layering process.
- **radiocarbon dating**: A method of estimating the age of an artifact or biological vestige based on the relative amounts of various isotopes of carbon present in a sample.

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18.5E: The Fossil Record and the Evolution of the Modern Horse

Learning Objectives

- Analyze the fossil record to understand the evolution of horses

Fossils provide evidence that organisms from the past are not the same as those found today, and demonstrate a progression of evolution. Scientists date and categorize fossils 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 forms over millions of years.

Case Study: Evolution of the Modern Horse

Highly detailed fossil records have been recovered for sequences in the evolution of modern horses. The fossil record of horses in North America is especially rich and contains transition fossils: fossils that show intermediate stages between earlier and later forms. The fossil record extends back to a dog-like ancestor some 55 million years ago, which gave rise to the first horse-like species 55 to 42 million years ago in the genus *Eohippus*.

The first equid fossil was found in the gypsum quarries in Montmartre, Paris in the 1820s. The tooth was sent to the Paris Conservatory, where Georges Cuvier identified it as a browsing equine related to the tapir. His sketch of the entire animal matched later skeletons found at the site. During the H.M.S. Beagle survey expedition, Charles Darwin had remarkable success with fossil hunting in Patagonia. In 1833 in Santa Fe, Argentina, he was "filled with astonishment" when he found a horse's tooth in the same stratum as fossils of giant armadillos and wondered if it might have been washed down from a later layer, but concluded this was "not very probable." In 1836, the anatomist Richard Owen confirmed the tooth was from an extinct species, which he subsequently named *Equus curvidens*.

The original sequence of species believed to have evolved into the horse was based on fossils discovered in North America in the 1870s by paleontologist Othniel Charles Marsh. The sequence, from *Eohippus* to the modern horse (*Equus*), was popularized by Thomas Huxley and became one of the most widely known examples of a clear evolutionary progression. The sequence of transitional fossils was assembled by the American Museum of Natural History into an exhibit that emphasized the gradual, "straight-line" evolution of the horse.

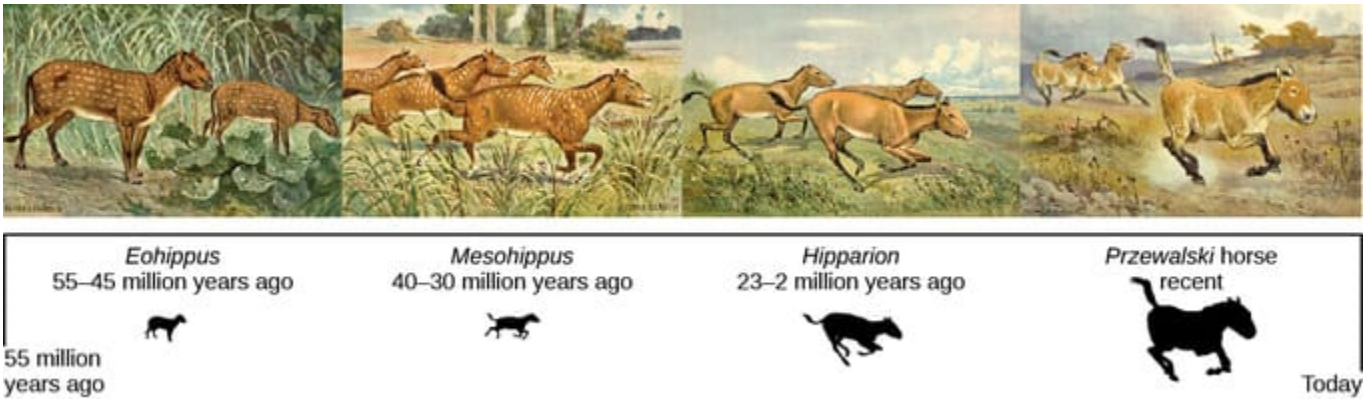


Figure $18.5E.1$: Horse evolution: This illustration shows an artist's renderings of species derived from fossils of the evolutionary history of the horse and its ancestors. The species depicted are only four from a very diverse lineage that contains many branches, dead ends, and adaptive radiations. 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.

Since then, as the number of equid fossils has increased, the actual evolutionary progression from *Eohippus* to *Equus* has been discovered to be much more complex and multibranched than was initially supposed. Detailed fossil information on the rate and distribution of new equid species has also revealed that the progression between species was not as smooth and consistent as

was once believed.

Although some transitions were indeed gradual progressions, a number of others were relatively abrupt in geologic time, taking place over only a few million years. Both anagenesis, a gradual change in an entire population ‘s gene frequency, and cladogenesis, a population “splitting” into two distinct evolutionary branches, occurred, and many species coexisted with “ancestor” species at various times.

Adaptation for Grazing

The series of fossils tracks the change in anatomy resulting from a gradual drying trend that changed the landscape from a forested habitat to a prairie habitat. Early horse ancestors were originally specialized for tropical forests, while modern horses are now adapted to life on drier land. Successive fossils show the evolution of teeth shapes and foot and leg anatomy to a grazing habit with adaptations for escaping predators.

The horse belongs to the order Perissodactyla (odd-toed ungulates), the members of which all share hoofed feet and an odd number of toes on each foot, as well as mobile upper lips and a similar tooth structure. This means that horses share a common ancestry with tapirs and rhinoceroses. 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. Paleozoologists have been able to piece together a more complete outline of the modern horse’s evolutionary lineage than that of any other animal.

Key Points

- A dog-like organism gave rise to the first horse ancestors 55-42 million years ago.
- The fossil record shows modern horses moved from tropical forests to prairie habitats, developed teeth, and grew in size.
- The first equid fossil was a tooth from the extinct species *Equus curvidens* found in Paris in the 1820s.
- Thomas Huxley popularized the evolutionary sequence of horses, which became one of the most common examples of clear evolutionary progression.
- Horse evolution was previously believed to be a linear progress, but after more fossils were discovered, it was determined the evolution of horses was more complex and multi-branched.
- Horses have evolved from gradual change (anagenesis) as well as abrupt progression and division (cladogenesis).

Key Terms

- **cladogenesis**: An evolutionary splitting event in which each branch and its smaller branches forms a clade.
- **equid**: A member of the horse family.
- **anagenesis**: Evolution of a new species through a large scale change in gene frequency so that the new species replaces the old, rather than branching to produce an additional species.

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18.5F: Homologous Structures

Learning Objectives

- Describe the connection between evolution and the appearance of homologous structures

Homologous Structures

Homology is the relationship between structures or DNA derived from the most recent common ancestor. A common example of homologous structures in evolutionary biology are the wings of bats and the arms of primates. Although these two structures do not look similar or have the same function, genetically, they come from the same structure of the last common ancestor. Homologous traits of organisms are therefore explained by descent from a common ancestor.

It's important to note that defining two structures as homologous depends on what ancestor is being described as the common ancestor. If we go all the way back to the beginning of life, all structures are homologous!

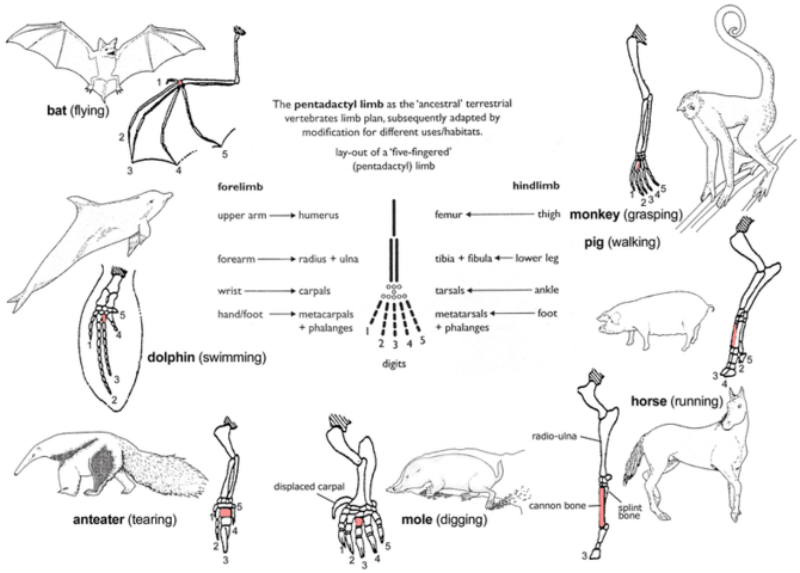


Figure $18.5F.1$: Homology in the forelimbs of vertebrates: The principle of homology illustrated by the adaptive radiation of the forelimb of mammals. All conform to the basic pentadactyl pattern but are modified for different usages. The third metacarpal is shaded throughout; the shoulder is crossed-hatched.

In genetics, homology is measured by comparing protein or DNA sequences. Homologous gene sequences share a high similarity, supporting the hypothesis that they share a common ancestor.

Homology can also be partial: new structures can evolve through the combination of developmental pathways or parts of them. As a result, hybrid or mosaic structures can evolve that exhibit partial homologies. For example, certain compound leaves of flowering plants are partially homologous both to leaves and shoots because they combine some traits of leaves and some of shoots.

Paralogous Structures

Homologous sequences are considered paralogous if they were separated by a gene duplication event; if a gene in an organism is duplicated to occupy two different positions in the same genome, then the two copies are paralogous.

A set of sequences that are paralogous are called paralogs of each other. Paralogs typically have the same or similar function, but

sometimes do not. It is considered that due to lack of the original selective pressure upon one copy of the duplicated gene, this copy is free to mutate and acquire new functions.

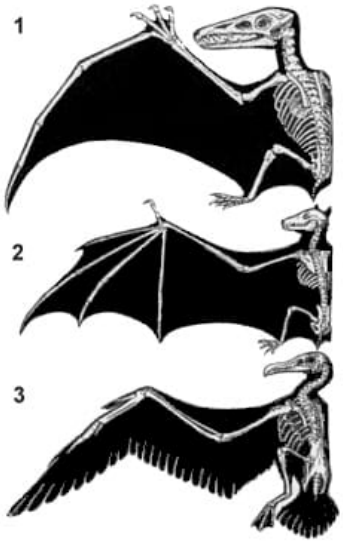


Figure $18.5F.1$: Homology vs. analogy: The wings of pterosaurs (1), bats (2), and birds (3) are analogous as wings, but homologous as forelimbs. This is because they are similar characteristically and even functionally, but evolved from different ancestral roots.

Paralogous genes often belong to the same species, but not always. For example, the hemoglobin gene of humans and the myoglobin gene of chimpanzees are considered paralogs. This is a common problem in bioinformatics; when genomes of different species have been sequenced and homologous genes have been found, one can not immediately conclude that these genes have the same or similar function, as they could be paralogs whose function has diverged.

Analogous Structures

The opposite of homologous structures are analogous structures, which are physically similar structures between two taxa that evolved separately (rather than being present in the last common ancestor). Bat wings and bird wings evolved independently and are considered analogous structures. Genetically, a bat wing and a bird wing have very little in common; the last common ancestor of bats and birds did not have wings like either bats or birds. Wings evolved independently in each lineage after diverging from ancestors with forelimbs that were not used as wings (terrestrial mammals and theropod dinosaurs, respectively).

It is important to distinguish between different hierarchical levels of homology in order to make informative biological comparisons. In the above example, the bird and bat wings are analogous as wings, but homologous as forelimbs because the organ served as a forearm (not a wing) in the last common ancestor of tetrapods.

Analogy is different than homology. Although analogous characteristics are superficially similar, they are not homologous because they are phylogenetically independent. The wings of a maple seed and the wings of an albatross are analogous but not homologous (they both allow the organism to travel on the wind, but they didn't both develop from the same structure). Analogy is commonly also referred to as homoplasy.

Key Points

- Homology is a relationship defined between structures or DNA derived from a common ancestor and illustrates descent from a common ancestor.
- Analogous structures are physically (but not genetically) similar structures that were not present the last common ancestor.
- Homology can also be partial; new structures can evolve through the combination or parts of developmental pathways.
- Analogy may also be referred to as homoplasy, which is further divided into parallelism, reversal, and convergence.

Key Terms

- **homology**: A correspondence of structures in two life forms with a common evolutionary origin, such as flippers and hands.
- **analogy**: The relationship between characteristics that are apparently similar but did not develop from the same structure
- **homoplasy**: A correspondence between the parts or organs of different species acquired as the result of parallel evolution or convergence.

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18.5G: Convergent Evolution

Learning Objectives

- Predict the circumstances supporting convergent evolution of two species

Convergent Evolution

Sometimes, similar phenotypes evolve independently in distantly related species. For example, flight has evolved in both bats and insects, and they both have wings, which are adaptations to flight. However, the wings of bats and insects have evolved from very different original structures. This phenomenon is called convergent evolution, where similar traits evolve independently in species that do not share a recent common ancestry.

Examples of Convergent Evolution

Convergent evolution describes the independent evolution of similar features in species of different lineages. The two species came to the same function, flying, but did so separately from each other. They have "converged" on this useful trait. Both sharks and dolphins have similar body forms, yet are only distantly related: sharks are fish and dolphins are mammals. Such similarities are a result of both populations being exposed to the same selective pressures. Within both groups, changes that aid swimming have been favored. Thus, over time, they developed similar appearances (morphology), even though they are not closely related.

One of the most well-known examples of convergent evolution is the camera eye of cephalopods (e.g., octopus), vertebrates (e.g., mammals), and cnidaria (e.g., box jellies). Their last common ancestor had at most a very simple photoreceptive spot, but a range of processes led to the progressive refinement of this structure to the advanced camera eye. There is, however, one subtle difference: the cephalopod eye is "wired" in the opposite direction, with blood and nerve vessels entering from the back of the retina, rather than the front as in vertebrates.

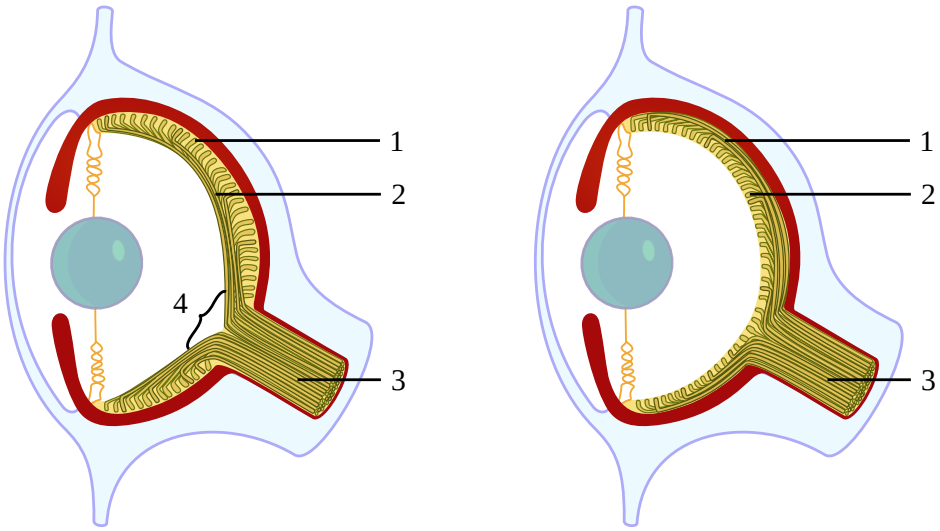


Figure $18.5G.1$: Eye evolution: Vertebrates and octopuses developed the camera eye independently. In the vertebrate version the nerve fibers pass in front of the retina, and there is a blind spot (4) where the nerves pass through the retina. In the octopus version, the eye is constructed the "right way out," with the nerves attached to the rear of the retina. This means that octopuses do not have a blind spot.

Convergent evolution is similar to, but distinguishable from, the phenomenon of parallel evolution. Parallel evolution occurs when two independent but similar species evolve in the same direction and thus independently acquire similar characteristics; for example, gliding frogs have evolved in parallel from multiple types of tree frog.

Analogous Structures

Traits arising through convergent evolution are analogous structures, in contrast to homologous structures, which have a common origin, but not necessarily similar function. The British anatomist Richard Owen was the first scientist to recognize the fundamental difference between analogies and homologies. Bat and pterosaur wings are an example of analogous structures, while the bat wing is homologous to human and other mammal forearms, sharing an ancestral state despite serving different functions.

Divergent Evolution

The opposite of convergent evolution is divergent evolution, whereby related species evolve different traits. On a molecular level, this can happen due to random mutation unrelated to adaptive changes.

Key Points

- Examples of convergent evolution include the relationship between bat and insect wings, shark and dolphin bodies, and vertebrate and cephalopod eyes.
- Analogous structures arise from convergent evolution, but homologous structures do not.
- Convergent evolution is the opposite of divergent evolution, in which related species evolve different traits.
- Convergent evolution is similar to parallel evolution, in which two similar but independent species evolve in the same direction and independently acquire similar characteristics.

Key Terms

- **parallel evolution**: the development of a similar trait in related, but distinct, species descending from the same ancestor, but from different clades
- **convergent evolution**: a trait of evolution in which species not of similar recent origin acquire similar properties due to natural selection
- **divergent evolution**: the process by which a species with similar traits become groups that are tremendously different from each other over many generations
- **morphology**: the form and structure of an organism

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18.5H: Vestigial Structures

Learning Objectives

- Discuss the connection between evolution and the existence of vestigial structures

What Are Vestigial Structures?

Some organisms possess structures with no apparent function which 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. Another example of a structure with no function is the human vermiform appendix. These unused structures without function are called vestigial structures. Other examples of vestigial structures are wings (which may have other functions) on flightless birds like the ostrich, leaves on some cacti, traces of pelvic bones in whales, and the sightless eyes of cave animals.

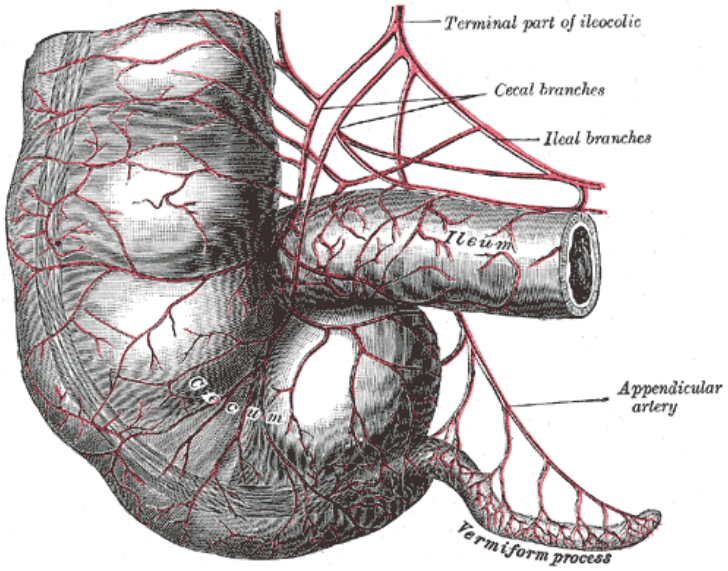


Figure $18.5H.1$: Vestigial appendix: In humans the vermiform appendix is a vestigial structure; it has lost much of its ancestral function.

There are also several reflexes and behaviors that are considered to be vestigial. The formation of goose bumps in humans under stress is a vestigial reflex its function in human ancestors was to raise the body's hair, making the ancestor appear larger and scaring off predators. The arrector pili muscle, which is a band of smooth muscle that connects the hair follicle to connective tissue, contracts and creates the goose bumps on skin.

Vestigial Structures in Evolution

Vestigial structures are often homologous to structures that function normally in other species. Therefore, vestigial structures can be considered evidence for evolution, the process by which beneficial heritable traits arise in populations over an extended period of time. The existence of vestigial traits can be attributed to changes in the environment and behavior patterns of the organism in question. As the function of the trait is no longer beneficial for survival, the likelihood that future offspring will inherit the "normal" form of it decreases. In some cases the structure becomes detrimental to the organism.

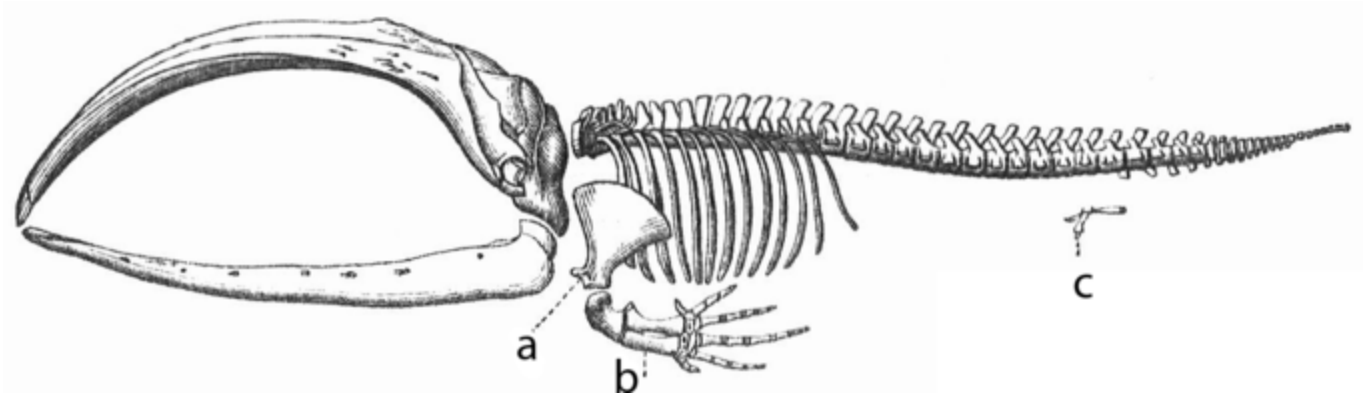


Figure $18.5H.1$: Whale Skeleton: The pelvic bones in whales are also a good example of vestigial evolution (whales evolved from four-legged land mammals and secondarily lost their hind legs). Letter c in the picture indicates the undeveloped hind legs of a baleen whale.

If there are no selection pressures actively lowering the fitness of the individual, the trait will persist in future generations unless the trait is eliminated through genetic drift or other random events.

Although in many cases the vestigial structure is of no direct harm, all structures require extra energy in terms of development, maintenance, and weight and are also a risk in terms of disease (e.g., infection, cancer). This provides some selective pressure for the removal of parts that do not contribute to an organism's fitness, but a structure that is not directly harmful will take longer to be 'phased out' than one that is. Some vestigial structures persist due to limitations in development, such that complete loss of the structure could not occur without major alterations of the organism's developmental pattern, and such alterations would likely produce numerous negative side-effects.

The vestigial versions of a structure can be compared to the original version of the structure in other species in order to determine the homology of the structure. Homologous structures indicate common ancestry with those organisms that have a functional version of the structure. Vestigial traits can still be considered adaptations because an adaptation is often defined as a trait that has been favored by natural selection. Adaptations, therefore, need not be adaptive, as long as they were at some point.

Key Points

- Structures that have no apparent function and appear to be residual parts from a past ancestor are called vestigial structures.
- Examples of vestigial structures include the human appendix, the pelvic bone of a snake, and the wings of flightless birds.
- Vestigial structures can become detrimental, but in most cases these structures are harmless; however, these structures, like any other structure, require extra energy and are at risk for disease.
- Vestigial structures, especially non-harmful ones, take a long time to be phased out since eliminating them would require major alterations that could result in negative side effects.

Key Terms

- **vestigial structure**: Genetically determined structures or attributes that have lost most or all of their ancestral function in a given species.
- **adaptation**: A modification of something or its parts that makes it more fit for existence under the conditions of its current environment.

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18.5I: Biogeography and the Distribution of Species

Learning Objectives

- Relate biogeography and the distribution of species

Distribution of Species

Biogeography is the study of the geographic distribution of living things and the abiotic factors that affect their distribution. Abiotic factors, such as temperature and rainfall, vary based on latitude and elevation, primarily. As these abiotic factors change, the composition of plant and animal communities also changes.

Patterns of Species Distribution

Ecologists who study biogeography examine patterns of species distribution. No species exists everywhere; for example, the Venus flytrap is endemic to a small area in North and South Carolina. An endemic species is one which is naturally found only in a specific geographic area that is usually restricted in size. Other species are generalists: species which live in a wide variety of geographic areas; the raccoon, for example, is native to most of North and Central America.

Since species distribution patterns are based on biotic and abiotic factors and their influences during the very long periods of time required for species evolution, early studies of biogeography were closely linked to the emergence of evolutionary thinking in the eighteenth century. Some of the most distinctive assemblages of plants and animals occur in regions that have been physically separated for millions of years by geographic barriers. Biologists estimate that Australia, for example, has between 600,000 and 700,000 species of plants and animals. Approximately 3/4 of living plant and mammal species are endemic species found solely in Australia.



Figure 18.5*I*.1: Australia: Australia is home to many endemic species. The (a) wallaby (*Wallabia bicolor*), a medium-sized member of the kangaroo family, is a pouched mammal, or marsupial. The (b) echidna (*Tachyglossus aculeatus*) is an egg-laying mammal.

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, such as 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.

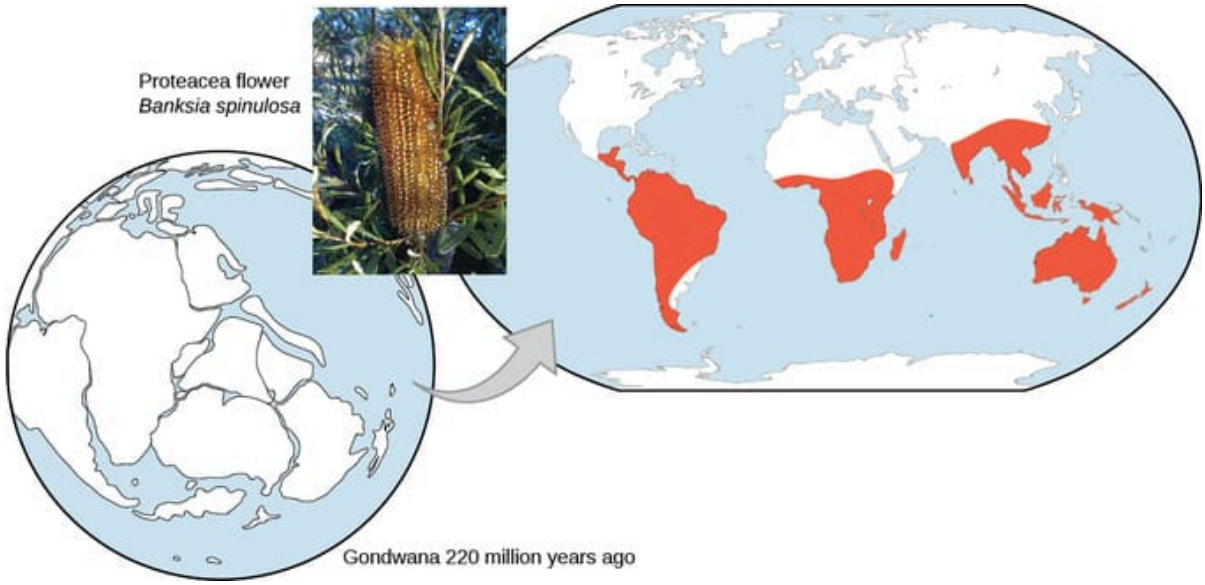


Figure 18.5I.1: Biogeography: The Proteacea family of plants evolved before the supercontinent Gondwana broke up. Today, members of this plant family are found throughout the southern hemisphere (shown in red).

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Key Points

- Biogeography is the study of geological species distribution, which is influenced by both biotic and abiotic factors.
- Some species are endemic and are only found in a particular region, while others are generalists and are distributed worldwide.
- Species that evolved before the breakup of continents are distributed worldwide.
- Species that evolved after the breakup of continents are found in only certain regions of the planet.

Key Terms

- **endemic**: unique to a particular area or region; not found in other places
- **generalist**: species which can thrive in a wide variety of environmental conditions
- **Pangaea**: supercontinent that included all the landmasses of the earth before the Triassic period and that broke up into Laurasia and Gondwana

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19: THE EVOLUTION OF POPULATIONS

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19.1: POPULATION EVOLUTION

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19.1A: Defining Population Evolution

Learning Objectives

- Describe how the forces of genetic drift, genetic hitchhiking, gene flow, and mutation can lead to differences in population variation

The Evolution of Populations

According to evolutionary theory, every organism from humans to beetles to plants to bacteria share a common ancestor. Millions of years of evolutionary pressure caused some organisms to died while others survived, leaving earth with the diverse life forms we have today. Within this diversity is unity; for example, all organisms are composed of cells and use DNA. The theory of evolution gives us a unifying theory to explain the similarities and differences within life's organisms and processes.



Figure 19.1A.1: Evolution on earth: Evolution has resulted in living things that may be single-celled or complex, multicellular organisms. They may be plants, animals, fungi, bacteria, or archaea. This diversity results from evolution.

Genetic Variation in Populations

A population is a group of individuals that can all interbreed, often distinguished as a species. Because these individuals can share genes and pass on combinations of genes to the next generation, the collection of these genes is called a gene pool. The process of evolution occurs *only* in populations and not in individuals. A single individual cannot evolve alone; evolution is the process of changing the gene frequencies within a gene pool. Five forces can cause genetic variation and evolution in a population: mutations, natural selection, genetic drift, genetic hitchhiking, and gene flow.

Mutations

Why do some organisms survive while others die? These surviving organisms generally possess traits or characteristics that bestow benefits that help them survive (e.g., better camouflage, faster swimming, or more efficient digestion). Each of these characteristics is the result of a mutation, or a change in the genetic code. Mutations occur spontaneously, but not all mutations are heritable; they are passed down to offspring only if the mutations occur in the gametes. These heritable mutations are responsible for the rise of new traits in a population.

Natural Selection

Just as mutations cause new traits in a population, natural selection acts on the frequency of those traits. Because there are more organisms than resources, all organisms are in a constant struggle for existence. In natural selection, those individuals with superior traits will be able to produce more offspring. The more offspring an organism can produce, the higher its fitness. As novel traits and behaviors arise from mutation, natural selection perpetuates the traits that confer a benefit.

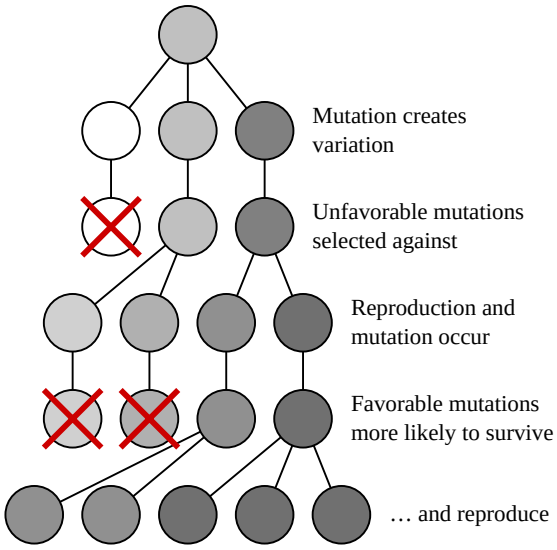


Figure 19.1A.1: Mutation and natural selection: As mutations create variation, natural selection affects the frequency of that trait in a population. Mutations that confer a benefit (such as running faster or digesting food more efficiently) can help that organism survive and reproduce, carrying the mutation to the next generation.

Genetic Drift

When selective forces are absent or relatively weak, gene frequencies tend to “drift” due to random events. This drift halts when the variation of the gene becomes “fixed” by either disappearing from the population or replacing the other variations completely. Even in the absence of selective forces, genetic drift can cause two separate populations that began with the same genetic structure to drift apart into two divergent populations.

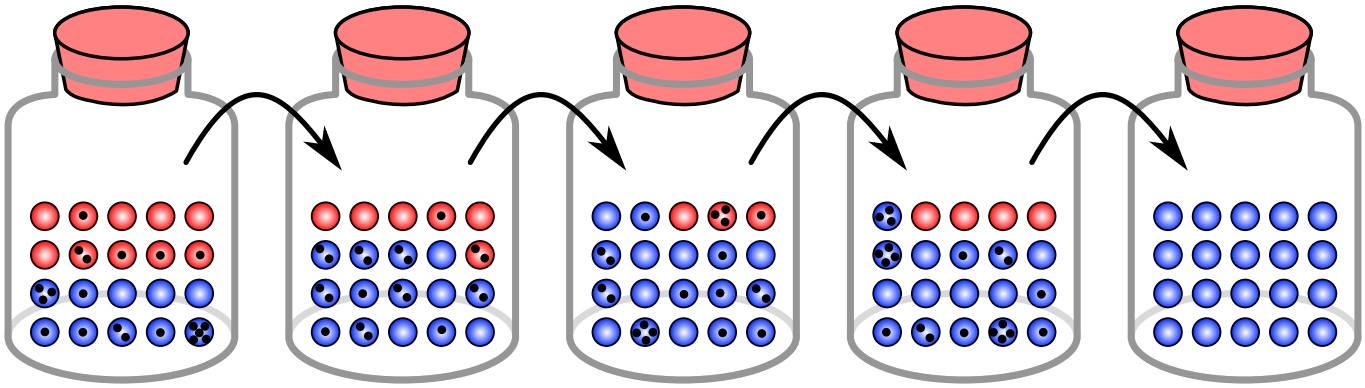


Figure 19.1A.1: Genetic drift and gene fixation: In this simulation, there is fixation in the blue gene variation within five generations. Images these dots are beetles and some of them are destroyed by a wildfire. As the surviving population changes over time, some traits (red) may be completely eliminated from the population, leaving only the beetles with other traits (blue).

Genetic Hitchhiking

When recombination occurs during sexual reproduction, genes are usually shuffled so that each parent gives its offspring a random assortment of its genetic variation. However, genes that are close together on the same chromosome are often assorted together. Therefore, the frequency of a gene may increase in a population through genetic hitchhiking if its proximal genes confer a benefit.

Gene Flow

Gene flow is the exchange of genes between populations or between species.If the gene pools between two populations are different, the exchange of genes can introduce variation that is advantageous or disadvantageous to one of the populations. If advantageous, this gene variation may replace all the other variations until the entire population exhibits that trait.

Key Points

- The theory of evolution gives us a unifying theory to explain the similarities and differences within life's organisms and processes.
- Populations (or gene pools) evolve as gene frequencies change; individual organisms cannot evolve.
- Variation in populations is determined by the genes present in the population's gene pool, which may be directly altered by mutation.
- Natural selection is the gradual process that increases the frequency of advantageous inherited traits (allowing it to survive and reproduce) and decreases the frequency of detrimental inherited traits within a population.
- A population's genetic makeup can also be affected by random chance events like genetic drift, or when genes are inherited together in genetic hitchhiking.

Key Terms

- **gene flow**: the transfer of alleles or genes from one population to another
- **genetic hitchhiking**: a phenomenon in which a gene increases in a population because it lies near genes on the same chromosome that are advantageous to an organism
- **genetic drift**: an overall shift of allele distribution in an isolated population, due to random fluctuations in the frequencies of individual alleles of the genes
- **fitness**: an individual's ability to propagate its genes
- **natural selection**: a process in which individual organisms or phenotypes that possess favorable traits are more likely to survive and reproduce
- **mutation**: any heritable change of the base-pair sequence of genetic material

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19.1B: Population Genetics

Learning Objectives

- Define a population gene pool and explain how the size of the gene pool can affect the evolutionary success of a population

Population Genetics

A gene for a particular characteristic may have several variations called alleles. These variations code for different traits associated with that characteristic. For example, in the ABO blood type system in humans, three alleles (I^A, I^B, or i) determine the particular blood-type protein on the surface of red blood cells. A human with a type I^A allele will display A-type proteins (antigens) on the surface of their red blood cells. Individuals with the phenotype of type A blood have the genotype I^AI^A or I^Ai, type B have I^BI^B or I^Bi, type AB have I^AI^B, and type O have ii.

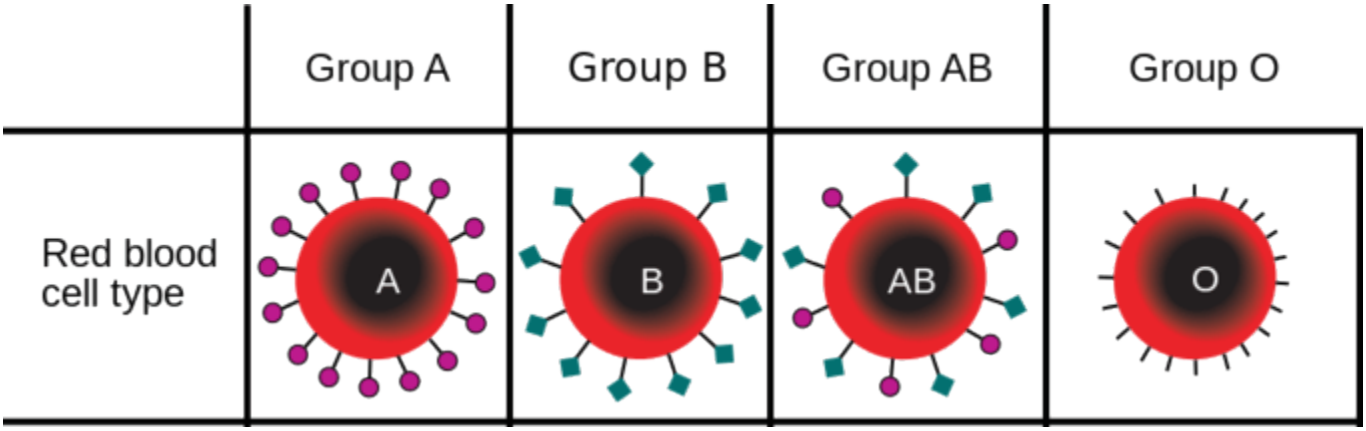


Figure $19.1B.1$: ABO blood type in humans: In humans, each blood type corresponds to a combination of two alleles, which represent a the type of antigens displayed on the outside of a red blood cell. Human blood types are A, B, AB, and O.

A diploid organism can only carry two alleles for a particular gene. In human blood type, the combinations are composed of two alleles such as I^AI^A or I^AI^B. Although each organism can only carry two alleles, more than those two alleles may be present in the larger population. For example, in a population of fifty people where all the blood types are represented, there may be more I^A alleles than i alleles. Population genetics is the study of how selective forces change a population through changes in allele and genotypic frequencies.

Allele Frequency

The allele frequency (or gene frequency) is the rate at which a specific allele appears within a population. In population genetics, the term evolution is defined as a change in the frequency of an allele in a population. Frequencies range from 0, present in no individuals, to 1, present in all individuals. The gene pool is the sum of all the alleles at all genes in a population.

Using the ABO blood type system as an example, the frequency of one of the alleles, for example I^A, is the number of copies of that allele divided by all the copies of the ABO gene in the population, i.e. all the alleles. Allele frequencies can be expressed as a decimal or as a percent and always add up to 1, or 100 percent, of the total population. For example, in a sample population of humans, the frequency of the I^A allele might be 0.26, which would mean that 26% of the chromosomes in that population carry the I^A allele. If we also know that the frequency of the I^B allele in this population is 0.14, then the frequency of the i allele is 0.6, which we obtain by subtracting all the known allele frequencies from 1 (thus: 1 – 0.26 – 0.14 = 0.6). A change in any of these allele frequencies over time would constitute evolution in the population.

Population Size and Evolution

When allele frequencies within a population change randomly with no advantage to the population over existing allele frequencies, the phenomenon is called genetic drift. The smaller a population, the more susceptible it is to mechanisms such as genetic drift as alleles are more likely to become fixed at 0 (absent) or 1 (universally present). Random events that alter allele frequencies will have a much larger effect when the gene pool is small. Genetic drift and natural selection usually occur simultaneously in populations, but the cause of the frequency change is often impossible to determine.

Natural selection also affects allele frequency. If an allele confers a phenotype that enables an individual to better survive or have more offspring, the frequency of that allele will increase. Because many of those offspring will also carry the beneficial allele and, therefore, the phenotype, they will have more offspring of their own that also carry the allele. Over time, the allele will spread throughout the population and may become fixed: every individual in the population carries the allele. If an allele is dominant but detrimental, it may be swiftly eliminated from the gene pool when the individual with the allele does not reproduce. However, a detrimental recessive allele can linger for generations in a population, hidden by the dominant allele in heterozygotes. In such cases, the only individuals to be eliminated from the population are those unlucky enough to inherit two copies of such an allele.

The Founder Effect

The founder effect occurs when part of a population becomes isolated and establishes a separate gene pool with its own allele frequencies. When a small number of individuals become the basis of a new population, this new population can be very different genetically from the original population if the founders are not representative of the original. Therefore, many different populations, with very different and uniform gene pools, can all originate from the same, larger population. Together, the forces of natural selection, genetic drift, and founder effect can lead to significant changes in the gene pool of a population.

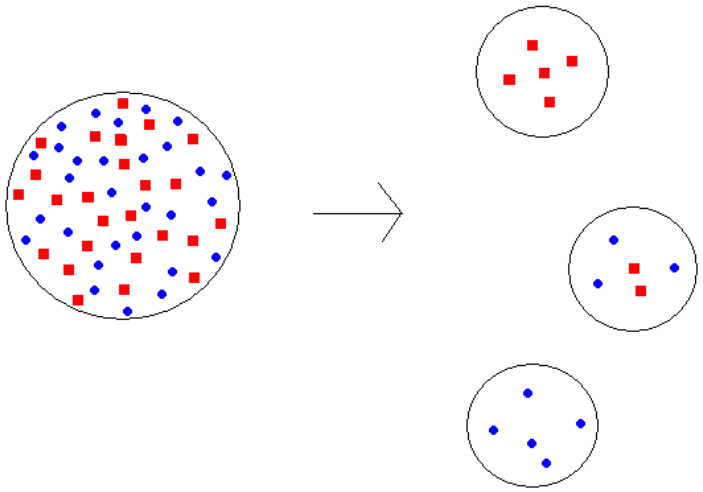


Figure 19.1B.1: The Founder Effect: Here are three possible outcomes of the founder effect, each with gene pools separate from the original populations.

Key Points

- A gene pool is the sum of all the alleles (variants of a gene) in a population.
- Allele frequencies range from 0 (present in no individuals) to 1 (present in all individuals); all allele frequencies for a given gene add up to 100 percent in a population.
- The smaller a population, the more susceptible it is to mechanisms like natural selection and genetic drift, as the effects of such mechanisms are magnified when the gene pool is small.
- The founder effect occurs when part of an original population establishes a new population with a separate gene pool, leading to less genetic variation in the new population.

Key Terms

- **allele**: one of a number of alternative forms of the same gene occupying a given position on a chromosome
- **gene pool**: the complete set of unique alleles that would be found by inspecting the genetic material of every living member of a species or population
- **founder effect**: a decrease in genetic variation that occurs when an entire population descends from a small number of founders

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19.1C: Hardy-Weinberg Principle of Equilibrium

Learning Objectives

- Use the Hardy Weinberg equation to calculate allelic and genotypic frequencies in a population

The Hardy-Weinberg principle states that a population's allele and genotype frequencies will remain constant in the absence of evolutionary mechanisms. Ultimately, the Hardy-Weinberg principle models a population without evolution under the following conditions:

1. no mutations
2. no immigration/emigration
3. no natural selection
4. no sexual selection
5. a large population

Although no real-world population can satisfy all of these conditions, the principle still offers a useful model for population analysis.

Hardy-Weinberg Equations and Analysis

According to the Hardy-Weinberg principle, the variable *p* often represents the frequency of a particular allele, usually a dominant one. For example, assume that *p* represents the frequency of the dominant allele, Y, for yellow pea pods. The variable *q* represents the frequency of the recessive allele, y, for green pea pods. If p and q are the only two possible alleles for this characteristic, then the sum of the frequencies must add up to 1, or 100 percent. We can also write this as p + q = 1.If the frequency of the Y allele in the population is 0.6, then we know that the frequency of the y allele is 0.4.

From the Hardy-Weinberg principle and the known allele frequencies, we can also infer the frequencies of the genotypes. Since each individual carries two alleles per gene (Y or y), we can predict the frequencies of these genotypes with a chi square. If two alleles are drawn at random from the gene pool, we can determine the probability of each genotype.

In the example, our three genotype possibilities are: pp (YY), producing yellow peas; pq (Yy), also yellow; or qq (yy), producing green peas. The frequency of homozygous pp individuals is p^2; the frequency of hereozygous pq individuals is 2pq; and the frequency of homozygous qq individuals is q^2. If p and q are the only two possible alleles for a given trait in the population, these genotypes frequencies will sum to one: $p^2 + 2pq + q^2 = 1$.

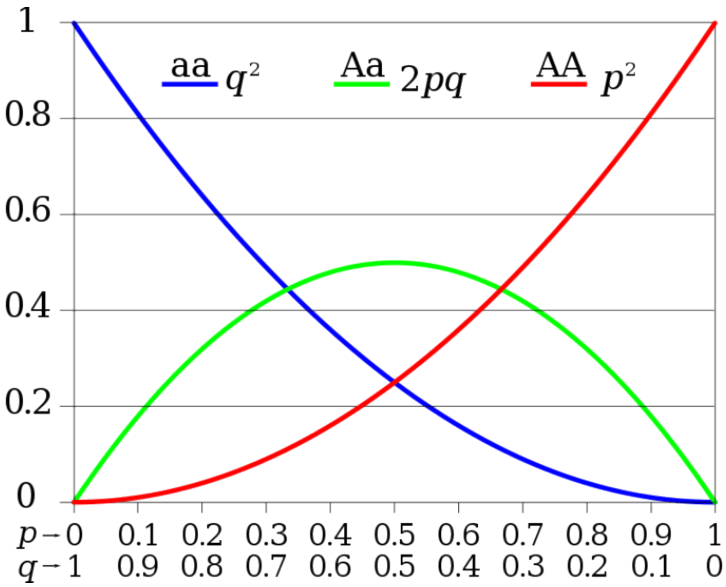


Figure 19.1C.1: Hardy-Weinberg proportions for two alleles: The horizontal axis shows the two allele frequencies *p* and *q* and the vertical axis shows the expected genotype frequencies.Each line shows one of the three possible genotypes.

In our example, the possible genotypes are homozygous dominant (YY), heterozygous (Yy), and homozygous recessive (yy). If we can only observe the phenotypes in the population, then we know only the recessive phenotype (yy). For example, in a garden of 100 pea plants, 86 might have yellow peas and 16 have green peas. We do not know how many are homozygous dominant (Yy) or heterozygous (Yy), but we do know that 16 of them are homozygous recessive (yy).

Therefore, by knowing the recessive phenotype and, thereby, the frequency of that genotype (16 out of 100 individuals or 0.16), we can calculate the number of other genotypes. If q^2 represents the frequency of homozygous recessive plants, then q^2 = 0.16. Therefore, q = 0.4.Because p + q = 1, then 1 – 0.4 = p, and we know that p = 0.6. The frequency of homozygous dominant plants (p^2) is $(0.6)^2$ = 0.36. Out of 100 individuals, there are 36 homozygous dominant (YY) plants. The frequency of heterozygous plants (2pq) is 2(0.6)(0.4) = 0.48. Therefore, 48 out of 100 plants are heterozygous yellow (Yy).

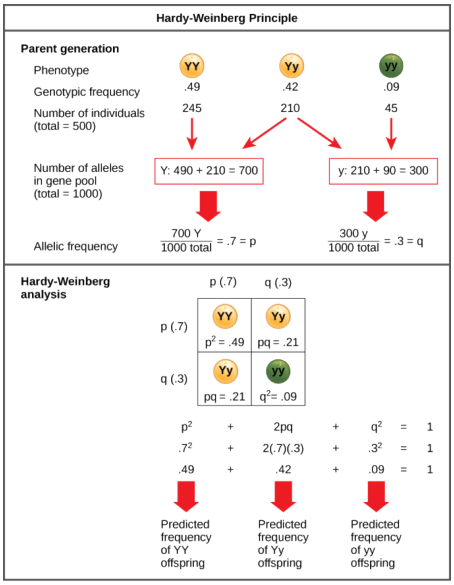


Figure 19.1C.1: The Hardy-Weinberg Principle: When populations are in the Hardy-Weinberg equilibrium, the allelic frequency is stable from generation to generation and the distribution of alleles can be determined. If the allelic frequency measured in the field differs from the predicted value, scientists can make inferences about what evolutionary forces are at play.

Applications of Hardy-Weinberg

The genetic variation of natural populations is constantly changing from genetic drift, mutation, migration, and natural and sexual selection. The Hardy-Weinberg principle gives scientists a mathematical baseline of a non-evolving population to which they can compare evolving populations. If scientists record allele frequencies over time and then calculate the expected frequencies based on Hardy-Weinberg values, the scientists can hypothesize the mechanisms driving the population's evolution.

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Key Points

- The Hardy-Weinberg principle assumes that in a given population, the population is large and is not experiencing mutation, migration, natural selection, or sexual selection.
- The frequency of alleles in a population can be represented by $p + q = 1$, with p equal to the frequency of the dominant allele and q equal to the frequency of the recessive allele.
- The frequency of genotypes in a population can be represented by $p^2+2pq+q^2= 1$, with p^2 equal to the frequency of the homozygous dominant genotype, 2pq equal to the frequency of the heterozygous genotype, and q^2 equal to the frequency of the recessive genotype.
- The frequency of alleles can be estimated by calculating the frequency of the recessive genotype, then calculating the square root of that frequency in order to determine the frequency of the recessive allele.

Key Terms

- **genotype**: the combination of alleles, situated on corresponding chromosomes, that determines a specific trait of an individual, such as “Aa” or “aa”
- **phenotype**: the appearance of an organism based on a multifactorial combination of genetic traits and environmental factors, especially used in pedigrees

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19.2: POPULATION GENETICS

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19.2A: Genetic Variation

19.2B: Genetic Drift

19.2C: Gene Flow and Mutation

19.2D: Nonrandom Mating and Environmental Variance

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19.2A: Genetic Variation

Learning Objectives

- Assess the ways in which genetic variance affects the evolution of populations

Genetic Variation

Genetic variation is a measure of the genetic differences that exist within a population. The genetic variation of an entire species is often called genetic diversity. Genetic variations are the differences in DNA segments or genes between individuals and each variation of a gene is called an allele.For example, a population with many different alleles at a single chromosome locus has a high amount of genetic variation. Genetic variation is essential for natural selection because natural selection can only increase or decrease frequency of alleles that already exist in the population.

Genetic variation is caused by:

- mutation
- random mating between organisms
- random fertilization
- crossing over (or recombination) between chromatids of homologous chromosomes during meiosis

The last three of these factors reshuffle alleles within a population, giving offspring combinations which differ from their parents and from others.

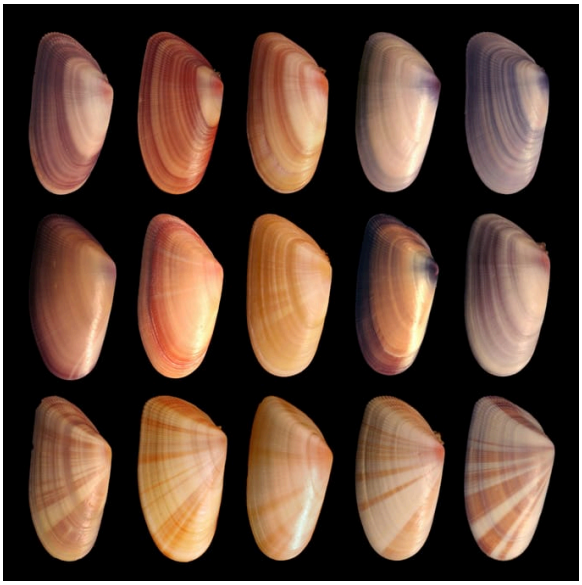


Figure 19.2A.1: Genetic variation in the shells of Donax variabilis: An enormous amount of phenotypic variation exists in the shells of Donax varabilis, otherwise known as the coquina mollusc. This phenotypic variation is due at least partly to genetic variation within the coquina population.

Evolution and Adaptation to the Environment

Variation allows some individuals within a population to adapt to the changing environment. Because natural selection acts directly only on phenotypes, more genetic variation within a population usually enables more phenotypic variation. Some new alleles increase an organism's ability to survive and reproduce, which then ensures the survival of the allele in the population. Other new alleles may be immediately detrimental (such as a malformed oxygen-carrying protein) and organisms carrying these

new mutations will die out. Neutral alleles are neither selected for nor against and usually remain in the population. Genetic variation is advantageous because it enables some individuals and, therefore, a population, to survive despite a changing environment.

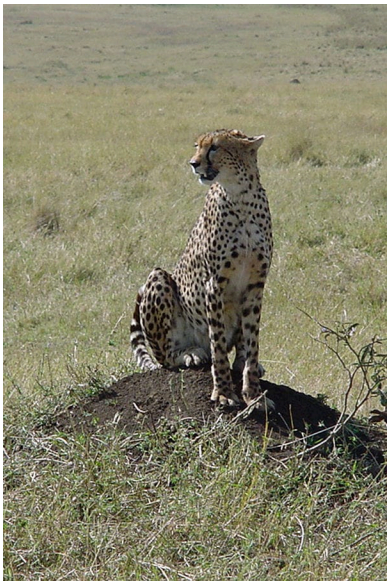


Figure 19.2A.1: Low genetic diversity in the wild cheetah population: Populations of wild cheetahs have very low genetic variation. Because wild cheetahs are threatened, their species has a very low genetic diversity. This low genetic diversity means they are often susceptible to disease and often pass on lethal recessive mutations; only about 5% of cheetahs survive to adulthood.

Geographic Variation

Some species display geographic variation as well as variation within a population. Geographic variation, or the distinctions in the genetic makeup of different populations, often occurs when populations are geographically separated by environmental barriers or when they are under selection pressures from a different environment. One example of geographic variation are clines: graded changes in a character down a geographic axis.

Sources of Genetic Variation

Gene duplication, mutation, or other processes can produce new genes and alleles and increase genetic variation. New genetic variation can be created within generations in a population, so a population with rapid reproduction rates will probably have high genetic variation. However, existing genes can be arranged in new ways from chromosomal crossing over and recombination in sexual reproduction. Overall, the main sources of genetic variation are the formation of new alleles, the altering of gene number or position, rapid reproduction, and sexual reproduction.

Key Points

- Genetic variation is an important force in evolution as it allows natural selection to increase or decrease frequency of alleles already in the population.
- Genetic variation can be caused by mutation (which can create entirely new alleles in a population), random mating, random fertilization, and recombination between homologous chromosomes during meiosis (which reshuffles alleles within an organism's offspring).
- Genetic variation is advantageous to a population because it enables some individuals to adapt to the environment while maintaining the survival of the population.

Key Terms

- **genetic diversity**: the level of biodiversity, refers to the total number of genetic characteristics in the genetic makeup of a

species
- **crossing over**: the exchange of genetic material between homologous chromosomes that results in recombinant chromosomes
- **phenotypic variation**: variation (due to underlying heritable genetic variation); a fundamental prerequisite for evolution by natural selection
- **genetic variation**: variation in alleles of genes that occurs both within and among populations

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19.2B: Genetic Drift

Learning Objectives

- Distinguish between selection and genetic drift

Genetic Drift vs. Natural Selection

Genetic drift is the converse of natural selection. The theory of natural selection maintains that some individuals in a population have traits that enable to survive and produce more offspring, while other individuals have traits that are detrimental and may cause them to die before reproducing. Over successive generation, these selection pressures can change the gene pool and the traits within the population. For example, a big, powerful male gorilla will mate with more females than a small, weak male and therefore more of his genes will be passed on to the next generation. His offspring may continue to dominate the troop and pass on their genes as well. Over time, the selection pressure will cause the allele frequencies in the gorilla population to shift toward large, strong males.

Unlike natural selection, genetic drift describes the effect of chance on populations in the absence of positive or negative selection pressure. Through random sampling, or the survival or and reproduction of a random sample of individuals within a population, allele frequencies within a population may change. Rather than a male gorilla producing more offspring because he is stronger, he may be the only male available when a female is ready to mate. His genes are passed on to future generation because of chance, not because he was the biggest or the strongest. Genetic drift is the shift of alleles within a population due to chance events that cause random samples of the population to reproduce or not.

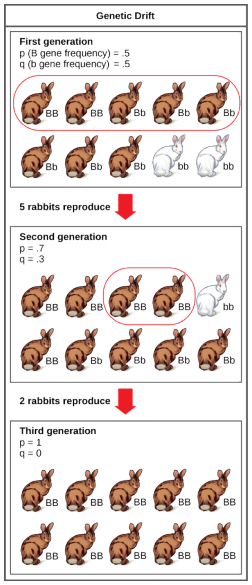


Figure $19.2B.1$: Effect of genetic drift: Genetic drift in a population can lead to the elimination of an allele from that population by chance. In this example, the brown coat color allele (B) is dominant over the white coat color allele (b). In the first generation, the two alleles occur with equal frequency in the population, resulting in p and q values of.5. Only half of the individuals reproduce, resulting in a second generation with p and q values of.7 and.3, respectively. Only two individuals in the second generation reproduce and, by chance, these individuals are homozygous dominant for brown coat color. As a result, in the third generation the recessive b allele is lost.

Small populations are more susceptible to the forces of genetic drift. Large populations, on the other hand, are buffered against the effects of chance. If one individual of a population of 10 individuals happens to die at a young age before leaving any offspring to the next generation, all of its genes (1/10 of the population's gene pool) will be suddenly lost. In a population of 100, that individual represents only 1 percent of the overall gene pool; therefore, genetic drift has much less impact on the larger population's genetic structure.

The Bottleneck Effect

Genetic drift can also be magnified by natural events, such as a natural disaster that kills a large portion of the population at random. The bottleneck effect occurs when only a few individuals survive and reduces variation in the gene pool of a population. The genetic structure of the survivors becomes the genetic structure of the entire population, which may be very different from the pre-disaster population.

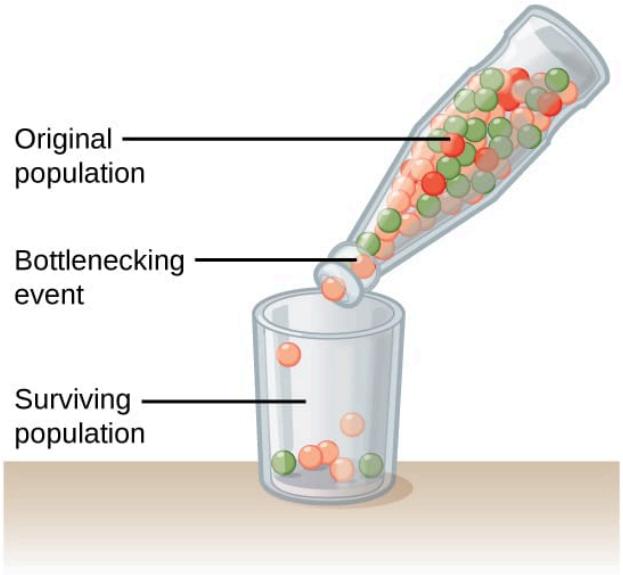


Figure $19.2B.1$: Effect of a bottleneck on a population: A chance event or catastrophe can reduce the genetic variability within a population.

The Founder Effect

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, it is improbable that those individuals are representative of the entire population, which results in the founder effect. The founder effect occurs when the genetic structure changes to match that of the new population's founding fathers and mothers.

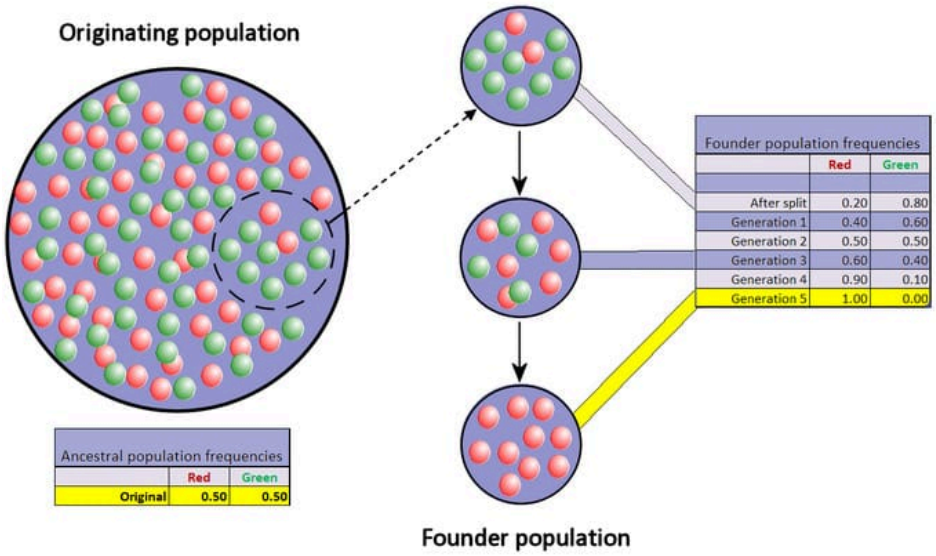


Figure $19.2B.1$: The Founder Effect: The founder effect occurs when a portion of the population (i.e. "founders") separates from the old population to start a new population with different allele frequencies.

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 was probably due to the fact that a higher-than-normal proportion of the founding colonists 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 blood marrow and congenital abnormalities, even cancer.

Drift and fixation

The Hardy–Weinberg principle states that within sufficiently large populations, the allele frequencies remain constant from one generation to the next unless the equilibrium is disturbed by migration, genetic mutation, or selection.

Because the random sampling can remove, but not replace, an allele, and because random declines or increases in allele frequency influence expected allele distributions for the next generation, genetic drift drives a population towards genetic uniformity over time. When an allele reaches a frequency of 1 (100%) it is said to be "fixed" in the population and when an allele reaches a frequency of 0 (0%) it is lost. Once an allele becomes fixed, genetic drift for that allele comes to a halt, and the allele frequency cannot change unless a new allele is introduced in the population via mutation or gene flow. Thus even while genetic drift is a random, directionless process, it acts to eliminate genetic variation over time.

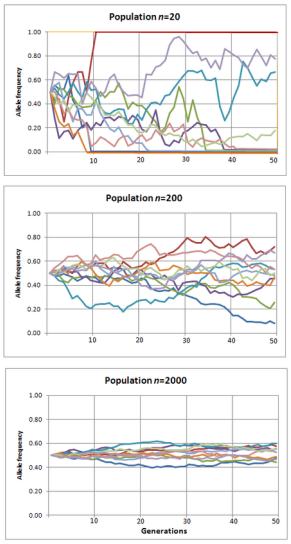


Figure $19.2B.1$: Genetic drift over time: Ten simulations of random genetic drift of a single given allele with an initial frequency distribution 0.5 measured over the course of 50 generations, repeated in three reproductively synchronous populations of different sizes. In these simulations, alleles drift to loss or fixation (frequency of 0.0 or 1.0) only in the smallest population.Effect of population size on genetic drift: Ten simulations each of random change in the frequency distribution of a single hypothetical allele over 50 generations for different sized populations; first population size n=20, second population n=200, and third population n=2000.

Key Points

- Genetic drift is the change in the frequency of an allele in a population due to random sampling and the random events that influence the survival and reproduction of those individuals.
- The bottleneck effect occurs when a natural disaster or similar event randomly kills a large portion (i.e. random sample) of the population, leaving survivors that have allele frequencies that were very different from the previous population.
- The founder effect occurs when a portion of the population (i.e. "founders") separates from the old population to start a new population with different allele frequencies.
- Small populations are more susceptible genetic drift than large populations, whose larger numbers can buffer the population against chance events.

Key Terms

- **genetic drift**: an overall shift of allele distribution in an isolated population, due to random sampling
- **founder effect**: a decrease in genetic variation that occurs when an entire population descends from a small number of founders
- **random sampling**: a subset of individuals (a sample) chosen from a larger set (a population) by chance

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19.2C: Gene Flow and Mutation

Learning Objectives

- Explain how gene flow and mutations can influence the allele frequencies of a population

Gene Flow

An important evolutionary force is gene flow: the flow of alleles in and out of a population due to the migration of individuals or gametes. While some populations are fairly stable, others experience more movement and fluctuation. Many plants, for example, send their pollen by wind, insects, or birds to pollinate other populations of the same species some distance away. Even a population that may initially appear to be stable, such as a pride of lions, can receive new genetic variation as developing males leave their mothers to form new prides with genetically-unrelated females. This variable flow of individuals in and out of the group not only changes the gene structure of the population, but can also introduce new genetic variation to populations in different geological locations and habitats.

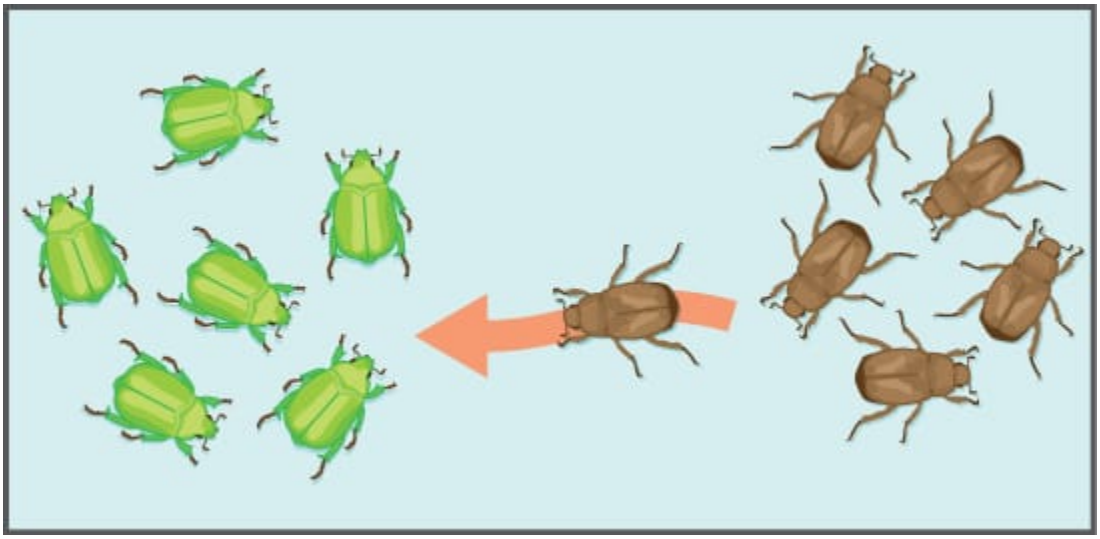


Figure $19.2C.1$: Gene flow: Gene flow can occur when an individual travels from one geographic location to another.

Maintained gene flow between two populations can also lead to a combination of the two gene pools, reducing the genetic variation between the two groups. Gene flow strongly acts against speciation, by recombining the gene pools of the groups, and thus, repairing the developing differences in genetic variation that would have led to full speciation and creation of daughter species.

For example, if a species of grass grows on both sides of a highway, pollen is likely to be transported from one side to the other and vice versa. If this pollen is able to fertilize the plant where it ends up and produce viable offspring, then the alleles in the pollen have effectively linked the population on one side of the highway with the other.

Mutation

Mutations are changes to an organism's DNA and are an important driver of diversity in populations. Species evolve because of the accumulation of mutations that occur over time. The appearance of new mutations is the most common way to introduce novel genotypic and phenotypic variance. Some mutations are unfavorable or harmful and are quickly eliminated from the population by natural selection. Others are beneficial and will spread through the population. Whether or not a mutation is beneficial or harmful is determined by whether it helps an organism survive to sexual maturity and reproduce. Some mutations have no effect on an organism and can linger, unaffected by natural selection, in the genome while others can have a dramatic effect on a gene and

the resulting phenotype.



Figure $19.2C.1$: Mutation in a garden rose: A mutation has caused this garden moss rose to produce flowers of different colors. This mutation has introduce a new allele into the population that increases genetic variation and may be passed on to the next generation.

Key Points

- Plant populations experience gene flow by spreading their pollen long distances.
- Animals experience gene flow when individuals leave a family group or herd to join other populations.
- The flow of individuals in and out of a population introduces new alleles and increases genetic variation within that population.
- Mutations are changes to an organism's DNA that create diversity within a population by introducing new alleles.
- Some mutations are harmful and are quickly eliminated from the population by natural selection; harmful mutations prevent organisms from reaching sexual maturity and reproducing.
- Other mutations are beneficial and can increase in a population if they help organisms reach sexual maturity and reproduce.

Key Terms

- **gene flow**: the transfer of alleles or genes from one population to another
- **mutation**: any heritable change of the base-pair sequence of genetic material

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19.2D: Nonrandom Mating and Environmental Variance

Learning Objectives

- Explain how environmental variance and nonrandom mating can change gene frequencies in a population

Nonrandom Mating

If individuals nonrandomly mate with other individuals in the population, i.e. they choose their mate, choices can drive evolution within a population. There are many reasons nonrandom mating occurs. One reason is simple mate choice or sexual selection; for example, female peahens may prefer peacocks with bigger, brighter tails. Traits that lead to more matings for an individual lead to more offspring and through natural selection, eventually lead to a higher frequency of that trait in the population. One common form of mate choice, called positive assortative mating, is an individual's preference to mate with partners that are phenotypically similar to themselves.



Figure $19.2D.1$: Assortative mating in the American Robin: The American Robin may practice assortative mating on plumage color, a melanin based trait, and mate with other robins who have the most similar shade of color. However, there may also be some sexual selection for more vibrant plumage which indicates health and reproductive performance.

Another cause of nonrandom mating is physical location. This is especially true in large populations spread over large geographic distances where not all individuals will have equal access to one another. Some might be miles apart through woods or over rough terrain, while others might live immediately nearby.

Environmental Variance

Genes are not the only players involved in determining population variation. Phenotypes are also influenced by other factors, such as the environment. A beachgoer is likely to have darker skin than a city dweller, for example, due to regular exposure to the sun, an environmental factor. Some major characteristics, such as gender, are determined by the environment for some species. For example, some turtles and other reptiles have temperature-dependent sex determination (TSD). TSD means that individuals develop into males if their eggs are incubated within a certain temperature range, or females at a different temperature range.



Figure 19.2D.1: Temperature-dependent sex determination: The sex of the American alligator (Alligator mississippiensis) is determined by the temperature at which the eggs are incubated. Eggs incubated at 30 degrees C produce females, and eggs incubated at 33 degrees C produce males.

Geographic separation between populations can lead to differences in the phenotypic variation between those populations. Such geographical variation is seen between most populations and can be significant. One type of geographic variation, called a cline, can be seen as populations of a given species vary gradually across an ecological gradient.

image

Geographic variation in moose: This graph shows geographical variation in moose; body mass increase positively with latitude. Bergmann's Rule is an ecologic principle which states that as latitude increases the body mass of a particular species increases. The data are taken from a Swedish study investigating the size of moose as latitude increases as shows the positive relationship between the two, supporting Bergmann's Rule.

Species of warm-blooded animals, for example, tend to have larger bodies in the cooler climates closer to the earth's poles, allowing them to better conserve heat. This is considered a latitudinal cline. Alternatively, flowering plants tend to bloom at different times depending on where they are along the slope of a mountain, known as an altitudinal cline.

If there is gene flow between the populations, the individuals will likely show gradual differences in phenotype along the cline. Restricted gene flow, on the other hand, can lead to abrupt differences, even speciation.

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Key Points

- Nonrandom mating can occur when individuals prefer mates with particular superior physical characteristics or by the preference of individuals to mate with individuals similar to themselves.
- Nonrandom mating can also occur when mates are chosen based on physical accessibility; that is, the availability of some mates over others.
- Phenotypes of individuals can also be influenced by the environment in which they live, such as temperature, terrain, or other factors.
- A cline occurs when populations of a given species vary gradually across an ecological gradient.

Key Terms

- **cline**: a gradation in a character or phenotype within a species or other group
- **sexual selection**: a mode of natural selection in which some individuals out-reproduce others of a population because they are better at securing mates
- **assortative mating**: between males and females of a species, the mutual attraction or selection, for reproductive purposes, of individuals with similar characteristics

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19.3: ADAPTIVE EVOLUTION

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19.3D: Sexual Selection

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19.3A: Natural Selection and Adaptive Evolution

Learning Objectives

- Explain how natural selection leads to adaptive evolution

An Introduction to Adaptive Evolution

Natural selection only acts on the population's heritable traits: selecting for beneficial alleles and, thus, increasing their frequency in the population, while selecting against deleterious alleles and, thereby, decreasing their frequency. This process is known as adaptive evolution. Natural selection does not act on individual alleles, however, but on entire organisms. An individual may carry a very beneficial genotype with a resulting phenotype that, for example, increases the ability to reproduce (fecundity), but if that same individual also carries an allele that results in a fatal childhood disease, that fecundity phenotype will not be passed on to the next generation because the individual will not live to reach reproductive age. Natural selection acts at the level of the individual; it selects for individuals with greater contributions to the gene pool of the next generation, known as an organism's evolutionary fitness (or Darwinian fitness).

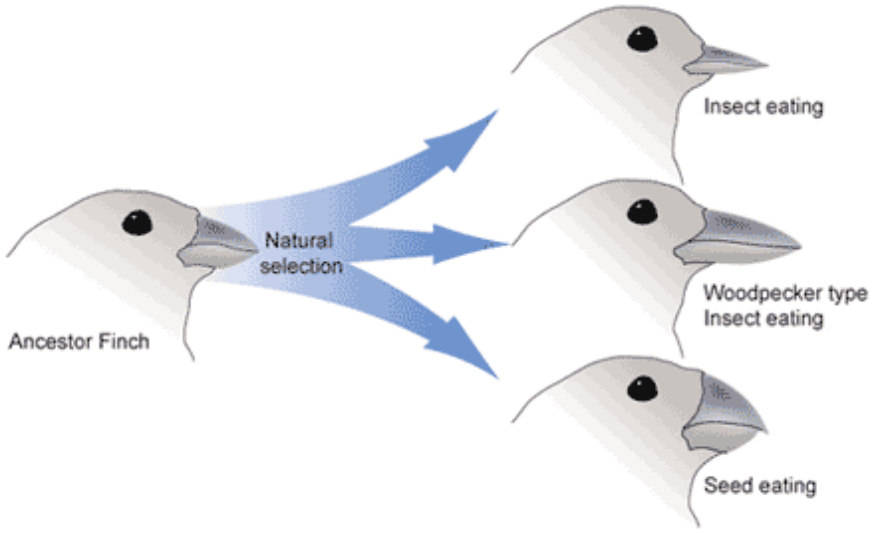


Figure 19.3A.1: Adaptive evolution in finches: Through natural selection, a population of finches evolved into three separate species by adapting to several difference selection pressures. Each of the three modern finches has a beak adapted to its life history and diet.

Fitness is often quantifiable and is measured by scientists in the field. However, it is not the absolute fitness of an individual that counts, but rather how it compares to the other organisms in the population. This concept, called relative fitness, allows researchers to determine which individuals are contributing additional offspring to the next generation and, thus, how the population might evolve.

There are several ways selection can affect population variation:

- stabilizing selection
- directional selection
- diversifying selection
- frequency-dependent selection
- sexual selection

As natural selection influences the allele frequencies in a population, individuals can either become more or less genetically similar and the phenotypes displayed can become more similar or more disparate. In the end, natural selection cannot produce

perfect organisms from scratch, it can only generate populations that are better adapted to survive and successfully reproduce in their environments through the aforementioned selections.

Galápagos with David Attenborough: Two hundred years after Charles Darwin set foot on the shores of the Galápagos Islands, David Attenborough travels to this wild and mysterious archipelago. Amongst the flora and fauna of these enchanted volcanic islands, Darwin formulated his groundbreaking theories on evolution. Journey with Attenborough to explore how life on the islands has continued to evolve in biological isolation, and how the ever-changing volcanic landscape has given birth to species and sub-species that exist nowhere else in the world.

Key Points

- Natural selection increases or decreases biological traits within a population, thereby selecting for individuals with greater evolutionary fitness.
- An individual with a high evolutionary fitness will provide more beneficial contributions to the gene pool of the next generation.
- Relative fitness, which compares an organism's fitness to the others in the population, allows researchers to establish how a population may evolve by determining which individuals are contributing additional offspring to the next generation.
- Stabilizing selection, directional selection, diversifying selection, frequency -dependent selection, and sexual selection all contribute to the way natural selection can affect variation within a population.

Key Terms

- **natural selection**: a process in which individual organisms or phenotypes that possess favorable traits are more likely to survive and reproduce
- **fecundity**: number, rate, or capacity of offspring production
- **Darwinian fitness**: the average contribution to the gene pool of the next generation that is made by an average individual of the specified genotype or phenotype

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19.3B: Stabilizing, Directional, and Diversifying Selection

Learning Objectives

- Contrast stabilizing selection, directional selection, and diversifying selection.

Stabilizing Selection

If natural selection favors an average phenotype by selecting against extreme variation, the population will undergo stabilizing selection. For example, in a population of mice that live in the woods, natural selection will tend to favor individuals that best blend in with the forest floor and are less likely to be spotted by predators. Assuming the ground is a fairly consistent shade of brown, those mice whose fur is most-closely matched to that color will most probably survive and reproduce, passing on their genes for their brown coat. Mice that carry alleles that make them slightly lighter or slightly darker will stand out against the ground and will more probably die from predation. As a result of this stabilizing selection, the population's genetic variance will decrease.

image

Stabilizing selection: Stabilizing selection occurs when the population stabilizes on a particular trait value and genetic diversity decreases.

Directional Selection

When the environment changes, populations will often undergo directional selection, which selects for phenotypes at one end of the spectrum of existing variation.

A classic example of this type of selection is the evolution of the peppered moth in eighteenth- and nineteenth-century England. Prior to the Industrial Revolution, the moths were predominately light in color, which allowed them to blend in with the light-colored trees and lichens in their environment. As soot began spewing from factories, the trees darkened and the light-colored moths became easier for predatory birds to spot.

image

Directional selection: Directional selection occurs when a single phenotype is favored, causing the allele frequency to continuously shift in one direction.

Over time, the frequency of the melanic form of the moth increased because their darker coloration provided camouflage against the sooty tree; they had a higher survival rate in habitats affected by air pollution. Similarly, the hypothetical mouse population may evolve to take on a different coloration if their forest floor habitat changed. The result of this type of selection is a shift in the population's genetic variance toward the new, fit phenotype.



Figure $19.3B.1$: The Evolution of the Peppered Moth: Typica and carbonaria morphs resting on the same tree.The light-colored typica (below the bark's scar) is nearly invisible on this pollution-free tree, camouflaging it from predators.

Diversifying (or Disruptive) Selection

Sometimes natural selection can select for two or more distinct phenotypes that each have their advantages. In these cases, the intermediate phenotypes are often less fit than their extreme counterparts. Known as diversifying or disruptive selection, this is seen in many populations of animals that have multiple male mating strategies, such as lobsters. Large, dominant alpha males obtain mates by brute force, while small males can sneak in for furtive copulations with the females in an alpha male's territory. In this case, both the alpha males and the "sneaking" males will be selected for, but medium-sized males, which cannot overtake the alpha males and are too big to sneak copulations, are selected against.

image

Diversifying (or disruptive) selection: Diversifying selection occurs when extreme values for a trait are favored over the intermediate values.This type of selection often drives speciation.

Diversifying selection can also occur when environmental changes favor individuals on either end of the phenotypic spectrum. Imagine a population of mice living at the beach where there is light-colored sand interspersed with patches of tall grass. In this scenario, light-colored mice that blend in with the sand would be favored, as well as dark-colored mice that can hide in the grass. Medium-colored mice, on the other hand, would not blend in with either the grass or the sand and, thus, would more probably be eaten by predators. The result of this type of selection is increased genetic variance as the population becomes more diverse.

Comparing Types of Natural Selection

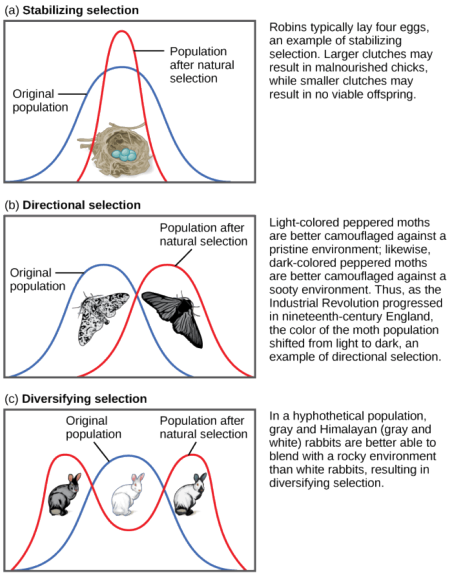


Figure $19.3B.1$: Types of natural selection: Different types of natural selection can impact the distribution of phenotypes within a population.In (a) stabilizing selection, an average phenotype is favored.In (b) directional selection, a change in the environment shifts the spectrum of phenotypes observed.In (c) diversifying selection, two or more extreme phenotypes are selected for, while the average phenotype is selected against.

Key Points

- Stabilizing selection results in a decrease of a population ‘s genetic variance when natural selection favors an average phenotype and selects against extreme variations.
- In directional selection, a population’s genetic variance shifts toward a new phenotype when exposed to environmental changes.
- Diversifying or disruptive selection increases genetic variance when natural selection selects for two or more extreme phenotypes that each have specific advantages.
- In diversifying or disruptive selection, average or intermediate phenotypes are often less fit than either extreme phenotype and are unlikely to feature prominently in a population.

Key Terms

- **directional selection**: a mode of natural selection in which a single phenotype is favored, causing the allele frequency to continuously shift in one direction
- **disruptive selection**: (or diversifying selection) a mode of natural selection in which extreme values for a trait are favored over intermediate values
- **stabilizing selection**: a type of natural selection in which genetic diversity decreases as the population stabilizes on a particular trait value

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19.3C: Frequency-Dependent Selection

Learning Objectives

- Describe frequency-dependent selection

Frequency-dependent Selection

Another type of selection, called frequency-dependent selection, favors phenotypes that are either common (positive frequency-dependent selection) or rare (negative frequency-dependent selection).

Negative Frequency-dependent Selection

An interesting example of this type of selection is seen in a unique group of lizards of the Pacific Northwest. Male common side-blotched lizards come in three throat-color patterns: orange, blue, and yellow. Each of these forms has a different reproductive strategy: orange males are the strongest and can fight other males for access to their females; blue males are medium-sized and form strong pair bonds with their mates; and yellow males are the smallest and look a bit like female, allowing them to sneak copulations. Like a game of rock-paper-scissors, orange beats blue, blue beats yellow, and yellow beats orange in the competition for females. The big, strong orange males can fight off the blue males to mate with the blue's pair-bonded females; the blue males are successful at guarding their mates against yellow sneaker males; and the yellow males can sneak copulations from the potential mates of the large, polygynous orange males.



Figure $19.3C.1$: Frequency-dependent selection in side-blotched lizards: A yellow-throated side-blotched lizard is smaller than either the blue-throated or orange-throated males and appears a bit like the females of the species, allowing it to sneak copulations. Frequency-dependent selection allows for both common and rare phenotypes of the population to appear in a frequency-aided cycle.

In this scenario, orange males will be favored by natural selection when the population is dominated by blue males, blue males will thrive when the population is mostly yellow males, and yellow males will be selected for when orange males are the most populous. As a result, populations of side-blotched lizards cycle in the distribution of these phenotypes. In one generation, orange might be predominant and then yellow males will begin to rise in frequency. Once yellow males make up a majority of the population, blue males will be selected for.Finally, when blue males become common, orange males will once again be favored.

An example of negative frequency-dependent selection can also be seen in the interaction between the human immune system and various infectious microbes such as pathogenic bacteria or viruses. As a particular human population is infected by a

common strain of microbe, the majority of individuals in the population become immune to it. This then selects for rarer strains of the microbe which can still infect the population because of genome mutations; these strains have greater evolutionary fitness because they are less common.

Positive Frequency-dependent Selection

An example of positive frequency-dependent selection is the mimicry of the warning coloration of dangerous species of animals by other species that are harmless. The scarlet kingsnake, a harmless species, mimics the coloration of the eastern coral snake, a venomous species typically found in the same geographical region. Predators learn to avoid both species of snake due to the similar coloration, and as a result the scarlet kingsnake becomes more common, and its coloration phenotype becomes more variable due to relaxed selection. This phenotype is therefore more "fit" as the population of species that possess it (both dangerous and harmless) becomes more numerous. In geographic areas where the coral snake is less common, the pattern becomes less advantageous to the kingsnake, and much less variable in its expression, presumably because predators in these regions are not "educated" to avoid the pattern.



Figure $19.3C.1$: Lampropeltis elapsoides, the scarlet kingsnake: The scarlet kingsnake mimics the coloration of the poisonous eastern coral snake. Positive frequency-dependent selection reinforces the common phenotype because predators avoid the distinct coloration.



Figure $19.3C.1$: Micrurus fulvius, the eastern coral snake: The eastern coral snake is poisonous.

Negative frequency-dependent selection serves to increase the population's genetic variance by selecting for rare phenotypes,

whereas positive frequency-dependent selection usually decreases genetic variance by selecting for common phenotypes.

Key Points

- Negative frequency -dependent selection selects for rare phenotypes in a population and increases a population's genetic variance.
- Positive frequency-dependent selection selects for common phenotypes in a population and decreases genetic variance.
- In the example of male side-blotched lizards, populations of each color pattern increase or decrease at various stages depending on their frequency; this ensures that both common and rare phenotypes continue to be cyclically present.
- Infectious agents such as microbes can exhibit negative frequency-dependent selection; as a host population becomes immune to a common strain of the microbe, less common strains of the microbe are automatically favored.
- Variation in color pattern mimicry by the scarlet kingsnake is dependent on the prevalence of the eastern coral snake, the model for this mimicry, in a particular geographical region. The more prevalent the coral snake is in a region, the more common and variable the scarlet kingsnake's color pattern will be, making this an example of positive frequency-dependent selection.

Key Terms

- **frequency-dependent selection**: the term given to an evolutionary process where the fitness of a phenotype is dependent on its frequency relative to other phenotypes in a given population
- **polygynous**: having more than one female as mate

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19.3D: Sexual Selection

Learning Objectives

- Discuss the effects of sexual dimorphism on the reproductive potential of an organism

Sexual Selection

The selection pressures on males and females to obtain matings is known as sexual selection. Sexual selection takes two major forms: intersexual selection (also known as 'mate choice' or 'female choice') in which males compete with each other to be chosen by females; and intrasexual selection (also known as 'male–male competition') in which members of the less limited sex (typically males) compete aggressively among themselves for access to the limiting sex. The limiting sex is the sex which has the higher parental investment, which therefore faces the most pressure to make a good mate decision.



Figure $19.3D.1$: Sexual selection in elk: This male elk has large antlers to compete with rival males for available females (intrasexual competition).Tn addition, the many points on his antlers represent health and longevity, and therefore he may be more desirable to females (intersexual selection).

Sexual Dimorphism

Males and females of certain species are often quite different from one another in ways beyond the reproductive organs. Males are often larger, for example, and display many elaborate colors and adornments, such as the peacock's tail, while females tend to be smaller and duller in decoration. These differences are called sexual dimorphisms and arise from the variation in male reproductive success.

Females almost always mate, while mating is not guaranteed for males. The bigger, stronger, or more decorated males usually obtain the vast majority of the total matings, while other males receive none. This can occur because the males are better at fighting off other males, or because females will choose to mate with the bigger or more decorated males. In either case, this variation in reproductive success generates a strong selection pressure among males to obtain those matings, resulting in the evolution of bigger body size and elaborate ornaments in order to increase their chances of mating. Females, on the other hand, tend to get a handful of selected matings; therefore, they are more likely to select more desirable males.



Figure $19.3D.1$: Sexual dimorphism: Morphological differences between males and females of the same species is known as sexual dimorphism.These differences can be observed in (a) peacocks and peahens, (b) Argiope appensa spiders (the female spider is the large one), and (c) wood ducks.

Sexual dimorphism varies widely among species; some species are even sex-role reversed. In such cases, females tend to have a greater variation in their reproductive success than males and are, correspondingly, selected for the bigger body size and elaborate traits usually characteristic of males.

The Handicap Principle

Sexual selection can be so strong that it selects for traits that are actually detrimental to the individual's survival, even though they maximize its reproductive success. For example, while the male peacock's tail is beautiful and the male with the largest, most colorful tail will more probably win the female, it is not a practical appendage. In addition to being more visible to predators, it makes the males slower in their attempted escapes. There is some evidence that this risk, in fact, is why females like the big tails in the first place. Because large tails carry risk, only the best males survive that risk and therefore the bigger the tail, the more fit the male. This idea is known as the handicap principle.

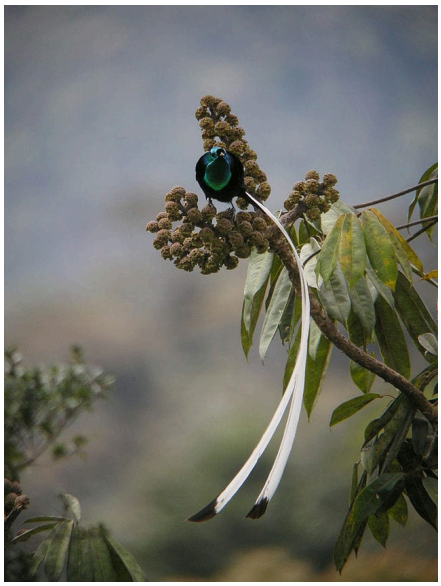


Figure $19.3D.1$: A male bird of paradise: This male bird of paradise carries an extremely long tail as the result of sexual selection.The tail is flamboyant and detrimental to the bird's own survival, but it increases his reproductive success.This may be an example of the handicap principle.

The Good Genes Hypothesis

The good genes hypothesis states that males develop these impressive ornaments to show off their efficient metabolism or their ability to fight disease. Females then choose males with the most impressive traits because it signals their genetic superiority, which they will then pass on to their offspring. Though it might be argued that females should not be so selective because it will likely reduce their number of offspring, if better males father more fit offspring, it may be beneficial. Fewer, healthier offspring may increase the chances of survival more than many, weaker offspring.

BBC Planet Earth – Birds of Paradise mating dance: Extraordinary Courtship displays from these weird and wonderful creatures. From episode 1 “Pole to Pole”. This is an example of the extreme behaviors that arise from intense sexual selection pressure.

Key Points

- Sexual selection often results in the development of secondary sexual characteristics, which help to maximize a species ‘ reproductive success, but do not provide any survival benefits.
- The handicap principle states that only the best males survive the risks from traits that may actually be detrimental to a species; therefore, they are more fit as mating partners.
- In the good genes hypothesis, females will choose males that show off impressive traits to ensure they pass on genetic superiority to their offspring.
- Sexual dimorphisms, obvious morphological differences between the sexes of a species, arise when there is more variance in the reproductive success of either males or females.

Key Terms

- **sexual dimorphism**: a physical difference between male and female individuals of the same species
- **sexual selection**: a type of natural selection, where members of the sexes acquire distinct forms because members choose mates with particular features or because competition for mates with certain traits succeed
- **handicap principle**: a theory that suggests that animals of greater biological fitness signal this status through a behavior or morphology that effectively lowers their chances of survival

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19.3E: No Perfect Organism

Learning Objectives

- Explain the limitations encountered in natural selection

No Perfect Organism

Natural selection is a driving force in evolution and can generate populations that are adapted to survive and successfully reproduce in their environments. However, natural selection cannot produce the perfect organism. Natural selection can only select on existing variation in the population; it cannot create anything from scratch. Therefore, the process of evolution is limited by a population's existing genetic variance, the physical proximity of alleles, non-beneficial intermediate morphs in a polymorphic population, and non-adaptive evolutionary forces.

Natural Selection Acts on Individuals, not Alleles

Natural selection is also limited because it acts on the phenotypes of individuals, not alleles. Some alleles may be more likely to be passed on with alleles that confer a beneficial phenotype because of their physical proximity on the chromosomes. Alleles that are carried together are in linkage disequilibrium. When a neutral allele is linked to beneficial allele, consequently meaning that it has a selective advantage, the allele frequency can increase in the population through genetic hitchhiking (also called genetic draft).

Any given individual may carry some beneficial alleles and some unfavorable alleles. Natural selection acts on the net effect of these alleles and corresponding fitness of the phenotype. As a result, good alleles can be lost if they are carried by individuals that also have several overwhelmingly bad alleles; similarly, bad alleles can be kept if they are carried by individuals that have enough good alleles to result in an overall fitness benefit.

Polymorphism

Furthermore, natural selection can be constrained by the relationships between different polymorphisms. One morph may confer a higher fitness than another, but may not increase in frequency because the intermediate morph is detrimental.



Figure $19.3E.1$:

Polymorphism in the grove snail: Color and pattern morphs of the grove snail, Cepaea nemoralis.The polymorphism, when two or more different genotypes exist within a given species, in grove snails seems to have several causes, including predation by thrushes.

For example, consider a hypothetical population of mice that live in the desert. Some are light-colored and blend in with the sand, while others are dark and blend in with the patches of black rock. The dark-colored mice may be more fit than the light-colored mice, and according to the principles of natural selection the frequency of light-colored mice is expected to decrease over time. However, the intermediate phenotype of a medium-colored coat is very bad for the mice: these cannot blend in with

either the sand or the rock and will more vulnerable to predators. As a result, the frequency of a dark-colored mice would not increase because the intermediate morphs are less fit than either light-colored or dark-colored mice. This a common example of disruptive selection.

Not all Evolution is Adaptive

Finally, it is important to understand that not all evolution is adaptive. While natural selection selects the fittest individuals and often results in a more fit population overall, other forces of evolution, including genetic drift and gene flow, often do the opposite by introducing deleterious alleles to the population's gene pool. Evolution has no purpose. It is not changing a population into a preconceived ideal. It is simply the sum of various forces and their influence on the genetic and phenotypic variance of a population.

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Key Points

- Natural selection is limited by a population ‘s existing genetic variation.
- Natural selection is limited through linkage disequilibrium, where alleles that are physically proximate on the chromosome are passed on together at greater frequencies.
- In a polymorphic population, two phenotypes may be maintained in the population despite the higher fitness of one morph if the intermediate phenotype is detrimental.
- Evolution is not purposefully adaptive; it is the result of various selection forces working together to influence genetic and phenotypical variances within a population.

Key Terms

- **linkage disequilibrium**: a non-random association of two or more alleles at two or more loci; normally caused by an interaction between genes
- **genetic hitchhiking**: changes in the frequency of an allele because of linkage with a positively or negatively selected allele at another locus
- **polymorphism**: the regular existence of two or more different genotypes within a given species or population

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20: PHYLOGENIES AND THE HISTORY OF LIFE

20.1: Organizing Life on Earth

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20.1: ORGANIZING LIFE ON EARTH

20.1A: Phylogenetic Trees

20.1B: Limitations of Phylogenetic Trees

20.1C: The Levels of Classification

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20.1A: Phylogenetic Trees

Learning Objectives

- Describe the various types of phylogenetic trees and how they organize life

Scientists use a tool called a phylogenetic tree, a type of diagram, to show the evolutionary pathways and connections among organisms. Scientists consider phylogenetic trees to be a hypothesis of the evolutionary past since one cannot go back to confirm the proposed relationships. In other words, a "tree of life", as it is sometimes called, can be constructed to illustrate when different organisms evolved and to show the relationships among different organisms.

Unlike a taxonomic classification diagram, a phylogenetic tree can be read like a map of evolutionary history. Many phylogenetic trees have a single lineage at the base representing a common ancestor. Scientists call such trees 'rooted,' which means there is a single ancestral lineage (typically drawn from the bottom or left) to which all organisms represented in the diagram relate. Notice in the rooted phylogenetic tree that the three domains (Bacteria, Archaea, and Eukarya) diverge from a single point and branch off. The small branch that plants and animals (including humans) occupy in this diagram shows how recent and miniscule these groups are compared with other organisms. Unrooted trees don't show a common ancestor but do show relationships among species.

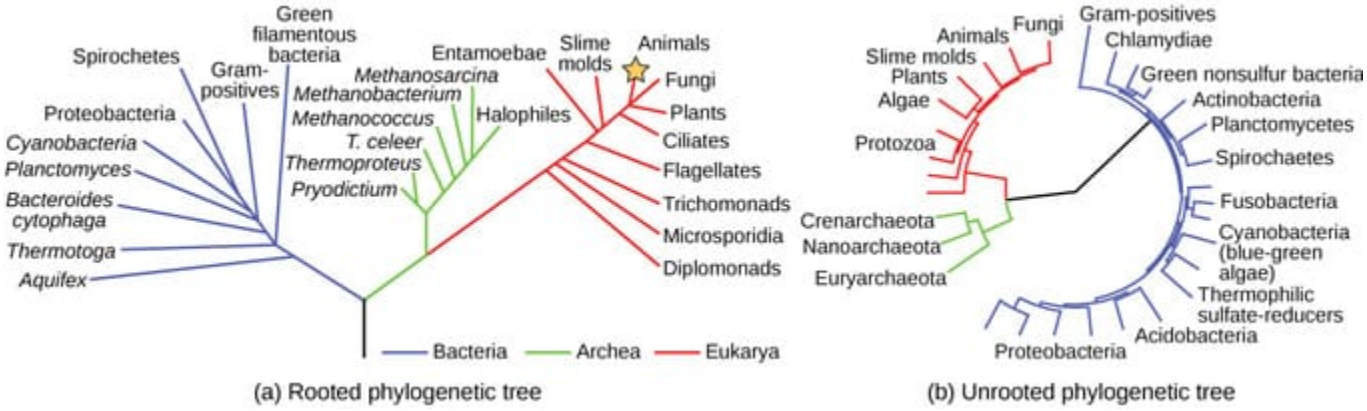


Figure 20.1A.1: Phylogenetic trees: Both of these phylogenetic trees shows the relationship of the three domains of life (Bacteria, Archaea, and Eukarya), but the (a) rooted tree attempts to identify when various species diverged from a common ancestor, while the (b) unrooted tree does not.

In a rooted tree, the branching indicates evolutionary relationships. The point where a split occurs, called a branch point, represents where a single lineage evolved into a distinct new one. A lineage that evolved early from the root and remains unbranched is called basal taxon. When two lineages stem from the same branch point, they are called sister taxa. A branch with more than two lineages is called a polytomy and serves to illustrate where scientists have not definitively determined all of the relationships. It is important to note that although sister taxa and polytomy do share an ancestor, it does not mean that the groups of organisms split or evolved from each other. Organisms in two taxa may have split apart at a specific branch point, but neither taxa gave rise to the other.

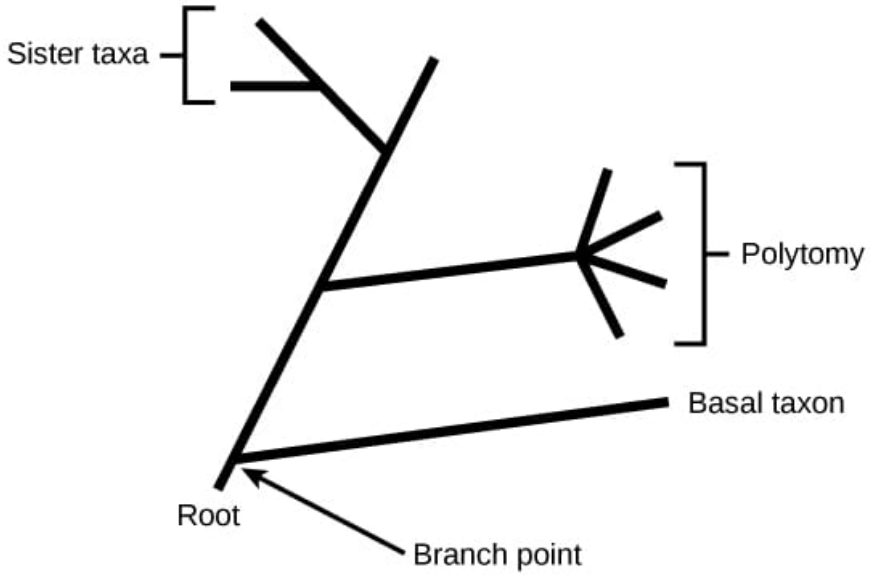


Figure 20.1A.1: Rooted phylogenetic trees: The root of a phylogenetic tree indicates that an ancestral lineage gave rise to all organisms on the tree. A branch point indicates where two lineages diverged. A lineage that evolved early and remains unbranched is a basal taxon. When two lineages stem from the same branch point, they are sister taxa. A branch with more than two lineages is a polytomy.

Rooted phylogenetic trees can serve as a pathway to understanding 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 back towards the "trunk" of the tree, one can discover that species' ancestors, as well as where lineages share a common ancestry. In addition, the tree can be used to study entire groups of organisms.

Another point to mention on phylogenetic tree structure is that rotation at branch points does not change the information. For example, if a branch point was rotated and the taxon order changed, this would not alter the information because the evolution of each taxon from the branch point was independent of the other.

Many disciplines within the study of biology contribute to understanding how past and present life evolved over time; together, these disciplines contribute to building, updating, and maintaining the "tree of life." Information is used to organize and classify organisms based on evolutionary relationships in a scientific field called systematics. Data may be collected from fossils, from studying the structure of body parts or molecules used by an organism, and by DNA analysis. By combining data from many sources, scientists can put together the phylogeny of an organism. Since phylogenetic trees are hypotheses, they will continue to change as new types of life are discovered and new information is learned.

Key Points

- Rooted trees have a single lineage at the base representing a common ancestor that connects all organisms presented in a phylogenetic diagram.
- Branch points in a phylogenetic tree represent a split where a single lineage evolved into a distinct new one, while basal taxon depict unbranched lineages that evolved early from the root.
- Unrooted trees portray relationships among species, but do not depict their common ancestor.
- Phylogenetic trees are hypotheses and are, therefore, modified as data becomes available.
- Systematics uses data from fossils, the study of bodily structures, molecules used by a species, and DNA analysis to contribute to the building, updating, and maintaining of phylogenetic trees.

Key Terms

- **polytomy**: a section of a phylogeny in which the evolutionary relationships cannot be fully resolved to dichotomies
- **basal taxon**: a lineage, displayed using a phylogenetic tree, that evolved early from the root and from which no other branches have diverged
- **systematics**: research into the relationships of organisms; the science of systematic classification
- **phylogeny**: the visual representation of the evolutionary history of organisms; based on rigorous analyses

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20.1B: Limitations of Phylogenetic Trees

Learning Objectives

- Identify the limitations of phylogenetic trees as representations of the organization of life

It may be easy to assume that more closely-related organisms look more alike; while this is often the case, it is not always true. If two closely-related lineages evolved under significantly varied surroundings or after the evolution of a major new adaptation, it is possible for the two groups to appear more different than other groups that are not as closely related. For example, the phylogenetic tree shows that lizards and rabbits both have amniotic eggs, whereas frogs do not; yet lizards and frogs appear more similar than lizards and rabbits.

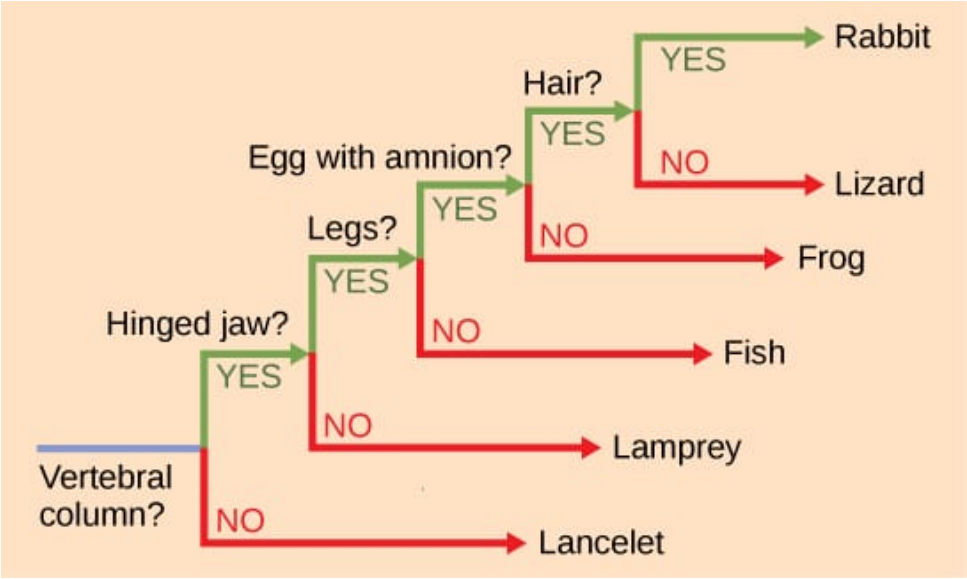


Figure $20.1B.1$: Limitations of phylogenetic trees: This ladder-like phylogenetic tree of vertebrates is rooted by an organism that lacked a vertebral column. At each branch point, organisms with different characters are placed in different groups based on the characteristics they share.

Another aspect of phylogenetic trees is that, unless otherwise indicated, the branches do not account for length of time, only the evolutionary order. In other words, the length of a branch does not typically mean more time passed; nor does a short branch mean less time passed, unless specified on the diagram. A tree may 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. For example, the tree in the diagram shows that the oldest trait is the vertebral column, followed by hinged jaws, and so forth. Remember, any phylogenetic tree is a part of the greater whole and, as with a real tree, it does not grow in only one direction after a new branch develops. So, simply 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 phenotypically similar to each other than to a close relative.

Key Points

- Closely-related species may not always look more alike, while groups that are not closely related yet evolved under similar conditions, may appear more similar to each other.
- In phylogenetic trees, branches do not usually account for length of time and only depict evolutionary order.
- Phylogenetic trees are like real trees in that they do not simply grow in only one direction after a new branch forms; the evolution of one organism does not necessarily signify the evolutionary end of another.

Key Terms

- **phenotypical**: of or pertaining to a phenotype: the appearance of an organism based on a multifactorial combination of genetic traits and environmental factors

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20.1C: The Levels of Classification

Learning Objectives

- Describe how taxonomic classification of organisms is accomplished and detail the levels of taxonomic classification from domain to species

Taxonomy (which literally means “arrangement law”) is the science of classifying organisms to construct internationally-shared classification systems with each organism placed into more and more inclusive groupings. Think about how a grocery store is organized. One large space is divided into departments, such as produce, dairy, and meats. Then each department further divides into aisles, then each aisle into categories and brands, and then, finally, a single product. This organization from larger to smaller, more-specific categories is called a hierarchical system.

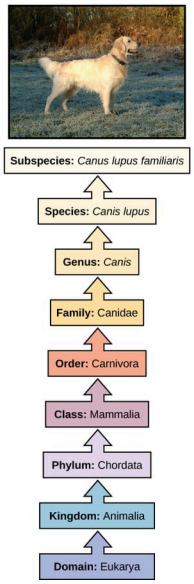


Figure $20.1C.1$: Hierarchical models: The taxonomic classification system uses a hierarchical model to organize living organisms into increasingly specific categories. The common dog, Canis lupus familiaris, is a subspecies of Canis lupus, which also includes the wolf and dingo.

The taxonomic classification system (also called the Linnaean system after its inventor, Carl Linnaeus, a Swedish botanist, zoologist, and physician) uses a hierarchical model. Moving from the point of origin, the groups become more specific, until one branch ends as a single species. For example, after the common beginning of all life, scientists divide organisms into three large categories called domains: Bacteria, Archaea, and Eukarya. Within each domain is a second category called a kingdom. After kingdoms, the subsequent categories of increasing specificity are: phylum, class, order, family, genus, and species.

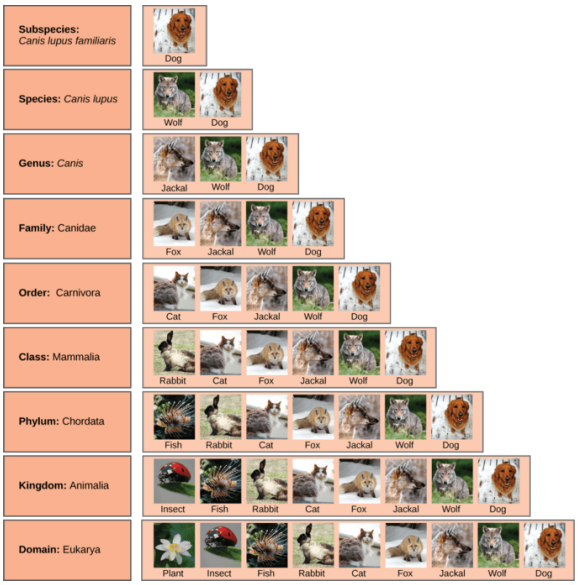


Figure $20.1C.1$: Levels in taxonomic classification: At each sublevel in the taxonomic classification system, organisms become more similar. Dogs and wolves are the same species because they can breed and produce viable offspring, but they are different enough to be classified as different subspecies.

The kingdom Animalia stems from the Eukarya domain. The full name of an organism technically has eight terms. For dogs, it is: Eukarya, Animalia, Chordata, Mammalia, Carnivora, Canidae, *Canis*, and *lupus*. Notice that each name is capitalized except for species and that genus and species names are italicized. Scientists generally refer to an organism only by its genus and species, which is its two-word scientific name, in what is called binomial nomenclature. Therefore, the scientific name of the dog is *Canis lupus*. The name at each level is also called a taxon. In other words, dogs are in order Carnivora. Carnivora is the name of 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; in this case, dog. Note that the dog is additionally a subspecies: the “familiaris” in *Canis lupus familiaris*. Subspecies are members of the same species that are capable of mating and reproducing viable offspring, but they are considered separate subspecies due to geographic or behavioral isolation or other factors.

Dogs actually share a domain (Eukarya) with the widest diversity of organisms, including plants and butterflies. At each sublevel, the organisms become more similar because they are more closely related. Historically, scientists classified organisms using physical characteristics, but as DNA technology developed, more precise phylogenies have been determined.

Recent genetic analysis and other advancements have found that some earlier phylogenetic classifications do not align with the evolutionary past; therefore, changes and updates must be made as new discoveries occur. Recall that phylogenetic trees are hypotheses and are modified as data becomes available. In addition, classification historically has focused on grouping organisms mainly by shared characteristics and does not necessarily illustrate how the various groups relate to each other from an evolutionary perspective. For example, despite the fact that a hippopotamus resembles a pig more than a whale, the hippopotamus may be the closest living relative to the whale.

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Key Points

- Categories within taxonomic classification are arranged in increasing specificity.
- The most general category in taxonomic classification is domain, which is the point of origin for all species; all species belong to one of these domains: Bacteria, Archaea, and Eukarya.
- Within each of the three domains, we find kingdoms, the second category within taxonomic classification, followed by subsequent categories that include phylum, class, order, family, genus, and species.
- At each classification category, organisms become more similar because they are more closely related.
- As scientific technology advances, changes to the taxonomic classification of many species must be altered as inaccuracies in classifications are discovered and corrected.

Key Terms

- **binomial nomenclature**: the scientific system of naming each species of organism with a Latinized name in two parts
- **taxon**: any of the taxonomic categories such as phylum or subspecies
- **Linnaeus**: Swedish botanist, physician and zoologist who laid the foundations for the modern scheme of nomenclature; known as the “father of modern taxonomy”

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20.2: DETERMINING EVOLUTIONARY RELATIONSHIPS



- Topic hierarchy

20.2A: Distinguishing between Similar Traits

20.2B: Building Phylogenetic Trees

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20.2A: Distinguishing between Similar Traits

Learning Objectives

- Explain the difference between homologous and analogous structures

Two Options for Similarities

In general, organisms that share similar physical features and genomes tend to be more closely related than those that do not. Such features that overlap both morphologically (in form) and genetically are referred to as homologous structures; they stem from developmental similarities that are based on evolution. For example, the bones in the wings of bats and birds have homologous structures.

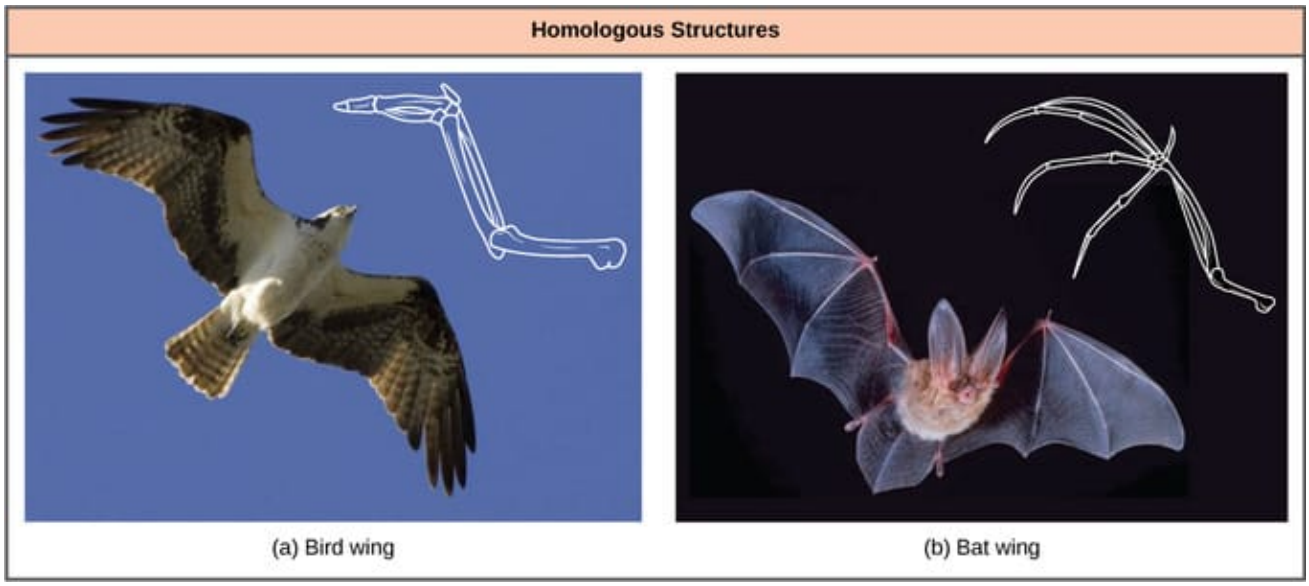


Figure 20.2A.1: Homologous structures: Bat and bird wings are homologous structures, indicating that bats and birds share a common evolutionary past.

Notice it is not simply a single bone, but rather a grouping of several bones arranged in a similar way. The more complex the feature, the more probable that any overlap is due to a common evolutionary past. Imagine two people from different countries both inventing a car with all the same parts and in exactly the same arrangement without any previous or shared knowledge. That outcome would be highly improbable. However, if two people both invented a hammer, it would be reasonable to conclude that both could have the original idea without the help of the other. The same relationship between complexity and shared evolutionary history is true for homologous structures in organisms.

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. Similarly, unrelated organisms may be distantly related, but appear very similar. This usually happens because both organisms developed common adaptations that evolved within similar environmental conditions. When similar characteristics occur because of environmental constraints and not due to a close evolutionary relationship, it is called an analogy or homoplasy. For example, insects use wings to fly like bats and birds, but the wing structure and embryonic origin is completely different. These are called analogous structures.



Figure 20.2A.1: Analogous structures: The (c) wing of a honeybee is similar in shape to a (b) bird wing and (a) bat wing, and it serves the same function. However, the honeybee wing is not composed of bones and has a distinctly-different structure and embryonic origin. These wing types (insect versus bat and bird) illustrate an analogy: similar structures that do not share an evolutionary history.

Similar traits can be either homologous or analogous. Homologous structures share a similar embryonic origin; analogous organs have a similar function. For example, the bones in the front flipper of a whale are homologous to the bones in the human arm. These structures are not analogous. The wings of a butterfly and the wings of a bird are analogous, but not homologous. Some structures are both analogous and homologous: the wings of a bird and the wings of a bat are both homologous and analogous. Scientists must determine which type of similarity a feature exhibits to decipher the phylogeny of the organisms being studied.

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 analysis, has blossomed. New computer programs not only confirm many earlier classified organisms, but also uncover previously-made errors. As with physical characteristics, even the DNA sequence can be tricky to read in some cases. For some situations, two very closely-related organisms can appear unrelated if a mutation occurred that caused a shift in the genetic code. An insertion or deletion mutation would move each nucleotide base over one place, causing two similar codes to appear unrelated.

Sometimes two segments of DNA code 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 both of these situations, computer technologies have been developed to help identify the actual relationships. Ultimately, the coupled use of both morphologic and molecular information is more effective in determining phylogeny.

Key Points

- Organisms may be very closely related, even though they look quite different, due to a minor genetic change that caused a major morphological difference.
- Unrelated organisms may appear very similar because both organisms developed common adaptations that evolved within similar environmental conditions.
- To determine the phylogeny of an organism, scientists must determine whether a similarity is homologous or analogous.
- The advancement of DNA technology, the area of molecular systematics, describes the use of information on the molecular level, including DNA analysis.

Key Terms

- **analogous**: when similar similar physical features occur in organisms because of environmental constraints and not due to

a close evolutionary relationship

- **homologous**: when similar physical features and genomes stem from developmental similarities that are based on evolution
- **phylogeny**: the evolutionary history of an organism
- **molecular systematics**: molecular phylogenetics is the analysis of hereditary molecular differences, mainly in DNA sequences, to gain information on an organism's evolutionary relationships

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20.2B: Building Phylogenetic Trees

Learning Objectives

- Describe the cladistics as a method used to create phylogenetic trees

After the homologous and analogous traits are sorted, scientists often organize the homologous traits using a system called cladistics. This system sorts organisms into clades: groups of organisms that descended from a single ancestor. For example, all of the organisms in the orange 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 all of the descendants from a branch point.

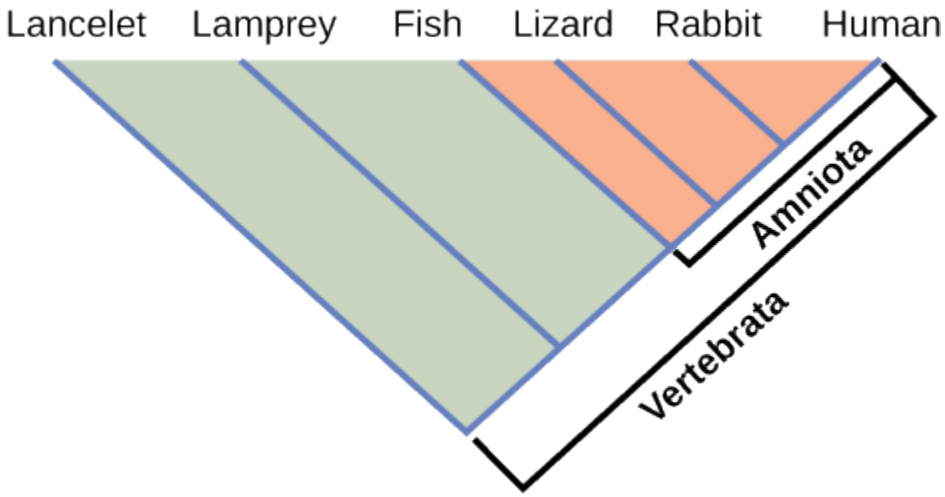


Figure $20.2B.1$: Common ancestors: Lizards, rabbits, and humans all descend from a common ancestor that had an amniotic egg. Thus, lizards, rabbits, and humans all belong to the clade Amniota. Vertebrata is a larger clade that also includes fish and lamprey.

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. Notice in the various examples of clades how each clade comes from a single point, whereas the non-clade groups show branches that do not share a single point.

Shared Characteristics

Organisms evolve from common ancestors and then diversify. Scientists use the phrase “descent with modification” because even though related organisms have many of the same characteristics and genetic codes, changes occur. This pattern repeats as one goes through the phylogenetic tree of life:

1. A change in the genetic makeup of an organism leads to a new trait which becomes prevalent in the group.
2. Many organisms descend from this point and have this trait.
3. New variations continue to arise: some are adaptive and persist, leading to new traits.
4. With new traits, a new branch point is determined (go back to step 1 and repeat).

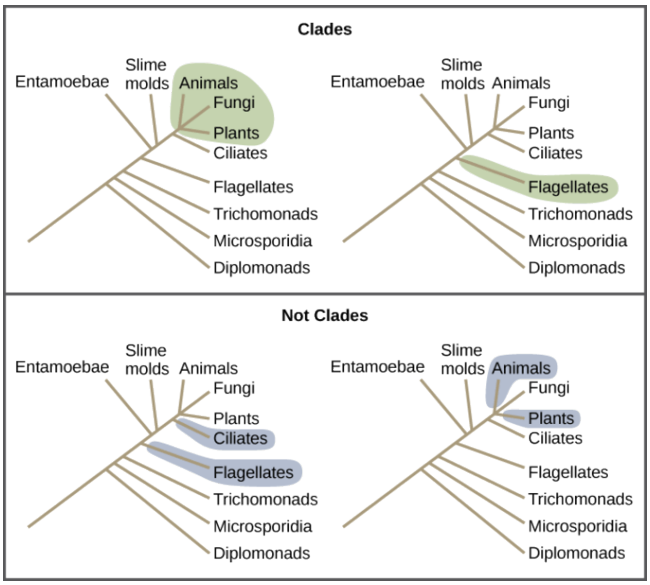


Figure $20.2B.1$: Examples of clades: All the organisms within a clade stem from a single point on the tree. A clade may contain multiple groups, as in the case of animals, fungi, and plants, or a single group, as in the case of flagellates. Groups that diverge at a different branch point, or that do not include all groups in a single branch point, are not considered clades.

If a characteristic is found in the ancestor of a group, it is considered a shared-ancestral character because all of the organisms in the taxon or clade have that trait. Now, consider the amniotic egg characteristic in the same figure. Only some of the organisms have this trait; to those that do, it is called a shared-derived character because this trait derived at some point, but does not include all of the ancestors in the tree. The tricky aspect to shared-ancestral and shared-derived characters is the fact that these terms are relative. The same trait can be considered one or the other depending on the particular diagram being used. These terms help scientists distinguish between clades in the building of phylogenetic trees.

Choosing the Right Relationships

Imagine being the person responsible for organizing all of the items in a department store properly; an overwhelming task. Organizing the evolutionary relationships of all life on earth proves much more difficult: scientists must span enormous blocks of time and work with information from long-extinct organisms. Trying to decipher the proper connections, especially given the presence of homologies and analogies, makes the task of building an accurate tree of life extraordinarily difficult. Add to that the advancement of DNA technology, which now provides large quantities of genetic sequences to be used and analyzed. Taxonomy is a subjective discipline: many organisms have more than one connection to each other, so each taxonomist will decide the order of connections.

To aid in the tremendous task of describing phylogenies accurately, scientists often use a concept called maximum parsimony, which means that events occurred in the simplest, most obvious way. For example, if a group of people entered a forest preserve to go hiking, based on the principle of maximum parsimony, one could predict that most of the people would hike on established trails rather than forge new ones. For scientists deciphering evolutionary pathways, the same idea is used: the pathway of evolution probably includes the fewest major events that coincide with the evidence at hand. Starting with all of the homologous traits in a group of organisms, scientists look for the most obvious and simple order of evolutionary events that led to the occurrence of those traits.

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Key Points

- Phylogenetic trees sort organisms into clades: groups of organisms that descended from a single ancestor.
- Organisms of a single clade are called a monophyletic group.
- Scientists use the phrase “descent with modification” because genetic changes occur even though related organisms have many of the same characteristics and genetic codes.
- A characteristic is considered a shared-ancestral character if it is found in the ancestor of a group and all of the organisms in the taxon or clade have that trait.
- If only some of the organisms have a certain trait, it is called a shared- derived character because this trait derived at some point, but does not include all of the ancestors in the clade.
- Scientists often use a concept called maximum parsimony, which means that events occurred in the simplest, most obvious way, to aid in the tremendous task of describing phylogenies accurately.

Key Terms

- **monophyletic**: of, pertaining to, or affecting a single phylum (or other taxon) of organisms
- **derived**: of, or pertaining to, conditions unique to the descendant species of a clade, and not found in earlier ancestral species
- **clades**: groups of organisms that descended from a single ancestor
- **ancestral**: of, pertaining to, derived from, or possessed by, an ancestor or ancestors; as, an ancestral estate
- **maximum parsimony**: the preferred phylogenetic tree is the tree that requires the least evolutionary change to explain some observed data

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20.3: PERSPECTIVES ON THE PHYLOGENETIC TREE

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20.3A: Limitations to the Classic Model of Phylogenetic Trees

20.3B: Horizontal Gene Transfer

20.3C: Endosymbiotic Theory and the Evolution of Eukaryotes

20.3D: Web, Network, and Ring of Life Models

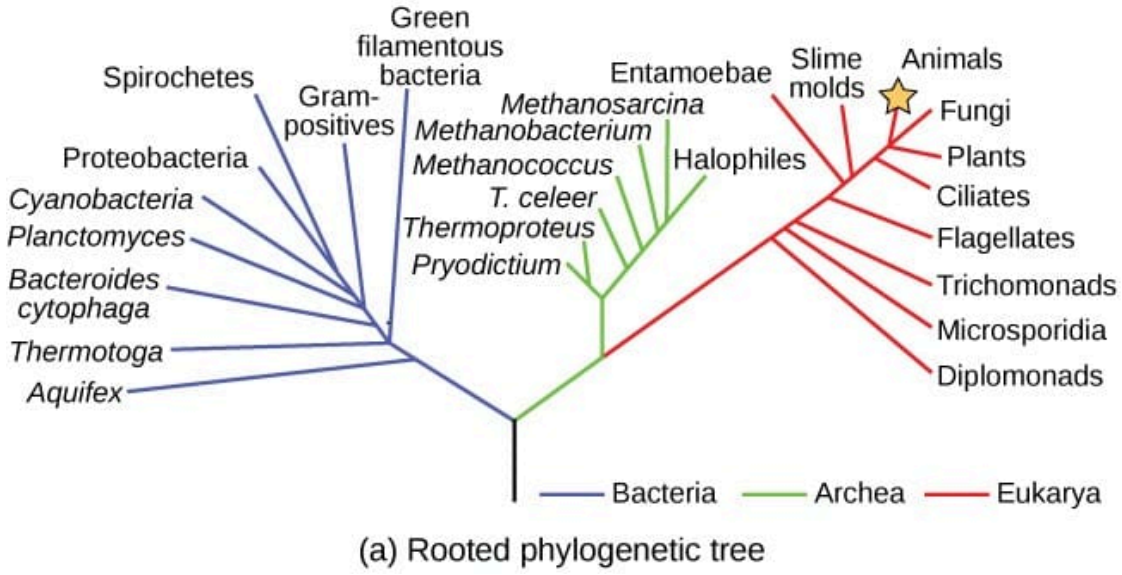
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20.3A: Limitations to the Classic Model of Phylogenetic Trees

Learning Objectives

- Identify the limitations to the classic model of phylogenetic trees

The concepts of phylogenetic modeling are constantly changing. It is one of the most dynamic fields of study in all of biology. Over the last several decades, new research has challenged scientists' ideas about how organisms are related. New models of these relationships have been proposed for consideration by the scientific community. Many phylogenetic trees have been shown as models of the evolutionary relationship among species. Phylogenetic trees originated with Charles Darwin, who sketched the first phylogenetic tree in 1837, which served as a pattern for subsequent studies for more than a century. The concept of a phylogenetic tree with a single trunk representing a common ancestor, with the branches representing the divergence of species from this ancestor, fits well with the structure of many common trees, such as the oak. However, evidence from modern DNA sequence analysis and newly-developed computer algorithms has caused skepticism about the validity of the standard tree model in the scientific community.



(a) Rooted phylogenetic tree

Figure 20.3A.1: Tree of life: The (a) concept of the "tree of life" goes back to an 1837 sketch by Charles Darwin. Like an (b) oak tree, the "tree of life" has a single trunk and many branches.

Classical thinking about prokaryotic evolution, included in the classic tree model, is that species evolve clonally. That is, they produce offspring themselves with only random mutations causing the descent into the variety of modern and extinct species known to science. This view is somewhat complicated in eukaryotes that reproduce sexually, but the laws of Mendelian genetics explain the variation in offspring, again, to be a result of a mutation within the species. The concept of genes being transferred between unrelated species was not considered as a possibility until relatively recently. Horizontal gene transfer (HGT), also known as lateral gene transfer, is the transfer of genes between unrelated species. HGT has been shown to be an ever-present phenomenon, with many evolutionists postulating a major role for this process in evolution, thus complicating the simple tree model. Genes have been shown to be passed between species which are only distantly related using standard phylogeny, thus adding a layer of complexity to the understanding of phylogenetic relationships. Finally, as an example of the ultimate gene transfer, theories of genome fusion between symbiotic or endosymbiotic organisms have been proposed to explain an event of great importance: the evolution of the first eukaryotic cell, without which humans could not have come into existence.

Key Points

- Charles Darwin sketched the first phylogenetic tree in 1837.
- A single trunk on a phylogenetic tree represents a common ancestor and the branches represent the divergence of species from this ancestor.
- Prokaryotes are assumed to evolve clonally in the classic tree model.
- Horizontal gene transfer is the transfer of genes between unrelated species and, as such, complicates the simple tree model.
- Ultimate gene transfer has provided theories of genome fusion between symbiotic or endosymbiotic organisms.

Key Terms

- **phylogenetic**: of, or relating to the evolutionary development of organisms
- **clonal**: pertaining to asexual reproduction
- **horizontal gene transfer**: the transfer of genetic material from one organism to another one that is not its offspring; especially common among bacteria

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20.3B: Horizontal Gene Transfer

Learning Objectives

- Explain how horizontal gene transfer can make resolution of phylogenies difficult

Horizontal gene transfer (HGT) is the introduction of genetic material from one species to another species by mechanisms other than the vertical transmission from parent(s) to offspring. These transfers allow even distantly-related species (using standard phylogeny) to share genes, influencing their phenotypes. It is thought that HGT is more prevalent in prokaryotes, but that only about 2% of the prokaryotic genome may be transferred by this process. Some researchers believe these estimates are premature; the actual importance of HGT to evolutionary processes must be viewed as a work in progress. As the phenomenon is investigated more thoroughly, it may be revealed to be more common. Many evolutionists postulate a major role for this process in evolution, thus complicating the simple tree model. A number of scientists believe that HGT and mutation appear to be (especially in prokaryotes) a significant source of genetic variation, which is the raw material for the process of natural selection. These transfers may occur between any two species that share an intimate relationship, thus adding a layer of complexity to the understanding or resolution of phylogenetic relationships.

Summary of Mechanisms of Prokaryotic and Eukaryotic HGT			
	Mechanism	**Mode of Transmission**	**Example**
Prokaryotes	transformation	DNA uptake	many prokaryotes
	transduction	bacteriophage (virus)	bacteria
	conjugation	pilus	many prokaryotes
	gene transfer agents	phage-like particles	purple non-sulfur bacteria
Eukaryotes	from food organisms	unknown	aphid
	jumping genes	transposons	rice and millet plants
	epiphytes/parasites	unknown	yew tree fungi
	from viral infections		

Figure $20.3B.1$: Mechanisms of prokaryotic and eukaryotic horizontal gene transfer: Horizontal gene transfer is the introduction of genetic material from one species to another species by mechanisms other than the vertical transmission from parent(s) to offspring. These transfers allow even distantly-related species (using standard phylogeny) to share genes, influencing their phenotypes. Examples of mechanisms of horizontal gene transfer are listed for both prokaryotic and eukaryotic organisms.

HGT in Prokaryotes

The mechanism of HGT has been shown to be quite common in the prokaryotic domains of Bacteria and Archaea, significantly changing the way their evolution is viewed. These gene transfers between species are the major mechanism whereby bacteria acquire resistance to antibiotics. Classically, this type of transfer was thought to occur by three different mechanisms:

- Transformation: naked DNA is taken up by a bacteria.
- Transduction: genes are transferred using a virus.
- Conjugation: the use a hollow tube called a pilus to transfer genes between organisms.

More recently, a fourth mechanism of gene transfer between prokaryotes has been discovered. Small, virus-like particles called gene transfer agents (GTAs) transfer random genomic segments from one species of prokaryote to another. GTAs have been shown to be responsible for genetic changes, sometimes at a very high frequency compared to other evolutionary processes.

The first GTA was characterized in 1974 using purple, non-sulfur bacteria. These GTAs, which are thought to be bacteriophages that lost the ability to reproduce on their own, carry random pieces of DNA from one organism to another. The ability of GTAs to act with high frequency has been demonstrated in controlled studies using marine bacteria. Gene transfer events in marine prokaryotes, either by GTAs or by viruses, have been estimated to be as high as 10^{13} per year in the Mediterranean Sea alone. GTAs and viruses are thought to be efficient HGT vehicles with a major impact on prokaryotic evolution.

HGT in Eukaryotes

Although it is easy to see how prokaryotes exchange genetic material by HGT, it was initially thought that this process was absent in eukaryotes. After all, prokaryotes are only single cells exposed directly to their environment, whereas the sex cells of multicellular organisms are usually sequestered in protected parts of the body. It follows from this idea that the gene transfers between multicellular eukaryotes should be more difficult. Indeed, it is thought that this process is rarer in eukaryotes and has a much smaller evolutionary impact than in prokaryotes. In spite of this fact, HGT between distantly-related organisms has been demonstrated in several eukaryotic species. It is possible that more examples will be discovered in the future.

In plants, gene transfer has been observed in species that cannot cross-pollinate by normal means. Transposons or “jumping genes” have been shown to transfer between rice and millet plant species. Furthermore, fungal species feeding on yew trees, from which the anti-cancer drug TAXOL® is derived from the bark, have acquired the ability to make taxol themselves; a clear example of gene transfer.

In animals, a particularly interesting example of HGT occurs within the aphid species. Aphids are insects that vary in color based on carotenoid content. Carotenoids are pigments made by a variety of plants, fungi, and microbes, which serve a variety of functions in animals who obtain these chemicals from their food. Humans require carotenoids to synthesize vitamin A and we obtain them by eating orange fruits and vegetables: carrots, apricots, mangoes, and sweet potatoes. On the other hand, aphids have acquired the ability to make the carotenoids on their own. According to DNA analysis, this ability is due to the transfer of fungal genes into the insect by HGT, presumably as the insect consumed fungi for food. A carotenoid enzyme called a desaturase is responsible for the red coloration seen in certain aphids. Furthermore, it has been shown that when this gene is inactivated by mutation, the aphids revert back to their more common green color.



Figure $20.3B.1$: HGT within the aphid species: (a) Red aphids get their color from red carotenoid pigment. Genes necessary to make this pigment are present in certain fungi. Scientists speculate that aphids acquired these genes through HGT after consuming fungi for food. If genes for making carotenoids are inactivated by mutation, the aphids revert back to (b) their green color. Red coloration makes the aphids much more conspicuous to predators, but evidence suggests that red aphids are more resistant to insecticides than green ones. Thus, red aphids may be more fit to survive in some environments than green ones.

Key Points

- It is thought that HGT is more prevalent in prokaryotes than eukaryotes, but that only about 2% of the prokaryotic genome may be transferred by this process.
- Many scientists believe that HGT and mutation appear to be (especially in prokaryotes) a significant source of genetic

variation, which is the raw material for the process of natural selection.
- HGT in prokaryotes occurs by four different mechanisms: transformation, transduction, conjugation, and via gene transfer agents.
- HGT occurs in plants through transposons (jumping genes), which transfer between different species of plants.
- An example of HGT in animals is the transfer (through consumption) of fungal genes into insects called aphids, which allows the aphids the ability to make carotenoids on their own.

Key Terms

- **transformation**: the alteration of a bacterial cell caused by the transfer of DNA from another, especially if pathogenic
- **transduction**: horizontal gene transfer mechanism in prokaryotes where genes are transferred using a virus
- **conjugation**: the temporary fusion of organisms, especially as part of sexual reproduction

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20.3C: Endosymbiotic Theory and the Evolution of Eukaryotes

Learning Objectives

- Describe the genome fusion hypothesis and its relationship to the evolution of eukaryotes

Genome Fusion and the Evolution of Eukaryotes

Scientists believe the ultimate event in HGT (horizontal gene transfer) occurs through genome fusion between different species when two symbiotic organisms become endosymbiotic. This occurs when one species is taken inside the cytoplasm of another species, which ultimately results in a genome consisting of genes from both the endosymbiont and the host. This mechanism is an aspect of the Endosymbiont Theory, which is accepted by a majority of biologists as the mechanism whereby eukaryotic cells obtained their mitochondria and chloroplasts. However, the role of endosymbiosis in the development of the nucleus is more controversial. Nuclear and mitochondrial DNA are thought to be of different (separate) evolutionary origin, with the mitochondrial DNA being derived from the circular genomes of bacteria that were engulfed by ancient prokaryotic cells. Mitochondrial DNA can be regarded as the smallest chromosome. Interestingly enough, mitochondrial DNA is inherited only from the mother. The mitochondrial DNA degrades in sperm when the sperm degrades in the fertilized egg or, in other instances, when the mitochondria located in the flagellum of the sperm fails to enter the egg.

Within the past decade, the process of genome fusion by endosymbiosis has been proposed to be responsible for the evolution of the first eukaryotic cells. Using DNA analysis and a new mathematical algorithm called conditioned reconstruction (CR), it has been proposed that eukaryotic cells developed from an endosymbiotic gene fusion between two species: one an Archaea and the other a Bacteria. As mentioned, some eukaryotic genes resemble those of Archaea, whereas others resemble those from Bacteria. An endosymbiotic fusion event would clearly explain this observation. On the other hand, this work is new and the CR algorithm is relatively unsubstantiated, which causes many scientists to resist this hypothesis.

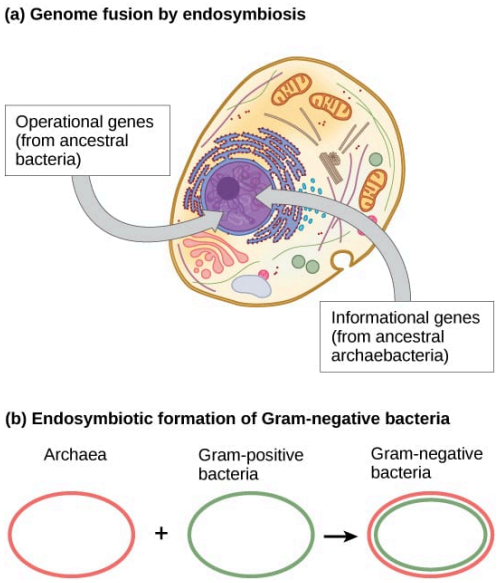


Figure $20.3C.1$: Endosymbiosis in eukaryotes: The theory that mitochondria and chloroplasts are endosymbiotic in origin is now widely accepted. More controversial is the proposal that (a) the eukaryotic nucleus resulted from the fusion of archaeal and bacterial genomes; and that (b) Gram-negative bacteria, which have two membranes, resulted from the fusion of Archaea and Gram-positive bacteria, each of which has a single membrane.

More recent work proposes that gram-negative bacteria, which are unique within their domain in that they contain two lipid bilayer membranes, did result from an endosymbiotic fusion of archaeal and bacterial species. The double membrane would be a

direct result of endosymbiosis, with the endosymbiont picking up the second membrane from the host as it was internalized. This mechanism has also been used to explain the double membranes found in mitochondria and chloroplasts. A lot of skepticism still surrounds this hypothesis; the ideas are still debated within the biological science community.

There are several other competing hypotheses as to the origin of eukaryotes and the nucleus. One idea about how the eukaryotic nucleus evolved is that prokaryotic cells produced an additional membrane which surrounded the bacterial chromosome. Some bacteria have the DNA enclosed by two membranes; however, there is no evidence of a nucleolus or nuclear pores. Other proteobacteria also have membrane-bound chromosomes. If the eukaryotic nucleus evolved this way, we would expect one of the two types of prokaryotes to be more closely-related to eukaryotes. Another hypothesis, the nucleus-first hypothesis, proposes the nucleus evolved in prokaryotes first, followed by a later fusion of the new eukaryote with bacteria that became mitochondria. The mitochondria-first hypothesis, however, proposes mitochondria were first established in a prokaryotic host, which subsequently acquired a nucleus (by fusion or other mechanisms) to become the first eukaryotic cell. Most interestingly, the eukaryote-first hypothesis proposes prokaryotes actually evolved from eukaryotes by losing genes and complexity. All of these hypotheses are testable. Only time and more experimentation will determine which hypothesis is best supported by data.

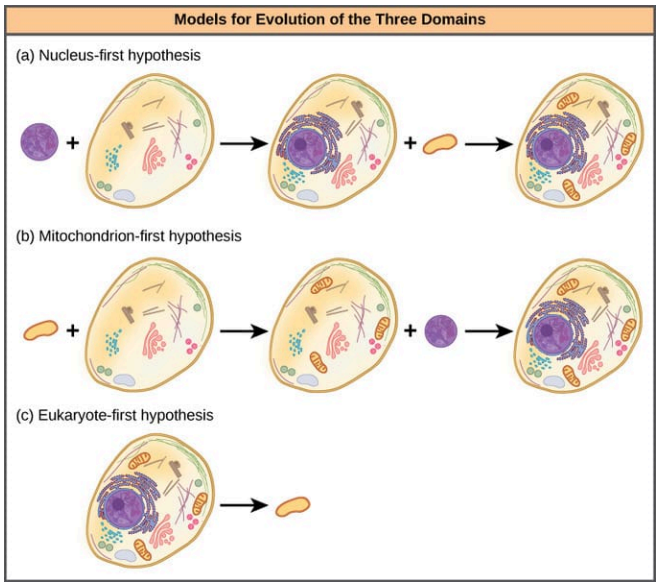


Figure $20.3C.1$: Three hypotheses of eukaryotic and prokaryotic evolution: Three alternate hypotheses of eukaryotic and prokaryotic evolution are (a) the nucleus-first hypothesis, (b) the mitochondrion-first hypothesis, and (c) the eukaryote-first hypothesis.

Key Points

- Two symbiotic organisms become endosymbiotic when one species is taken inside the cytoplasm of another species, resulting in genome fusion.
- Genome fusion, by endosymbiosis, between two species, one an Archaea and the other a Bacteria, has been proposed as responsible for the evolution of the first eukaryotic cells.
- Gram-negative bacteria are proposed to result from an endosymbiotic fusion of archaeal and bacterial species through a mechanism that has also been used to explain the double membranes found in mitochondria and chloroplasts.
- The nucleus-first hypothesis proposes the nucleus evolved in prokaryotes first, followed by a later fusion of the new eukaryote with bacteria that became mitochondria.
- The mitochondria-first hypothesis proposes mitochondria were first established in a prokaryotic host, which subsequently acquired a nucleus to become the first eukaryotic cell.
- The eukaryote-first hypothesis proposes prokaryotes actually evolved from eukaryotes by losing genes and complexity.

Key Terms

- **genome fusion**: a result of endosymbiosis when a genome consists of genes from both the endosymbiont and the host.
- **symbiotic**: of a relationship with mutual benefit between two individuals or organisms
- **endosymbiosis**: when one symbiotic species is taken inside the cytoplasm of another symbiotic species and both become endosymbiotic

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20.3D: Web, Network, and Ring of Life Models

Learning Objectives

- Describe the web, network, and ring of life models of phylogenetic trees

The recognition of the importance of Horizontal gene transfer (HGT), especially in the evolution of prokaryotes, has caused some to propose abandoning the classic “tree of life” model. In 1999, a phylogenetic model that resembles a web or a network more than a tree was proposed. The hypothesis is that eukaryotes evolved not from a single prokaryotic ancestor, but from a pool of many species that were sharing genes by HGT mechanisms. Some individual prokaryotes were responsible for transferring the bacteria that caused mitochondrial development in the new eukaryotes, whereas other species transferred the bacteria that gave rise to chloroplasts. This model is often called the “web of life.” In an effort to save the tree analogy, some have proposed using the Ficus tree with its multiple trunks as a phylogenetic tree to represent the evolutionary role for HGT.

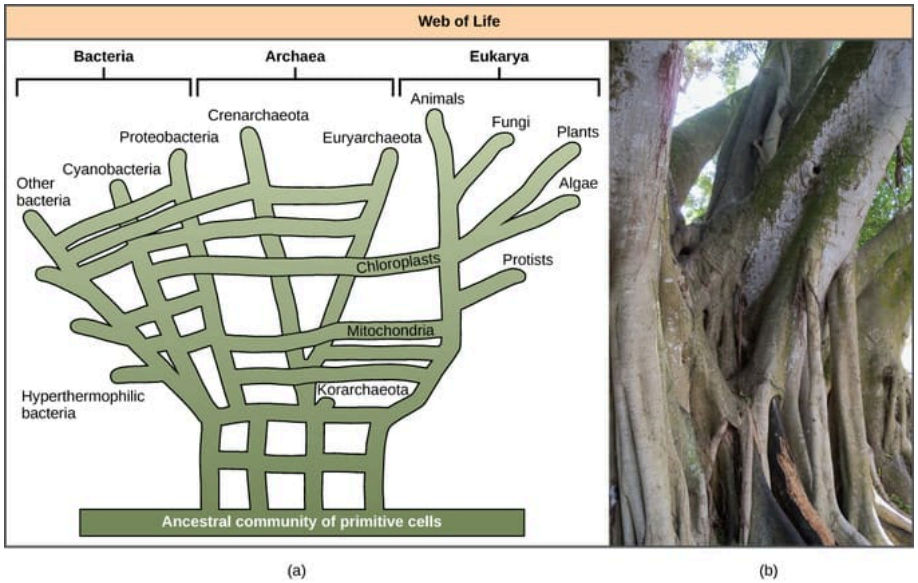


Figure $20.3D.1$: Phylogenetic web of life model: In the (a) phylogenetic model proposed by W. Ford Doolittle, the “tree of life” arose from a community of ancestral cells, has multiple trunks, and has connections between branches where horizontal gene transfer has occurred. Visually, this concept is better represented by (b) the multi-trunked Ficus than by the single trunk of the oak, similar to the tree drawn by Darwin.

Others have proposed abandoning any tree-like model of phylogeny in favor of a ring structure. The ” ring of life ” is a phylogenetic model where all three domains of life evolved from a pool of primitive prokaryotes. Using the conditioned reconstruction algorithm, it proposes a ring-like model in which species of all three domains (Archaea, Bacteria, and Eukarya) evolved from a single pool of gene-swapping prokaryotes. This structure is proposed as the best fit for data from extensive DNA analyses; the ring model is the only one that adequately takes HGT and genomic fusion into account. However, phylogeneticists remain highly skeptical of this model.

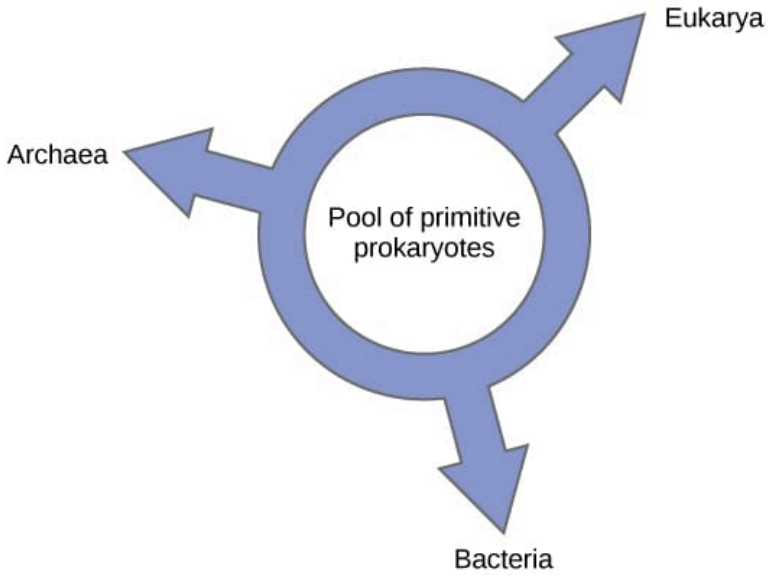


Figure 20.3D.1: Phylogenetic ring of life model: According to the "ring of life" phylogenetic model, the three domains of life evolved from a pool of primitive prokaryotes.

In summary, the "tree of life" model proposed by Darwin must be modified to include HGT. This does not mean a tree, web, or a ring will correlate completely to an accurate description of phylogenetic relationships of life. A consequence of the new thinking about phylogenetic models is the idea that Darwin's original conception of the phylogenetic tree is too simple, but made sense based on what was known at that time.

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Key Points

- A phylogenetic model that resembles a web or a network was proposed since eukaryotes evolved not from a single prokaryotic ancestor, but from a pool of many species that were sharing genes by HGT mechanisms.
- A phylogenetic model that resembles a ring was proposed in which species of all three domains, Archaea, Bacteria, and Eukarya, evolved from a single pool of gene-swapping prokaryotes.
- Phylogenetic models will continue to evolve as phylogeneticists remain highly skeptical of the current tree, web, and ring models.

Key Terms

- **web of life**: a phylogenetic model that resembles a web or a network more than a tree
- **ring of life**: a phylogenetic model where all three domains of life (Archaea, Bacteria, and Eukarya) evolved from a pool of primitive prokaryotes

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21: VIRUSES

21.1: Viral Evolution, Morphology, and Classification

21.1A: Discovery and Detection of Viruses

21.1B: Evolution of Viruses

21.1C: Viral Morphology

21.1D: Virus Classification

21.2: Virus Infections and Hosts

21.2A: Steps of Virus Infections

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21.3: Prevention and Treatment of Viral Infections

21.3A: Vaccines and Immunity

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21.4: Prions and Viroids

21.4.1: 21-4A- Prions and Viroids

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21.1: VIRAL EVOLUTION, MORPHOLOGY, AND CLASSIFICATION

- Topic hierarchy

21.1A: Discovery and Detection of Viruses

21.1B: Evolution of Viruses

21.1C: Viral Morphology

21.1D: Virus Classification

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21.1A: Discovery and Detection of Viruses

Learning Objectives

- Describe how viruses were first discovered and how they are detected

Discovery and Detection

Viruses were first discovered after the development of a porcelain filter, called the Chamberland-Pasteur filter, which could remove all bacteria visible in the microscope from any liquid sample. In 1886, Adolph Meyer demonstrated that a disease of tobacco plants, tobacco mosaic disease, could be transferred from a diseased plant to a healthy one via liquid plant extracts. In 1892, Dmitri Ivanowski showed that this disease could be transmitted in this way even after the Chamberland-Pasteur filter had removed all viable bacteria from the extract. Still, it was many years before it was proven that these "filterable" infectious agents were not simply very small bacteria, but were a new type of tiny, disease-causing particle.

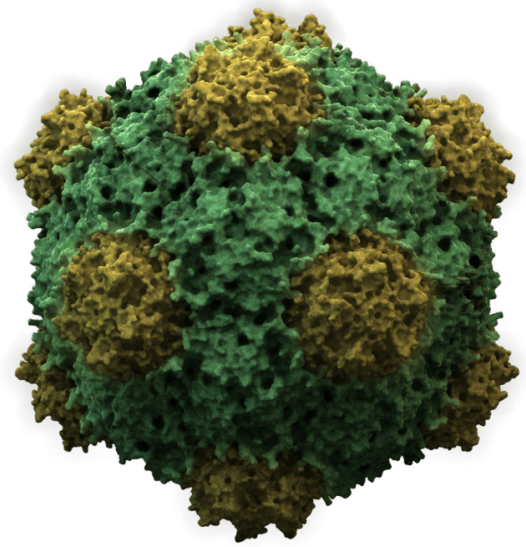


Figure 21.1A.1: The structure of the icosahedral cowpea mosaic virus: In the past, viruses were classified by the type of nucleic acid they contained, DNA or RNA, and whether they had single- or double-stranded nucleic acid.

Virions, single virus particles, are very small, about 20–250 nanometers in diameter. These individual virus particles are the infectious form of a virus outside the host cell. Unlike bacteria (which are about 100 times larger), we cannot see viruses with a light microscope, with the exception of some large virions of the poxvirus family. It was not until the development of the electron microscope in the late 1930s that scientists got their first good view of the structure of the tobacco mosaic virus (TMV) and other viruses. The surface structure of virions can be observed by both scanning and transmission electron microscopy, whereas the internal structures of the virus can only be observed in images from a transmission electron microscope. The use of these technologies has enabled the discovery of many viruses of all types of living organisms. They were initially grouped by shared morphology. Later, groups of viruses were classified by the type of nucleic acid they contained, DNA or RNA, and whether their nucleic acid was single- or double-stranded. More recently, molecular analysis of viral replicative cycles has further refined their classification.

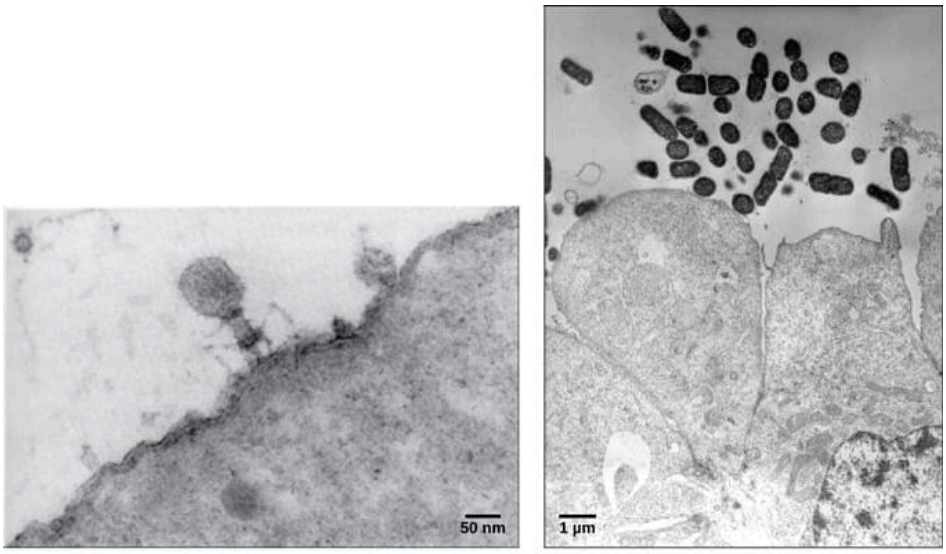


Figure 21.1A.1: Examples of transmission electron micrographs of viruses: In these transmission electron micrographs, (a) a virus is dwarfed by the bacterial cell it infects, while (b) these E. coli cells are dwarfed by cultured colon cells.

Key Points

- Virions, single virus particles, are 20–250 nanometers in diameter.
- In the past, viruses were classified by the type of nucleic acid they contained, DNA or RNA, and whether they had single- or double-stranded nucleic acid.
- Molecular analysis of viral replicative cycles is now more routinely used to classify viruses.

Key Terms

- **virus**: a submicroscopic infectious organism, now understood to be a non-cellular structure consisting of a core of DNA or RNA surrounded by a protein coat
- **virion**: a single individual particle of a virus (the viral equivalent of a cell)

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21.1B: Evolution of Viruses

Learning Objectives

- Describe the difficulties in determining the origin of viruses

Although biologists have accumulated a significant amount of knowledge about how present-day viruses evolve, much less is known about how viruses originated in the first place. When exploring the evolutionary history of most organisms, scientists can look at fossil records and similar historic evidence. However, viruses do not fossilize, so researchers must conjecture by investigating how today's viruses evolve and by using biochemical and genetic information to create speculative virus histories.

While most findings agree that viruses don't have a single common ancestor, scholars have yet to find one hypothesis about virus origins that is fully accepted in the field. One possible hypothesis, called devolution or the regressive hypothesis, proposes to explain the origin of viruses by suggesting that viruses evolved from free-living cells. However, many components of how this process might have occurred are a mystery. A second hypothesis (called escapist or the progressive hypothesis) accounts for viruses having either an RNA or a DNA genome and suggests that viruses originated from RNA and DNA molecules that escaped from a host cell. A third hypothesis posits a system of self-replication similar to that of other self-replicating molecules, probably evolving alongside the cells they rely on as hosts; studies of some plant pathogens support this hypothesis.

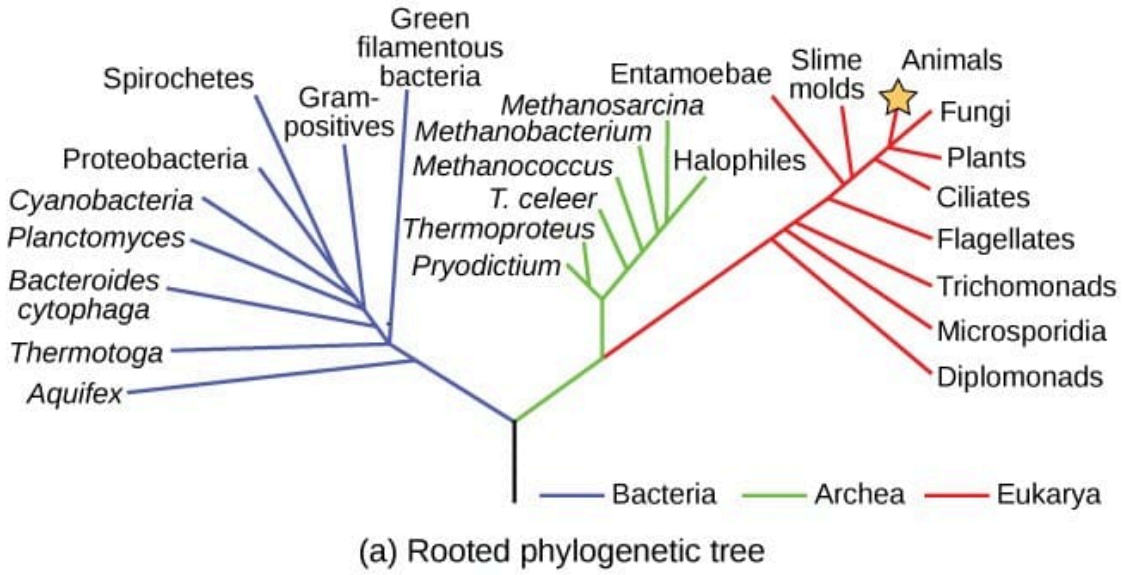


Figure 21.1B.1: Common ancestor tree of life: This phylogenetic tree of the three domains of life (Bacteria, Archaea, and Eukarya) attempts to identify when various species diverged from a common ancestor. Finding a common ancestor for viruses has proven to be far more difficult, especially since they do not fossilize.

As technology advances, scientists may develop and refine further hypotheses to explain the origin of viruses. The emerging field called virus molecular systematics attempts to do just that through comparisons of sequenced genetic material. These researchers hope to one day better understand the origin of viruses, a discovery that could lead to advances in the treatments for the ailments they produce.

Key Points

- Scientists agree that viruses don't have a single common ancestor, but have yet to agree on a single hypothesis about virus origins.
- The devolution or the regressive hypothesis suggests that viruses evolved from free-living cells.
- The escapist or the progressive hypothesis suggests that viruses originated from RNA and DNA molecules that escaped from a host cell.

- The self-replicating hypothesis posits a system of self-replication that most probably involves evolution alongside the host cells.

Key Terms

- **self-replicating**: able to generate a copy of itself
- **devolution**: degeneration (as opposed to evolution)

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21.1C: Viral Morphology

Learning Objectives

- Describe the relationship between the viral genome, capsid, and envelope

Viruses are acellular, meaning they are biological entities that do not have a cellular structure. Therefore, they lack most of the components of cells, such as organelles, ribosomes, and the plasma membrane. A virion consists of a nucleic acid core, an outer protein coating or capsid, and sometimes an outer envelope made of protein and phospholipid membranes derived from the host cell. The capsid is made up of protein subunits called capsomeres. Viruses may also contain additional proteins, such as enzymes. The most obvious difference between members of viral families is their morphology, which is quite diverse. An interesting feature of viral complexity is that host and virion complexity are uncorrelated. Some of the most intricate virion structures are observed in bacteriophages, viruses that infect the simplest living organisms: bacteria.

Morphology

Viruses come in many shapes and sizes, but these are consistent and distinct for each viral family. In general, the shapes of viruses are classified into four groups: filamentous, isometric (or icosahedral), enveloped, and head and tail. Filamentous viruses are long and cylindrical. Many plant viruses are filamentous, including TMV (tobacco mosaic virus). Isometric viruses have shapes that are roughly spherical, such as poliovirus or herpesviruses. Enveloped viruses have membranes surrounding capsids. Animal viruses, such as HIV, are frequently enveloped. Head and tail viruses infect bacteria. They have a head that is similar to icosahedral viruses and a tail shape like filamentous viruses.

Many viruses use some sort of glycoprotein to attach to their host cells via molecules on the cell called viral receptors. For these viruses, attachment is a requirement for later penetration of the cell membrane, allowing them to complete their replication inside the cell. The receptors that viruses use are molecules that are normally found on cell surfaces and have their own physiological functions. Viruses have simply evolved to make use of these molecules for their own replication.

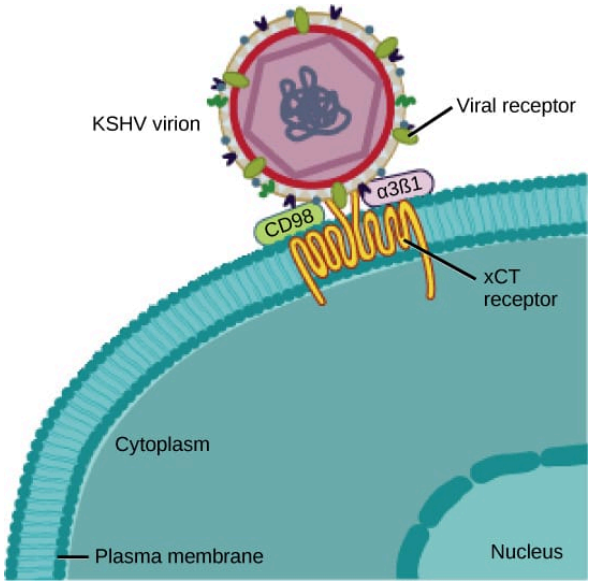


Figure $21.1C.1$: Example of a virus attaching to its host cell: The KSHV virus binds the xCT receptor on the surface of human cells. This attachment allows for later penetration of the cell membrane and replication inside the cell.

Overall, the shape of the virion and the presence or absence of an envelope tell us little about what disease the virus may cause or what species it might infect, but they are still useful means to begin viral classification. Among the most complex virions known, the T4 bacteriophage, which infects the *Escherichia coli* bacterium, has a tail structure that the virus uses to attach to host cells and a head structure that houses its DNA. Adenovirus, a non-enveloped animal virus that causes respiratory illnesses in humans,

uses glycoprotein spikes protruding from its capsomeres to attach to host cells. Non-enveloped viruses also include those that cause polio (poliovirus), plantar warts (papillomavirus), and hepatitis A (hepatitis A virus).

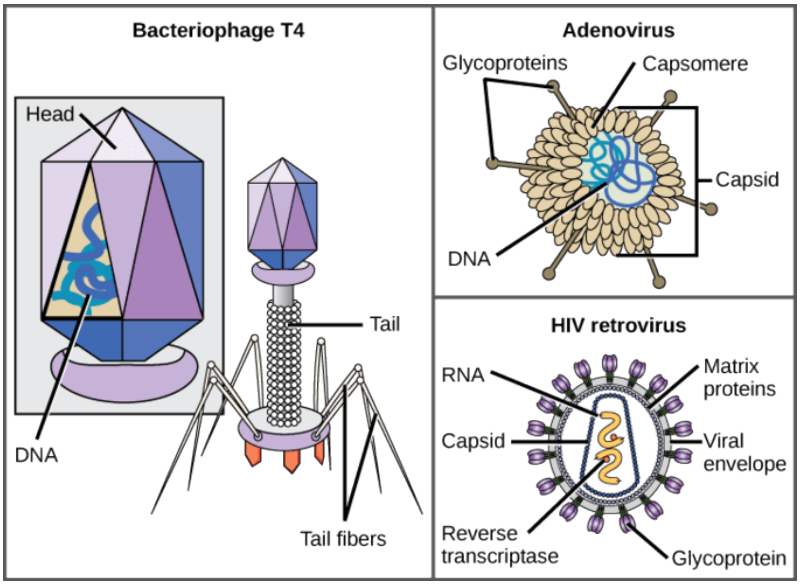


Figure 21.1C.1: Examples of virus shapes: Viruses can be either complex in shape or relatively simple. This figure shows three relatively-complex virions: the bacteriophage T4, with its DNA-containing head group and tail fibers that attach to host cells; adenovirus, which uses spikes from its capsid to bind to host cells; and HIV, which uses glycoproteins embedded in its envelope to bind to host cells.

Enveloped virions like HIV consist of nucleic acid and capsid proteins surrounded by a phospholipid bilayer envelope and its associated proteins. Glycoproteins embedded in the viral envelope are used to attach to host cells. Other envelope proteins include the matrix proteins that stabilize the envelope and often play a role in the assembly of progeny virions. Chicken pox, influenza, and mumps are examples of diseases caused by viruses with envelopes. Because of the fragility of the envelope, non-enveloped viruses are more resistant to changes in temperature, pH, and some disinfectants than are enveloped viruses.

Types of Nucleic Acid

Unlike nearly all living organisms that use DNA as their genetic material, viruses may use either DNA or RNA. The virus core contains the genome or total genetic content of the virus. Viral genomes tend to be small, containing only those genes that encode proteins that the virus cannot obtain from the host cell. This genetic material may be single- or double-stranded. It may also be linear or circular. While most viruses contain a single nucleic acid, others have genomes that have several, called segments.

In DNA viruses, the viral DNA directs the host cell's replication proteins to synthesize new copies of the viral genome and to transcribe and translate that genome into viral proteins. DNA viruses cause human diseases, such as chickenpox, hepatitis B, and some venereal diseases, like herpes and genital warts.

RNA viruses contain only RNA as their genetic material. To replicate their genomes in the host cell, the RNA viruses encode enzymes that can replicate RNA into DNA, which cannot be done by the host cell. These RNA polymerase enzymes are more likely to make copying errors than DNA polymerases and, therefore, often make mistakes during transcription. For this reason, mutations in RNA viruses occur more frequently than in DNA viruses. This causes them to change and adapt more rapidly to their host. Human diseases caused by RNA viruses include hepatitis C, measles, and rabies.

Key Points

- Viruses are classified into four groups based on shape: filamentous, isometric (or icosahedral), enveloped, and head and tail.
- Many viruses attach to their host cells to facilitate penetration of the cell membrane, allowing their replication inside the cell.
- Non-enveloped viruses can be more resistant to changes in temperature, pH, and some disinfectants than are enveloped viruses.
- The virus core contains the small single- or double-stranded genome that encodes the proteins that the virus cannot get

from the host cell.

Key Terms

- **capsid**: the outer protein shell of a virus
- **envelope**: an enclosing structure or cover, such as a membrane
- **filamentous**: Having the form of threads or filaments
- **isometric**: of, or being a geometric system of three equal axes lying at right angles to each other (especially in crystallography)

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21.1D: Virus Classification

Learning Objectives

- Describe how viruses are classified

To understand the features shared among different groups of viruses, a classification scheme is necessary. However, most viruses are not thought to have evolved from a common ancestor, so the methods that scientists use to classify living things are not very useful. Biologists have used several classification systems in the past, based on the morphology and genetics of the different viruses. However, these earlier classification methods grouped viruses based on which features of the virus they were using to classify them. The most commonly-used classification method today is called the Baltimore classification scheme which is based on how messenger RNA (mRNA) is generated in each particular type of virus. The surface structure of virions can be observed by both scanning and transmission electron microscopy, whereas the internal structures of the virus can only be observed in images from a transmission electron microscope.

Past Systems of Classification

Viruses are classified in several ways: by factors such as their core content, the structure of their capsids, and whether they have an outer envelope. Viruses may use either DNA or RNA as their genetic material. The virus core contains the genome or total genetic content of the virus. Viral genomes tend to be small, containing only those genes that encode proteins that the virus cannot obtain from the host cell. This genetic material may be single- or double-stranded. It may also be linear or circular. While most viruses contain a single nucleic acid, others have genomes that have several, which are called segments. The type of genetic material (DNA or RNA) and its structure (single- or double-stranded, linear or circular, and segmented or non-segmented) are used to classify the virus core structures.

Virus Classification by Genome Structure and Core	
Core Classifications	**Examples**
RNA	Rabies virus, retroviruses
DNA	Herpesviruses, smallpox virus
Single-stranded	Rabies virus, retroviruses
Double-stranded	Herpesviruses, smallpox virus
Linear	Rabies virus, retroviruses, herpesviruses, smallpox virus
Circular	Papillomaviruses, many bacteriophages
Non-segmented: genome consists of a single segment of genetic material	Parainfluenza viruses
Segmented: genome is divided into multiple segments	Influenza viruses

Figure 21.1*D*.1: Virus classification by genome structure and core: The type of genetic material (DNA or RNA) and its structure (single- or double-stranded, linear or circular, and segmented or non-segmented) are used to classify the virus core structures.

Viruses can also be classified by the design of their capsids. Isometric viruses have shapes that are roughly spherical, such as poliovirus or herpesviruses. Enveloped viruses have membranes surrounding capsids. Animal viruses, such as HIV, are frequently enveloped. Head and tail viruses infect bacteria and have a head that is similar to icosahedral viruses and a tail shape like filamentous viruses. Capsids are classified as naked icosahedral, enveloped icosahedral, enveloped helical, naked helical, and complex. For example, the tobacco mosaic virus has a naked helical capsid. The adenovirus has an icosahedral capsid.

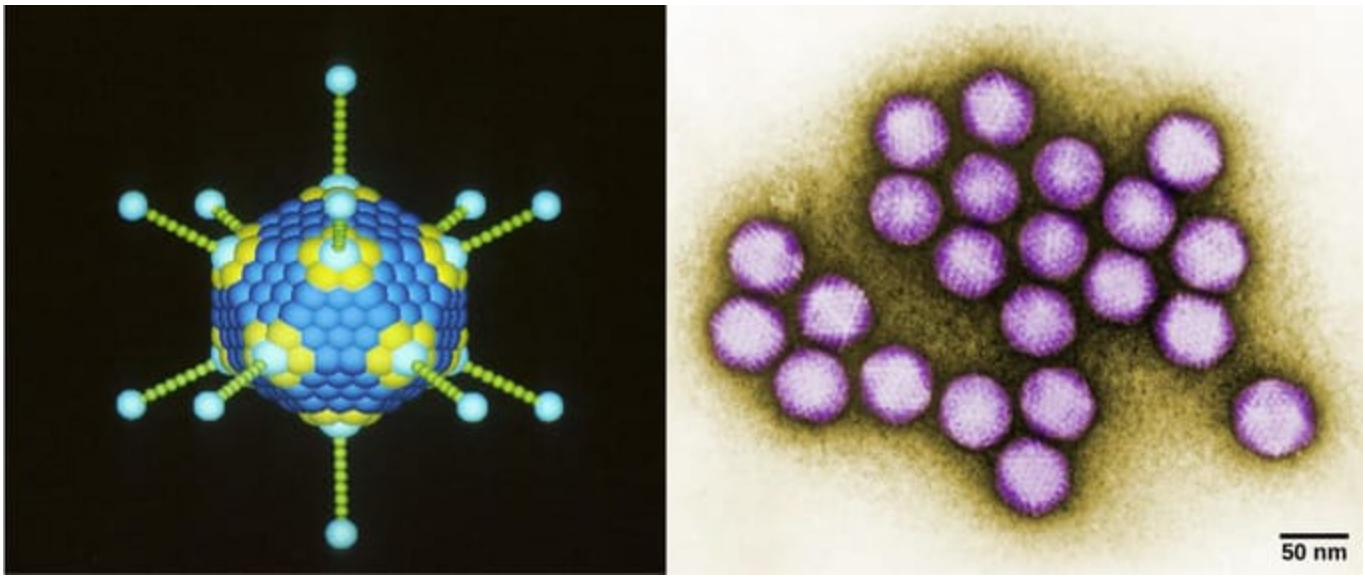


Figure 21.1D.1: Adenovirus classification: Adenovirus (left) is depicted with a double-stranded DNA genome enclosed in an icosahedral capsid that is 90–100 nm across. The virus, shown clustered in the micrograph (right), is transmitted orally and causes a variety of illnesses in vertebrates, including human eye and respiratory infections.

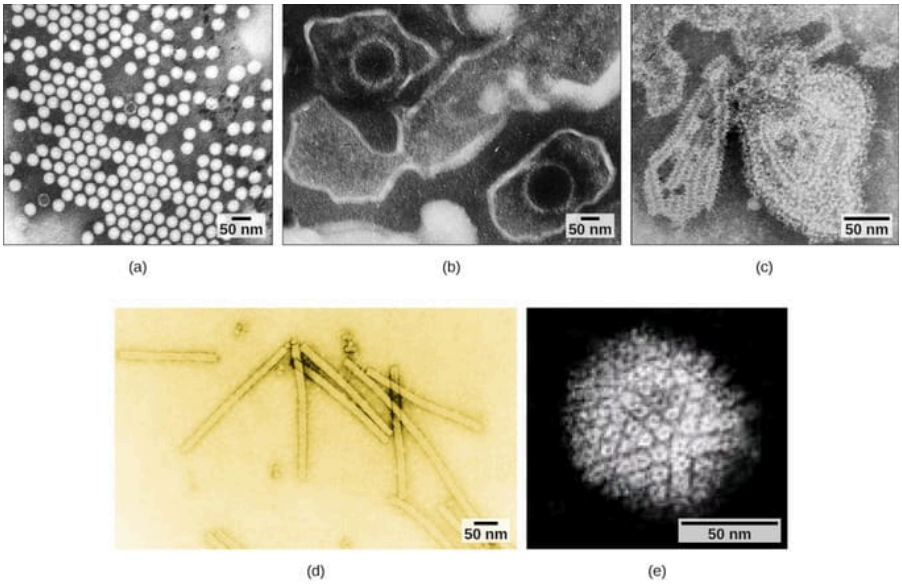


Figure 21.1D.1: Transmission electron micrograph of viruses: Transmission electron micrographs of various viruses show their structures. The capsid of the (a) polio virus is naked icosahedral; (b) the Epstein-Barr virus capsid is enveloped icosahedral; (c) the mumps virus capsid is an enveloped helix; (d) the tobacco mosaic virus capsid is naked helical; and (e) the herpesvirus capsid is complex.

Virus Classification by Capsid Structure	
Capsid Classification	**Examples**
Naked icosahedral	Hepatitis A virus, polioviruses
Enveloped icosahedral	Epstein-Barr virus, herpes simplex virus, rubella virus, yellow fever virus, HIV-1
Enveloped helical	Influenza viruses, mumps virus, measles virus, rabies virus
Naked helical	Tobacco mosaic virus
Complex with many proteins; some have combinations of icosahedral and helical capsid structures	Herpesviruses, smallpox virus, hepatitis B virus, T4 bacteriophage

Figure 21.1D.1: Virus classification by capsid structure: Viruses can also be classified by the design of their capsids which are classified as naked icosahedral, enveloped icosahedral, enveloped helical, naked helical, and complex.

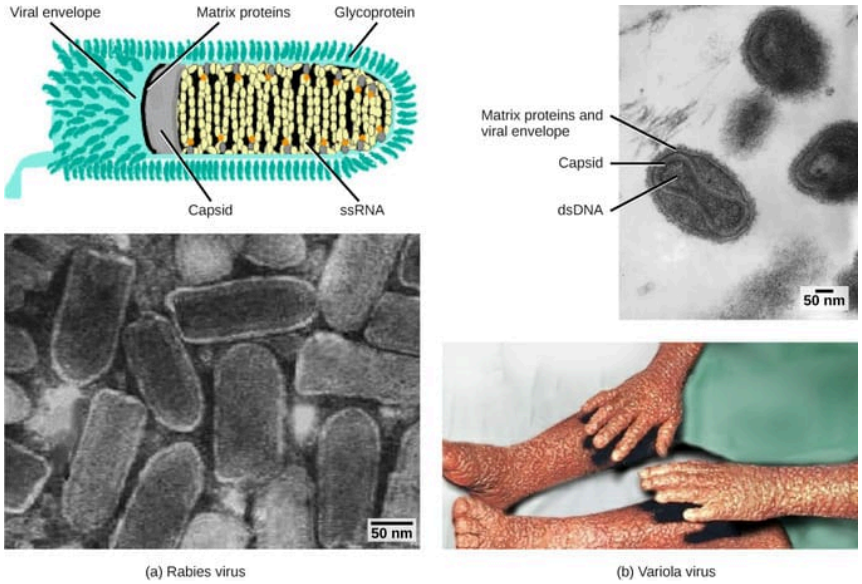


Figure 21.1D.1: Example of viruses classified by caspid design: Viruses are classified based on their core genetic material and capsid design. (a) Rabies virus has a single-stranded RNA (ssRNA) core and an enveloped helical capsid, whereas (b) variola virus, the causative agent of smallpox, has a double-stranded DNA (dsDNA) core and a complex capsid.

Baltimore Classification

The most commonly-used system of virus classification was developed by Nobel Prize-winning biologist David Baltimore in the early 1970s. In addition to the differences in morphology and genetics mentioned above, the Baltimore classification scheme groups viruses according to how the mRNA is produced during the replicative cycle of the virus. Viruses can contain double-stranded DNA (dsDNA), single-stranded DNA (ssDNA), double-stranded RNA (dsRNA), single-stranded RNA with a positive polarity (ssRNA), ssRNA with a negative polarity, diploid (two copies) ssRNA, and partial dsDNA genomes. Positive polarity means that the genomic RNA can serve directly as mRNA and a negative polarity means that their sequence is complementary to the mRNA.

Baltimore Classification

Group	Characteristics	Mode of mRNA Production	Example
I	Double-stranded DNA	mRNA is transcribed directly from the DNA template	Herpes simplex (herpesvirus)
II	Single-stranded DNA	DNA is converted to double-stranded form before RNA is transcribed	Canine parvovirus (parvovirus)
III	Double-stranded RNA	mRNA is transcribed from the RNA genome	Childhood gastroenteritis (rotavirus)
IV	Single stranded RNA (+)	Genome functions as mRNA	Common cold (pircornavirus)
V	Single stranded RNA (-)	mRNA is transcribed from the RNA genome	Rabies (rhabdovirus)
VI	Single stranded RNA viruses with reverse transcriptase	Reverse transcriptase makes DNA from the RNA genome; DNA is then incorporated in the host genome; mRNA is transcribed from the incorporated DNA	Human immunodeficiency virus (HIV)
VII	Double stranded DNA viruses with reverse transcriptase	The viral genome is double-stranded DNA, but viral DNA is replicated through an RNA intermediate; the RNA may serve directly as mRNA or as a template to make mRNA	Hepatitis B virus (hepadnavirus)

Figure 21.1D.1: Baltimore classification: The Baltimore classification scheme, the most commonly used, was developed by Nobel Prize-winning biologist David Baltimore in the early 1970s. The scheme groups viruses according to how the mRNA is produced during the replicative cycle of the virus, in addition to the differences in morphology and genetics.

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Key Points

- The type of genetic material, either DNA or RNA, and whether its structure is single- or double-stranded, linear or circular, and segmented or non-segmented are factors for classification.
- Virus capsids can be classified as naked icosahedral, enveloped icosahedral, enveloped helical, naked helical, and complex.
- Virus can either have an envelope or not.
- A more recent system, the Baltimore classification scheme, groups viruses into seven classes according to how the mRNA is produced during the replicative cycle of the virus.

Key Terms

- **Baltimore classification**: a classification scheme that groups viruses into seven classes according to how the mRNA is produced during the replicative cycle of the virus
- **messenger RNA**: Messenger RNA (mRNA) is a molecule of RNA that encodes a chemical “blueprint” for a protein product.

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21.2: VIRUS INFECTIONS AND HOSTS

- Topic hierarchy

21.2A: Steps of Virus Infections

21.2B: The Lytic and Lysogenic Cycles of Bacteriophages

21.2C: Animal Viruses

21.2D: Plant Viruses

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21.2A: Steps of Virus Infections

Learning Objectives

- List the steps of viral replication and explain what occurs at each step

Steps of Virus Infections

A virus must use cell processes to replicate. The viral replication cycle can produce dramatic biochemical and structural changes in the host cell, which may cause cell damage. These changes, called cytopathic (causing cell damage) effects, can change cell functions or even destroy the cell. Some infected cells, such as those infected by the common cold virus known as rhinovirus, die through lysis (bursting) or apoptosis (programmed cell death or "cell suicide"), releasing all progeny virions at once. The symptoms of viral diseases result from the immune response to the virus, which attempts to control and eliminate the virus from the body and from cell damage caused by the virus. Many animal viruses, such as HIV (Human Immunodeficiency Virus), leave the infected cells of the immune system by a process known as budding, where virions leave the cell individually. During the budding process, the cell does not undergo lysis and is not immediately killed. However, the damage to the cells that the virus infects may make it impossible for the cells to function normally, even though the cells remain alive for a period of time. Most productive viral infections follow similar steps in the virus replication cycle: attachment, penetration, uncoating, replication, assembly, and release.

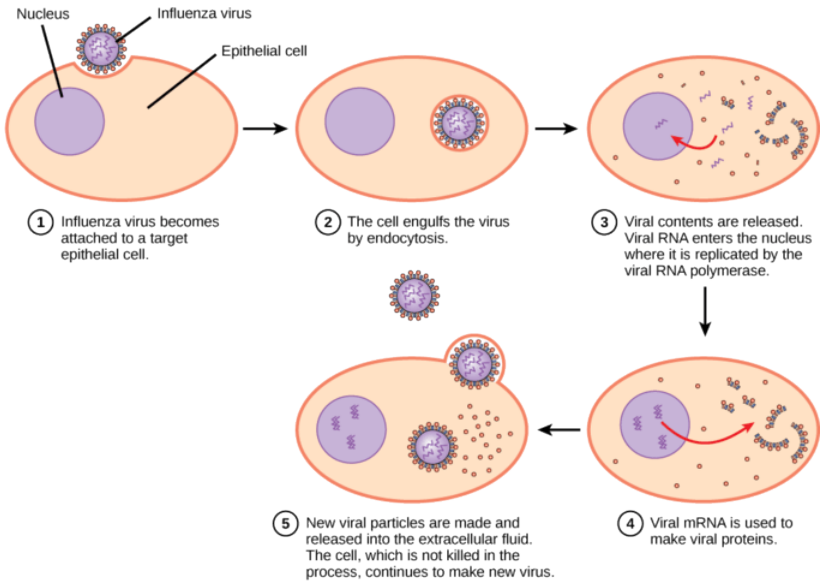


Figure 21.2A.1: Pathway to viral infection: In influenza virus infection, glycoproteins attach to a host epithelial cell. As a result, the virus is engulfed. RNA and proteins are made and assembled into new virions.

Attachment

A virus attaches to a specific receptor site on the host cell membrane through attachment proteins in the capsid or via glycoproteins embedded in the viral envelope. The specificity of this interaction determines the host (and the cells within the host) that can be infected by a particular virus. This can be illustrated by thinking of several keys and several locks where each key will fit only one specific lock.

Entry

The nucleic acid of bacteriophages enters the host cell naked, leaving the capsid outside the cell. Plant and animal viruses can

enter through endocytosis, in which the cell membrane surrounds and engulfs the entire virus. Some enveloped viruses enter the cell when the viral envelope fuses directly with the cell membrane. Once inside the cell, the viral capsid is degraded and the viral nucleic acid is released, which then becomes available for replication and transcription.

Replication and Assembly

The replication mechanism depends on the viral genome. DNA viruses usually use host cell proteins and enzymes to make additional DNA that is transcribed to messenger RNA (mRNA), which is then used to direct protein synthesis. RNA viruses usually use the RNA core as a template for synthesis of viral genomic RNA and mRNA. The viral mRNA directs the host cell to synthesize viral enzymes and capsid proteins, and to assemble new virions. Of course, there are exceptions to this pattern. If a host cell does not provide the enzymes necessary for viral replication, viral genes supply the information to direct synthesis of the missing proteins. Retroviruses, such as HIV, have an RNA genome that must be reverse transcribed into DNA, which then is incorporated into the host cell genome.

To convert RNA into DNA, retroviruses must contain genes that encode the virus-specific enzyme reverse transcriptase, which transcribes an RNA template to DNA. Reverse transcription never occurs in uninfected host cells; the needed enzyme, reverse transcriptase, is only derived from the expression of viral genes within the infected host cells. The fact that HIV produces some of its own enzymes not found in the host has allowed researchers to develop drugs that inhibit these enzymes. These drugs, including the reverse transcriptase inhibitor AZT, inhibit HIV replication by reducing the activity of the enzyme without affecting the host's metabolism. This approach has led to the development of a variety of drugs used to treat HIV and has been effective at reducing the number of infectious virions (copies of viral RNA) in the blood to non-detectable levels in many HIV-infected individuals.

Egress

The last stage of viral replication is the release of the new virions produced in the host organism. They are then able to infect adjacent cells and repeat the replication cycle. As you have learned, some viruses are released when the host cell dies, while other viruses can leave infected cells by budding through the membrane without directly killing the cell.

Key Points

- Viral replication involves six steps: attachment, penetration, uncoating, replication, assembly, and release.
- During attachment and penetration, the virus attaches itself to a host cell and injects its genetic material into it.
- During uncoating, replication, and assembly, the viral DNA or RNA incorporates itself into the host cell's genetic material and induces it to replicate the viral genome.
- During release, the newly-created viruses are released from the host cell, either by causing the cell to break apart, waiting for the cell to die, or by budding off through the cell membrane.

Key Terms

- **virion**: a single individual particle of a virus (the viral equivalent of a cell)
- **glycoprotein**: a protein with covalently-bonded carbohydrates
- **retrovirus**: a virus that has a genome consisting of RNA

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21.2B: The Lytic and Lysogenic Cycles of Bacteriophages

Learning Objectives

- Describe the lytic and lysogenic cycles of bacteriophages

Different Hosts and Their Viruses

Viruses are often very specific as to which hosts and which cells within the host they will infect. This feature of a virus makes it specific to one or a few species of life on earth. So many different types of viruses exist that nearly every living organism has its own set of viruses that try to infect its cells. Even the smallest and simplest of cells, prokaryotic bacteria, may be attacked by specific types of viruses.



Figure $21.2B.1$: Bacteriophage: This transmission electron micrograph shows bacteriophages attached to a bacterial cell.

Bacteriophages

Bacteriophages are viruses that infect bacteria. Bacteriophages may have a lytic cycle or a lysogenic cycle, and a few viruses are capable of carrying out both. When infection of a cell by a bacteriophage results in the production of new virions, the infection is said to be productive.

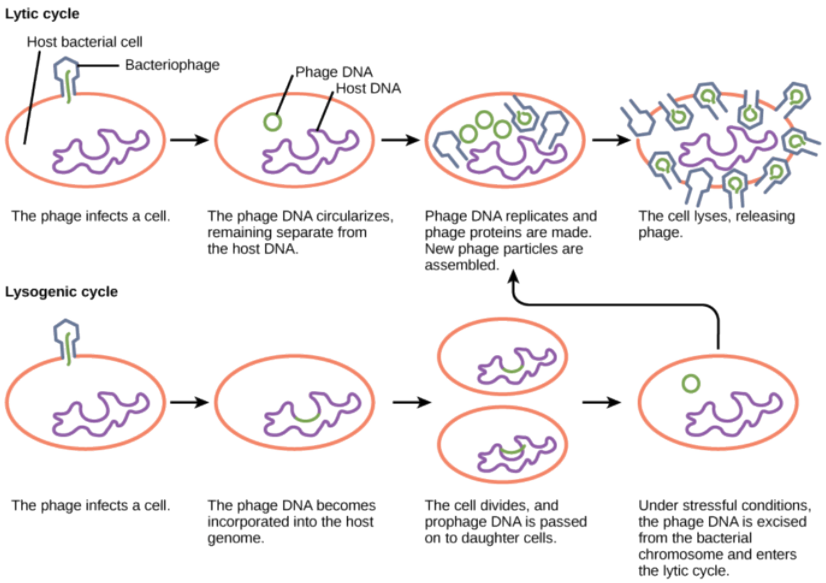


Figure $21.2B.1$: Lytic versus lysogenic cycle: A temperate bacteriophage has both lytic and lysogenic cycles. In the lytic cycle, the phage replicates and lyses the host cell. In the lysogenic cycle, phage DNA is incorporated into the host genome, where it is passed on to subsequent generations. Environmental stressors such as starvation or exposure to toxic chemicals may cause the prophage to excise and enter the lytic cycle.

Lytic Cycle

With lytic phages, bacterial cells are broken open (lysed) and destroyed after immediate replication of the virion. As soon as the cell is destroyed, the phage progeny can find new hosts to infect. An example of a lytic bacteriophage is T4, which infects *E. coli* found in the human intestinal tract. Lytic phages are more suitable for phage therapy.

Some lytic phages undergo a phenomenon known as lysis inhibition, where completed phage progeny will not immediately lyse out of the cell if extracellular phage concentrations are high.

Lysogenic Cycle

In contrast, the lysogenic cycle does not result in immediate lysing of the host cell. Those phages able to undergo lysogeny are known as temperate phages. Their viral genome will integrate with host DNA and replicate along with it fairly harmlessly, or may even become established as a plasmid. The virus remains dormant until host conditions deteriorate, perhaps due to depletion of nutrients; then, the endogenous phages (known as prophages) become active. At this point they initiate the reproductive cycle, resulting in lysis of the host cell. As the lysogenic cycle allows the host cell to continue to survive and reproduce, the virus is reproduced in all of the cell's offspring. An example of a bacteriophage known to follow the lysogenic cycle and the lytic cycle is the phage lambda of E. coli.

Latency Period

Viruses that infect plant or animal cells may also undergo infections where they are not producing virions for long periods. An example is the animal herpes viruses, including herpes simplex viruses, which cause oral and genital herpes in humans. In a process called latency, these viruses can exist in nervous tissue for long periods of time without producing new virions, only to leave latency periodically and cause lesions in the skin where the virus replicates. Even though there are similarities between lysogeny and latency, the term lysogenic cycle is usually reserved to describe bacteriophages.

Key Points

- Viruses are species specific, but almost every species on Earth can be affected by some form of virus.
- The lytic cycle involves the reproduction of viruses using a host cell to manufacture more viruses; the viruses then burst out

of the cell.
- The lysogenic cycle involves the incorporation of the viral genome into the host cell genome, infecting it from within.

Key Terms

- **latency**: The ability of a pathogenic virus to lie dormant within a cell.
- **bacteriophage**: A virus that specifically infects bacteria.
- **lytic cycle**: The normal process of viral reproduction involving penetration of the cell membrane, nucleic acid synthesis, and lysis of the host cell.
- **lysogenic cycle**: A form of viral reproduction involving the fusion of the nucleic acid of a bacteriophage with that of a host, followed by proliferation of the resulting prophage.

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21.2C: Animal Viruses

Learning Objectives

- Describe various animal viruses and the diseases they cause

Animal Viruses

Animal viruses, unlike the viruses of plants and bacteria, do not have to penetrate a cell wall to gain access to the host cell. Non-enveloped or “naked” animal viruses may enter cells in two different ways. When a protein in the viral capsid binds to its receptor on the host cell, the virus may be taken inside the cell via a vesicle during the normal cell process of receptor-mediated endocytosis. An alternative method of cell penetration used by non-enveloped viruses is for capsid proteins to undergo shape changes after binding to the receptor, creating channels in the host cell membrane. The viral genome is then “injected” into the host cell through these channels in a manner analogous to that used by many bacteriophages. Enveloped viruses also have two ways of entering cells after binding to their receptors: receptor-mediated endocytosis and fusion. Many enveloped viruses enter the cell by receptor-mediated endocytosis in a fashion similar to some non-enveloped viruses. On the other hand, fusion only occurs with enveloped virions. These viruses, which include HIV among others, use special fusion proteins in their envelopes to cause the envelope to fuse with the plasma membrane of the cell, thus releasing the genome and capsid of the virus into the cell cytoplasm.

After making their proteins and copying their genomes, animal viruses complete the assembly of new virions and exit the cell. Using the example of HIV, enveloped animal viruses may bud from the cell membrane as they assemble themselves, taking a piece of the cell’s plasma membrane in the process. On the other hand, non-enveloped viral progeny, such as rhinoviruses, accumulate in infected cells until there is a signal for lysis or apoptosis, and all virions are released together.

Animal viruses are associated with a variety of human diseases. Some of them follow the classic pattern of acute disease, where symptoms worsen for a short period followed by the elimination of the virus from the body by the immune system with eventual recovery from the infection. Examples of acute viral diseases are the common cold and influenza. Other viruses cause long-term chronic infections, such as the virus causing hepatitis C, whereas others, like herpes simplex virus, cause only intermittent symptoms. Still other viruses, such as human herpes viruses 6 and 7, which in some cases can cause the minor childhood disease roseola, often successfully cause productive infections without causing any symptoms at all in the host; these patients have an asymptomatic infection.

In hepatitis C infections, the virus grows and reproduces in liver cells, causing low levels of liver damage. The damage is so low that infected individuals are often unaware that they are infected, with many infections only detected by routine blood work on patients with risk factors such as intravenous drug use. Since many of the symptoms of viral diseases are caused by immune responses, a lack of symptoms is an indication of a weak immune response to the virus. This allows the virus to escape elimination by the immune system and persist in individuals for years, while continuing to produce low levels of progeny virions in what is known as a chronic viral disease. Chronic infection of the liver by this virus leads to a much greater chance of developing liver cancer, sometimes as much as 30 years after the initial infection.

As mentioned, herpes simplex virus can remain in a state of latency in nervous tissue for months, even years. As the virus “hides” in the tissue and makes few if any viral proteins, there is nothing for the immune response to act against; immunity to the virus slowly declines. Under certain conditions, including various types of physical and psychological stress, the latent herpes simplex virus may be reactivated and undergo a lytic replication cycle in the skin, causing the lesions associated with the disease. Once virions are produced in the skin and viral proteins are synthesized, the immune response is again stimulated and resolves the skin lesions in a few days by destroying viruses in the skin. As a result of this type of replicative cycle, appearances of cold sores and genital herpes outbreaks only occur intermittently, even though the viruses remain in the nervous tissue for life. Latent infections are common with other herpes viruses as well, including the varicella-zoster virus that causes chickenpox. After having a chickenpox infection in childhood, the varicella-zoster virus can remain latent for many years and reactivate in adults to cause the painful condition known as “shingles”.

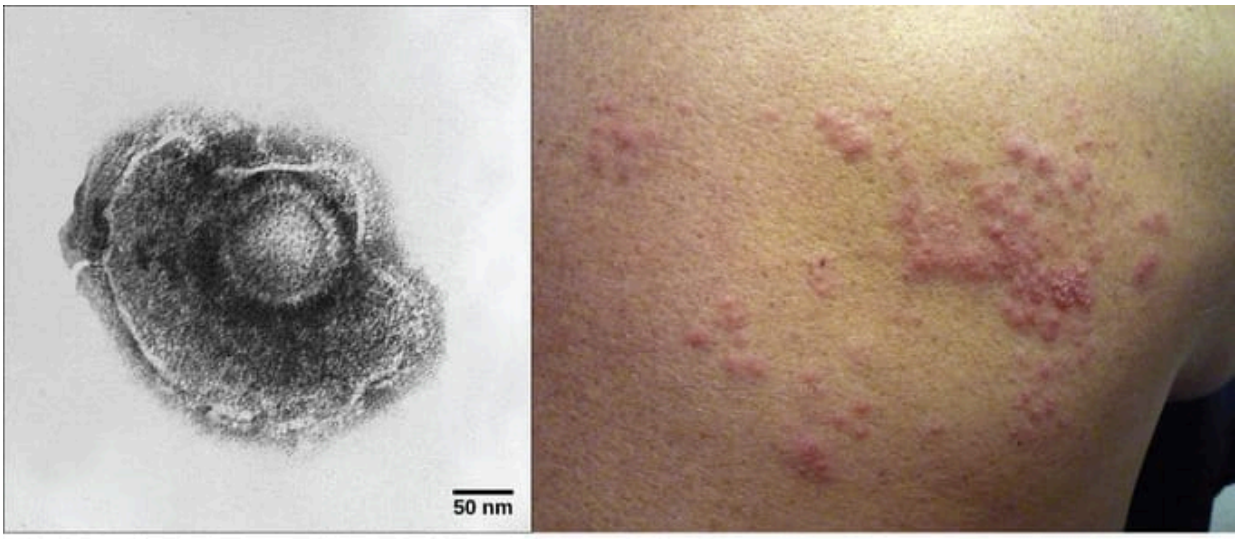


Figure $21.2C.1$: Chicken pox virus: (a) Varicella-zoster, the virus that causes chickenpox, has an enveloped icosahedral capsid visible in this transmission electron micrograph. Its double-stranded DNA genome incorporates into the host DNA and reactivates after latency in the form of (b) shingles, often exhibiting a rash.

Key Points

- Animal viruses may enter a host cell by either receptor -mediated endocytosis or by changing shape and entering the cell through the cell membrane.
- Viruses cause diseases in humans and other animals; they often have to run their course before symptoms disappear.
- Examples of viral animal diseases include hepatitis C, chicken pox, and shingles.

Key Terms

- **receptor-mediated endocytosis**: a process by which cells internalize molecules (endocytosis) by the inward budding of plasma membrane vesicles containing proteins with receptor sites specific to the molecules being internalized

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21.2D: Plant Viruses

Learning Objectives

- Give examples of plant viruses and explain why they can be costly to the economy

Plant Viruses

Plant viruses, like other viruses, contain a core of either DNA or RNA. As plant viruses have a cell wall to protect their cells, their viruses do not use receptor-mediated endocytosis to enter host cells as is seen with animal viruses. For many plant viruses to be transferred from plant to plant, damage to some of the plants' cells must occur to allow the virus to enter a new host. This damage is often caused by weather, insects, animals, fire, or human activities such as farming or landscaping. Additionally, plant offspring may inherit viral diseases from parent plants.

Plant viruses can be transmitted by a variety of vectors: through contact with an infected plant's sap, by living organisms such as insects and nematodes, and through pollen. When plant viruses are transferred between different plants, this is known as horizontal transmission; when they are inherited from a parent, this is called vertical transmission.

Symptoms of viral diseases vary according to the virus and its host. One common symptom is hyperplasia: the abnormal proliferation of cells that causes the appearance of plant tumors known as galls. Other viruses induce hypoplasia, or decreased cell growth, in the leaves of plants, causing thin, yellow areas to appear. Still other viruses affect the plant by directly killing plant cells; a process known as cell necrosis. Other symptoms of plant viruses include malformed leaves, black streaks on the stems of the plants, altered growth of stems, leaves, or fruits, and ring spots, which are circular or linear areas of discoloration found in a leaf.



Figure $21.2D.1$: Oak tree galls: Galls are abnormal plant growth or swellings comprised of plant tissue. Galls are usually found on foliage or twigs. These unusual deformities are caused by plant growth-regulating chemicals or stimuli produced by an insect or other arthropod pest species. The chemicals produced by these causal organisms interfere with normal plant cell growth.

Plant viruses can seriously disrupt crop growth and development, significantly affecting our food supply. They are responsible for poor crop quality and quantity globally, and can bring about huge economic losses annually. Other viruses may damage plants used in landscaping. Some viruses that infect agricultural food plants include the name of the plant they infect, such as tomato spotted wilt virus, bean common mosaic virus, and cucumber mosaic virus. In plants used for landscaping, two of the most common viruses are peony ring spot and rose mosaic virus. There are far too many plant viruses to discuss each in detail, but symptoms of bean common mosaic virus result in lowered bean production and stunted, unproductive plants. In the ornamental

rose, the rose mosaic disease causes wavy yellow lines and colored splotches on the leaves of the plant.

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Key Points

- Plants have cell walls which protect them from viruses entering their cells, so some type of damage must occur in order for them to become infected.
- When viruses are passed between plants, it is called horizontal transmission; when they are passed from the parent plant to the offspring, it is called vertical transmission.
- Symptoms of plant virus infection include malformed leaves, black streaks on the stems, discoloration of the leaves and fruits, and ring spots.
- Plant viruses can cause major disruptions to crop growth, which in turn can have a major impact on the economy.

Key Terms

- **horizontal transmission**: the transmission of an infectious agent, such as bacterial, fungal, or viral infection, between members of the same species that are not in a parent-child relationship
- **vertical transmission**: the transmission of an infection or other disease from the female of the species to the offspring

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21.3: PREVENTION AND TREATMENT OF VIRAL INFECTIONS

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- Topic hierarchy

21.3A: Vaccines and Immunity

21.3B: Vaccines and Anti-Viral Drugs for Treatment

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21.3A: Vaccines and Immunity

Learning Objectives

- Explain how vaccination protects vaccinated individuals and the community

Vaccines for Prevention

While we do have limited numbers of effective antiviral drugs, such as those used to treat HIV and influenza, the primary method of controlling viral disease is by vaccination, which is intended to prevent outbreaks by building immunity to a virus or virus family. Vaccines may be prepared using live viruses, killed viruses, or molecular subunits of the virus. The killed viral vaccines and subunit viruses are both incapable of causing disease.



Figure 21.3A.1: Vaccinations: Vaccinations are designed to boost immunity to a virus to prevent infection.

Live viral vaccines are designed in the laboratory to cause few symptoms in recipients while giving them protective immunity against future infections. Polio was one disease that represented a milestone in the use of vaccines. Mass immunization campaigns in the 1950s and 1960s significantly reduced the incidence of the disease, which caused muscle paralysis in children and generated great fear in the general population when regional epidemics occurred. The success of the polio vaccine paved the way for the routine dispensation of childhood vaccines against measles, mumps, rubella, chickenpox, and other diseases.

The danger of using live vaccines, which are usually more effective than killed vaccines, is low, but significant since the possibility that these viruses will revert to their disease-causing form by back mutations is still present. Live vaccines are usually made by attenuating (weakening) the “wild-type” (disease-causing) virus by growing it in the laboratory in tissues or at temperatures different from what the virus is accustomed to in the host. Adaptations to these new cells or temperatures induce mutations in the genomes of the virus, allowing it to grow better in the laboratory while inhibiting its ability to cause disease when reintroduced into conditions found in the host. These attenuated viruses still cause infection, but since they do not grow very well, they allow the immune response to develop in time to prevent major disease. Back mutations occur when the vaccine undergoes mutations in the host such that it readapts to the host and can again cause disease, which can then be spread to other humans in an epidemic. This type of scenario happened as recently as 2007 in Nigeria where mutations in a polio vaccine led to an epidemic of polio in that country.

Some vaccines are in continuous development because certain viruses, such as influenza and HIV, have a high mutation rate compared to other viruses and normal host cells. With influenza, mutations in the surface molecules of the virus help the organism evade the protective immunity that may have been obtained in a previous influenza season, making it necessary for individuals to

get vaccinated every year. Other viruses, such as those that cause the childhood diseases measles, mumps, and rubella, mutate so infrequently that the same vaccine is used year after year.

Key Points

- Vaccinations are prepared with live viruses, killed viruses, or molecular subunits of the virus.
- A live vaccine consists of a small dose of the active virus.
- A killed vaccine contains the inactivated virus.
- It is possible, though rare, for live vaccines to cause the disease they're used to prevent.
- Live vaccines are made by growing the virus in a lab, which causes mutations that allow them to grow better in the lab than in the host, thereby inhibiting their ability to cause disease.
- Even though live vaccines are designed to cause few symptoms, back mutations can occur and cause the virus to readapt to the host and the disease to spread.

Key Terms

- **vaccination**: inoculation in order to protect against a particular disease or strain of disease; causes a primary immune response without illness, allowing the secondary response to destroy subsequent infection
- **live vaccine**: consists of an active microbe (virus or bacteria)
- **killed vaccine**: (inactivated vaccine) consists of virus particles which are grown in culture and then killed using a method such as with heat or formaldehyde

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21.3B: Vaccines and Anti-Viral Drugs for Treatment

Learning Objectives

- Give examples of treatments with anti-viral drugs

Vaccines and Anti-viral Drugs for Treatment

In some cases, vaccines can be used to treat an active viral infection. The concept behind this is that by giving the vaccine, immunity is boosted without adding more disease-causing virus. In the case of rabies, a fatal neurological disease transmitted via the saliva of rabies virus-infected animals, the progression of the disease from the time of the animal bite to the time it enters the central nervous system may be two weeks or longer. This is enough time to vaccinate an individual who suspects that they have been bitten by a rabid animaL; their boosted immune response is sufficient to prevent the virus from entering nervous tissue. Thus, the potentially-fatal neurological consequences of the disease are averted; the individual only has to recover from the infected bite. This approach is also being used for the treatment of Ebola virus, one of the fastest and most deadly viruses on earth. Transmitted by bats and great apes, this disease can cause death in 70–90 percent of infected humans within two weeks. Using newly-developed vaccines that boost the immune response in this way, there is hope that affected individuals will be better able to control the virus, potentially saving a greater percentage of infected persons from a rapid and very painful death.

Another way of treating viral infections is the use of antiviral drugs. These drugs often have limited success in curing viral disease, but in many cases, they have been used to control and reduce symptoms for a wide variety of viral diseases. For most viruses, these drugs can inhibit the virus by blocking the actions of one or more of its proteins. It is important that the targeted proteins be encoded by viral genes and that these molecules are not present in a healthy host cell. In this way, viral growth is inhibited without damaging the host. There are large numbers of antiviral drugs available to treat infections, some specific for a particular virus and others that can affect multiple viruses.

Antivirals have been developed to treat genital herpes (herpes simplex II) and influenza. For genital herpes, drugs such as acyclovir can reduce the number and duration of episodes of active viral disease during which patients develop viral lesions in their skin cells. As the virus remains latent in nervous tissue of the body for life, this drug is not curative, but can make the symptoms of the disease more manageable. For influenza, drugs like Tamiflu (oseltamivir) can reduce the duration of “flu” symptoms by one or two days, but the drug does not prevent symptoms entirely. Tamiflu works by inhibiting an enzyme (viral neuraminidase) that allows new virions to leave their infected cells. Thus, Tamiflu inhibits the spread of virus from infected to uninfected cells. Other antiviral drugs, such as Ribavirin, have been used to treat a variety of viral infections, although its mechanism of action against certain viruses remains unclear.

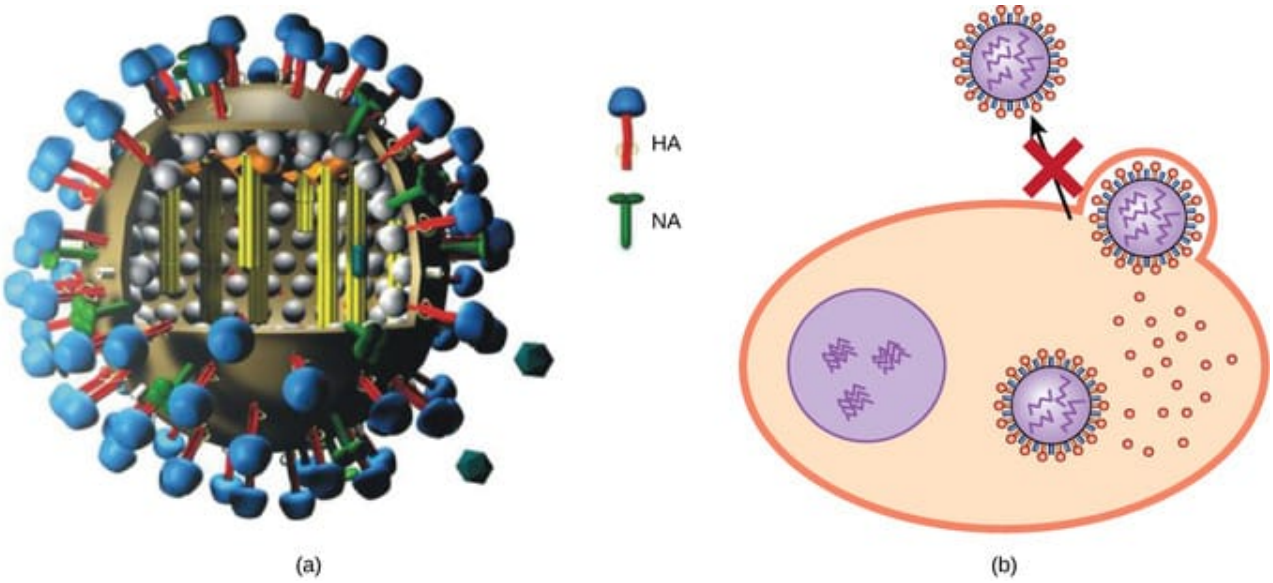


Figure $21.3B.1$: Tamiflu: (a) Tamiflu inhibits a viral enzyme called neuraminidase (NA) found in the influenza viral envelope. (b) Neuraminidase cleaves the connection between viral hemagglutinin (HA), also found in the viral envelope, and glycoproteins on the host cell surface. Inhibition of neuraminidase prevents the virus from detaching from the host cell, thereby blocking further infection.

Anti-HIV Drugs

By far, the most successful use of antivirals has been in the treatment of the retrovirus HIV, which causes a disease that, if untreated, is usually fatal within 10–12 years after infection. Anti-HIV drugs have been able to control viral replication to the point that individuals receiving these drugs survive for a significantly longer time than the untreated.

Anti-HIV drugs inhibit viral replication at many different phases of the HIV replicative cycle. Drugs have been developed that inhibit the fusion of the HIV viral envelope with the plasma membrane of the host cell (fusion inhibitors), the conversion of its RNA genome into double-stranded DNA (reverse transcriptase inhibitors), the integration of the viral DNA into the host genome (integrase inhibitors), and the processing of viral proteins (protease inhibitors).

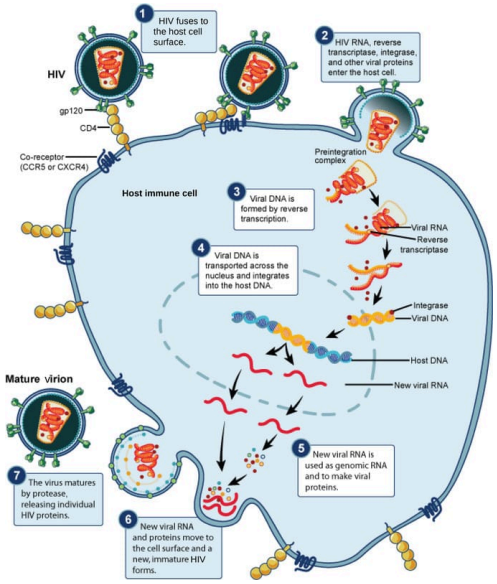


Figure $21.3B.1$: HIV: HIV, an enveloped, icosahedral virus, attaches to the CD4 receptor of an immune cell and fuses with the cell membrane. Viral contents are released into the cell where viral enzymes convert the single-stranded RNA genome into DNA and incorporate it into the host genome.

When any of these drugs are used individually, the high mutation rate of the virus allows it to easily and rapidly develop resistance

to the drug, limiting the drug's effectiveness. The breakthrough in the treatment of HIV was the development of HAART, highly-active anti-retroviral therapy, which involves a mixture of different drugs, sometimes called a drug "cocktail." By attacking the virus at different stages of its replicative cycle, it is much more difficult for the virus to develop resistance to multiple drugs at the same time. Still, even with the use of combination HAART therapy, there is concern that, over time, the virus will develop resistance to this therapy. Thus, new anti-HIV drugs are constantly being developed with the hope of continuing the battle against this highly fatal virus.

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Key Points

- Vaccines can boost an individual's immune response and control viruses, such as Ebola and rabies, before they become deadly.
- Anti-viral drugs inhibit the virus by blocking the actions of its proteins; they are used to control and reduce symptoms for viral diseases.
- Tamiflu can reduce flu symptoms by inhibiting the enzyme neuraminidase, which blocks the virus from spreading to uninfected cells.
- Anti-HIV drugs inhibit and control viral replication at many different phases of the HIV replication cycle, so patients taking these drugs have a higher survival rate.
- Viruses can develop resistance to individual anti-viral drugs.
- The treatment of HIV involves a mixture of different drugs (fusion inhibitors, reverse transcriptase inhibitors, integrase inhibitors, and protease inhibitors) in a cocktail; viruses have greater difficulty gaining resistance to multiple drugs.

Key Terms

- **virion**: a single individual particle of a virus (the viral equivalent of a cell)
- **anti-viral drug**: a class of medication, such as antibiotics, that inhibits the virus by blocking the actions of one or more of its proteins
- **Ebola virus**: an extremely contagious virus of African origin that causes Ebola fever, spread through contact with bodily fluids or secretions of infected persons and by airborne particles

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21.4: PRIONS AND VIROIDS

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- Topic hierarchy

21.4.1: 21-4A- Prions and Viroids

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21.4.1: 21-4A- Prions and Viroids

Learning Objectives

- Describe prions and viroids and their basic properties

Prions

Prions, so-called because they are proteinaceous, are infectious particles, smaller than viruses, that contain no nucleic acids (neither DNA nor RNA). Historically, the idea of an infectious agent that did not use nucleic acids was considered impossible, but pioneering work by Nobel Prize-winning biologist Stanley Prusiner has convinced the majority of biologists that such agents do indeed exist.

Fatal neurodegenerative diseases, such as kuru in humans and bovine spongiform encephalopathy (BSE) in cattle (commonly known as “mad cow disease”), were shown to be transmitted by prions. The disease was spread by the consumption of meat, nervous tissue, or internal organs between members of the same species. Kuru, native to humans in Papua New Guinea, was spread from human to human via ritualistic cannibalism. BSE, originally detected in the United Kingdom, spread between cattle by the practice of including cattle nervous tissue in feed for other cattle. Individuals with kuru and BSE show symptoms of loss of motor control and unusual behaviors, such as uncontrolled bursts of laughter with kuru, followed by death. Kuru was controlled by inducing the population to abandon its ritualistic cannibalism.

On the other hand, BSE was initially thought to affect only cattle. Cattle that died of BSE had developed lesions or “holes” in the brain, causing the brain tissue to resemble a sponge. Later on in the outbreak, however, it was shown that a similar encephalopathy in humans known as variant Creutzfeldt-Jakob disease (CJD) could be acquired from eating beef from animals with BSE, sparking bans by various countries on the importation of British beef and causing considerable economic damage to the British beef industry. BSE still exists in various areas. Although a rare disease, individuals that acquire CJD are difficult to treat. The disease spreads from human to human by blood, so many countries have banned blood donation from regions associated with BSE.

The cause of spongiform encephalopathies, such as kuru and BSE, is an infectious structural variant of a normal cellular protein called PrP (prion protein). It is this variant that constitutes the prion particle. PrP exists in two forms: PrP^{C}, the normal form of the protein, and PrP^{SC}, the infectious form. Once introduced into the body, the PrP^{SC} contained within the prion binds to PrP^{C} and converts it to PrP^{SC}. This leads to an exponential increase of the PrP^{SC} protein, which aggregates. PrP^{SC} is folded abnormally; the resulting conformation (shape) is directly responsible for the lesions seen in the brains of infected cattle. Thus, although not without some detractors among scientists, the prion appears to be an entirely new form of infectious agent; the first one found whose transmission is not reliant upon genes made of DNA or RNA.

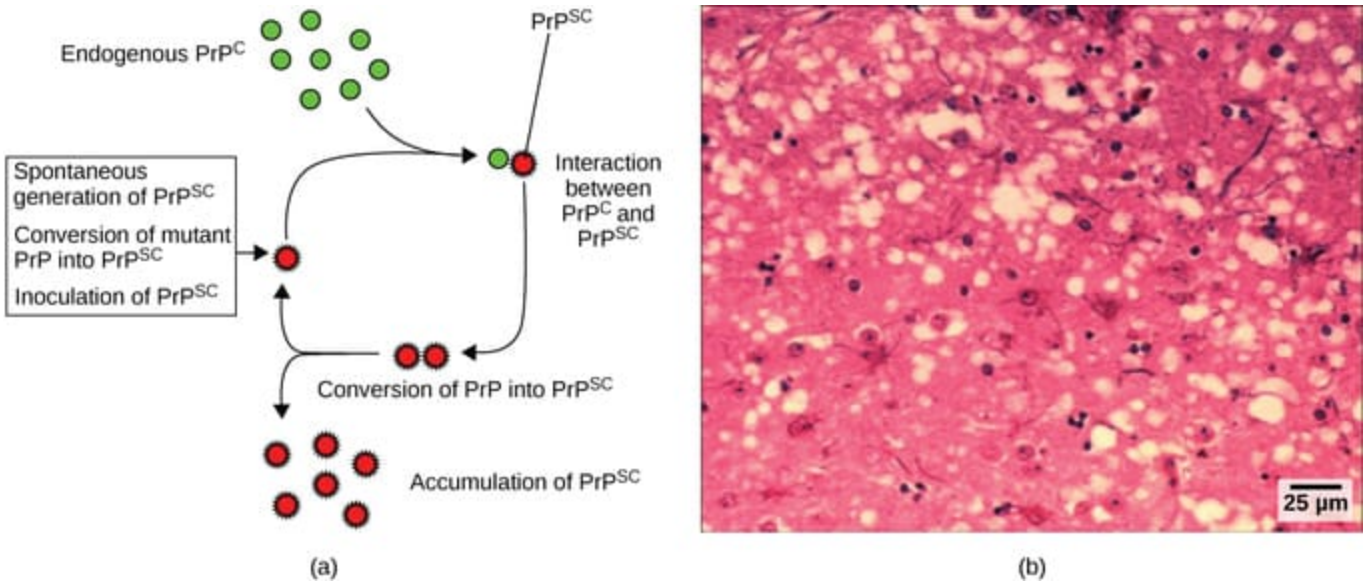


Figure 21.4.1.1: Example of the formation of a prion: (a) Endogenous normal prion protein (PrPc) is converted into the disease-causing form (PrPsc) when it encounters this variant form of the protein. PrPsc may arise spontaneously in brain tissue, especially if a mutant form of the protein is present, or it may occur via the spread of misfolded prions consumed in food into brain tissue. (b) This prion-infected brain tissue, visualized using light microscopy, shows the vacuoles that give it a spongy texture, typical of transmissible spongiform encephalopathies.

Viroids

Viroids are plant pathogens: small, single-stranded, circular RNA particles that are much simpler than a virus. They do not have a capsid or outer envelope, but, as with viruses, can reproduce only within a host cell. Viroids do not, however, manufacture any proteins. They produce only a single, specific RNA molecule. Human diseases caused by viroids have yet to be identified.

Viroid-infected plants are responsible for crop failures and the loss of millions of dollars in agricultural revenue each year. Some of the plants they infect include potatoes, cucumbers, tomatoes, chrysanthemums, avocados, and coconut palms.



Figure 21.4.1.1: Potatoes infected by a viroid: These potatoes have been infected by the potato spindle tuber viroid (PSTV). It is typically spread when infected knives are used to cut healthy potatoes, which are then planted.

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Key Points

- The prion appears to be the first infectious agent found whose transmission is not reliant upon genes made of DNA or RNA.
- An infectious structural variant of a normal cellular protein called PrP (prion protein) is known to cause spongiform encephalopathies.
- Prions have been implicated in fatal neurodegenerative diseases, such as kuru in humans and bovine spongiform encephalopathy (BSE) in cattle.
- Loss of motor control and unusual behaviors are common symptoms of individuals with kuru and BSE; symptoms are usually followed by death.
- Viroids do not have a capsid or outer envelope and can reproduce only within a host cell.
- Viroids are not known to cause any human diseases, but they are responsible for crop failures and the loss of millions of dollars in agricultural revenue each year.

Key Terms

- **prion**: a self-propagating misfolded conformer of a protein that is responsible for a number of diseases that affect the brain and other neural tissue
- **proteinaceous**: of, pertaining to, or consisting of protein
- **viroid**: plant pathogens that consist of just a short section of RNA, but without the protein coat typical of viruses

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22: PROKARYOTES- BACTERIA AND ARCHAEA

- Topic hierarchy

22.1: Prokaryotic Diversity

22.1A: Classification of Prokaryotes

22.1B: The Origins of Archaea and Bacteria

22.1C: Extremophiles and Biofilms

22.2: Structure of Prokaryotes

22.2A: Basic Structures of Prokaryotic Cells

22.2B: Prokaryotic Reproduction

22.3: Prokaryotic Metabolism

22.3A: Energy and Nutrient Requirements for Prokaryotes

22.3B: The Role of Prokaryotes in Ecosystems

22.4: Bacterial Diseases in Humans

22.4A: History of Bacterial Diseases

22.4B: Biofilms and Disease

22.4C: Antibiotics- Are We Facing a Crisis?

22.4D: Bacterial Foodborne Diseases

22.5: Beneficial Prokaryotes

22.5A: Symbiosis between Bacteria and Eukaryotes

22.5B: Early Biotechnology- Cheese, Bread, Wine, Beer, and Yogurt

22.5C: Prokaryotes and Environmental Bioremediation

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22.1: PROKARYOTIC DIVERSITY



- Topic hierarchy

22.1A: Classification of Prokaryotes

22.1B: The Origins of Archaea and Bacteria

22.1C: Extremophiles and Biofilms

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22.1A: Classification of Prokaryotes

Learning Objectives

- Discuss the origins of prokaryotic organisms in terms of the geologic timeline

Evolution of Prokaryotes

In the recent past, scientists grouped living things into five kingdoms (animals, plants, fungi, protists, and prokaryotes) based on several criteria such as: the absence or presence of a nucleus and other membrane-bound organelles, the absence or presence of cell walls, multicellularity, etc. In the late 20th century, the pioneering work of Carl Woese and others compared sequences of small-subunit ribosomal RNA (SSU rRNA) which resulted in a more fundamental way to group organisms on earth. Based on differences in the structure of cell membranes and in rRNA, Woese and his colleagues proposed that all life on earth evolved along three lineages, called domains. The domain Bacteria comprises all organisms in the kingdom Bacteria, the domain Archaea comprises the rest of the prokaryotes, and the domain Eukarya comprises all eukaryotes, including organisms in the kingdoms Animalia, Plantae, Fungi, and Protista.

The current model of the evolution of the first, living organisms is that these were some form of prokaryotes, which may have evolved out of protobionts. In general, the eukaryotes are thought to have evolved later in the history of life. However, some authors have questioned this conclusion, arguing that the current set of prokaryotic species may have evolved from more complex eukaryotic ancestors through a process of simplification. Others have argued that the three domains of life arose simultaneously, from a set of varied cells that formed a single gene pool.

Two of the three domains, Bacteria and Archaea, are prokaryotic. Based on fossil evidence, prokaryotes were the first inhabitants on Earth, appearing 3.5 to 3.8 billion years ago during the Precambrian Period. These organisms are abundant and ubiquitous; that is, they are present everywhere. In addition to inhabiting moderate environments, they are found in extreme conditions: from boiling springs to permanently frozen environments in Antarctica; from salty environments like the Dead Sea to environments under tremendous pressure, such as the depths of the ocean; and from areas without oxygen, such as a waste management plant, to radioactively-contaminated regions, such as Chernobyl. Prokaryotes reside in the human digestive system and on the skin, are responsible for certain illnesses, and serve an important role in the preparation of many foods.



Figure 22.1A.1: Prokaryotes in extreme environments: Certain prokaryotes can live in extreme environments such as the Morning Glory pool, a hot spring in Yellowstone National Park. The spring's vivid blue color is from the prokaryotes that thrive in its very hot waters.

Key Points

- All living things can be classified into three main groups called domains; these include the Archaea, the Bacteria, and the Eukarya.
- Prokaryotes arose during the Precambrian Period 3.5 to 3.8 billion years ago.
- Prokaryotic organisms can live in every type of environment on Earth, from very hot, to very cold, to super haline, to very acidic.
- The domains Bacteria and Archaea are the ones containing prokaryotic organisms.
- The Archaea are prokaryotes that inhabit extreme environments, such as inside of volcanoes, while Bacteria are more common organisms, such as *E. coli*.

Key Terms

- **prokaryote**: an organism whose cell (or cells) are characterized by the absence of a nucleus or any other membrane-bound organelles
- **domain**: in the three-domain system, the highest rank in the classification of organisms, above kingdom: Bacteria, Archaea, and Eukarya
- **archaea**: a taxonomic domain of single-celled organisms lacking nuclei, formerly called archaebacteria, but now known to differ fundamentally from bacteria

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22.1B: The Origins of Archaea and Bacteria

Learning Objectives

- Distinguish bacteria from archaea in terms of their origins

Prokaryotes, the First Inhabitants of Earth

When and where did life begin? What were the conditions on earth when life began? Prokaryotes were the first forms of life on earth, existing for billions of years before plants and animals appeared. The earth and its moon are thought to be about 4.54 billion years old. This estimate is based on evidence from radiometric dating of meteorite material together with other substrate material from earth and the moon. Early earth had a very different atmosphere (contained less molecular oxygen) than it does today and was subjected to strong radiation; thus, the first organisms would have flourished where they were more protected, such as in ocean depths or beneath the surface of the earth. Also at this time, strong volcanic activity was common on Earth. It is probable that these first organisms, the first prokaryotes, were adapted to very high temperatures. Early earth was prone to geological upheaval and volcanic eruption, and was subject to bombardment by mutagenic radiation from the sun. The first organisms were prokaryotes that could withstand these harsh conditions.

Although probable prokaryotic cell fossils date to almost 3.5 billion years ago, most prokaryotes do not have distinctive morphologies; fossil shapes cannot be used to identify them as Archaea. Instead, chemical fossils of unique lipids are more informative because such compounds do not occur in other organisms. Some publications suggest that archaean or eukaryotic lipid remains are present in shales dating from 2.7 billion years ago. Such lipids have also been detected in Precambrian formations. The oldest such traces come from the Isua district of west Greenland, which include earth's oldest sediments, formed 3.8 billion years ago. The archaeal lineage may be the most ancient that exists on earth.

Within prokaryotes, archaeal cell structure is most similar to that of gram-positive bacteria, largely because both have a single lipid bilayer and usually contain a thick sacculus of varying chemical composition. In phylogenetic trees based upon different gene / protein sequences of prokaryotic homologs, the archaeal homologs are more closely related to those of Gram-positive bacteria. Archaea and gram-positive bacteria also share conserved indels in a number of important proteins, such as Hsp70 and glutamine synthetase.

It has been proposed that the archaea evolved from gram-positive bacteria in response to antibiotic selection pressure. This is suggested by the observation that archaea are resistant to a wide variety of antibiotics that are primarily produced by gram-positive bacteria and that these antibiotics primarily act on the genes that distinguish archaea from bacteria. The evolution of Archaea in response to antibiotic selection, or any other competitive selective pressure, could also explain their adaptation to extreme environments (such as high temperature or acidity) as the result of a search for unoccupied niches to escape from antibiotic-producing organisms.

Microbial Mats

Microbial mats or large biofilms may represent the earliest forms of life on earth; there is fossil evidence of their presence starting about 3.5 billion years ago. A microbial mat is a multi-layered sheet of prokaryotes that includes mostly bacteria, but also archaea. Microbial mats are a few centimeters thick, typically growing where different types of materials interface, mostly on moist surfaces. The various types of prokaryotes that comprise the mats use different metabolic pathways, which is the reason for their various colors. Prokaryotes in a microbial mat are held together by a glue-like sticky substance that they secrete called extracellular matrix.

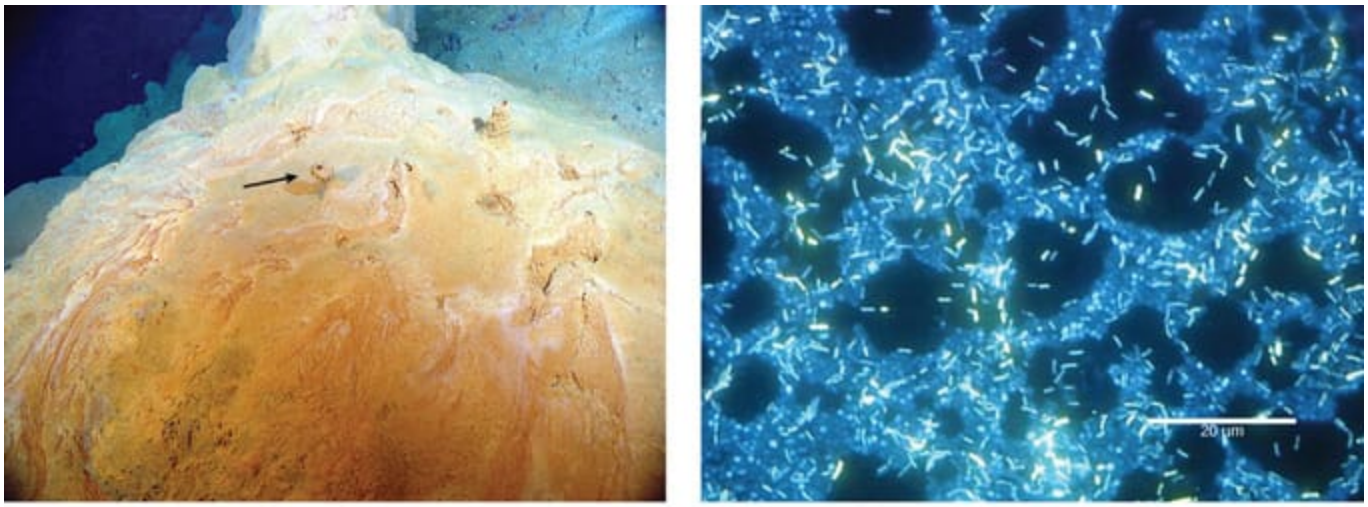


Figure $22.1B.1$: Microbial mat: This (a) microbial mat, about one meter in diameter, grows over a hydrothermal vent in the Pacific Ocean in a region known as the “Pacific Ring of Fire.” The mat helps retain microbial nutrients. Chimneys, such as the one indicated by the arrow, allow gases to escape. (b) In this micrograph, bacteria are visualized using fluorescence microscopy.

The first microbial mats likely obtained their energy from chemicals found near hydrothermal vents. A hydrothermal vent is a breakage or fissure in the earth’s surface that releases geothermally-heated water. With the evolution of photosynthesis about 3 billion years ago, some prokaryotes in microbial mats came to use a more widely-available energy source, sunlight, whereas others were still dependent on chemicals from hydrothermal vents for energy and food.

Stromatolites

Fossilized microbial mats represent the earliest record of life on earth. A stromatolite is a sedimentary structure formed when minerals are precipitated out of water by prokaryotes in a microbial mat. Stromatolites form layered rocks made of carbonate or silicate. Although most stromatolites are artifacts from the past, there are places on earth where stromatolites are still forming. For example, growing stromatolites have been found in the Anza-Borrego Desert State Park in San Diego County, California.



Figure $22.1B.1$: Stromatolites: (a) These living stromatolites are located in Shark Bay, Australia. (b) These fossilized stromatolites, found in Glacier National Park, Montana, are nearly 1.5 billion years old.

Key Points

- The first prokaryotes were adapted to the extreme conditions of early earth.
- It has been proposed that archaea evolved from gram-positive bacteria as a response to antibiotic selection pressures.

- Microbial mats and stromatolites represent some of the earliest prokaryotic formations that have been found.

Key Terms

- **stromatolite**: a laminated, columnar, rock-like structure built over geologic time by microorganisms such as cyanobacteria
- **gram-positive**: that is stained violet by Gram's method due to the presence of a peptidoglycan cell wall
- **sacculus**: a small sac
- **indel**: either an insertion or deletion mutation in the genetic code

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22.1C: Extremophiles and Biofilms

Learning Objectives

- Discuss the distinguishing features of extremophiles and the environments that produce biofilms

Microbes Are Adaptable: Life in Moderate and Extreme Environments

Some organisms have developed strategies that allow them to survive harsh conditions. Prokaryotes thrive in a vast array of environments; some grow in conditions that would seem very normal to us, whereas others are able to thrive and grow under conditions that would kill a plant or animal. Almost all prokaryotes have a cell wall: a protective structure that allows them to survive in both hyper- and hypo-osmotic conditions. Some soil bacteria are able to form endospores that resist heat and drought, thereby allowing the organism to survive until favorable conditions recur. These adaptations, along with others, allow bacteria to be the most abundant life form in all terrestrial and aquatic ecosystems.

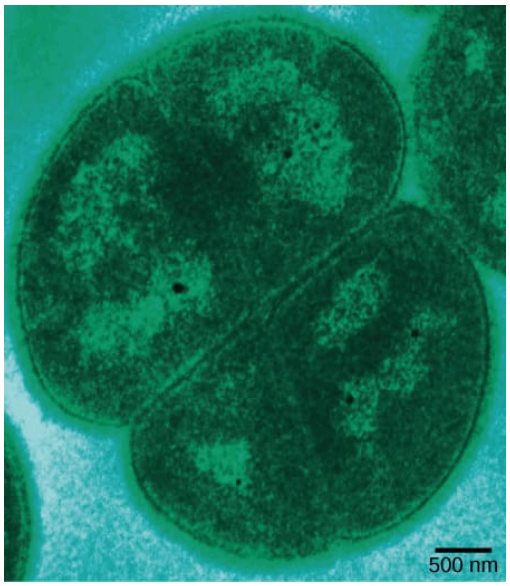


Figure $22.1C.1$: Bacteria and radiation tolerance: Deinococcus radiodurans, visualized in this false color transmission electron micrograph, is a prokaryote that can tolerate very high doses of ionizing radiation. It has developed DNA repair mechanisms that allow it to reconstruct its chromosome even if it has been broken into hundreds of pieces by radiation or heat.

Other bacteria and archaea are adapted to grow under extreme conditions and are called extremophiles, meaning “lovers of extremes.” Extremophiles have been found in all kinds of environments: the depth of the oceans, hot springs, the Arctic and the Antarctic, in very dry places, deep inside earth, in harsh chemical environments, and in high radiation environments, just to mention a few. These organisms give us a better understanding of prokaryotic diversity and raise the possibility of finding new prokaryotic species that may lead to the discovery of new therapeutic drugs or have industrial applications. Because they have specialized adaptations that allow them to live in extreme conditions, many extremophiles cannot survive in moderate environments. There are many different groups of extremophiles. They are identified based on the conditions in which they grow best. Several habitats are extreme in multiple ways. For example, a soda lake is both salty and alkaline, so organisms that live in a soda lake must be both alkaliphiles and halophiles. Other extremophiles, like radioresistant organisms, do not prefer an extreme environment (in this case, one with high levels of radiation), but have adapted to survive in it.

Prokaryotes in the Dead Sea

One example of a very harsh environment is the Dead Sea, a hypersaline basin that is located between Jordan and Israel. Hypersaline environments are essentially concentrated seawater. In the Dead Sea, the sodium concentration is 10 times higher

than that of seawater. The water also contains high levels of magnesium (about 40 times higher than in seawater) that would be toxic to most living things. Iron, calcium, and magnesium, elements that form divalent ions (Fe^{2+}, Ca^{2+}, and Mg^{2+}), produce what is commonly referred to as “hard” water. Taken together, the high concentration of divalent cations, the acidic pH (6.0), and the intense solar radiation flux make the Dead Sea a unique, and uniquely hostile, ecosystem.



Figure 22.1C.1: Halophile habitats: (a) The Dead Sea is hypersaline. Nevertheless, salt-tolerant bacteria thrive in this sea. (b) These halobacteria cells can form salt-tolerant bacterial mats.

The Ecology of Biofilms

Until a couple of decades ago, microbiologists used to think of prokaryotes as isolated entities living apart. This model, however, does not reflect the true ecology of prokaryotes, most of which prefer to live in communities where they can interact. A biofilm is a microbial community held together in a gummy-textured matrix that consists primarily of polysaccharides secreted by the organisms, together with some proteins and nucleic acids. Biofilms grow attached to surfaces. Some of the best-studied biofilms are composed of prokaryotes, although fungal biofilms have also been described, as well as some composed of a mixture of fungi and bacteria.

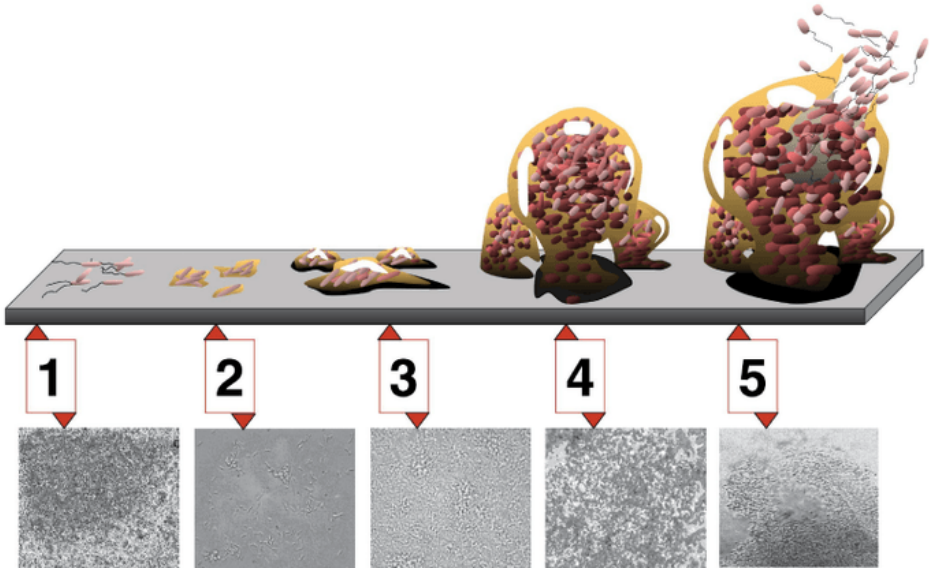


Figure 22.1C.1: Biofilm Development: Five stages of biofilm development are shown. During stage 1, initial attachment, bacteria adhere to a solid surface via weak van der Waals interactions. During stage 2, irreversible attachment, hairlike appendages called pili permanently anchor the bacteria to the surface. During stage 3, maturation I, the biofilm grows through cell division and recruitment of other bacteria. An extracellular matrix composed primarily of polysaccharides holds the biofilm together. During stage 4, maturation II, the biofilm continues to grow and takes on a more complex shape. During stage 5, dispersal, the biofilm matrix is partly broken down, allowing some bacteria to escape and colonize another surface. Micrographs of a Pseudomonas aeruginosa biofilm in each of the stages of development are shown.

Biofilms are present almost everywhere: they can cause the clogging of pipes and readily colonize surfaces in industrial settings. In recent, large-scale outbreaks of bacterial contamination of food, biofilms have played a major role. They also colonize household surfaces, such as kitchen counters, cutting boards, sinks, and toilets, as well as places on the human body, such as the surfaces of our teeth.

Interactions among the organisms that populate a biofilm, together with their protective exopolysaccharidic (EPS) environment, make these communities more robust than free-living, or planktonic, prokaryotes. The sticky substance that holds bacteria together also excludes most antibiotics and disinfectants, making biofilm bacteria hardier than their planktonic counterparts. Overall, biofilms are very difficult to destroy because they are resistant to many common forms of sterilization.

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Key Points

- Prokaryotes live in all environments, no matter how extreme they may be.
- Bacteria that prefer very salty environments are called halophiles, while those that live in very acidic environments are called acidophiles.
- An example of a habitat that halophiles can colonize is the Dead Sea, a body of water that is 10 times saltier than regular ocean water.
- A biofilm is a microbial community held together in a gummy-textured matrix that consists primarily of polysaccharides secreted by the organisms.
- Biofilms can be found clogging pipes, on kitchen counters, or even on the surface of one's teeth.

Key Terms

- **extremophile**: an organism that lives under extreme conditions of temperature, salinity, etc; commercially important as a source of enzymes that operate under similar conditions
- **halophile**: an organism that lives and thrives in an environment of high salinity, often requiring such an environment; a form of extremophile
- **alkaliphile**: any organism that lives and thrives in an alkaline environment, such as a soda lake; a form of extremophile

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22.2: STRUCTURE OF PROKARYOTES

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- Topic hierarchy

22.2A: Basic Structures of Prokaryotic Cells

22.2B: Prokaryotic Reproduction

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22.2A: Basic Structures of Prokaryotic Cells

Learning Objectives

- Describe the basic structure of a typical prokaryote

The Prokaryotic Cell

Prokaryotes are unicellular organisms that lack organelles or other internal membrane-bound structures. Therefore, they do not have a nucleus, but, instead, generally have a single chromosome: a piece of circular, double-stranded DNA located in an area of the cell called the nucleoid. Most prokaryotes have a cell wall outside the plasma membrane.

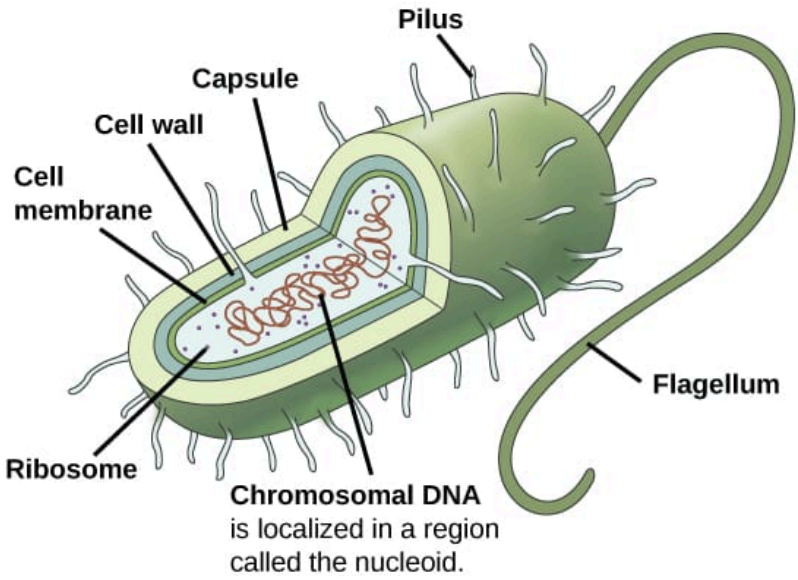


Figure 22.2A.1: Prokaryotic cell structure: The features of a typical prokaryotic cell are shown.

The composition of the cell wall differs significantly between the domains Bacteria and Archaea, the two domains of life into which prokaryotes are divided. The composition of their cell walls also differs from the eukaryotic cell walls found in plants (cellulose) or fungi and insects (chitin). The cell wall functions as a protective layer and is responsible for the organism's shape. Some bacteria have a capsule outside the cell wall. Other structures are present in some prokaryotic species, but not in others. For example, the capsule found in some species enables the organism to attach to surfaces, protects it from dehydration and attack by phagocytic cells, and increases its resistance to our immune responses. Some species also have flagella used for locomotion and pili used for attachment to surfaces. Plasmids, which consist of extra-chromosomal DNA, are also present in many species of bacteria and archaea.

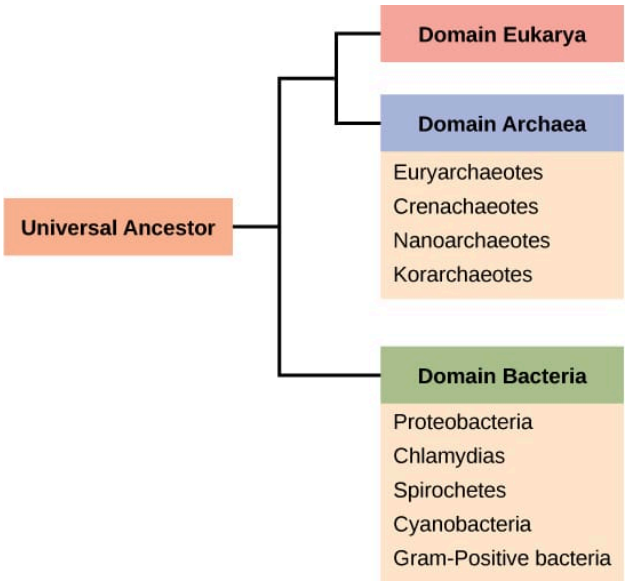


Figure 22.2A.1: Domains of life: Bacteria and Archaea are both prokaryotes, but differ enough to be placed in separate domains. An ancestor of modern Archaea is believed to have given rise to Eukarya, the third domain of life. Archaeal and bacterial phyla are shown; the evolutionary relationship between these phyla is still open to debate.

The Plasma Membrane

The plasma membrane is a thin lipid bilayer (6 to 8 nanometers) that completely surrounds the cell and separates the inside from the outside. Its selectively-permeable nature keeps ions, proteins, and other molecules within the cell, preventing them from diffusing into the extracellular environment, while other molecules may move through the membrane. The general structure of a cell membrane is a phospholipid bilayer composed of two layers of lipid molecules. In archaeal cell membranes, isoprene (phytanyl) chains linked to glycerol replace the fatty acids linked to glycerol in bacterial membranes. Some archaeal membranes are lipid monolayers instead of bilayers.

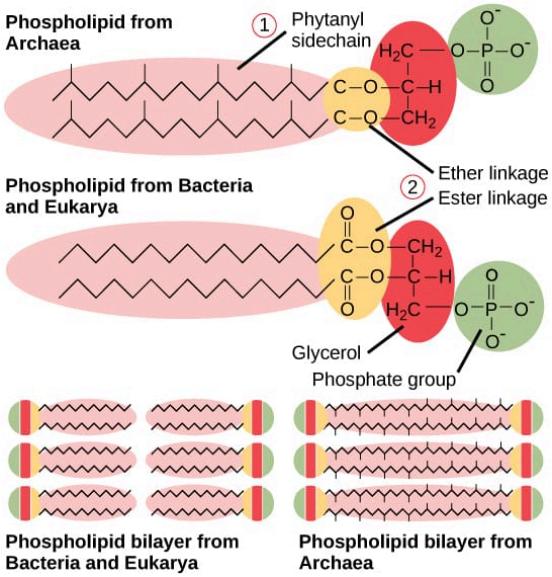


Figure 22.2A.1: Plasma membrane structure: Archaeal phospholipids differ from those found in Bacteria and Eukarya in two ways. First, they have branched phytanyl sidechains instead of linear ones. Second, an ether bond instead of an ester bond connects the lipid to the glycerol.

The Cell Wall

The cytoplasm of prokaryotic cells has a high concentration of dissolved solutes. Therefore, the osmotic pressure within the cell

is relatively high. The cell wall is a protective layer that surrounds some cells and gives them shape and rigidity. It is located outside the cell membrane and prevents osmotic lysis (bursting due to increasing volume). The chemical composition of the cell walls varies between archaea and bacteria. It also varies between bacterial species.

Bacterial cell walls contain peptidoglycan composed of polysaccharide chains that are cross-linked by unusual peptides containing both L- and D-amino acids, including D-glutamic acid and D-alanine. Proteins normally have only L-amino acids; as a consequence, many of our antibiotics work by mimicking D-amino acids and, therefore, have specific effects on bacterial cell wall development. There are more than 100 different forms of peptidoglycan. S-layer (surface layer) proteins are also present on the outside of cell walls of both archaea and bacteria.

Bacteria are divided into two major groups: gram-positive and gram-negative, based on their reaction to gram staining. Note that all gram-positive bacteria belong to one phylum; bacteria in the other phyla (Proteobacteria, Chlamydias, Spirochetes, Cyanobacteria, and others) are gram-negative. The gram-staining method is named after its inventor, Danish scientist Hans Christian Gram (1853–1938). The different bacterial responses to the staining procedure are ultimately due to cell wall structure. Gram-positive organisms typically lack the outer membrane found in gram-negative organisms. Up to 90 percent of the cell wall in gram-positive bacteria is composed of peptidoglycan, with most of the rest composed of acidic substances called teichoic acids. Teichoic acids may be covalently linked to lipids in the plasma membrane to form lipoteichoic acids. Lipoteichoic acids anchor the cell wall to the cell membrane. Gram-negative bacteria have a relatively thin cell wall composed of a few layers of peptidoglycan (only 10 percent of the total cell wall), surrounded by an outer envelope containing lipopolysaccharides (LPS) and lipoproteins. This outer envelope is sometimes referred to as a second lipid bilayer. The chemistry of this outer envelope is very different, however, from that of the typical lipid bilayer that forms plasma membranes.

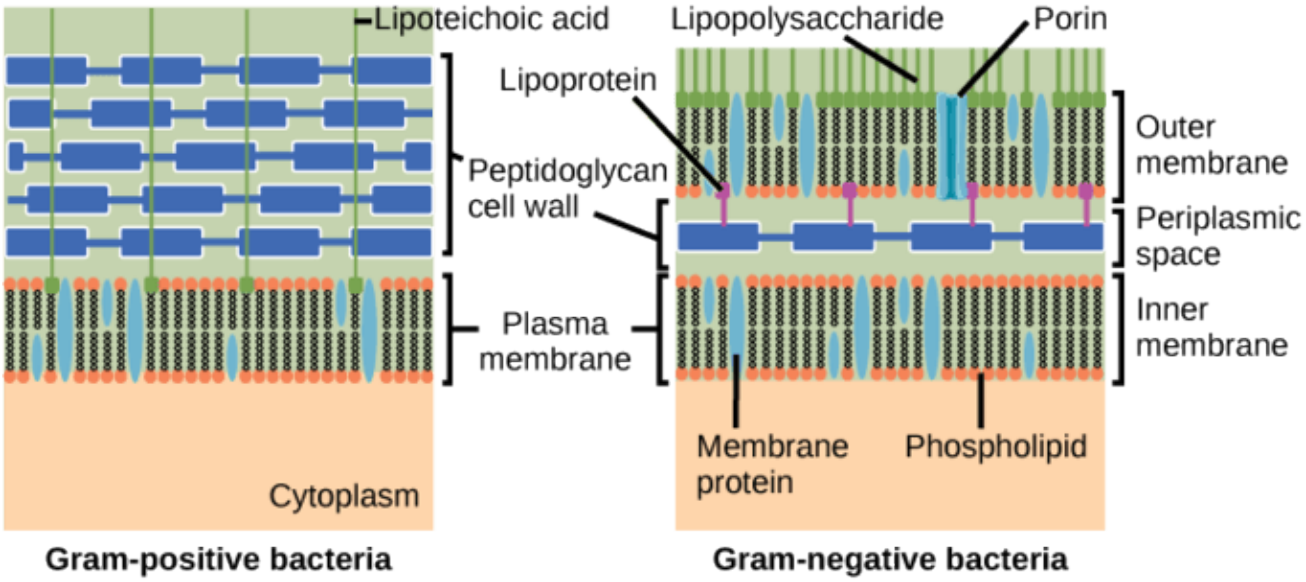


Figure 22.2A.1: Gram-positive and gram-negative bacteria: Bacteria are divided into two major groups: gram-positive and gram-negative. Both groups have a cell wall composed of peptidoglycan: in gram-positive bacteria, the wall is thick, whereas in gram-negative bacteria, the wall is thin. In gram-negative bacteria, the cell wall is surrounded by an outer membrane that contains lipopolysaccharides and lipoproteins. Porins, proteins in this cell membrane, allow substances to pass through the outer membrane of gram-negative bacteria. In gram-positive bacteria, lipoteichoic acid anchors the cell wall to the cell membrane.

Key Points

- Prokaryotic cells lack a defined nucleus, but have a region in the cell, termed the nucleoid, in which a single chromosomal, circular, double-stranded DNA molecule is located.
- Archaeal membranes have replaced the fatty acids of bacterial membranes with isoprene; some archaeal membranes are monolayer rather than bilayer.
- Prokaryotes can be further classified based on the composition of the cell wall in terms of the amount of peptidoglycan present.
- Gram-positive organisms typically lack the outer membrane found in gram-negative organisms and contain a large amount of peptidoglycan in the cell wall, roughly 90%.
- Gram-negative bacteria have a relatively thin cell wall composed of a few layers of peptidoglycan.

- Gram-negative bacteria have a relatively thin cell wall composed of a few layers of peptidoglycan.

Key Terms

- **nucleoid**: the irregularly-shaped region within a prokaryote cell where the genetic material is localized
- **plasmid**: a circle of double-stranded DNA that is separate from the chromosomes, which is found in bacteria and protozoa
- **osmotic pressure**: the hydrostatic pressure exerted by a solution across a semipermeable membrane from a pure solvent

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22.2B: Prokaryotic Reproduction

Learning Objectives

- Distinguish among the types of reproduction in prokaryotes

Reproduction

Reproduction in prokaryotes is asexual and usually takes place by binary fission. The DNA of a prokaryote exists as as a single, circular chromosome. Prokaryotes do not undergo mitosis; rather the chromosome is replicated and the two resulting copies separate from one another, due to the growth of the cell. The prokaryote, now enlarged, is pinched inward at its equator and the two resulting cells, which are clones, separate. Binary fission does not provide an opportunity for genetic recombination or genetic diversity, but prokaryotes can share genes by three other mechanisms.

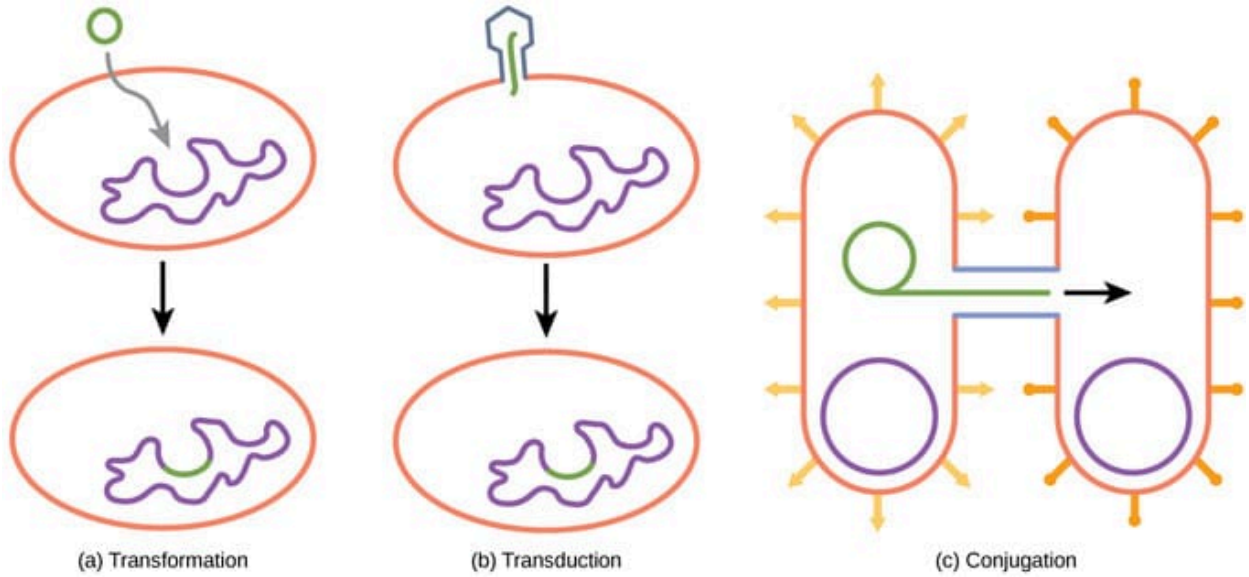


Figure $22.2B.1$: Modes of prokaryote reproduction: Besides binary fission, there are three other mechanisms by which prokaryotes can exchange DNA. In (a) transformation, the cell takes up prokaryotic DNA directly from the environment. The DNA may remain separate as plasmid DNA or be incorporated into the host genome. In (b) transduction, a bacteriophage injects DNA into the cell that contains a small fragment of DNA from a different prokaryote. In (c) conjugation, DNA is transferred from one cell to another via a mating bridge that connects the two cells after the pilus draws the two bacteria close enough to form the bridge.

In transformation, the prokaryote takes in DNA found in its environment that is shed by other prokaryotes. If a nonpathogenic bacterium takes up DNA for a toxin gene from a pathogen and incorporates the new DNA into its own chromosome, it, too, may become pathogenic. In transduction, bacteriophages, the viruses that infect bacteria, sometimes also move short pieces of chromosomal DNA from one bacterium to another. Transduction results in a recombinant organism. Archaea are not affected by bacteriophages, but instead have their own viruses that translocate genetic material from one individual to another. In conjugation, DNA is transferred from one prokaryote to another by means of a pilus, which brings the organisms into contact with one another. The DNA transferred can be in the form of a plasmid or as a hybrid, containing both plasmid and chromosomal DNA.

Reproduction can be very rapid: a few minutes for some species. This short generation time, coupled with mechanisms of genetic recombination and high rates of mutation, result in the rapid evolution of prokaryotes, allowing them to respond to environmental changes (such as the introduction of an antibiotic) very rapidly.

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Key Points

- Binary fission is a type of reproduction in which the chromosome is replicated and the resultant prokaryote is an exact copy of the parental prokaryate, thus leaving no opportunity for genetic diversity.
- Transformation is a type of prokaryotic reproduction in which a prokaryote can take up DNA found within the environment that has originated from other prokaryotes.
- Transduction is a type of prokaryotic reproduction in which a prokaryote is infected by a virus which injects short pieces of chromosomal DNA from one bacterium to another.
- Conjugation is a type of prokaryotic reproduction in which DNA is transferred between prokaryotes by means of a pilus.

Key Terms

- **transformation**: the alteration of a bacterial cell caused by the transfer of DNA from another, especially if pathogenic
- **transduction**: horizontal gene transfer mechanism in prokaryotes where genes are transferred using a virus
- **binary fission**: the process whereby a cell divides asexually to produce two daughter cells
- **conjugation**: the temporary fusion of organisms, especially as part of sexual reproduction

- **pilus**: a hairlike appendage found on the cell surface of many bacteria

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22.3: PROKARYOTIC METABOLISM

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- Topic hierarchy

22.3A: Energy and Nutrient Requirements for Prokaryotes

22.3B: The Role of Prokaryotes in Ecosystems

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22.3A: Energy and Nutrient Requirements for Prokaryotes

Learning Objectives

- Summarize what prokaryotes need to remain alive and functioning

Needs of Prokaryotes

The diverse environments and ecosystems on Earth have a wide range of conditions in terms of temperature, available nutrients, acidity, salinity, and energy sources. Prokaryotes are very well equipped to make their living out of a vast array of nutrients and conditions. To live, prokaryotes need a source of energy, a source of carbon, and some additional nutrients.

Macronutrients

Cells are essentially a well-organized assemblage of macromolecules and water. Recall that macromolecules are produced by the polymerization of smaller units called monomers. For cells to build all of the molecules required to sustain life, they need certain substances, collectively called nutrients. When prokaryotes grow in nature, they obtain their nutrients from the environment. Nutrients that are required in large amounts are called macronutrients, whereas those required in smaller or trace amounts are called micronutrients. Just a handful of elements are considered macronutrients: carbon, hydrogen, oxygen, nitrogen, phosphorus, and sulfur. (A mnemonic for remembering these elements is the acronym CHONPS.)

Why are these macronutrients needed in large amounts? They are the components of organic compounds in cells. Carbon is the major element in all macromolecules: carbohydrates, proteins, nucleic acids, lipids, and many other compounds. Carbon accounts for about 50 percent of the composition of the cell. Nitrogen represents 12 percent of the total dry weight of a typical cell and is a component of proteins, nucleic acids, and other cell constituents. Most of the nitrogen available in nature is either atmospheric nitrogen (N_2) or another inorganic form. Diatomic (N_2) nitrogen, however, can be converted into an organic form only by certain organisms, called nitrogen-fixing organisms. Both hydrogen and oxygen are part of many organic compounds and of water. Phosphorus is required by all organisms for the synthesis of nucleotides and phospholipids. Sulfur is part of the structure of some amino acids such as cysteine and methionine. It is also present in several vitamins and coenzymes. Other important macronutrients are potassium (K), magnesium (Mg), calcium (Ca), and sodium (Na). Although these elements are required in smaller amounts, they are very important for the structure and function of the prokaryotic cell.

Micronutrients

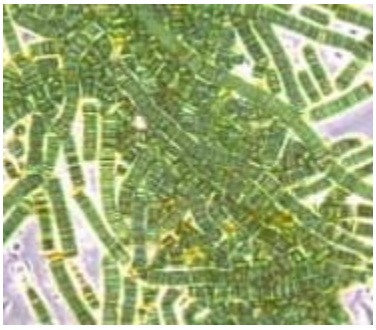


Figure 22.3A.1: Filaments of photosynthetic cyanobacteria: Cyanobacteria are an example of phototrophic prokaryotes.

In addition to these macronutrients, prokaryotes require various metallic elements in small amounts. These are referred to as micronutrients or trace elements. For example, iron is necessary for the function of the cytochromes involved in electron-transport reactions. Some prokaryotes require other elements (such as boron (B), chromium (Cr), and manganese (Mn)) primarily as enzyme cofactors.

The Ways in Which Prokaryotes Obtain Energy

Prokaryotes can use different sources of energy to assemble macromolecules from smaller molecules. Phototrophs (or phototrophic organisms) obtain their energy from sunlight. Chemotrophs (or chemosynthetic organisms) obtain their energy from chemical compounds. Chemotrophs that can use organic compounds as energy sources are called chemoorganotrophs. Those that can also use inorganic compounds as energy sources are called chemolithotrophs.

The Ways in Which Prokaryotes Obtain Carbon

Just as prokaryotes can use different sources of energy, they can also utilize different sources of carbon compounds. Recall that organisms that are able to fix inorganic carbon are called autotrophs. Autotrophic prokaryotes synthesize organic molecules from carbon dioxide. In contrast, heterotrophic prokaryotes obtain carbon from organic compounds. To make the picture more complex, the terms that describe how prokaryotes obtain energy and carbon can be combined. Thus, photoautotrophs use energy from sunlight and carbon from carbon dioxide and water, whereas chemoheterotrophs obtain energy and carbon from an organic chemical source. Chemolithoautotrophs obtain their energy from inorganic compounds, while building their complex molecules from carbon dioxide. Table 1 summarizes carbon and energy sources in prokaryotes.

Carbon and Energy Sources in Prokaryotes				
Energy Sources			**Carbon Sources**	
Light	Chemicals		Carbon dioxide	Organic compounds
Phototrophs	Chemotrophs		Autotrophs	Heterotrophs
	Organic chemicals	Inorganic chemicals		
	Chemo-organotrophs	Chemolithotrophs		

Figure 22.3A.1: Table 1. Carbon and energy sources in prokaryotes: This table summarizes the types of energy and carbon sources for different types of prokaryotes.

Key Points

- The main components of the organic compounds in a prokaryotic cell are macronutrients (such as carbon, hydrogen, oxygen, nitrogen, phosphorus, and sulfur) that make up important biomolecules, including proteins and nucleic acids.
- Nutrients that are needed by prokaryotes in small quantities to perform cellular functions, including certain electron transport chain reactions, are known as micronutrients (e.g., iron, boron, chromium, and manganese).
- Autotrophic prokaryotes are able to fix inorganic compounds, such as carbon dioxide, to obtain carbon, while heterotrophic prokaryotes use organic compounds as their source of carbon.

Key Terms

- **macronutrient**: any of the elements required in large amounts by all living things
- **chemotroph**: an organism that obtains energy by the oxidation of electron-donating molecules in the environment
- **micronutrient**: a mineral, vitamin, or other substance that is essential, even in very small quantities, for growth or metabolism

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22.3B: The Role of Prokaryotes in Ecosystems

Learning Objectives

- Give examples of the beneficial roles played by prokaryotes in different ecosystems

Role of Prokaryotes in Ecosystems

Prokaryotes are ubiquitous: There is no niche or ecosystem in which they are not present. Prokaryotes play many roles in the environments they occupy, but the roles they play in the carbon and nitrogen cycles are vital to life on earth.

Prokaryotes and the Carbon Cycle

Carbon is one of the most important macronutrients. Prokaryotes play an important role in the carbon cycle. Carbon is cycled through earth's major reservoirs: land, the atmosphere, aquatic environments, sediments and rocks, and biomass. The movement of carbon is via carbon dioxide, which is removed from the atmosphere by land plants and marine prokaryotes and is returned to the atmosphere via the respiration of chemoorganotrophic organisms, including prokaryotes, fungi, and animals. Although the largest carbon reservoir in terrestrial ecosystems is in rocks and sediments, that carbon is not readily available.

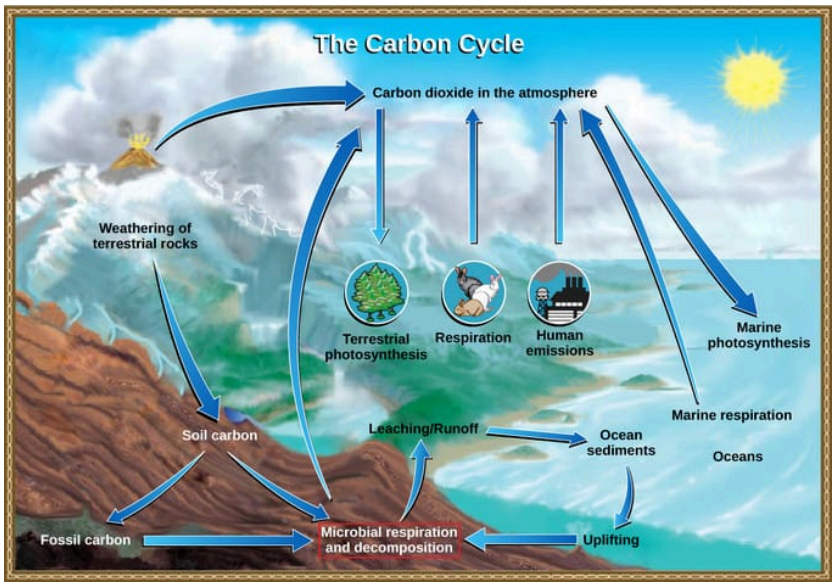


Figure $22.3B.1$: Carbon cycle: Prokaryotes play a significant role in continuously moving carbon through the biosphere.

A large amount of available carbon is found in land plants, which are producers that use carbon dioxide from the air to synthesize carbon compounds. Related to this, one very significant source of carbon compounds is humus, which is a mixture of organic materials from dead plants and prokaryotes that have resisted decomposition. Consumers such as animals use organic compounds generated by producers, releasing carbon dioxide to the atmosphere. Then, bacteria and fungi, collectively called decomposers, carry out the breakdown (decomposition) of plants and animals and their organic compounds. The most important contributor of carbon dioxide to the atmosphere is microbial decomposition of dead material (dead animals, plants, and humus).

In aqueous environments and their anoxic sediments, there is another carbon cycle taking place. In this case, the cycle is based on one-carbon compounds. In anoxic sediments, prokaryotes, mostly archaea, produce methane (CH_4). This methane moves into the zone above the sediment, which is richer in oxygen and supports bacteria called methane oxidizers that oxidize methane to carbon dioxide, which then returns to the atmosphere.

Prokaryotes and the Nitrogen Cycle

Nitrogen is a very important element for life because it is part of proteins and nucleic acids. As a macronutrient in nature, it is recycled from organic compounds to ammonia, ammonium ions, nitrate, nitrite, and nitrogen gas by myriad processes, many of which are carried out solely by prokaryotes; they are key to the nitrogen cycle. The largest pool of nitrogen available in the terrestrial ecosystem is gaseous nitrogen from the air, but this nitrogen is not usable by plants, which are primary producers. Gaseous nitrogen is transformed, or "fixed," into more-readily available forms such as ammonia through the process of nitrogen fixation by natural means, especially by microorganisms (prokayotes) in the soil. Ammonia can then be used by plants or converted to other forms.

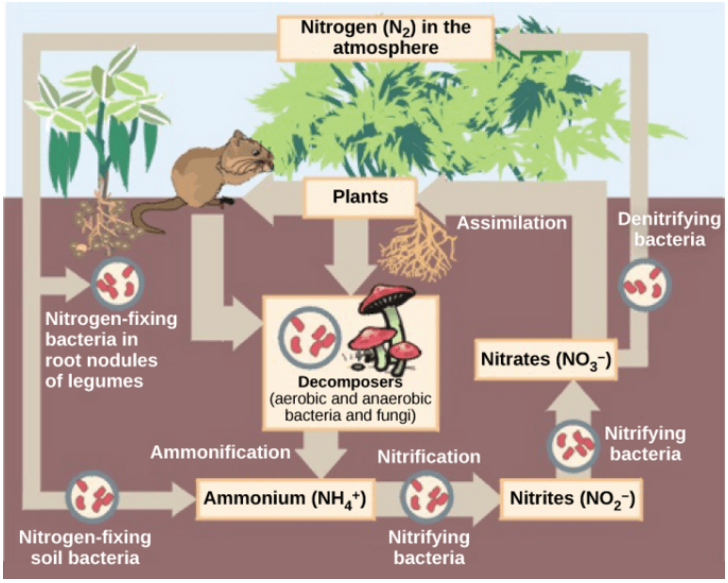


Figure $22.3B.1$: Nitrogen cycle: Prokaryotes play a key role in the nitrogen cycle.

Another source of ammonia is ammonification, the process by which ammonia is released during the decomposition of nitrogen-containing organic compounds. Ammonia released to the atmosphere, however, represents only 15 percent of the total nitrogen released; the rest is as N_2 and N_2O. Ammonia is catabolized anaerobically by some prokaryotes, yielding N_2 as the final product. Nitrification is the conversion of ammonium to nitrite and nitrate. Nitrification in soils is carried out by bacteria belonging to the genera *Nitrosomas*, *Nitrobacter*, and *Nitrospira*. The bacteria perform the reverse process, the reduction of nitrate from the soils to gaseous compounds such as N_2O, NO, and N_2, a process called denitrification.

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Key Points

- Carbon and nitrogen are both macronutrients that are necessary for life on earth; prokaryotes play vital roles in their cycles.
- The carbon cycle is maintained by prokaryotes that remove carbon dioxide and return it to the atmosphere.
- Prokaryotes play a major role in the nitrogen cycle by fixing atomspheric nitrogen into ammonia that plants can use and by converting ammonia into other forms of nitrogen sources.

Key Terms

- **carbon cycle**: the physical cycle of carbon through the earth's biosphere, geosphere, hydrosphere, and atmosphere that includes such processes as photosynthesis, decomposition, respiration and carbonification
- **nitrogen cycle**: the natural circulation of nitrogen, in which atmospheric nitrogen is converted to nitrogen oxides and deposited in the soil, where it is used by organisms or decomposed back to elemental nitrogen
- **nitrogen fixation**: the conversion of atmospheric nitrogen into ammonia and organic derivatives, by natural means, especially by microorganisms in the soil, into a form that can be assimilated by plants

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22.4: BACTERIAL DISEASES IN HUMANS

22.4A: History of Bacterial Diseases
22.4B: Biofilms and Disease
22.4C: Antibiotics- Are We Facing a Crisis?
22.4D: Bacterial Foodborne Diseases

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22.4A: History of Bacterial Diseases

Learning Objectives

- Give examples of historical, new, and re-emerging bacterial diseases in humans

There are records about infectious diseases as far back as 3000 B.C.E. A number of significant pandemics caused by bacteria have been documented over several hundred years. Some of the most memorable pandemics led to the decline of cities and nations. In the 21st century, infectious diseases remain among the leading causes of death worldwide, despite advances made in medical research and treatments in recent decades. A disease spreads when the pathogen that causes it is passed from one person to another. For a pathogen to cause disease, it must be able to reproduce in the host's body and damage the host in some way.

The Plague of Athens

In 430 B.C.E., the Plague of Athens killed one-quarter of the Athenian troops that were fighting in the great Peloponnesian War and weakened Athens' dominance and power. The plague impacted people living in overcrowded Athens as well as troops aboard ships that had to return to Athens. The source of the plague may have been identified recently when researchers from the University of Athens were able to use DNA from teeth recovered from a mass grave. The scientists identified nucleotide sequences from a pathogenic bacterium, *Salmonella enterica* serovar typhi, which causes typhoid fever. This disease is commonly seen in overcrowded areas and has caused epidemics throughout recorded history.



Figure 22.4A.1: Salmonella enterica serovar typhi: Salmonella enterica serovar typhi, the causative agent of typhoid fever, is a gram-negative, rod-shaped gamma protobacterium. Typhoid fever, which is spread through feces, causes intestinal hemorrhage, high fever, delirium and dehydration. Today, between 16 and 33 million cases of this re-emerging disease occur annually, resulting in over 200,000 deaths. Carriers of the disease can be asymptomatic. In a famous case in the early 1900s, a cook named Mary Mallon unknowingly spread the disease to over fifty people, three of whom died. Other Salmonella serotypes cause food poisoning.

Bubonic Plagues

From 541 to 750 C.E.., an outbreak of what was likely a bubonic plague (the Plague of Justinian), eliminated one-quarter to one-half of the human population in the eastern Mediterranean region. The population in Europe dropped by 50 percent during this outbreak. The bubonic plague would strike Europe more than once.

One of the most devastating pandemics was the Black Death (1346 to 1361) that is believed to have been another outbreak of bubonic plague caused by the bacterium *Yersinia pestis*. It is thought to have originated initially in China and spread along the Silk Road, a network of land and sea trade routes, to the Mediterranean region and Europe, carried by rat fleas living on black rats that were always present on ships. The Black Death reduced the world's population from an estimated 450 million to about 350 to 375 million. Bubonic plague struck London hard again in the mid-1600s. In modern times, approximately 1,000 to 3,000 cases of plague arise globally each year. Although contracting bubonic plague before antibiotics meant almost certain death, the bacterium responds to several types of modern antibiotics; mortality rates from plague are now very low.



Figure 22.4A.1: Bubonic plague: The (a) Great Plague of London killed an estimated 200,000 people, or about twenty percent of the city's population. The causative agent, the (b) bacterium Yersinia pestis, is a gram-negative, rod-shaped bacterium from the class Gamma Proteobacteria. The disease is transmitted through the bite of an infected flea, which is infected by a rodent. Symptoms include swollen lymph nodes, fever, seizure, vomiting of blood, and (c) gangrene.

Migration of Diseases to New Populations

Over the centuries, Europeans tended to develop genetic immunity to endemic infectious diseases, but when European conquerors reached the western hemisphere, they brought with them disease-causing bacteria and viruses, which triggered epidemics that completely devastated populations of Native Americans who had no natural resistance to many European diseases. It has been estimated that up to 90 percent of Native Americans died from infectious diseases after the arrival of Europeans, making conquest of the New World a foregone conclusion.

Emerging and Re-emerging Diseases

The distribution of a particular disease is dynamic. Therefore, changes in the environment, the pathogen, or the host population can dramatically impact the spread of a disease. According to the World Health Organization (WHO), an emerging disease is one that has appeared in a population for the first time, or that may have existed previously, but is rapidly increasing in incidence or geographic range. This definition also includes re-emerging diseases that were previously under control. Approximately 75 percent of recently-emerging infectious diseases affecting humans are zoonotic diseases. Zoonoses, diseases that primarily infect animals and are transmitted to humans, are of both viral and bacterial origins. Brucellosis is an example of a prokaryotic zoonosis that is re-emerging in some regions. Necrotizing fasciitis (commonly known as flesh-eating bacteria) has been increasing in virulence for the last 80 years, for unknown reasons.

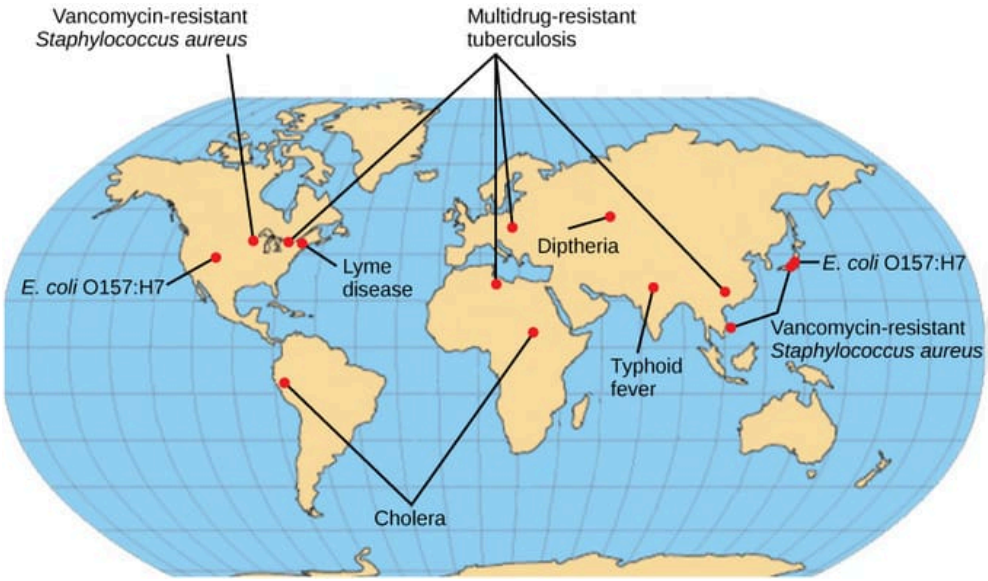


Figure 22.4A.1: Regions of bacterial disease emergence: The map shows regions where bacterial diseases are emerging or reemerging.

Some of the currently-emerging diseases are not actually new, but are diseases that were catastrophic in the past. They devastated populations, became dormant for a while, but have re-emerged, sometimes more virulent than before. Such was the case with bubonic plague. Other diseases, like tuberculosis, were never eradicated, but were under control in some regions of the world until re-emerging, mostly in urban centers with high concentrations of immunocompromised people. The WHO has identified certain diseases whose worldwide re-emergence should be monitored. Among these are two viral diseases (dengue fever and yellow fever) and three bacterial diseases (diphtheria, cholera, and bubonic plague). The war against infectious diseases has no foreseeable end.

Key Points

- A pathogen must be able to reproduce in the host's body and damage the host in some way to cause disease.
- Before antibiotics, contracting plagues usually meant death; however, most bacterium associated with these plagues respond to modern antibiotics; mortality rates from these diseases are now very low.
- Emerging diseases include those that have appeared in a population for the first time or that may have existed previously, but are rapidly spreading; this also includes re-emerging diseases that were previously under control.
- The spread of disease can be impacted dramatically by changes in the environment, the pathogen, or the host population.

Key Terms

- **zoonosis**: an animal disease that can be transmitted to humans
- **plague**: an epidemic or pandemic caused by any pestilence
- **pathogen**: any organism or substance, especially a microorganism, capable of causing disease, such as bacteria, viruses, protozoa, or fungi

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22.4B: Biofilms and Disease

Learning Objectives

- Give examples of the roles played by biofilms in human diseases

Biofilms and Disease

Biofilms are complex colonies of bacteria (often containing several species) that exchange chemical signals to coordinate the release of toxins that will attack the host. Once established, they are very difficult to destroy as they are highly resistant to antimicrobial treatments and host defense. Biofilms form when microorganisms adhere to the surface of some object in a moist environment and begin to reproduce. They grow virtually everywhere in almost any environment where there is a combination of moisture, nutrients, and a surface. Biofilms are responsible for diseases such as infections in patients with cystic fibrosis, Legionnaires' disease, and otitis media. They produce dental plaque and colonize catheters, prostheses, transcutaneous and orthopedic devices, contact lenses, and internal devices such as pacemakers. They also form in open wounds and burned tissue. In healthcare environments, biofilms grow on hemodialysis machines, mechanical ventilators, shunts, and other medical equipment. In fact, 65 percent of all infections acquired in the hospital (nosocomial infections) are attributed to biofilms. Biofilms are also related to diseases contracted from food because they colonize the surfaces of vegetable leaves and meat, as well as food-processing equipment that is not adequately cleaned.

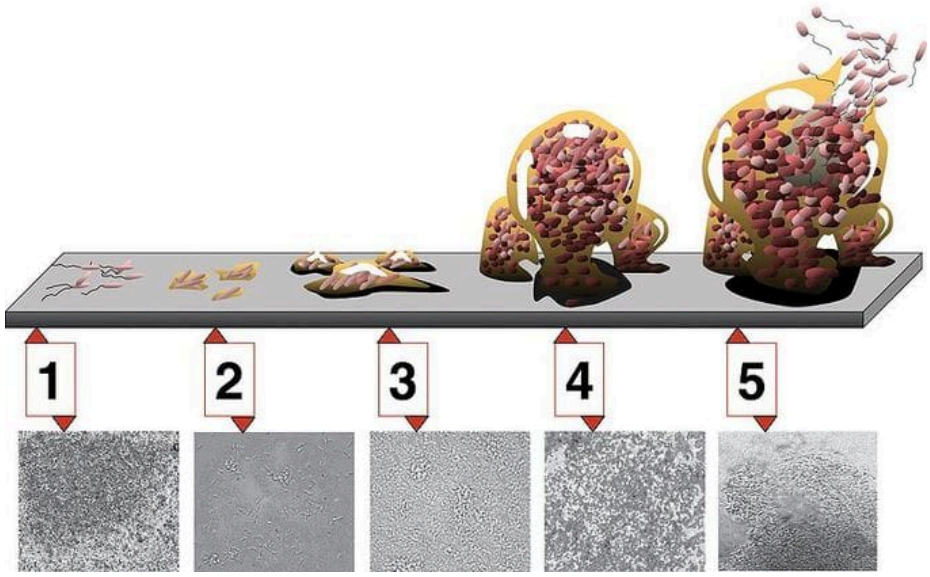


Figure $22.4B.1$: The Five Stages of Biofilm Development: Stage 1: initial attachment; stage 2: irreversible attachment; stage 3: maturation I; stage 4: maturation II; stage 5: dispersion. Each stage of development in the diagram is paired with a photomicrograph of a developing Pseudomonas aeruginosa biofilm. All photomicrographs are shown at the same scale.

Biofilm infections develop gradually and often do not cause immediate symptoms. They are rarely resolved by host defense mechanisms. Once an infection by a biofilm is established, it is very difficult to eradicate because biofilms tend to be resistant to most of the methods used to control microbial growth, including antibiotics. Biofilms respond poorly or only temporarily to antibiotics. It has been said that they can resist up to 1,000 times the antibiotic concentrations used to kill the same bacteria when they are free-living or planktonic. An antibiotic dose that large would harm the patient; therefore, scientists are working on new ways to eradicate biofilms.

Key Points

- Once a biofilm infection is established, it is very difficult to eradicate because biofilms exhibit great resistance to most

methods used to control microbial growth, including antibiotics.
- Biofilms are able to grow anywhere there is an optimal combination of moisture, nutrients, and a surface.
- Biofilms are responsible for diseases such as infections in patients and readily settle within wounds and burns; they can also easily colonize medical devices and other surfaces where sterility is vital for health.

Key Terms

- **biofilm**: a thin film of mucus created by and containing a colony of bacteria and other microorganisms
- **nosocomial**: contracted in a hospital, or arising from hospital treatment

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22.4C: Antibiotics- Are We Facing a Crisis?

Learning Objectives

- Discuss antibiotic resistance.

The word antibiotic comes from the Greek word “anti” meaning “against” and “bios” meaning “life.” An antibiotic is a chemical, produced either by microbes or synthetically, that is hostile to the growth of other organisms. Today’s news and other media often address concerns about an antibiotic crisis. Are the antibiotics that easily treated bacterial infections in the past becoming obsolete? Are there new “superbugs”: bacteria that have evolved to become more resistant to our arsenal of antibiotics? Is this the beginning of the end of antibiotics? All these questions challenge the healthcare community.

One of the main causes of resistant bacteria is the abuse of antibiotics. The imprudent and excessive use of antibiotics has resulted in the natural selection of resistant forms of bacteria. The antibiotic kills most of the infecting bacteria; therefore, only the resistant forms remain. These resistant forms reproduce, resulting in an increase in the proportion of resistant forms over non-resistant ones. Another major misuse of antibiotics is in patients with colds or the flu, for which antibiotics are useless. There is also the excessive use of antibiotics in livestock along with the routine use of antibiotics in animal feed, both of which promote bacterial resistance. In the United States, 70 percent of the antibiotics produced are fed to animals. Because they are given to livestock in low doses, the probability of resistance developing is maximized. These resistant bacteria are readily transferred to humans.

One of the Superbugs: MRSA

The imprudent use of antibiotics has paved the way for bacteria to expand populations of resistant forms. For example, *Staphylococcus aureus*, often called “staph,” is a common bacterium that can live in the human body and is usually easily treated with antibiotics. A very dangerous strain, however, methicillin-resistant *Staphylococcus aureus* (MRSA) has made the news over the past few years. This strain is resistant to many commonly-used antibiotics, including methicillin, amoxicillin, penicillin, and oxacillin. MRSA can cause infections of the skin, but it can also infect the bloodstream, lungs, urinary tract, or sites of injury. While MRSA infections are common among people in healthcare facilities, they have also appeared in healthy people who have not been hospitalized, but who live or work in tight populations (like military personnel and prisoners). Researchers have expressed concern about the way this latter source of MRSA targets a much younger population than those residing in care facilities. The Journal of the American Medical Association (JAMA) reported that, among MRSA-afflicted persons in healthcare facilities, the average age is 68, whereas people with “community-associated MRSA” (CA-MRSA) have an average age of 23.

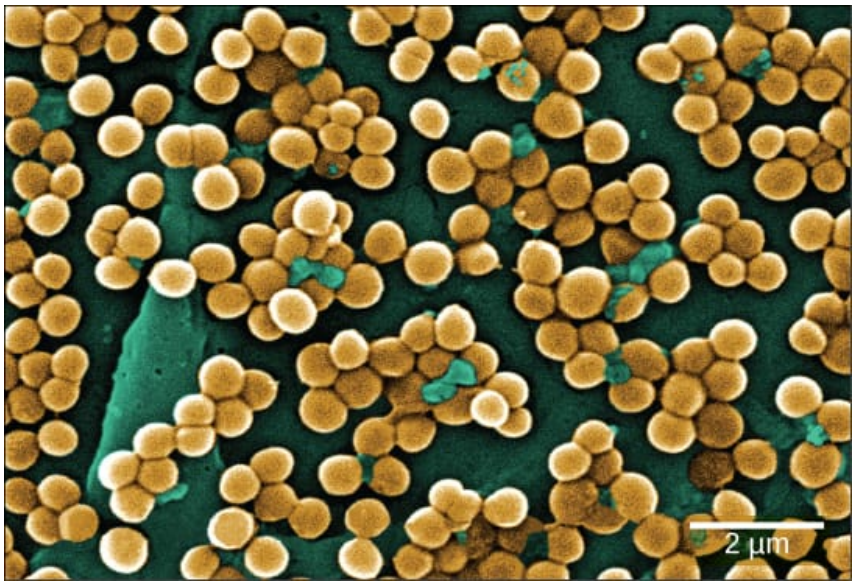


Figure 22.4C.1: MRSA, a superbug: This scanning electron micrograph shows methicillin-resistant Staphylococcus aureus bacteria, commonly known as MRSA. S. aureus is not always pathogenic, but can cause diseases such as food poisoning and skin and respiratory infections.

In summary, the medical community is facing an antibiotic crisis. Some scientists believe that after years of being protected from bacterial infections by antibiotics, we may be returning to a time in which a simple bacterial infection could again devastate the human population. Researchers are developing new antibiotics, but it takes many years of research and clinical trials, plus financial investments in the millions of dollars, to generate an effective and approved drug.

Reference

Naimi, TS, LeDell, KH, Como-Sabetti, K, et al. Comparison of community- and health care-associated methicillin-resistant *Staphylococcus aureus* infection. JAMA 290 (2003): 2976–84, doi: 10.1001/jama.290.22.2976.

Key Points

- In antibiotic resistance, antibiotics will kill most of the infecting bacteria leaving behind only the resistant forms, which reproduce, resulting in an increase in the proportion of resistant forms over non-resistant ones.
- Cold and flu treatments and the medication of livestock are examples of antibiotic misuse responsible for bacterial resistance.
- Methicillin-resistant *Staphylococcus aureus* (MRSA) is an example of a dangerous antibiotic-resistant strain of bacteria that can infect sick, as well as healthy people.
- Due to the growing resistance to antibiotics, scientists believe that we may be returning to a time in which a simple bacterial infection could again detrimentally impact human populations.

Key Terms

- **antibiotic**: any substance that can destroy or inhibit the growth of bacteria and similar microorganisms

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22.4D: Bacterial Foodborne Diseases

Learning Objectives

- Give examples of bacterial foodborne diseases in humans

Prokaryotes are everywhere. They readily colonize the surface of any type of material. Food is not an exception. Most of the time, prokaryotes colonize food and food-processing equipment in the form of a biofilm. Outbreaks of bacterial infection related to food consumption are common. A foodborne disease (colloquially called "food poisoning") is an illness resulting from the consumption of pathogenic bacteria, viruses, or other parasites that contaminate food. Although the United States has one of the safest food supplies in the world, the U.S. Centers for Disease Control and Prevention (CDC) has reported that "76 million people get sick, more than 300,000 are hospitalized, and 5,000 Americans die each year from foodborne illness."

The characteristics of foodborne illnesses have changed over time. In the past, sporadic cases of botulism, the potentially fatal disease produced by a toxin from the anaerobic bacterium *Clostridium botulinum*, were relatively common. Some of the sources for this bacterium were non-acidic canned foods, homemade pickles, and processed meat and sausages. The can, jar, or package created a suitable anaerobic environment where *Clostridium* could grow. However, proper sterilization and canning procedures have reduced the incidence of this disease.

While people may tend to think of foodborne illnesses as associated with animal-based foods, most cases are now linked to produce. There have been serious, produce-related outbreaks associated with raw spinach in the United States and with vegetable sprouts in Germany. These types of outbreaks have become more common. The raw spinach outbreak in 2006 was produced by the bacterium *E. coli* serotype O157:H7. A serotype is a strain of bacteria that carries a set of similar antigens on its cell surface. There are often many different serotypes of a bacterial species. Most *E. coli* are not particularly dangerous to humans, but serotype O157:H7 can cause bloody diarrhea and is potentially fatal.

All types of food can potentially be contaminated with bacteria. Recent outbreaks of *Salmonella* reported by the CDC occurred in foods as diverse as peanut butter, alfalfa sprouts, and eggs. A deadly outbreak in Germany in 2010 was caused by *E. coli* contamination of vegetable sprouts. The strain that caused the outbreak was found to be a new serotype not previously involved in other outbreaks, which indicates that *E. coli* is continuously evolving.

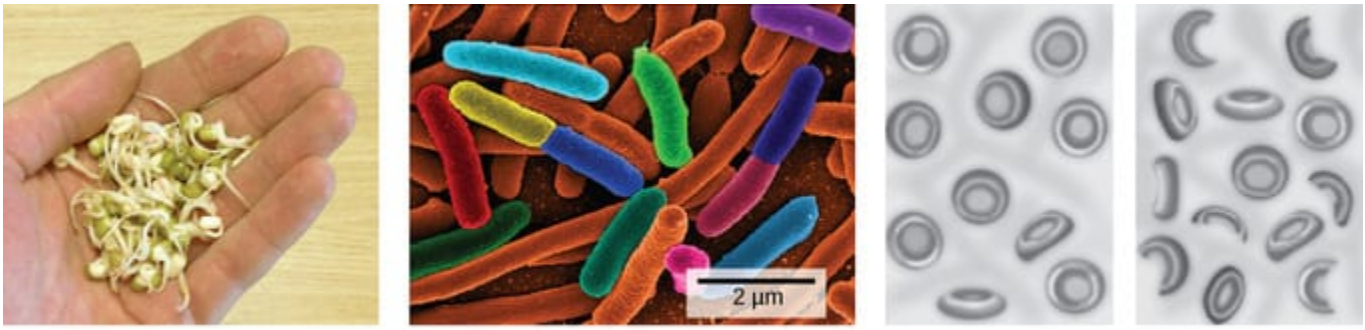


Figure $22.4D.1$: Bacterial illnesses from food: (a) Vegetable sprouts grown at an organic farm were the cause of an (b) E. coli outbreak that killed 32 people and sickened 3,800 in Germany in 2011. The strain responsible, E. coli O104:H4, produces Shiga toxin, a substance that inhibits protein synthesis in the host cell. The toxin (c) destroys red blood cells, resulting in bloody diarrhea. Deformed red blood cells clog the capillaries of the kidney, which can lead to kidney failure, as happened to 845 patients in the 2011 outbreak. Kidney failure is usually reversible, but some patients experience kidney problems years later.

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Key Points

- Food and food-processing equipment are usually colonized by biofilms.
- A foodborne disease is an illness resulting from the consumption of pathogenic bacteria, viruses, or other parasites that contaminate animal or plant-based food.
- Proper sterilization techniques and canning procedures have reduced the incidence of botulism.
- *E. coli* outbreaks have become more common as new strains continue to evolve.

Key Terms

- **serotype**: a group of microorganisms characterized by a specific set of antigens
- **botulism**: poisoning caused by the toxin from Clostridium botulinum, a type of anaerobic bacteria that grows in improperly-prepared food

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22.5: BENEFICIAL PROKARYOTES

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- Topic hierarchy

22.5A: Symbiosis between Bacteria and Eukaryotes
22.5B: Early Biotechnology- Cheese, Bread, Wine, Beer, and Yogurt
22.5C: Prokaryotes and Environmental Bioremediation

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22.5A: Symbiosis between Bacteria and Eukaryotes

Learning Objectives

- Explain the need for nitrogen fixation and how it is accomplished

Cooperation between Bacteria and Eukaryotes: Nitrogen Fixation

Nitrogen is a very important element for living things because it is part of the nucleotides and amino acids that are the building blocks of nucleic acids and proteins, respectively. Nitrogen is usually the most limiting element in terrestrial ecosystems. Atmospheric nitrogen, N_2, provides the largest pool of available nitrogen. However, eukaryotes cannot use atmospheric, gaseous nitrogen to synthesize macromolecules. Fortunately, nitrogen can be "fixed," meaning it is converted into ammonia (NH_3) either biologically or abiotically. Abiotic nitrogen fixation occurs as a result of lightning or by industrial processes.

Bacterial Nitrogen Fixation

Biological nitrogen fixation (BNF) is exclusively carried out by prokaryotes: soil bacteria, cyanobacteria, and *Frankia spp.* (filamentous bacteria interacting with actinorhizal plants such as alder, bayberry, and sweet fern). After photosynthesis and cellular respiration, BNF is the second most important biological process on Earth. The equation representing the process is as follows, where P_i stands for inorganic phosphate: $N_2 + 16ATP + 8^- + 8H^+ \; 2NH_3 + 16ADP + 16P_i + H_2$

The total fixed nitrogen through BNF is about 100 to 180 million metric tons per year. Biological processes contribute 65 percent of the nitrogen used in agriculture.

Types of Bacteria

Cyanobacteria are the most important nitrogen fixers in aquatic environments. In soil, members of the genus Clostridium are examples of free-living, nitrogen-fixing bacteria. Other bacteria live symbiotically with legume plants, providing the most important source of BNF. Symbionts may fix more nitrogen in soils than free-living organisms by a factor of 10. Soil bacteria, collectively called rhizobia, are able to symbiotically interact with legumes to form nodules: specialized structures where nitrogen fixation occurs. Nitrogenase, the enzyme that fixes nitrogen, is inactivated by oxygen, so the nodule provides an oxygen-free area for nitrogen fixation to take place. This process provides a natural and inexpensive plant fertilizer as it converts (reduces) atmospheric nitrogen to ammonia, which is easily usable by plants. The use of legumes is an excellent alternative to chemical fertilization and is of special interest to sustainable agriculture, which seeks to minimize the use of chemicals and conserve natural resources. Through symbiotic nitrogen fixation, the plant benefits from using an endless source of nitrogen: the atmosphere. Bacteria benefit from using photosynthates (carbohydrates produced during photosynthesis) from the plant and having a protected niche. Additionally, the soil benefits from being naturally fertilized. Therefore, the use of rhizobia as biofertilizers is a sustainable practice.

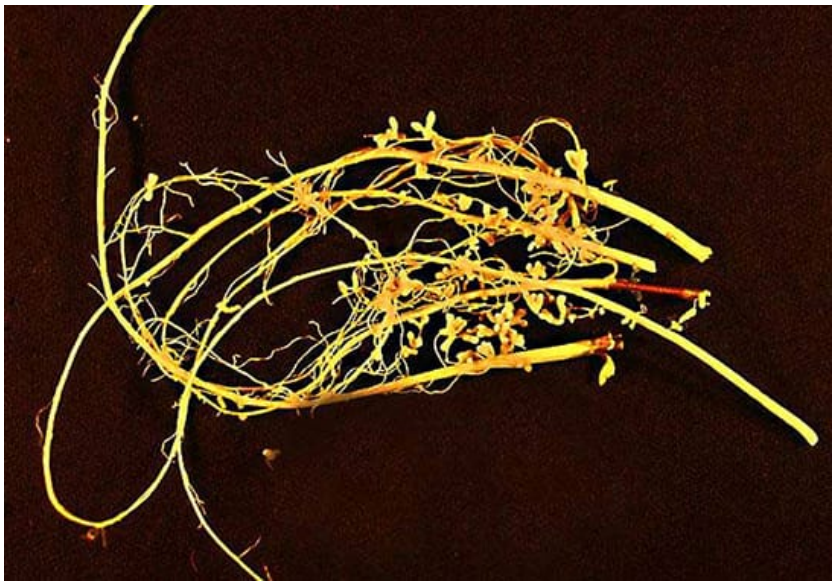


Figure 22.5A.1: Location of Nitrogen Fixation: Soybean (Glycine max) is a legume that interacts symbiotically with the soil bacterium Bradyrhizobium japonicum to form specialized structures on the roots called nodules where nitrogen fixation occurs.

Some legumes, like soybeans, are also key sources of agricultural protein. Some of the most important legumes are soybean, peanuts, peas, chickpeas, and beans. Other legumes, such as alfalfa, are used to feed cattle.

Key Points

- Prokaryotes perform biological nitrogen fixation (BNF) to convert nitrogen gas from the atmosphere into ammonia, which can be used by eukaryotes to form important biomolecules such as amino acids and nucleic acids.
- Although most nitrogen fixation is performed by prokaryotes, abiotic processes, such as industrial processes and lightning, can also fix nitrogen.
- Some bacteria form symbiotic relationships with legumes, which provide oxygen-free nodules on their roots for nitrogen fixation to occur; this process allows ammonia to form naturally from atomspheric nitrogen to act as fertilizer for soils.

Key Terms

- **abiotic**: nonliving, inanimate, characterized by the absence of life; of inorganic matter
- **nitrogen fixation**: the conversion of atmospheric nitrogen into ammonia and organic derivatives, by natural means, especially by microorganisms in the soil, into a form that can be assimilated by plants
- **legume**: a large family of herbs, shrubs, and trees that bear nodules on the roots that contain nitrogen-fixing bacteria

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22.5B: Early Biotechnology- Cheese, Bread, Wine, Beer, and Yogurt

Learning Objectives

- Discuss the origins of food biotechnology as indicated by the production of cheese, bread, wine, beer, and yogurt

Early Biotechnology: Cheese, Bread, Wine, Beer, and Yogurt

According to the United Nations Convention on Biological Diversity, biotechnology is “any technological application that uses biological systems, living organisms, or derivatives thereof, to make or modify products or processes for specific use. ” The concept of “specific use” involves some sort of commercial application. Genetic engineering, artificial selection, antibiotic production, and cell culture are current topics of study in biotechnology. However, humans have used prokaryotes before the term biotechnology was even coined. Some of the products are as simple as cheese, bread, wine, beer, and yogurt,which employ both bacteria and other microbes, such as yeast.

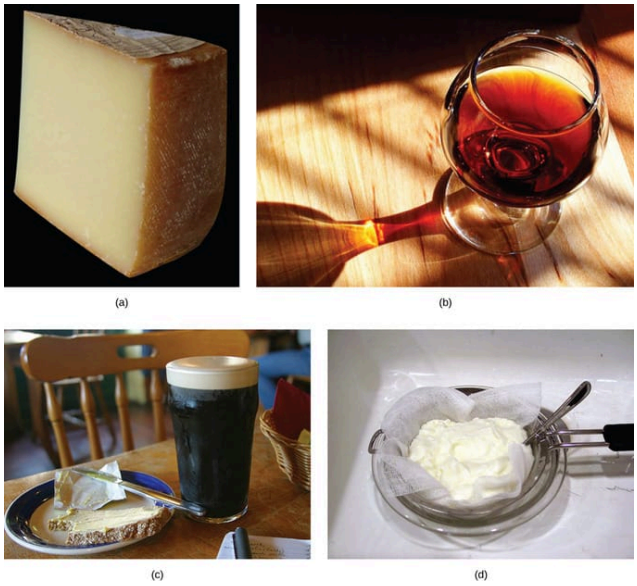


Figure $22.5B.1$: Products made using prokaryotes: Some of the products derived from the use of prokaryotes in early biotechnology include (a) cheese, (b) wine, (c) beer and bread, and (d) yogurt.

Cheese production began around 4,000–7,000 years ago when humans began to breed animals and process their milk. Fermentation, in this case, preserves nutrients because milk will spoil relatively quickly, but when processed as cheese, it is more stable. A required step in cheese-making is separating the milk into solid curds and liquid whey. This usually is done by acidifying the milk and adding rennet. The acidification can be accomplished directly by the addition of an acid like vinegar, but usually starter bacteria are employed instead. These starter bacteria convert milk sugars into lactic acid. The same bacteria (and the enzymes they produce) also play a large role in the eventual flavor of aged cheeses. Most cheeses are made with starter bacteria from the *Lactococci*, *Lactobacilli*, or *Streptococci* families. As a cheese ages, microbes and enzymes transform texture and intensify flavor. This transformation is largely a result of the breakdown of casein proteins and milkfat into a complex mix of amino acids, amines, and fatty acids. Some cheeses have additional bacteria or molds intentionally introduced before or during aging. In traditional cheesemaking, these microbes might already be present in the aging room; they are simply allowed to settle and grow on the stored cheeses. More often today, prepared cultures are used, giving more consistent results and putting fewer constraints on the environment where the cheese ages.

Records of brewing beer date back about 6,000 years to the Sumerians. Evidence indicates that the Sumerians discovered fermentation by chance. Wine has been produced for about 4,500 years. The production of beer and wine use microbes, including

both yeast and bacteria, to produce ethanol during fermentation as well as provide flavor to the beverage. Similarly, bread is one of the oldest prepared foods. Bread-making also uses the fermentation of yeast and some bacteria for leavening and flavor. Additionally, evidence suggests that cultured milk products, such as yogurt, have existed for at least 4,000 years. These products use prokaryotes (as with cheese) to provide flavor and to protect the food product from other unwanted microbes.

Key Points

- Prokaryotes and other microbes are beneficial to some food production by transforming textures, providing flavors, producing ethanol, and providing protection from unwanted microbes.
- Bacteria breakdown proteins and fats into a complex mix of amino acids, amines, and fatty acids; this processing alters the food product.
- Many food production processes rely on the fermentation of prokaryotes and other microbes to produce the desired flavors; in the case of beer and wine, they also affect the desired amount of ethanol.

Key Terms

- **fermentation**: an anaerobic biochemical reaction, in yeast, for example, in which enzymes catalyze the conversion of sugars to alcohol or acetic acid with the evolution of carbon dioxide
- **biotechnology**: the use of living organisms (especially microorganisms) in industrial, agricultural, medical, and other technological applications

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22.5C: Prokaryotes and Environmental Bioremediation

Learning Objectives

- Give examples of the use of prokaryotes in enviromental bioremediation

Using Prokaryotes to Clean up Our Planet: Bioremediation

Microbial bioremediation is the use of prokaryotes (or microbial metabolism) to remove pollutants. Bioremediation has been used to remove agricultural chemicals (pesticides, fertilizers) that leach from soil into groundwater and the subsurface. Certain toxic metals and oxides, such as selenium and arsenic compounds, can also be removed from water by bioremediation. The reduction of SeO_4^{-2} to SeO_3^{-2} and to Se^0 (metallic selenium) is a method used to remove selenium ions from water. Mercury is an example of a toxic metal that can be removed from an environment by bioremediation. As an active ingredient of some pesticides, mercury is used in industry and is also a by-product of certain processes, such as battery production. Methyl mercury is usually present in very low concentrations in natural environments, but it is highly toxic because it accumulates in living tissues. Several species of bacteria can carry out the biotransformation of toxic mercury into nontoxic forms. These bacteria, such as *Pseudomonas aeruginosa*, can convert Hg^{+2} into elemental Hg^0, which is nontoxic to humans.

One of the most useful and interesting examples of the use of prokaryotes for bioremediation purposes is the cleanup of oil spills. The importance of prokaryotes to petroleum bioremediation has been demonstrated in several oil spills in recent years, such as the Exxon Valdez spill in Alaska (1989), the Prestige oil spill in Spain (2002), the spill into the Mediterranean from a Lebanon power plant (2006), and, more recently, the BP oil spill in the Gulf of Mexico (2010). To clean up these spills, bioremediation is promoted by the addition of inorganic nutrients that help bacteria to grow. Hydrocarbon-degrading bacteria feed on hydrocarbons in the oil droplet, breaking down the hydrocarbons. Some species, such as *Alcanivorax borkumensis*, produce surfactants that solubilize the oil, whereas other bacteria degrade the oil into carbon dioxide. In the case of oil spills in the ocean, ongoing, natural bioremediation tends to occur if there are oil-consuming bacteria in the ocean prior to the spill. In addition to naturally occurring oil-degrading bacteria, humans select and engineer bacteria that possess the same capability with increased efficacy and the spectrum of hydrocarbon compounds that can be processed. Under ideal conditions, it has been reported that up to 80 percent of the non-volatile components in oil can be degraded within one year of the spill. Other oil fractions containing aromatic and highly-branched hydrocarbon chains are more difficult to remove and remain in the environment for longer periods of time.



Figure $22.5C.1$: Bioremediation in the Exxon Valdez oil spill: (a) Cleaning up oil after the Valdez spill in Alaska, workers hosed oil from beaches and then used a floating boom to corral the oil, which was finally skimmed from the water surface. Some species of bacteria are able to solubilize and degrade the oil. (b) One of the most catastrophic consequences of oil spills is the damage to fauna.

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Key Points

- To clean up oil spills, bacteria are introduced to the area of the spill where they break down the hydrocarbons of the oil into carbon dioxide; this is an example of bioremediation.
- Toxic metals, such as mercury (II), can be converted into nontoxic forms, such as mercury (0), by bacteria.
- Using natural organisms as examples, scientists can engineer bacteria for improved bioremediation of desired pollutants.
- Bioremediation can remove oil, some pesticides, fertilizers, and toxic chemicals, such as arsenic, from the environment.

Key Terms

- **bioremediation**: the use of biological organisms, usually microorganisms, to remove contaminants, especially from soil or polluted water
- **biotransformation**: the changes (both chemical and physical) that occur to a substance (especially a drug) by the actions of enzymes within an organism

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23: PROTISTS

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23.1: EUKARYOTIC ORIGINS

- Topic hierarchy

23.1A: Early Eukaryotes

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23.1C: Endosymbiosis and the Evolution of Eukaryotes

23.1D: The Evolution of Mitochondria

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23.1A: Early Eukaryotes

Learning Objectives

- Discuss the origins of eukaryotes in terms of the geologic time line

Origins of Eukaryotes

Humans have been familiar with macroscopic organisms (organisms big enough to see with the unaided eye) since before there was a written history. It is likely that most cultures distinguished between animals and land plants, but most probably included the macroscopic fungi as plants. Therefore, it became an interesting challenge to deal with the world of microorganisms once microscopes were developed a few centuries ago. Many different naming schemes were used over the last couple of centuries, but it has become the most common practice to refer to eukaryotes that are not land plants, animals, or fungi as protists.

Most protists are microscopic, unicellular organisms that are abundant in soil, freshwater, brackish, and marine environments. They are also common in the digestive tracts of animals and in the vascular tissues of plants. Others invade the cells of other protists, animals, and plants. Not all protists are microscopic. Some have huge, macroscopic cells, such as the plasmodia (giant amoebae) of myxomycete slime molds or the marine green alga *Caulerpa*, which can have single cells that can be several meters in size. Some protists are multicellular, such as the red, green, and brown seaweeds. It is among the protists that one finds the wealth of ways that organisms can grow. They are among the first organisms to evolve with the rise of eukaryotes.

Eukaryotes in a Geological Time Frame

The oldest fossil evidence of eukaryotes, cells measuring 10 µm or greater, is about 2 billion years old. All fossils older than this appear to be prokaryotes. It is probable that today's eukaryotes are descended from an ancestor that had a prokaryotic cellular organization. The last common ancestor (LCA) of today's Eukarya had several characteristics that included: cells with nuclei that divided mitotically and contained linear chromosomes where the DNA was associated with histones; a cytoskeleton and endomembrane system; and the ability to make cilia/flagella during at least part of its life cycle. The LCA was aerobic because it had mitochondria that were the result of an aerobic alpha-proteobacterium that lived inside a host cell. Whether this host had a nucleus at the time of the initial symbiosis remains unknown. The LCA may have had a cell wall for at least part of its life cycle, but more data are needed to confirm this hypothesis. Today's eukaryotes are very diverse in their shapes, organization, life cycles, and number of cells per individual.

While today's atmosphere is about one-fifth molecular oxygen (O_2), geological evidence shows that it originally lacked O_2. Without oxygen, aerobic respiration would not be expected; living things would have relied on fermentation instead. At some point before about 3.5 billion years ago, some prokaryotes evolved the ability to photosynthesize. Cyanobacteria used water as a hydrogen source and released O_2 as a waste product. Originally, oxygen-rich environments were probably localized around places where cyanobacteria were active, but by about 2 billion years ago, geological evidence shows that oxygen was building up to higher concentrations in the atmosphere. Oxygen levels similar to today's levels only arose within the last 700 million years. Recall that the first fossils that we believe to be eukaryotes date to about 2 billion years old, so they appeared as oxygen levels were increasing.

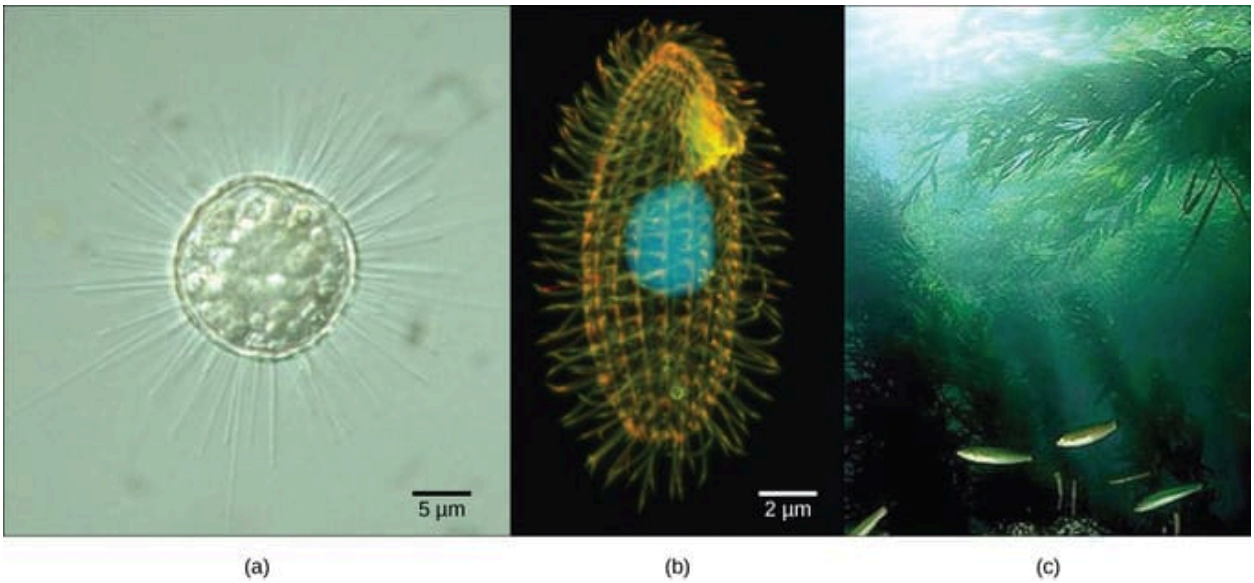


Figure 23.1A.1: Protist varieties: Protists range from the microscopic, single-celled (a) Acanthocystis turfacea and the (b) ciliate Tetrahymena thermophila, both visualized here using light microscopy, to the enormous, multicellular (c) kelps (Chromalveolata) that extend for hundreds of feet in underwater "forests. "

Key Points

- On a geological time line, protists are among the first organisms that evolved after prokaryotes.
- Today's eukaryotes evolved from a common ancestor with the following features: a nucleus that divided via mitosis, DNA associated with histones, a cytoskeleton and endomembrane system, the ability to make cilia/flagella.
- Protists vary widely in size, from single cells approximately 10 µm in size to multicellular seaweeds that are visible with the naked eye.

Key Terms

- **cyanobacteria**: photosynthetic prokaryotic microorganisms, of phylum Cyanobacteria, once known as blue-green algae
- **aerobic**: living or occurring only in the presence of oxygen
- **endomembrane**: all the membraneous components inside a eukaryotic cell, including the nuclear envelope, endoplastic reticulum, and Golgi apparatus

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23.1B: Characteristics of Eukaryotic DNA

Learning Objectives

- Compare and contrast prokaryotic DNA to eukaryotic DNA

Characteristics of Eukaryotic DNA compared to Prokaryotic DNA

Prokaryotic cells are known to be much less complex than eukaryotic cells since eukaryotic cells are considered to be present at a later point of evolution. It is probable that eukaryotic cells evolved from prokaryotic cells. Differences in complexity can be seen at the cellular level.

The single characteristic that is both necessary and sufficient to define an organism as a eukaryote is a nucleus surrounded by a nuclear envelope with nuclear pores. All extant eukaryotes have cells with nuclei; most of a eukaryotic cell's genetic material is contained within the nucleus. In contrast, prokaryotic DNA is not contained within a nucleus, but rather is attached to the plasma membrane and contained in the form of a nucleoid, an irregularly-shaped region that is not surrounded by a nuclear membrane.

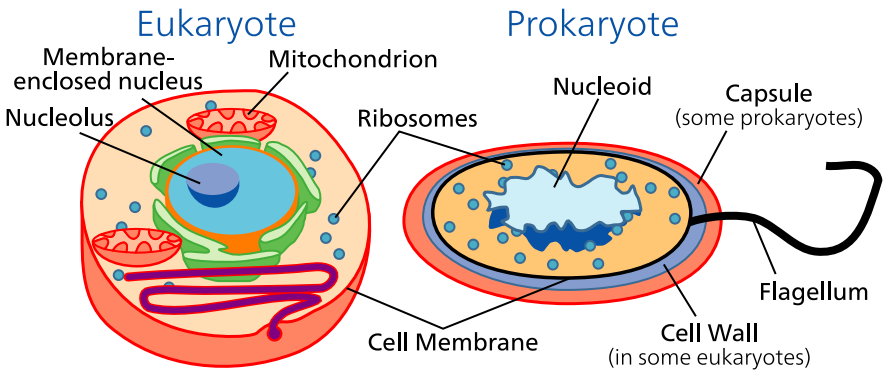


Figure $23.1B.1$: Cellular location of eukaryotic and prokaryotic DNA: Eukaryotic DNA is stored in a nucleus, whereas prokaryotic DNA is in the cytoplasm in the form of a nucleoid.

Eukaryotic DNA is packed into bundles of chromosomes, each consisting of a linear DNA molecule coiled around basic (alkaline) proteins called histones, which wind the DNA into a more compact form. Prokaryotic DNA is found in circular, non-chromosomal form. In addition, prokaryotes have plasmids, which are smaller pieces of circular DNA that can replicate separately from prokaryotic genomic DNA. Because of the linear nature of eukaryotic DNA, repeating non-coding DNA sequences called telomeres are present on either end of the chromosomes as protection from deterioration.

Mitosis, a process of nuclear division wherein replicated chromosomes are divided and separated using elements of the cytoskeleton, is universally present in eukaryotes. The cytoskeleton contains structural and motility components called actin microfilaments and microtubules. All extant eukaryotes have these cytoskeletal elements. Prokaryotes on the other hand undergo binary fission in a process where the DNA is replicated, then separates to two poles of the cell, and, finally, the cell fully divides.

A major DNA difference between eukaryotes and prokaryotes is the presence of mitochondrial DNA (mtDNA) in eukaryotes. Because eukaryotes have mitochondria and prokaryotes do not, eukaryotic cells contain mitochondrial DNA in addition to DNA contained in the nucleus and ribosomes. The mtDNA is composed of significantly fewer base pairs than nuclear DNA and encodes only a few dozen genes, depending on the organism.

Key Points

- Prokaryotic genomic DNA is attached to the plasma membrane in the form of a nucleoid, in contrast to eukaryotic DNA, which is located in a nucleus.
- Eukaryotic DNA is linear, compacted into chromosomes by histones, and has telomeres at each end to protect from

deterioration.
- Prokaryotes contain circular DNA in addition to smaller, transferable DNA plasmids.
- Eukaryotic cells contain mitochondrial DNA in addition to nuclear DNA.
- Eukaryotes separate replicated chromosomes by mitosis, using cytoskeletal proteins, whereas prokaryotes divide more simply via binary fission.

Key Terms

- **telomere**: either of the repetitive nucleotide sequences at each end of a eukaryotic chromosome, which protect the chromosome from degradation
- **plasmid**: a circle of double-stranded DNA that is separate from the chromosomes, which is found in bacteria and protozoa

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23.1C: Endosymbiosis and the Evolution of Eukaryotes

Learning Objectives

- Describe the general concept of endosymbiosis and the evolution of eukaryotes

Endosymbiosis and the Evolution of Eukaryotes

To fully understand eukaryotic organisms, it is necessary to understand that all extant eukaryotes are descendants of a chimeric organism that was a composite of a host cell and the cell(s) of an alpha-proteobacterium that "took up residence" inside the host. This major theme in the origin of eukaryotes is known as endosymbiosis, where one cell engulfs another such that the engulfed cell survives and both cells benefit. Over many generations, a symbiotic relationship can result in two organisms that depend on each other so completely that neither could survive on its own. Endosymbiotic events probably contributed to the origin of the last common ancestor (LCA) of today's eukaryotes.

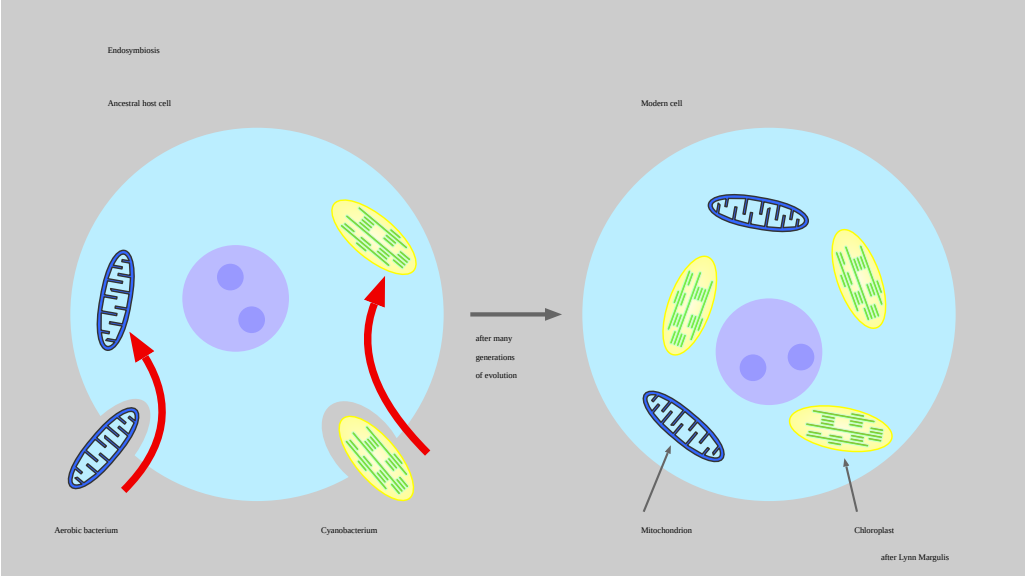


Figure $23.1C.1$: Endosymbiosis: Modern eukaryotic cells evolved from more primitive cells that engulfed bacteria with useful properties, such as energy production. Combined, the once-independent organisms flourished and evolved into a single organism.

Endosymbiotic Theory

The endosymbiotic theory was first articulated by the Russian botanist Konstantin Mereschkowski in 1905. Mereschkowski was familiar with work by botanist Andreas Schimper, who had observed in 1883 that the division of chloroplasts in green plants closely resembled that of free-living cyanobacteria. Schimper had tentatively proposed that green plants arose from a symbiotic union of two organisms. Ivan Wallin extended the idea of an endosymbiotic origin to mitochondria in the 1920s. These theories were initially dismissed or ignored. More detailed electron microscopic comparisons between cyanobacteria and chloroplasts combined with the discovery that plastids (organelles associated with photosynthesis) and mitochondria contain their own DNA led to a resurrection of the idea in the 1960s. The endosymbiotic theory was advanced and substantiated with microbiological evidence by Lynn Margulis in 1967.

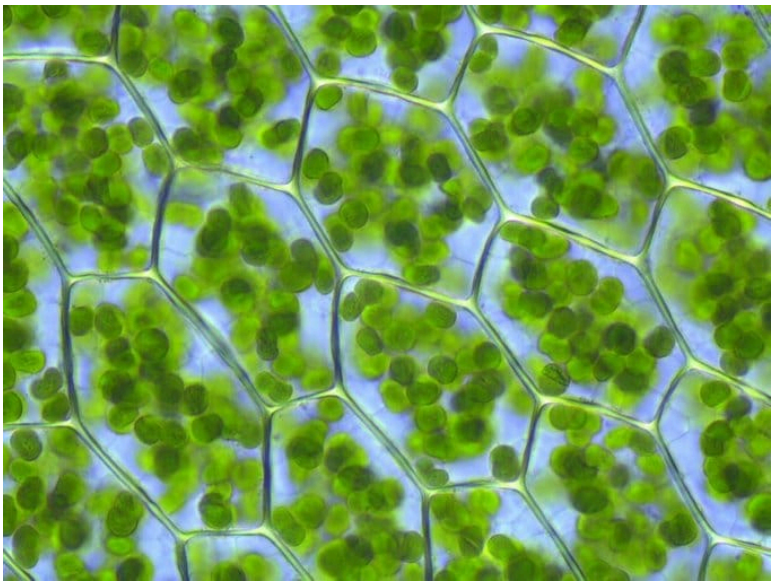


Figure $23.1C.1$: Chloroplasts in plants: A eukaryote with mitochondria engulfed a cyanobacterium in an event of serial primary endosymbiosis, creating a lineage of cells with both organelles. These cyanobacteria have become chloroplasts in modern plant cells. The cyanobacterial endosymbiont already had a double membrane.

In 1981 she argued that eukaryotic cells originated as communities of interacting entities, including endosymbiotic spirochetes that developed into eukaryotic flagella and cilia. This last idea has not received much acceptance because flagella lack DNA and do not show ultrastructural similarities to bacteria or archaea. According to Margulis and Dorion Sagan, “Life did not take over the globe by combat, but by networking” (*i.e.*, by cooperation). The possibility that the peroxisome organelles may have an endosymbiotic origin has also been considered, although they lack DNA. Christian de Duve proposed that they may have been the first endosymbionts, allowing cells to withstand growing amounts of free molecular oxygen in the earth’s atmosphere. However, it now appears that they may be formed *de novo*, contradicting the idea that they have a symbiotic origin.

It is believed that over millennia these endosymbionts transferred some of their own DNA to the host cell’s nucleus during the evolutionary transition from a symbiotic community to an instituted eukaryotic cell (called “serial endosymbiosis”). This hypothesis is thought to be possible because it is known today from scientific observation that transfer of DNA occurs between bacteria species, even if they are not closely related. Bacteria can take up DNA from their surroundings and have a limited ability to incorporate it into their own genome.

Key Points

- Endosymbiosis is the concept of one cell engulfing another and both cells benefiting from the relationship.
- Endosymbiosis was originally considered after the observation of the similarity between plant chloroplasts and free-living cyanobacteria.
- Peroxisomes may have been the first endosymbionts, caused by the increasing amount of atmospheric oxygen at that point in geological time.
- Over time, endosymbionts may have transferred some of their DNA to the host nucleus, thus becoming dependent on the host for survival and completing full integration into a single organism.

Key Terms

- **cyanobacteria**: photosynthetic prokaryotic microorganisms, of phylum Cyanobacteria, once known as blue-green algae
- **peroxisome**: a eukaryotic organelle that is the source of the enzymes that catalyze the production and breakdown of hydrogen peroxide and are responsible for the oxidation of long-chain fatty acids
- **endosymbiont**: an organism that lives within the body or cells of another organism

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23.1D: The Evolution of Mitochondria

Learning Objectives

- Explain the relationship between endosymbiosis and mitochondria to the evolution of eukaryotes

Relationship between Endosymbiosis and Mitochondria

One of the major features distinguishing prokaryotes from eukaryotes is the presence of mitochondria. Eukaryotic cells contain anywhere from one to several thousand mitochondria, depending on the cell's level of energy consumption. Each mitochondrion measures between 1 to 10 µm in length and exists in the cell as an organelle that can be ovoid to worm-shaped to intricately branched. Mitochondria arise from the division of existing mitochondria. They may fuse together. They move around inside the cell by interactions with the cytoskeleton. However, mitochondria cannot survive outside the cell. As the amount of oxygen increased in the atmosphere billions of years ago and as successful aerobic prokaryotes evolved, evidence suggests that an ancestral cell with some membrane compartmentalization engulfed a free-living aerobic prokaryote, specifically an alpha-proteobacterium, thereby giving the host cell the ability to use oxygen to release energy stored in nutrients. Alpha-proteobacteria are a large group of bacteria that includes species symbiotic with plants, disease organisms that can infect humans via ticks, and many free-living species that use light for energy. Several lines of evidence support the derivation of mitochondria from this endosymbiotic event. Most mitochondria are shaped like alpha-proteobacteria and are surrounded by two membranes, which would result when one membrane-bound organism engulfs another into a vacuole. The mitochondrial inner membrane involves substantial infoldings called cristae that resemble the textured, outer surface of alpha-proteobacteria. The matrix and inner membrane are rich with enzymes necessary for aerobic respiration.

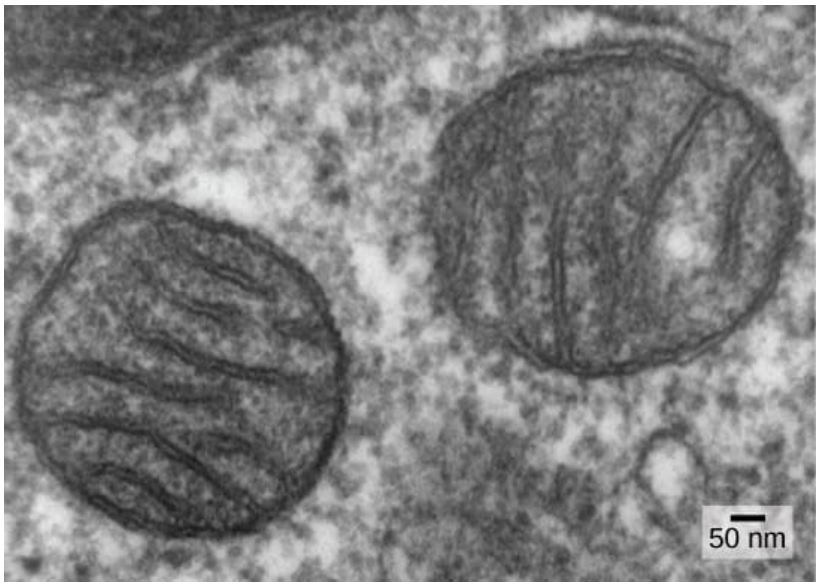


Figure $23.1D.1$: Micrograph of mammaliam mitochondria: In this transmission electron micrograph of mitochondria in a mammalian lung cell, the cristae, infoldings of the mitochondrial inner membrane, can be seen in cross-section.

Mitochondria divide independently by a process that resembles binary fission in prokaryotes. Specifically, mitochondria are not formed *de novo* by the eukaryotic cell; they reproduce within the cell and are distributed between two cells when cells divide. Therefore, although these organelles are highly integrated into the eukaryotic cell, they still reproduce as if they are independent organisms within the cell. However, their reproduction is synchronized with the activity and division of the cell. Mitochondria have their own circular DNA chromosome that is stabilized by attachments to the inner membrane and carries genes similar to genes expressed by alpha-proteobacteria. Mitochondria also have special ribosomes and transfer RNAs that resemble these components in prokaryotes. These features all support that mitochondria were once free-living prokaryotes.

Mitochondrial Genes

Mitochondria that carry out aerobic respiration have their own genomes, with genes similar to those in alpha-proteobacteria. However, many of the genes for respiratory proteins are located in the nucleus. When these genes are compared to those of other organisms, they appear to be of alpha-proteobacterial origin. Additionally, in some eukaryotic groups, such genes are found in the mitochondria, whereas in other groups, they are found in the nucleus. This has been interpreted as evidence that genes have been transferred from the endosymbiont chromosome to the host genome. This loss of genes by the endosymbiont is probably one explanation why mitochondria cannot live without a host.

Despite the transfer of genes between mitochondria and the nucleus, mitochondria retain much of their own independent genetic material. One possible explanation for mitochondria retaining control over some genes is that it may be difficult to transport hydrophobic proteins across the mitochondrial membrane as well as ensure that they are shipped to the correct location, which suggests that these proteins must be produced within the mitochondria. Another possible explanation is that there are differences in codon usage between the nucleus and mitochondria, making it difficult to be able to fully transfer the genes. A third possible explanation is that mitochondria need to produce their own genetic material so as to ensure metabolic control in eukaryotic cells, which indicates that mtDNA directly influences the respiratory chain and the reduction/oxidation processes of the mitochondria.

Key Points

- Eukaryotic cells contain varying amounts of mitochondria, depending on the cells' energy needs.
- Mitochondria have many features that suggest they were formerly independent organisms, including their own DNA, cell-independent division, and physical characteristics similar to alpha-proteobacteria.
- Some mitochondrial genes transferred to the nuclear genome over time, yet mitochondria retained some genetic material for reasons not completely understood.
- The hypothesized transfer of genes from mitochondria to the host cell's nucleus likely explains why mitochondria are not able to survive outside the host cell.

Key Terms

- **crista**: cristae (singular crista) are the internal compartments formed by the inner membrane of a mitochondrion
- **vacuole**: a large, membrane-bound, fluid-filled compartment in a cell's cytoplasm
- **endosymbiosis**: when one symbiotic species is taken inside the cytoplasm of another symbiotic species and both become endosymbiotic

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23.1E: The Evolution of Plastids

Learning Objectives

- Explain the relationship between endosymbiosis and plastids to the evolution of eukaryotes

Plastids

Some groups of eukaryotes are photosynthetic: their cells contain, in addition to the standard eukaryotic organelles, another kind of organelle called a plastid. There are three type of plastids: chloroplasts, chromoplasts, and leucoplasts. Chloroplasts are plastids that conduct photosynthesis. Chromoplasts are plastids that synthesize and store pigments. Leucoplasts are plastids located in the non-synthetic tissues of a plant (*e.g.*, roots) and generally store non-pigment molecules.

Like mitochondria, plastids appear to have a primary endosymbiotic origin, but differ in that they derive from cyanobacteria rather than alpha-proteobacteria. Cyanobacteria are a group of photosynthetic bacteria with all the conventional structures of prokaryotes. Unlike most prokaryotes, however, they have extensive, internal membrane-bound compartments called thylakoids, which contain chlorophyll and are the site of the light-dependent reactions of photosynthesis. In addition to thylakoids, chloroplasts found in eukaryotes have a circular DNA chromosome and ribosomes similar to those of cyanobacteria. Each chloroplast is surrounded by two membranes, suggestive of primary endosymbiosis. The outer membrane surrounding the plastid is thought have derived from the vacuole in the host, while the inner membrane is thought to have derived from the plasma membrane of the endosymbiont.

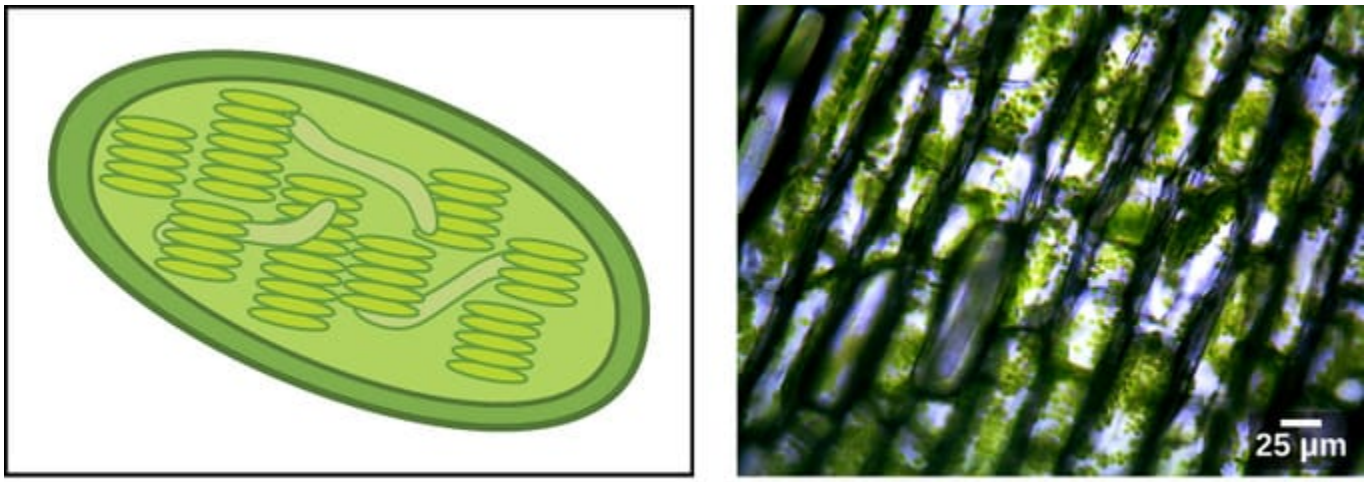


Figure $23.1E.1$: Chloroplast: (a) This chloroplast cross-section illustrates its elaborate inner membrane organization. Stacks of thylakoid membranes compartmentalize photosynthetic enzymes and provide scaffolding for chloroplast DNA. (b) The chloroplasts can be seen as small green spheres.

There is also, as with the case of mitochondria, strong evidence that many of the genes of the endosymbiont transferred to the nucleus. Plastids, like mitochondria, cannot live independently outside the host. In addition, like mitochondria, plastids derive from the binary fission of other plastids. Researchers have suggested that the endosymbiotic event that led to Archaeplastida (land plants, red and green algae) occurred 1 to 1.5 billion years ago, at least 500 million years after the fossil record suggests the presence of eukaryotes.

Secondary Endosymbiosis in Chlorarachniophytes

Endosymbiosis involves one cell engulfing another to produce, over time, a co-evolved relationship in which neither cell could

survive alone. The chloroplasts of red and green algae, for instance, are derived from the engulfment of a photosynthetic cyanobacterium by an early prokaryote. This leads to the question of the possibility of a cell containing an endosymbiont to become engulfed itself, resulting in a secondary endosymbiosis. Not all plastids in eukaryotes derive directly from primary endosymbiosis. Some of the major groups of algae became photosynthetic by secondary endosymbiosis; that is, by taking in either green algae or red algae as endosymbionts. Numerous microscopic and genetic studies support this conclusion; secondary plastids are surrounded by three or more membranes; some secondary plastids even have clear remnants of the nucleus of endosymbiotic algae.

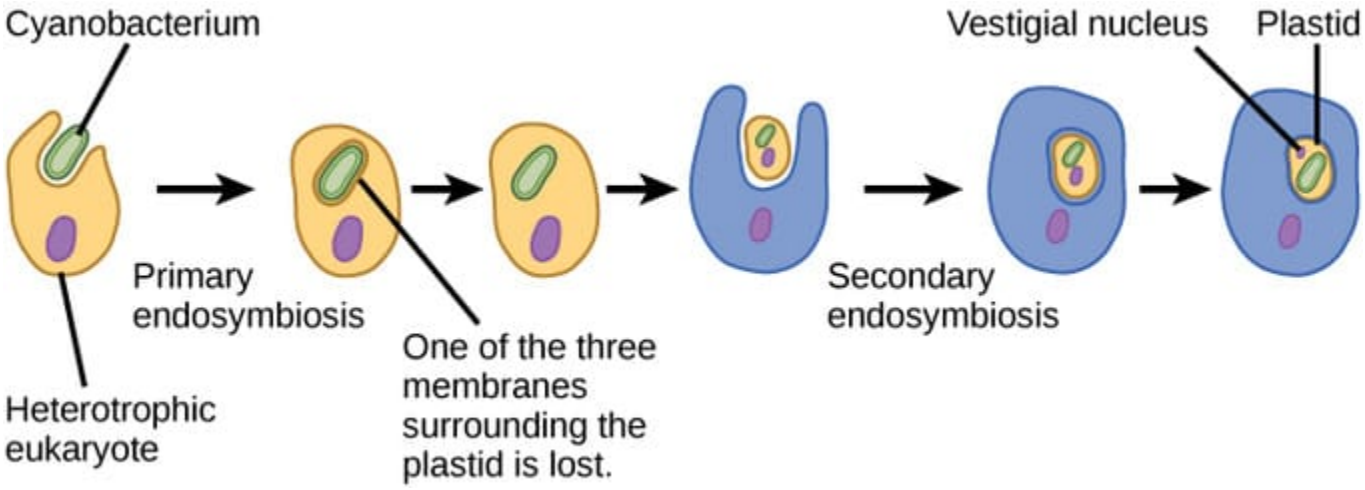


Figure $23.1E.1$: Primary and secondary endosymbiosis: The hypothesized process of endosymbiotic events leading to the evolution of chlorarachniophytes is shown. In a primary endosymbiotic event, a heterotrophic eukaryote consumed a cyanobacterium. In a secondary endosymbiotic event, the cell resulting from primary endosymbiosis was consumed by a second cell. The resulting organelle became a plastid in modern chlorarachniophytes.

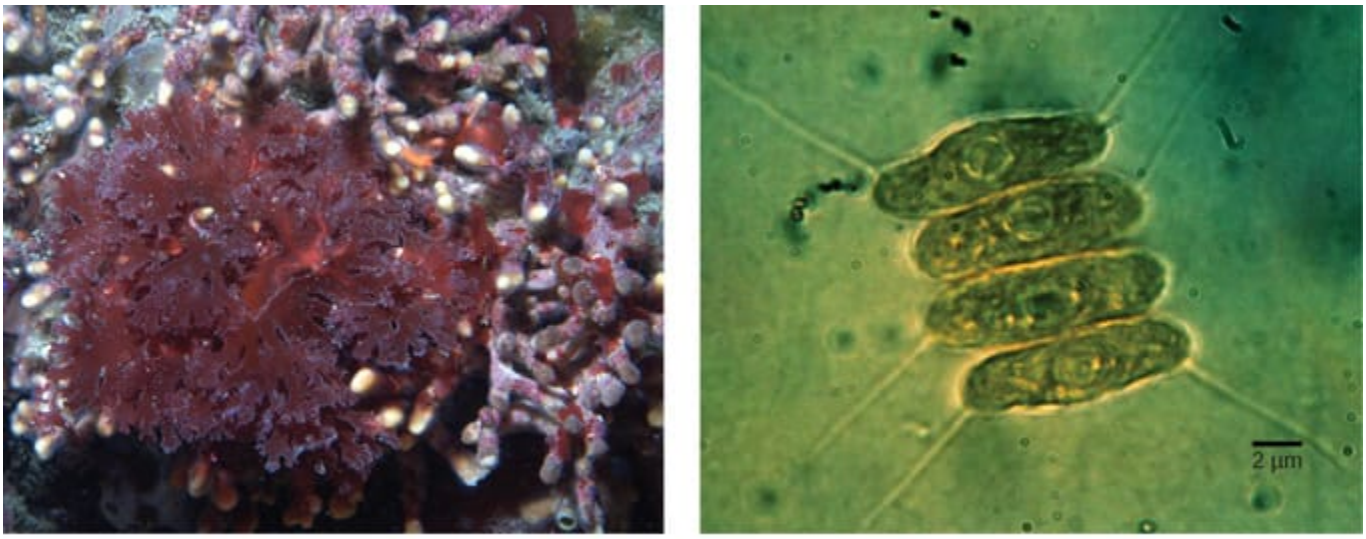


Figure $23.1E.1$: Red and green algae: (a) Red algae and (b) green algae (visualized by light microscopy) share similar DNA sequences with photosynthetic cyanobacteria. Scientists speculate that, in a process called endosymbiosis, an ancestral prokaryote engulfed a photosynthetic cyanobacterium that evolved into modern-day chloroplasts.

Molecular and morphological evidence suggest that the chlorarachniophyte protists are derived from a secondary endosymbiotic event. Chlorarachniophytes are rare algae indigenous to tropical seas and sand. These protists are thought to have originated when a eukaryote engulfed a green alga, the latter of which had already established an endosymbiotic relationship with a photosynthetic cyanobacterium. Several lines of evidence support that chlorarachniophytes evolved from secondary endosymbiosis. The chloroplasts contained within the green algal endosymbionts are capable of photosynthesis, making chlorarachniophytes photosynthetic. The green algal endosymbiont also exhibits a stunted vestigial nucleus. In fact, it appears that chlorarachniophytes are the products of a recent (on the scale of evolution) secondary endosymbiotic event. The plastids of chlorarachniophytes are surrounded by four membranes: the first two correspond to the inner and outer membranes of

the photosynthetic cyanobacterium, the third corresponds to the green alga, and the fourth corresponds to the vacuole that surrounded the green alga when it was engulfed by the chlorarachniophyte ancestor.

The process of secondary endosymbiosis is not unique to chlorarachniophytes. In fact, secondary endosymbiosis of green algae also led to euglenid protists, whereas secondary endosymbiosis of red algae led to the evolution of dinoflagellates, apicomplexans, and stramenopiles.

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Key Points

- Chloroplasts, chromoplasts, and leucoplasts are each a type of plastid.
- Plastids in eukaryotes derive from primary endosymbiosis with ancient cyanobacteria.
- Chlorarachniophytes are a type of algae that resulted from secondary endosymbiosis, when a eukaryote engulfed a green alga (which itself was a product of primary endosymbiosis with a cyanobacterium).
- Plastids share several features with mitochondria, including having their own DNA and the ability to replicate by binary fission.

Key Terms

- **chloroplast**: an organelle found in the cells of green plants and photosynthetic algae where photosynthesis takes place
- **thylakoid**: a folded membrane within plant chloroplasts from which grana are made, used in photosynthesis
- **plastid**: any of various organelles found in the cells of plants and algae, often concerned with photosynthesis

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23.2: CHARACTERISTICS OF PROTISTS

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- Topic hierarchy

23.2A: Cell Structure, Metabolism, and Motility

23.2B: Protist Life Cycles and Habitats

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23.2A: Cell Structure, Metabolism, and Motility

Learning Objectives

- Describe the metabolism and structure of protists, explaining the structures that provide their motility

Cell Structure

The cells of protists are among the most elaborate and diverse of all cells. Most protists are microscopic and unicellular, but some true multicellular forms exist. A few protists live as colonies that behave in some ways as a group of free-living cells and in other ways as a multicellular organism. Still other protists are composed of enormous, multinucleate, single cells that look like amorphous blobs of slime, or in other cases, similar to ferns. Many protist cells are multinucleated; in some species, the nuclei are different sizes and have distinct roles in protist cell function.

Single protist cells range in size from less than a micrometer to thousands of square meters (giant kelp). Animal-like cell membranes or plant-like cell walls envelope protist cells. In other protists, glassy silica-based shells or pellicles of interlocking protein strips encase the cells. The pellicle functions like a flexible coat of armor, preventing the protist from external damage without compromising its range of motion.

Metabolism

Protists exhibit many forms of nutrition and may be aerobic or anaerobic. Protists that store energy by photosynthesis belong to a group of photoautotrophs and are characterized by the presence of chloroplasts. Other protists are heterotrophic and consume organic materials (such as other organisms) to obtain nutrition. Amoebas and some other heterotrophic protist species ingest particles by a process called phagocytosis in which the cell membrane engulfs a food particle and brings it inward, pinching off an intracellular membranous sac, or vesicle, called a food vacuole. The vesicle containing the ingested particle, the phagosome, then fuses with a lysosome containing hydrolytic enzymes to produce a phagolysosome, which breaks down the food particle into small molecules that diffuse into the cytoplasm for use in cellular metabolism. Undigested remains ultimately exit the cell via exocytosis.

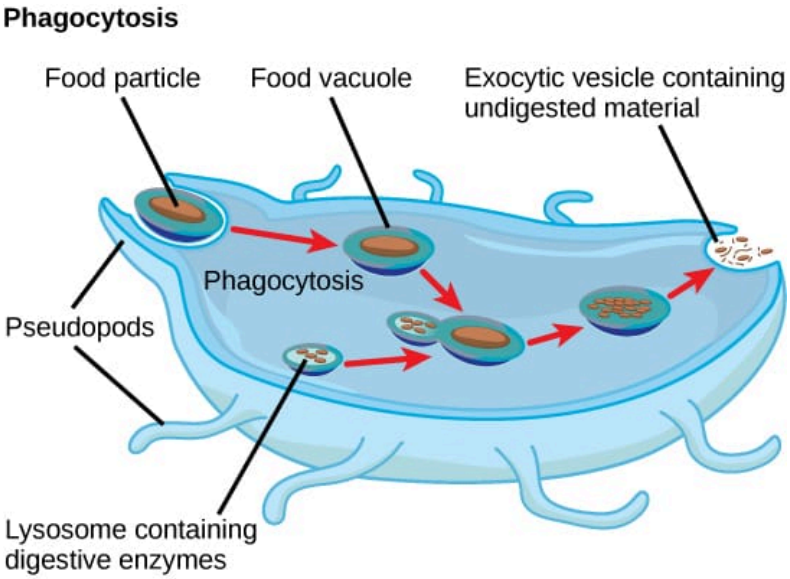


Figure 23.2A.1: Protist metabolism: The stages of phagocytosis include the engulfment of a food particle, the digestion of the particle using enzymes contained within a lysosome, and the expulsion of undigested materials from the cell.

Subtypes of heterotrophs, called saprobes, absorb nutrients from dead organisms or their organic wastes. Some protists function

as mixotrophs, obtaining nutrition by photoautotrophic or heterotrophic routes, depending on whether sunlight or organic nutrients are available.

Motility

The majority of protists are motile, but different types of protists have evolved varied modes of movement. Protists such as euglena have one or more flagella, which they rotate or whip to generate movement. Paramecia are covered in rows of tiny cilia that they beat to swim through liquids. Other protists, such at amoebae, form cytoplasmic extensions called pseudopodia anywhere on the cell, anchor the pseudopodia to a surface, and pull themselves forward. Some protists can move toward or away from a stimulus; a movement referred to as taxis. Protists accomplish phototaxis, movement toward light, by coupling their locomotion strategy with a light-sensing organ.

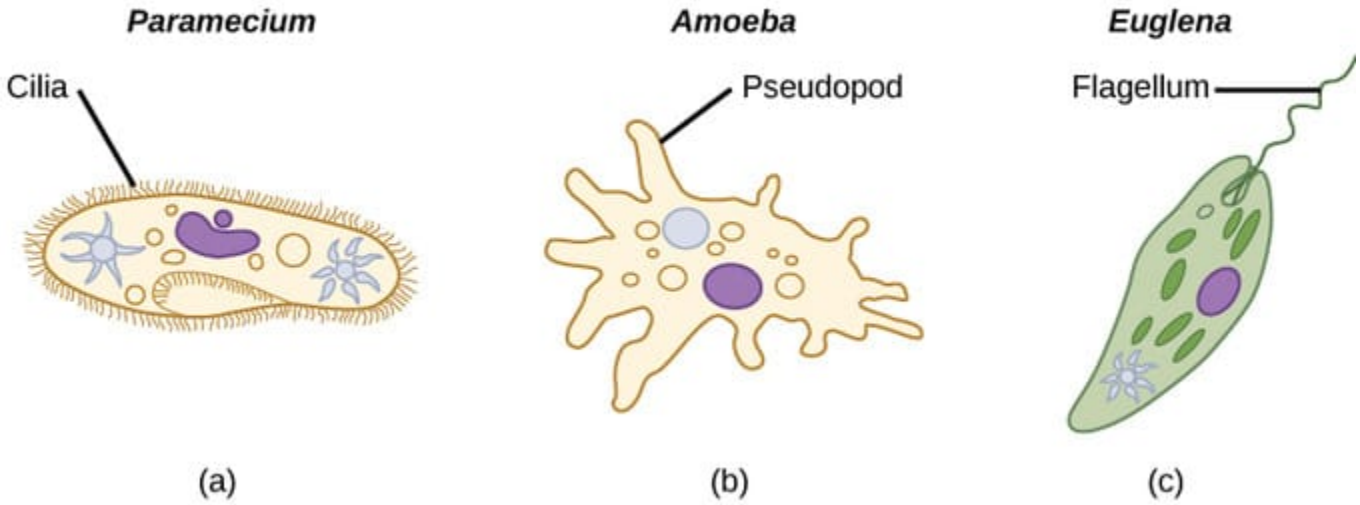


Figure 23.2A.1: Different types of motility in protists: Protists use various methods for transportation. (a) A paramecium waves hair-like appendages called cilia. (b) An amoeba uses lobe-like pseudopodia to anchor itself to a solid surface and pull itself forward. (c) Euglena uses a whip-like tail called a flagellum.

Key Points

- Protist cells may contain a single nucleus or many nuclei; they range in size from microscopic to thousands of meters in area.
- Protists may have animal-like cell membranes, plant-like cell walls, or may be covered by a pellicle.
- Some protists are heterotrophs and ingest food by phagocytosis, while other types of protists are photoautotrophs and store energy via photosynthesis.
- Most protists are motile and generate movement with cilia, flagella, or pseudopodia.

Key Terms

- **amorphous**: lacking a definite form or clear shape
- **multinucleate**: having more than one nucleus
- **pellicle**: cuticle, the hard protective outer layer of certain life forms
- **taxis**: the movement of an organism in response to a stimulus; similar to kinesis, but more direct
- **phagocytosis**: the process where a cell incorporates a particle by extending pseudopodia and drawing the particle into a vacuole of its cytoplasm
- **phagosome**: a membrane-bound vacuole within a cell containing foreign material captured by phagocytosis

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23.2B: Protist Life Cycles and Habitats

Learning Objectives

- Describe the habitats and life cycles of various protists

Life Cycle of Slime Molds

Protist life cycles range from simple to extremely elaborate. Certain parasitic protists have complicated life cycles and must infect different host species at different developmental stages to complete their life cycle. Some protists are unicellular in the haploid form and multicellular in the diploid form, which is a strategy also employed by animals. Other protists have multicellular stages in both haploid and diploid forms, a strategy called alternation of generations that is also used by plants.

Plasmodial slime molds

The slime molds are categorized on the basis of their life cycles into plasmodial or cellular types. Plasmodial slime molds are composed of large, multinucleate cells and move along surfaces like an amorphous blob of slime during their feeding stage. The slime mold glides along, lifting and engulfing food particles, especially bacteria. Upon maturation, the plasmodium takes on a net-like appearance with the ability to form fruiting bodies, or sporangia, during times of stress. Meiosis produces haploid spores within the sporangia. Spores disseminate through the air or water to potentially land in more favorable environments. If this occurs, the spores germinate to form amoeboid or flagellate haploid cells that can combine with each other and produce a diploid zygotic slime mold to complete the life cycle.

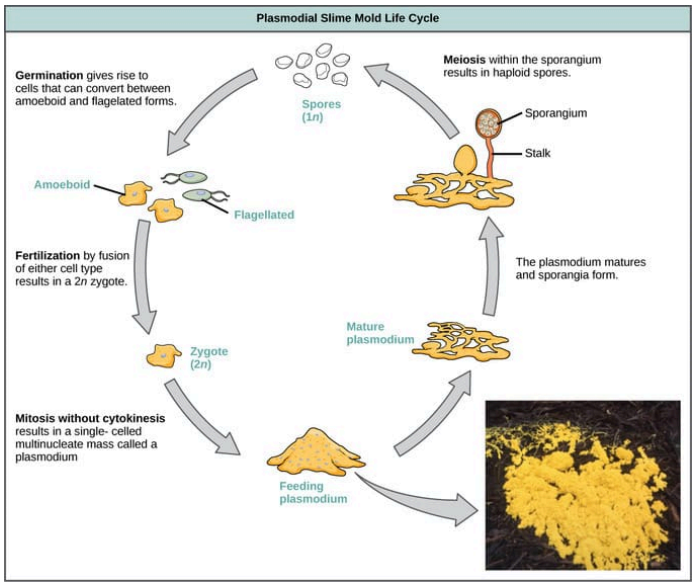


Figure $23.2B.1$: Plasmodial slime mold life cycle: Haploid spores develop into amoeboid or flagellated forms, which are then fertilized to form a diploid, multinucleate mass called a plasmodium. This plasmodium is net-like and, upon maturation, forms a sporangium on top of a stalk. The sporangium forms haploid spores through meiosis, after which the spores disseminate, germinate, and begin the life cycle anew. The brightly-colored plasmodium in the inset photo is a single-celled, multinucleate mass.

Cellular slime molds

The cellular slime molds function as independent amoeboid cells when nutrients are abundant. When food is depleted, cellular slime molds aggregate into a mass of cells that behaves as a single unit called a slug. Some cells in the slug contribute to a 2–3-millimeter stalk, which dries up and dies in the process. Cells atop the stalk form an asexual fruiting body that

contains haploid spores. As with plasmodial slime molds, the spores are disseminated and can germinate if they land in a moist environment. One representative genus of the cellular slime molds is *Dictyostelium*, which commonly exists in the damp soil of forests.

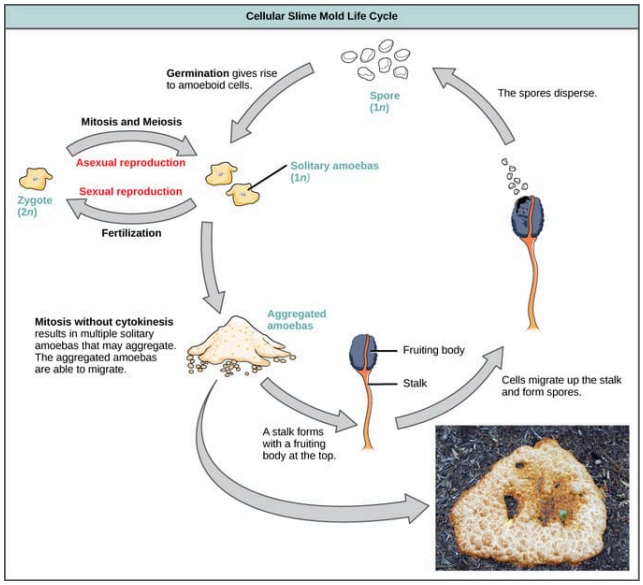


Figure $23.2B.1$: Cellular slime mold life cycle: Cellular slime molds may engage in two forms of life cycles: as solitary amoebas when nutrients are abundant or as aggregated amoebas (inset photo) when nutrients are scarce. In aggregate form, some individuals contribute to the formation of a stalk, on top of which sits a fruiting body full of spores that disseminate and germinate in the proper moist environment.

Habitats of Various Protists

There are over 100,000 described living species of protists. Nearly all protists exist in some type of aquatic environment, including freshwater and marine environments, damp soil, and even snow. Paramecia are a common example of aquatic protists. Due to their abundance and ease of use as research organisms, they are often subjects of study in classrooms and laboratories. In addition to aquatic protists, several protist species are parasites that infect animals or plants and, therefore, live in their hosts. Amoebas can be human parasites and can cause dysentery while inhabiting the small intestine. Other protist species live on dead organisms or their wastes and contribute to their decay. Approximately 1000 species of slime mold thrive on bacteria and fungi within rotting trees and other plants in forests around the world, contributing to the life cycle of these ecosystems.

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Key Points

- Slime molds are categorized on the basis of their life cycles into plasmodial or cellular types, both of which end their life cycle in the form of dispersed spores.
- Plasmodial slime molds form a single-celled, multinucleate mass, whereas cellular slime molds form an aggregated mass of separate amoebas that are able to migrate as a unified whole.
- Slimes molds feed primarily on bacteria and fungi and contribute to the decomposition of dead plants.

Key Terms

- **haploid**: of a cell having a single set of unpaired chromosomes
- **sporangia**: an enclosure in which spores are formed (also called a fruiting body)
- **plasmodium**: a mass of cytoplasm, containing many nuclei, created by the aggregation of amoeboid cells of slime molds during their vegetative phase
- **diploid**: of a cell, having a pair of each type of chromosome, one of the pair being derived from the ovum and the other from the spermatozoon

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23.3: GROUPS OF PROTISTS

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23.3A: Excavata

23.3B: Chromalveolata- Alveolates

23.3C: Chromalveolata- Stramenopiles

23.3D: Rhizaria

23.3E: Archaeplastida

23.3F: Amoebozoa and Opisthokonta

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23.3A: Excavata

Learning Objectives

- Describe characteristics of Excavates, including Diplomonads, Parabasalids and Euglenozoans

Excavata

Many of the protist species classified into the supergroup Excavata are asymmetrical, single-celled organisms with a feeding groove “excavated” from one side. This supergroup includes heterotrophic predators, photosynthetic species, and parasites. Its subgroups are the diplomonads, parabasalids, and euglenozoans.

Diplomonads

Among the Excavata are the diplomonads, which include the intestinal parasite, *Giardia lamblia*. Until recently, these protists were believed to lack mitochondria. Mitochondrial remnant organelles, called mitosomes, have since been identified in diplomonads, but these mitosomes are essentially nonfunctional. Diplomonads exist in anaerobic environments and use alternative pathways, such as glycolysis, to generate energy. Each diplomonad cell has two identical nuclei and uses several flagella for locomotion.



Giardia lamblia

The mammalian intestinal parasite *Giardia lamblia,*visualized here using scanning electron microscopy, is a waterborne protist that causes severe diarrhea when ingested.

Parabasalids

A second Excavata subgroup, the parabasalids, also exhibits semi-functional mitochondria. In parabasalids, these structures function anaerobically and are called hydrogenosomes because they produce hydrogen gas as a byproduct. Parabasalids move with flagella and membrane rippling. *Trichomonas vaginalis*, a parabasalid that causes a sexually-transmitted disease in humans, employs these mechanisms to transit through the male and female urogenital tracts. *T. vaginalis* causes trichomoniasis, which appears in an estimated 180 million cases worldwide each year. Whereas men rarely exhibit symptoms during an infection with

this protist, infected women may become more susceptible to secondary infection with human immunodeficiency virus (HIV) or genital wart virus infection, which causes over 90% of cervical cancer. Pregnant women infected with *T. vaginalis* are at an increased risk of serious complications, such as pre-term delivery.

Euglenozoans

Euglenozoans includes parasites, heterotrophs, autotrophs, and mixotrophs, ranging in size from 10 to 500 µm. Euglenoids move through their aquatic habitats using two long flagella that guide them toward light sources sensed by a primitive ocular organ called an eyespot. The familiar genus, *Euglena*, encompasses some mixotrophic species that display a photosynthetic capability only when light is present. In the dark, the chloroplasts of *Euglena* shrink up and temporarily cease functioning; the cells, instead, take up organic nutrients from their environment.

The human parasite, *Trypanosoma brucei*, belongs to a different subgroup of Euglenozoa, the kinetoplastids. The kinetoplastid subgroup is named after the kinetoplast, a DNA mass carried within the single, oversized mitochondrion possessed by each of these cells. This subgroup includes several parasites, collectively called trypanosomes, which cause devastating human diseases by infecting an insect species during a portion of their life cycle. *T. brucei* develops in the gut of the tsetse fly after the fly bites an infected human or other mammalian host. The parasite then travels to the insect salivary glands to be transmitted to another human or other mammal when the infected tsetse fly consumes another blood meal. *T. brucei* is common in central Africa and is the causative agent of African sleeping sickness, a disease associated with severe chronic fatigue and coma; it can be fatal if left untreated.

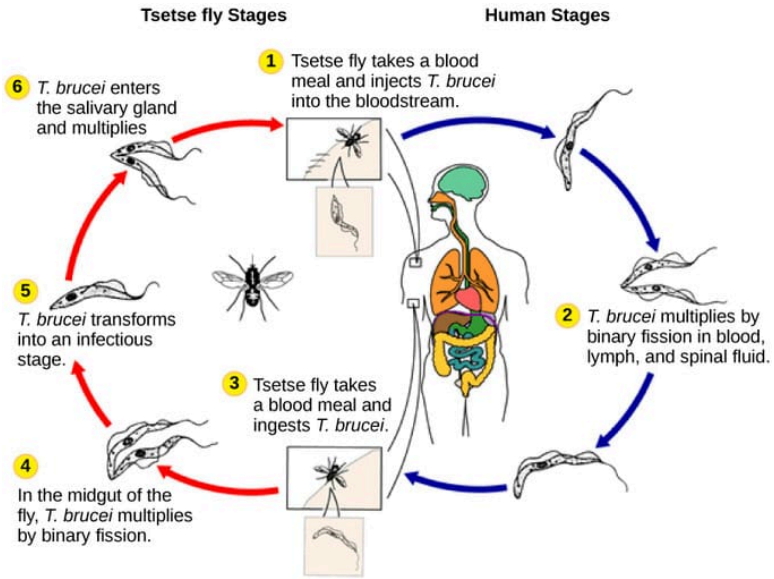


Figure 23.3A.1: Life cycle of *Trypanosoma brucei*: *Trypanosoma brucei,* the causative agent of sleeping sickness, spends part of its life cycle in the tsetse fly and part in humans.

Key Points

- Excavata are a supergroup of protists that are defined by an asymmetrical appearance with a feeding groove that is “excavated” from one side; it includes various types of organisms which are parasitic, photosynthetic and heterotrophic predators.
- Excavata includes the protists: Diplomonads, Parabasalids and Euglenozoans.
- Diplomonads are defined by the presence of a nonfunctional, mitochrondrial-remnant organelle called a mitosome.
- Parabasalids are characterized by a semi-functional mitochondria referred to as a hydrogenosome; they are comprised of parasitic protists, such as *Trichomonas vaginalis*.
- Euglenozoans can be classified as mixotrophs, heterotrophs, autotrophs, and parasites; they are defined by their use of flagella for movement.

Key Terms

- **mitosome**: an organelle found within certain unicellular eukaryotes which lack mitochondria
- **hydrogenosome**: a membrane-bound organelle found in ciliates, trichomonads, and fungi which produces molecular hydrogen and ATP
- **kinetoplast**: a disk-shaped mass of circular DNA inside a large mitochondrion, found specifically in protozoa of the class Kinetoplastea

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23.3B: Chromalveolata- Alveolates

Learning Objectives

- Evaluate traits associated with protists classified as alveolates which include dinoflagellates, apicomplexans, and ciliates

Chromalveolata

Current evidence suggests that species classified as chromalveolates are derived from a common ancestor that engulfed a photosynthetic red algal cell, which itself had already evolved chloroplasts from an endosymbiotic relationship with a photosynthetic prokaryote. Therefore, the ancestor of chromalveolates is believed to have resulted from a secondary endosymbiotic event. However, some chromalveolates appear to have lost red alga-derived plastid organelles or lack plastid genes altogether. Therefore, this supergroup should be considered a hypothesis-based working group that is subject to change and can be subdivided into alveolates and stramenopiles.

Alveolates

A large body of data supports that the alveolates are derived from a shared common ancestor. The alveolates are named for the presence of an alveolus, or membrane-enclosed sac, beneath the cell membrane. The exact function of the alveolus is unknown, but it may be involved in osmoregulation. The alveolates are further categorized into the dinoflagellates, the apicomplexans, and the ciliates.

Dinoflagellates

Dinoflagellates exhibit extensive morphological diversity and can be photosynthetic, heterotrophic, or mixotrophic. Many dinoflagellates are encased in interlocking plates of cellulose with two perpendicular flagella that fit into the grooves between the cellulose plates. One flagellum extends longitudinally and a second encircles the dinoflagellate. Together, the flagella contribute to the characteristic spinning motion of dinoflagellates. These protists exist in freshwater and marine habitats; they are a component of plankton.

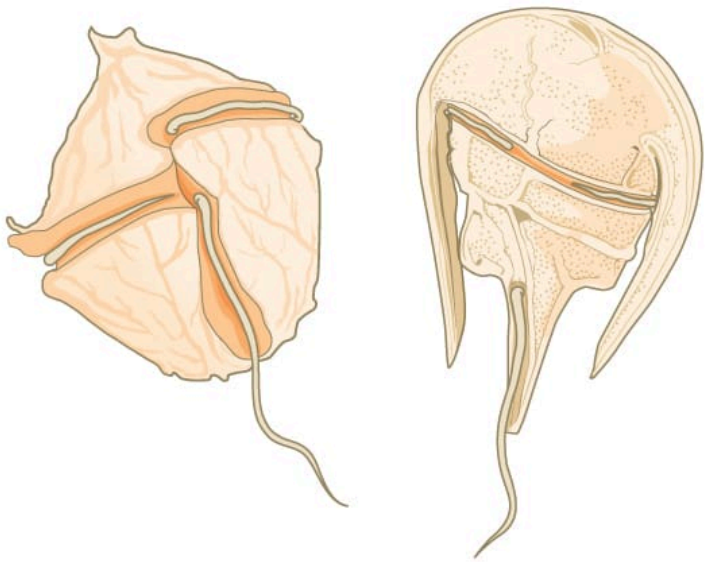


Figure $23.3B.1$: Dinoflagellates: The dinoflagellates exhibit great diversity in shape. Many are encased in cellulose armor and have two flagella that fit in grooves between the plates. Movement of these two perpendicular flagella causes a spinning motion.

Some dinoflagellates generate light, called bioluminescence, when they are jarred or stressed. Large numbers of marine dinoflagellates (billions or trillions of cells per wave) can emit light and cause an entire breaking wave to twinkle or take on a brilliant blue color. For approximately 20 species of marine dinoflagellates, population explosions (called blooms) during the summer months can tint the ocean with a muddy red color. This phenomenon is called a red tide and results from the abundant red pigments present in dinoflagellate plastids. In large quantities, these dinoflagellate species secrete an asphyxiating toxin that can kill fish, birds, and marine mammals. Red tides can be massively detrimental to commercial fisheries; humans who consume these protists may become poisoned.



Figure $23.3B.1$: Bioluminescence: Bioluminescence is emitted from dinoflagellates in a breaking wave, as seen from the New Jersey coast.

Apicomplexans

The apicomplexan protists are so named because their microtubules, fibrin, and vacuoles are asymmetrically distributed at one end of the cell in a structure called an apical complex. The apical complex is specialized for entry and infection of host cells. Indeed, all apicomplexans are parasitic. This group includes the genus *Plasmodium*, which causes malaria in humans. Apicomplexan life cycles are complex, involving multiple hosts and stages of sexual and asexual reproduction.

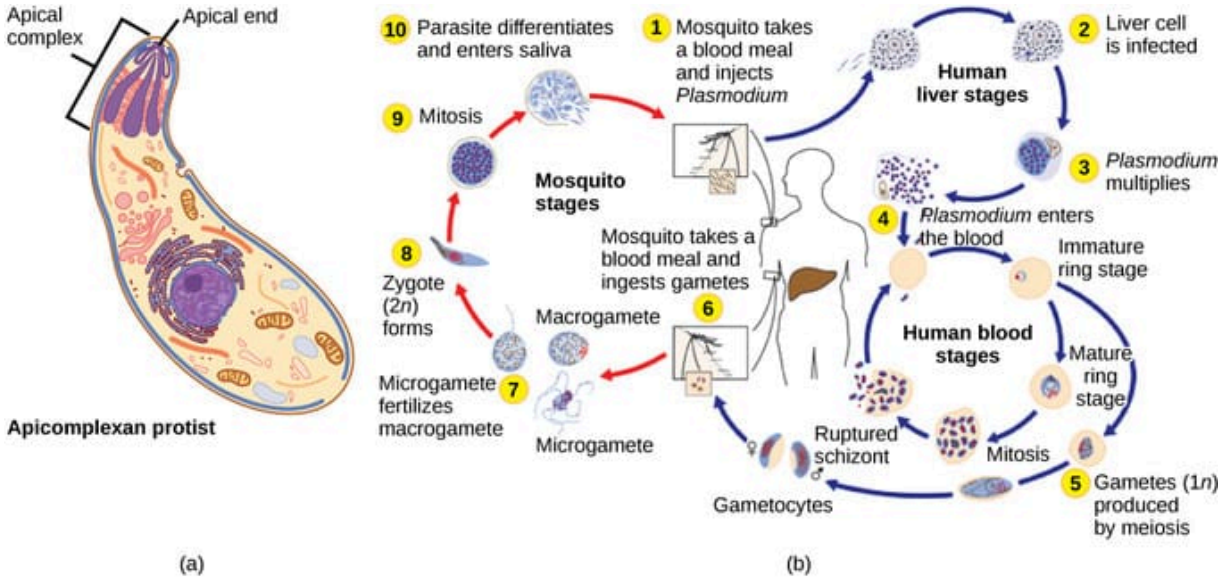


Figure $23.3B.1$: Parasitic apicomplexans: (a) Apicomplexans are parasitic protists. They have a characteristic apical complex that enables them to infect host cells. (b) Plasmodium, the causative agent of malaria, has a complex life cycle typical of apicomplexans.

Ciliates

The ciliates, which include *Paramecium* and *Tetrahymena*, are a group of protists 10 to 3,000 micrometers in length that are covered in rows, tufts, or spirals of tiny cilia. By beating their cilia synchronously or in waves, ciliates can coordinate directed movements and ingest food particles. Certain ciliates have fused cilia-based structures that function like paddles, funnels, or fins. Ciliates also are surrounded by a pellicle, providing protection without compromising agility. The genus *Paramecium* includes protists that have organized their cilia into a plate-like primitive mouth called an oral groove, which is used to capture and digest bacteria. Food captured in the oral groove enters a food vacuole where it combines with digestive enzymes. Waste particles are expelled by an exocytic vesicle that fuses at a specific region on the cell membrane: the anal pore. In addition to a vacuole-based digestive system, *Paramecium* also uses contractile vacuoles: osmoregulatory vesicles that fill with water as it enters the cell by osmosis and then contract to squeeze water from the cell.

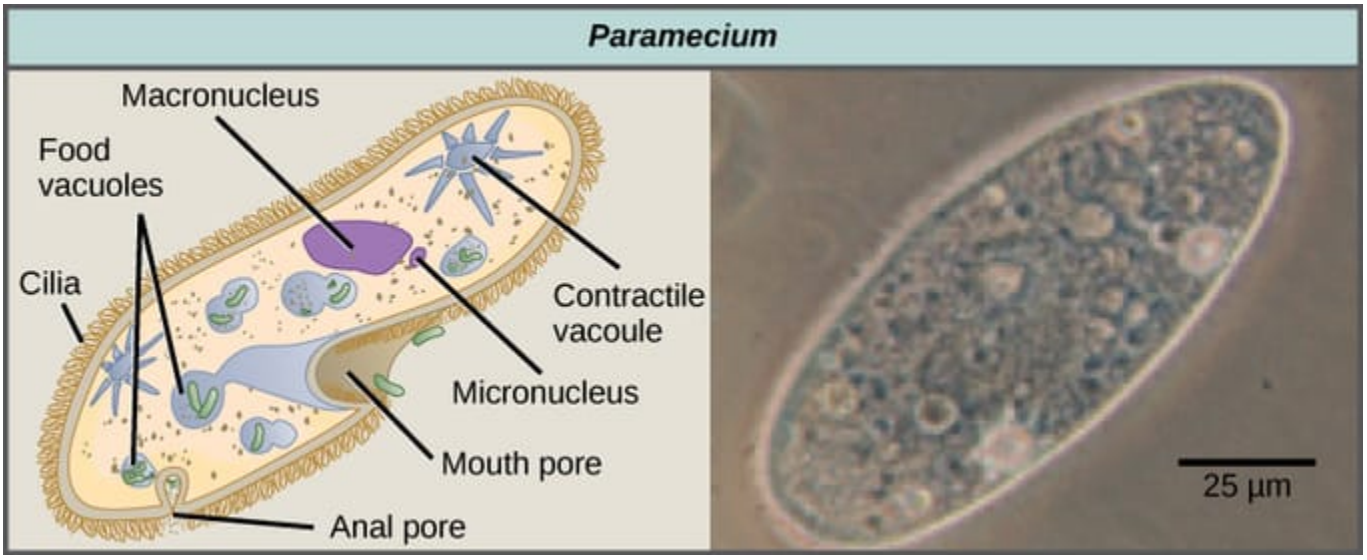


Figure $23.3B.1$: Paramecium: Paramecium has a primitive mouth (called an oral groove) to ingest food and an anal pore to excrete it. Contractile vacuoles allow the organism to excrete excess water. Cilia enable the organism to move.

Paramecium has two nuclei, a macronucleus and a micronucleus, in each cell. The micronucleus is essential for sexual reproduction, whereas the macronucleus directs asexual binary fission and all other biological functions. The process of sexual reproduction in *Paramecium* underscores the importance of the micronucleus to these protists. *Paramecium* and most other ciliates reproduce sexually by conjugation. This process begins when two different mating types of *Paramecium* make physical contact and join with a cytoplasmic bridge. The diploid micronucleus in each cell then undergoes meiosis to produce four haploid micronuclei. Three of these degenerate in each cell, leaving one micronucleus that then undergoes mitosis, generating two haploid micronuclei. The cells each exchange one of these haploid nuclei and move away from each other. A similar process occurs in bacteria that have plasmids. Fusion of the haploid micronuclei generates a completely novel diploid pre-micronucleus in each conjugative cell. This pre-micronucleus undergoes three rounds of mitosis to produce eight copies, while the original macronucleus disintegrates. Four of the eight pre-micronuclei become full-fledged micronuclei, whereas the other four perform multiple rounds of DNA replication and then become new macronuclei. Two cell divisions then yield four new paramecia from each original conjugative cell.

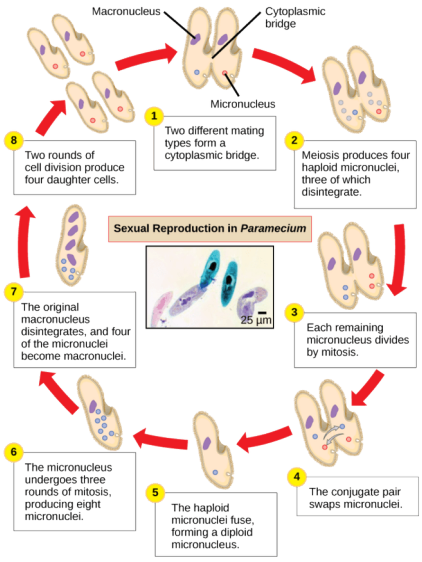


Figure $23.3B.1$: Paramecium: sexual reproduction: The complex process of sexual reproduction in *Paramecium*creates eight daughter cells from two original cells. Each cell has a macronucleus and a micronucleus. During sexual reproduction, the macronucleus dissolves and is replaced by a micronucleus.

Key Points

- Alveolates are classified under the group Chromalveolata which developed as a result of a secondary endosymbiotic event.
- Dinoflagellates are defined by their flagella structure which lays perpendicular and fits into the cellulose plates of the dinoflagellate, promoting a spinning motion.
- Apicomplexans are defined by the asymmetrical distribution of their microtubules, fibrin, and vacuoles; they include the parasitic protist *Plasmodium* which causes malaria.
- Ciliates are defined by the presence of cilia (such as the oral groove in the *Paramecium)*, which beat synchronously to aid the organism in locomotion and obtaining nutrients.
- Ciliates are defined by the presence of cilia, which beat synchronously, to aid the organism in locomotion and obtaining nutrients, such as the oral groove in the *Paramecium*.

Key Terms

- **osmoregulation**: the homeostatic regulation of osmotic pressure in the body in order to maintain a constant water content
- **plastid**: any of various organelles found in the cells of plants and algae, often concerned with photosynthesis
- **conjugation**: the temporary fusion of organisms, especially as part of sexual reproduction

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23.3C: Chromalveolata- Stramenopiles

Learning Objectives

- Describe characteristics of the following Stramenophiles: diatoms, brown algae, golden algae, and oomycetes

Chromalveolates

Current evidence suggests that chromalveolates have an ancestor which resulted from a secondary endosymbiotic event. The species which fall under the classification of chromalveolates have evolved from a common ancestor that engulfed a photosynthetic red algal cell. This red algal cell had previously evolved chloroplasts from an endosymbiotic relationship with a photosynthetic prokaryote. Chromalveolates include very important photosynthetic organisms, such as diatoms, brown algae, and significant disease agents in animals and plants. The chromalveolates can be subdivided into alveolates and stramenopiles.

Stramenopiles

A subgroup of chromalveolates, the stramenopiles, also referred to as heterokonts, includes photosynthetic marine algae and heterotrophic protists. The unifying feature of this group is the presence of a textured, or "hairy," flagellum. Many stramenopiles also have an additional flagellum that lacks hair-like projections. Members of this subgroup range in size from single-celled diatoms to the massive and multicellular kelp.

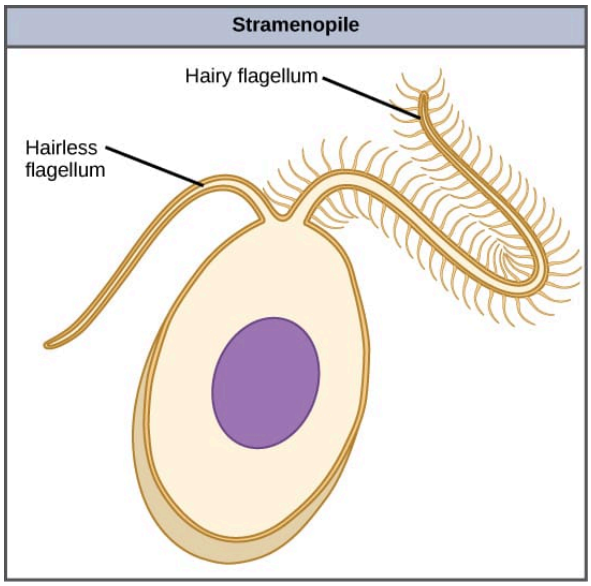


Figure $23.3C.1$: Stramenophile structure: This stramenopile cell has a single hairy flagellum and a secondary smooth flagellum.

Diatoms

The diatoms are unicellular photosynthetic protists that encase themselves in intricately patterned, glassy cell walls composed of silicon dioxide in a matrix of organic particles. These protists are a component of freshwater and marine plankton. Most species of diatoms reproduce asexually, although some instances of sexual reproduction and sporulation also exist. Some diatoms exhibit a slit in their silica shell called a raphe. By expelling a stream of mucopolysaccharides from the raphe, the diatom can attach to surfaces or propel itself in one direction.

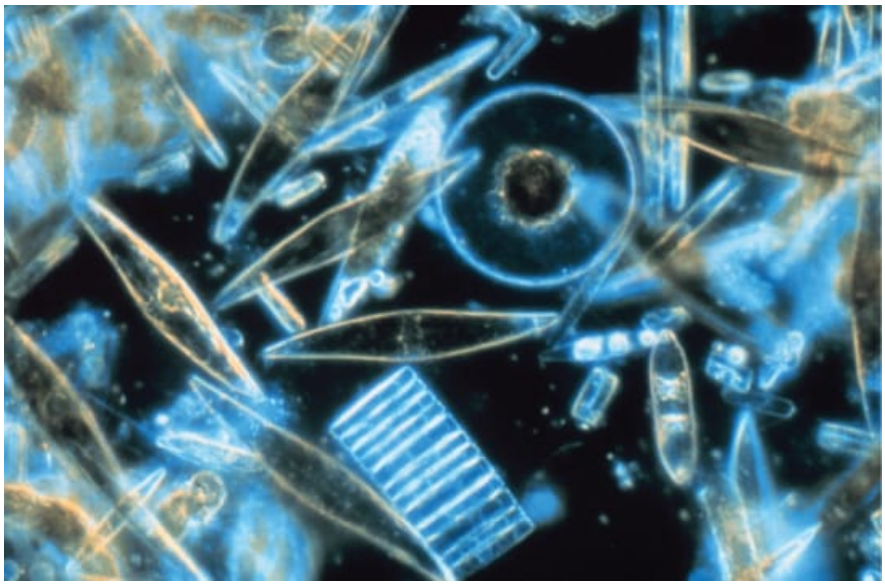


Figure 23.3C.1: Diatoms: Assorted diatoms, visualized here using light microscopy, live among annual sea ice in McMurdo Sound, Antarctica. Diatoms range in size from 2 to 200 µm.

During periods of nutrient availability, diatom populations bloom to numbers greater than can be consumed by aquatic organisms. The excess diatoms die and sink to the sea floor where they are not easily reached by saprobes that feed on dead organisms. As a result, the carbon dioxide that the diatoms had consumed and incorporated into their cells during photosynthesis is not returned to the atmosphere. In general, this process by which carbon is transported deep into the ocean is described as the biological carbon pump because carbon is "pumped" to the ocean depths where it is inaccessible to the atmosphere as carbon dioxide. The biological carbon pump is a crucial component of the carbon cycle that helps to maintain lower atmospheric carbon dioxide levels.

Golden Algae

Like diatoms, golden algae are largely unicellular, although some species can form large colonies. Their characteristic gold color results from their extensive use of carotenoids, a group of photosynthetic pigments that are generally yellow or orange in color. Golden algae are found in both freshwater and marine environments, where they form a major part of the plankton community.

Brown Algae

The brown algae are primarily marine, multicellular organisms that are known colloquially as seaweeds. Giant kelps are a type of brown algae. Some brown algae have evolved specialized tissues that resemble terrestrial plants, with root-like holdfasts, stem-like stipes, and leaf-like blades that are capable of photosynthesis. The stipes of giant kelps are enormous, extending in some cases for 60 meters. A variety of algal life cycles exists, but the most complex is alternation of generations in which both haploid and diploid stages involve multicellularity. For instance, compare this life cycle to that of humans. In humans, haploid gametes produced by meiosis (sperm and egg) combine in fertilization to generate a diploid zygote that undergoes many rounds of mitosis to produce a multicellular embryo and then a fetus. However, the individual sperm and egg themselves never become multicellular beings. In the brown algae genus *Laminaria*, haploid spores develop into multicellular gametophytes, which produce haploid gametes that combine to produce diploid organisms that then become multicellular organisms with a different structure from the haploid form. Terrestrial plants also have evolved alternation of generations.

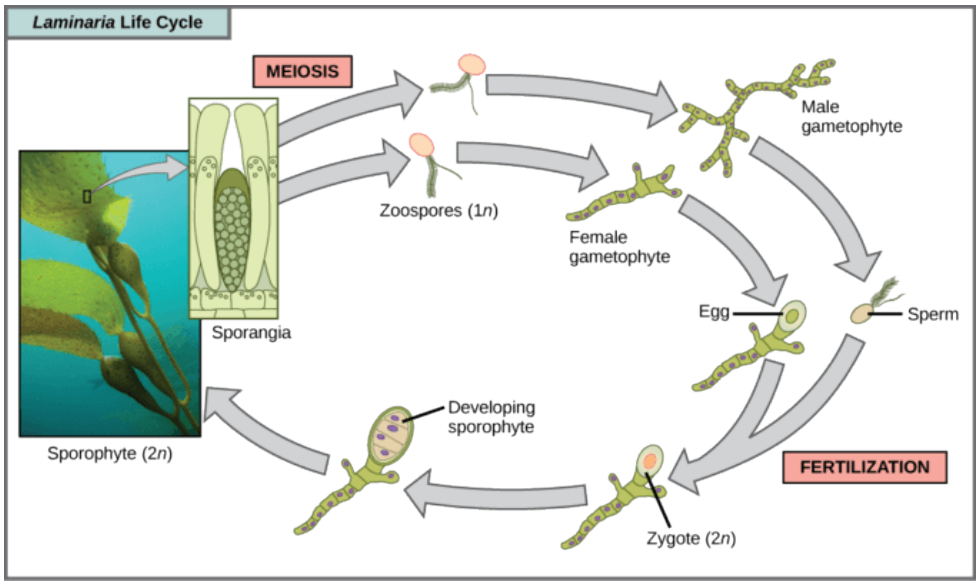


Figure $23.3C.1$: Brown algae life cycle: Several species of brown algae, such as the *Laminaria* shown here, have evolved life cycles in which both the haploid (gametophyte) and diploid (sporophyte) forms are multicellular. The gametophyte is different in structure from the sporophyte.

Oomycetes

The water molds, oomycetes ("egg fungus"), were so-named based on their fungus-like morphology, but molecular data have shown that the water molds are not closely related to fungi. The oomycetes are characterized by a cellulose-based cell wall and an extensive network of filaments that allow for nutrient uptake. As diploid spores, many oomycetes have two oppositely-directed flagella (one hairy and one smooth) for locomotion. The oomycetes are non-photosynthetic and include many saprobes and parasites. The saprobes appear as white fluffy growths on dead organisms. Most oomycetes are aquatic, but some parasitize terrestrial plants. One plant pathogen is *Phytophthora infestans*, the causative agent of late blight of potatoes, such as occurred in the nineteenth century Irish potato famine.



Figure $23.3C.1$: Oomycete: A saprobic oomycete engulfs a dead insect.

Key Points

- Stramenophiles, also referred to as heterokonts, are a subclass of chromalveolata, and are identified by the presence of a "hairy" flagellum.

- Diatoms, present in both freshwater and marine plankton, are unicellular photosynthetic protists that are characterized by the presence of a cell wall composed of silicon dioxide that displays intricate patterns.
- Golden algae, present in both freshwater and marine plankton communities, are unicellular photosynthetic protists characterized by the presence of carotenoids (yellow-orange photosynthetic pigments).
- Oomycetes, commonly referred to as water molds, are characterized by their fungus-like morphology, a cellulose-based cell wall, and a filamentous network used for nutrient uptake.
- Oomycetes, commonly referred to as water molds, are characterized by their fungus-like morphology, a cellulose-based cell wall and a filamentous network used for nutrient uptake.

Key Terms

- **stipe**: the stem of a kelp
- **raphe**: a ridge or seam on an organ, bodily tissue, or other structure, especially at the join between two halves or sections
- **saprobe**: an organism that lives off of dead or decaying organic material

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23.3D: Rhizaria

Learning Objectives

- Describe characteristics associated with Rhizaria

The Rhizaria supergroup includes many of the amoebas, most of which have threadlike or needle-like pseudopodia. Pseudopodia function to trap and engulf food particles and to direct movement in rhizarian protists. These pseudopods project outward from anywhere on the cell surface and can anchor to a substrate. The protist then transports its cytoplasm into the pseudopod, thereby moving the entire cell. This type of motion, called cytoplasmic streaming, is used by several diverse groups of protists as a means of locomotion or as a method to distribute nutrients and oxygen.

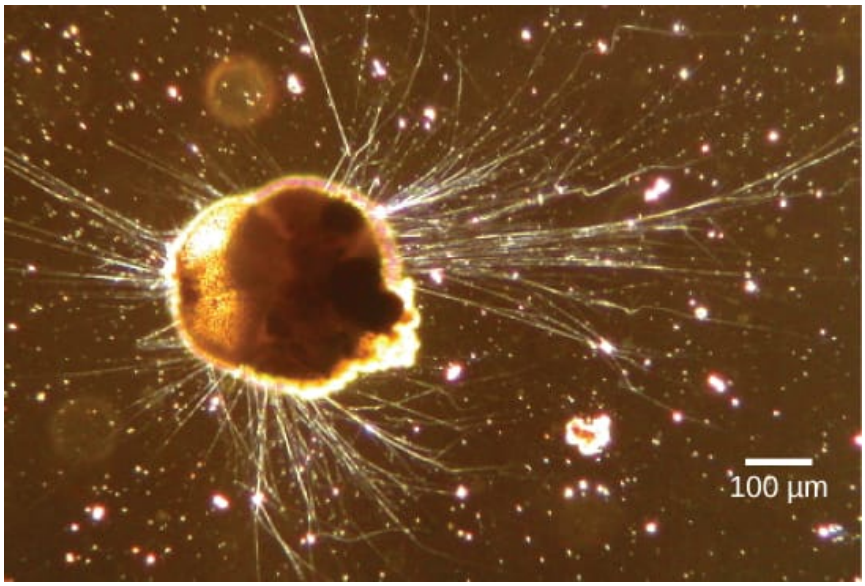


Figure $23.3D.1$: Ammonia tepida: Ammonia tepida, a Rhizaria species viewed here using phase contrast light microscopy, exhibits many threadlike pseudopodia.

Forams

Foraminiferans, or forams, are unicellular heterotrophic protists, ranging from approximately 20 micrometers to several centimeters in length; they occasionally resemble tiny snails. As a group, the forams exhibit porous shells, called tests, that are built from various organic materials and typically hardened with calcium carbonate. The tests may house photosynthetic algae, which the forams can harvest for nutrition. Foram pseudopodia extend through the pores and allow the forams to move, feed, and gather additional building materials. Foraminiferans are also useful as indicators of pollution and changes in global weather patterns.

The life-cycle involves an alternation between haploid and diploid phases. The haploid phase initially has a single nucleus, and divides to produce gametes with two flagella. The diploid phase is multinucleate, and after meiosis fragments to produce new organisms. The benthic forms has multiple rounds of asexual reproduction between sexual generations.

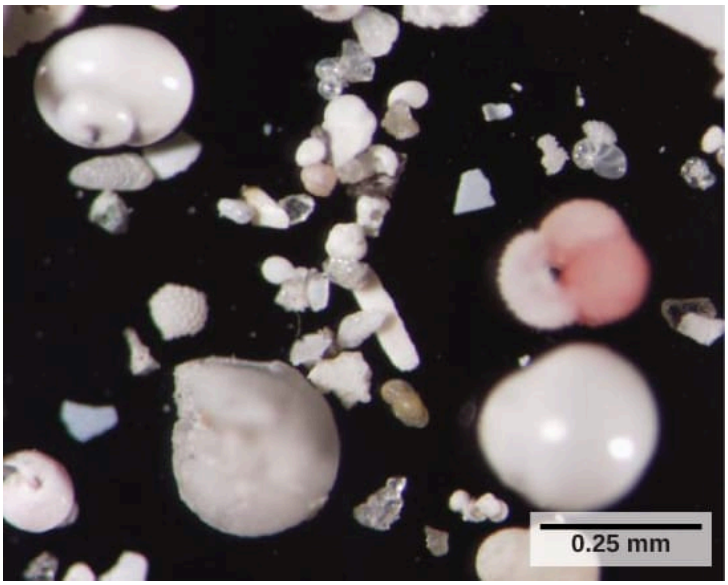


Figure $23.3D.1$: Forams: These shells from foraminifera sank to the sea floor.

Radiolarians

A second subtype of Rhizaria, the radiolarians, exhibit intricate exteriors of glassy silica with radial or bilateral symmetry. Radiolarians display needle-like pseudopods that are supported by microtubules which radiate outward from the cell bodies of these protists and function to catch food particles. The shells of dead radiolarians sink to the ocean floor, where they may accumulate in 100 meter-thick depths. Preserved, sedimented radiolarians are very common in the fossil record.

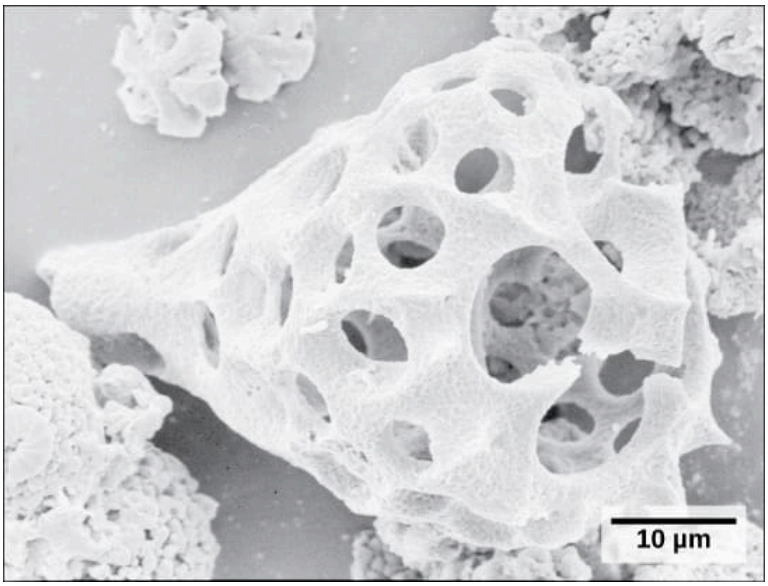


Figure $23.3D.1$: Radiolarian shell: This fossilized radiolarian shell was imaged using a scanning electron microscope.

Key Points

- The needle-like pseudopodia are used to carry out a process called cytoplasmic streaming which is a means of locomotion or distributing nutrients and oxygen.
- Two major subclassifications of Rhizaria include Forams and Radiolarians.
- Forams are characterized as unicellular heterotrophic protists that have porous shells, referred to as tests, which can contain photosynthetic algae that the foram can use as a nutrient source.
- Radiolarians are characterized by a glassy silica exterior that displays either bilateral or radial symmetry.

Key Terms

- **pseudopodia**: temporary projections of eukaryotic cells
- **test**: the external calciferous shell of a foram

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23.3E: Archaeplastida

Learning Objectives

- Describe the relationship between red algae, green algae, and land plants

Red algae and green algae are included in the supergroup Archaeplastida. It is well documented that land plants evolved from a common ancestor of these protists; their closest relatives are found within this group. Molecular evidence supports that all Archaeplastida are descendants of an endosymbiotic relationship between a heterotrophic protist and a cyanobacterium. The red and green algae include unicellular, multicellular, and colonial forms

Red Algae

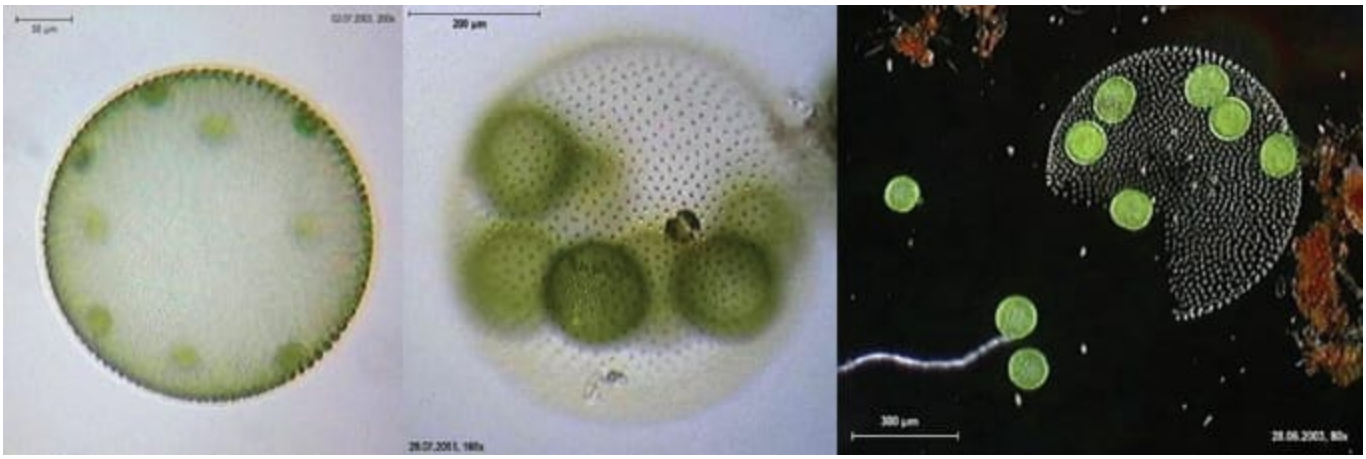
Red algae, or rhodophytes, are primarily multicellular, lack flagella, and range in size from microscopic, unicellular protists to large, multicellular forms grouped into the informal seaweed category. The red algae life cycle is an alternation of generations. Some species of red algae contain phycoerythrins, photosynthetic accessory pigments that are red in color and outcompete the green tint of chlorophyll, making these species appear as varying shades of red. Other protists classified as red algae lack phycoerythrins and are parasites. Red algae are common in tropical waters where they have been detected at depths of 260 meters. Other red algae exist in terrestrial or freshwater environments.

Green Algae: Chlorophytes and Charophytes

The most abundant group of algae is the green algae. The green algae exhibit similar features to the land plants, particularly in terms of chloroplast structure. It is well supported that this group of protists share a relatively-recent common ancestors with land plants. The green algae are subdivided into the chlorophytes and the charophytes. The charophytes are the closest-living relatives of land plants, resembling them in morphology and reproductive strategies. Charophytes are common in wet habitats where their presence often signals a healthy ecosystem.

The chlorophytes exhibit great diversity of form and function. Chlorophytes primarily inhabit freshwater and damp soil; they are a common component of plankton. *Chlamydomonas* is a simple, unicellular chlorophyte with a pear-shaped morphology and two opposing, anterior flagella that guide this protist toward light sensed by its eyespot. More complex chlorophyte species exhibit haploid gametes and spores that resemble *Chlamydomonas*.

The chlorophyte *Volvox* is one of only a few examples of a colonial organism, which behaves in some ways like a collection of individual cells, but in other ways like the specialized cells of a multicellular organism. Volvox colonies contain 500 to 60,000 cells, each with two flagella, contained within a hollow, spherical matrix composed of a gelatinous glycoprotein secretion. Individual *Volvox* cells move in a coordinated fashion and are interconnected by cytoplasmic bridges. Only a few of the cells reproduce to create daughter colonies, an example of basic cell specialization in this organism.



Volvox aureus

Volvox aureus is a green alga in the supergroup Archaeplastida. This species exists as a colony, consisting of cells immersed in a gel-like matrix and intertwined with each other via hair-like cytoplasmic extensions.

True multicellular organisms, such as the sea lettuce, *Ulva*, are represented among the chlorophytes. In addition, some chlorophytes exist as large, multinucleate, single cells. Species in the genus *Caulerpa* exhibit flattened, fern-like foliage and can reach lengths of 3 meters. *Caulerpa* species undergo nuclear division, but their cells do not complete cytokinesis, remaining instead as massive and elaborate single cells.



Caulerpa taxifolia

Caulerpa taxifolia is a chlorophyte consisting of a single cell containing potentially thousands of nuclei.

Key Points

- Archaeplastida are typically associated with their relationship to land plants; in addition, molecular evidence shows that Archaeplastida evolved from an endosymbiotic relationship between a heterotrophic protist and a cyanobacterium.
- Red algae (rhodophytes), are classified as Archaeplastida and are most often characterized by the presence of the red pigment phycoerythrin; however, there are red algae that lack phycoerythrins and can be classified as parasites.

- Red algae typically exist as multicellular protists that lack flagella; however, they can also exist as unicellular organisms.
- Green algae are the most abundant group of algae and can be further classified as chlorophytes and charophytes.
- Charophytes are the green algae which resemble land plants and are their closest living relative.
- Chlorophytes are the green algae which exhibit a wide range of forms; they can be unicellular, multicellular, or colonial.

Key Terms

- **endosymbiotic**: that lives within a body or cells of another organism
- **plankton**: a generic term for all the organisms that float in the sea

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23.3F: Amoebozoa and Opisthokonta

Learning Objectives

- Describe characteristics of Amoebozoa

Amoebozoa

Protists are eukaryotic organisms that are classified as unicellular, colonial, or multicellular organisms that do not have specialized tissues. This identifying property sets protists apart from other organisms within the Eukarya domain. The amoebozoans are classified as protists with pseudopodia which are used in locomotion and feeding. Amoebozoans live in marine environments, fresh water, or in soil. In addition to the defining pseudopodia, they also lack a shell and do not have a fixed body. The pseudopodia which are characteristically exhibited include extensions which can be tube-like or flat lobes, rather than the hair-like pseudopodia of rhizarian amoeba. Rhizarian amoeba are amoeboids with filose, reticulose, or microtubule-supported pseudopods and include the groups: Cercozoa, Foraminifera, and Radiolaria and are classified as bikonts. The Amoebozoa include several groups of unicellular amoeba-like organisms that are free-living or parasites that are classified as unikonts. The best known and most well-studied member of this group is the slime mold. Additional members include the Archamoebae, Tubulinea, and Flabellinea.

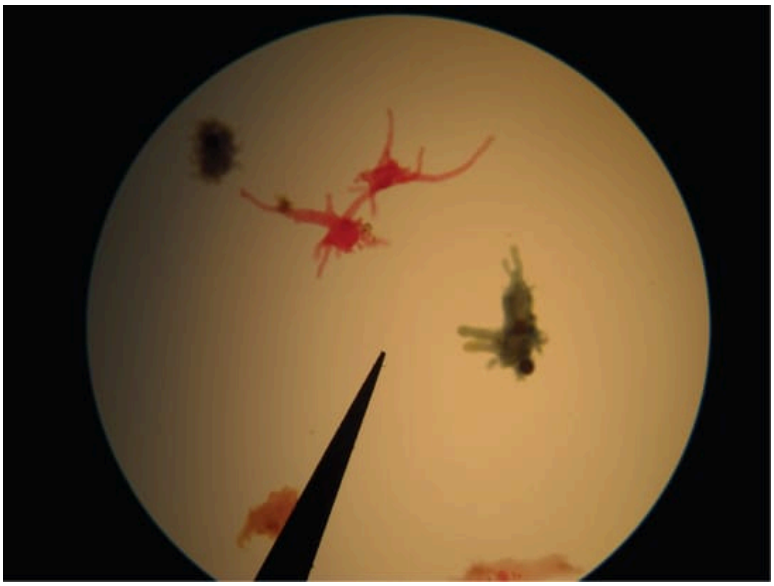


Figure $23.3F.1$: Pseudopodia structures: Amoebae with tubular and lobe-shaped pseudopodia, such as the ones seen under this microscope, would be morphologically classified as amoebozoans.

Slime Molds

A subset of the amoebozoans, the slime molds, has several morphological similarities to fungi that are thought to be the result of convergent evolution. For instance, during times of stress, some slime molds develop into spore -generating fruiting bodies, similar to fungi.

The slime molds are categorized on the basis of their life cycles into plasmodial or cellular types. Plasmodial slime molds are composed of large, multinucleate cells that move along surfaces like an amorphous blob of slime during their feeding stage. Food particles are lifted and engulfed into the slime mold as it glides along. Upon maturation, the plasmodium takes on a net-like appearance with the ability to form fruiting bodies, or sporangia, during times of stress. Haploid spores are produced by meiosis within the sporangia. These spores can be disseminated through the air or water to potentially land in more favorable environments. If this occurs, the spores germinate to form ameboid or flagellate haploid cells that can combine with each other

and produce a diploid zygotic slime mold to complete the life cycle.



Figure $23.3F.1$: Badhamia utricularis: Badhamia utricularis: an example of a plasmodial slime mold with the ability to form a fruiting body.

The cellular slime molds function as independent amoeboid cells when nutrients are abundant. When food is depleted, cellular slime molds pile onto each other into a mass of cells that behaves as a single unit called a slug. Some cells in the slug contribute to a 2–3-millimeter stalk, drying up and dying in the process. Cells atop the stalk form an asexual fruiting body that contains haploid spores. As with plasmodial slime molds, the spores are disseminated and can germinate if they land in a moist environment. One representative genus of the cellular slime molds is Dictyostelium, which commonly exists in the damp soil of forests.



Figure $23.3F.1$: Plasmodial slime mold: Physarum polycephalum: Physarum polycephalum is an example of a cellular slime mold.

Archamoebae, Flabellinea, and Tubulinea

The Archamoebae are a group of Amoebozoa distinguished by the absence of mitochondria. They include genera that are internal parasites or commensals of animals (*Entamoeba* and *Endolimax*). A few species are human pathogens, causing diseases such as amoebic dysentery. The other genera of archamoebae live in freshwater habitats and are unusual among amoebae in possessing flagella. Most have a single nucleus and flagellum, but the giant amoeba, *Pelomyxa*, has many of each.

The Tubulinea are a major grouping of Amoebozoa, including most of the larger and more familiar amoebae like *Amoeba*, *Arcella*, and *Difflugia*. During locomotion, most Tubulinea have a roughly cylindrical form or produce numerous cylindrical pseudopods. Each cylinder advances by a single central stream of cytoplasm, granular in appearance, and has no subpseudopodia. This distinguishes them from other amoeboid groups, although in some members this is not the normal type of locomotion.

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Key Points

- Amoebozoa (amoebas) can live in either marine and fresh water or in soil.
- Amoebozoa are characterized by the presence of pseudopodia, which are extensions that can be either tube-like or flat lobes and are used for locomotion and feeding.
- Amooebozoa can be further divided into subclassifications that include slime molds; these can be found as both plasmodial and cellular types.
- Plasmodial slime molds are characterized by the presence of large, multinucleate cells that have the ability to glide along the surface and engulf food particles as they move.
- Cellular molds are characterized by the presence of independent amoeboid cells during times of nutrient abundancy and the development of a cellular mass, called a slug, during times of nutrient depletion.
- Archamoebae, Flabellinea, and Tubulinea are also groups of Amoebozoa; their defining characteristics include: Archamoebae lack mitochondria; Flabellinea flatten during locomotion and lack a shell and flagella; Tubulinea have a rough cylindrical form during locomotion with cylindrical pseudopodia.

Key Terms

- **rhizaria**: a species-rich supergroup of mostly unicellular eukaryotes that for the most part are amoeboids with filose, reticulose, or microtubule-supported pseudopods
- **plasmodium**: a mass of cytoplasm, containing many nuclei, created by the aggregation of amoeboid cells of slime molds during their vegetative phase
- **sporangia**: an enclosure in which spores are formed (also called a fruiting body)

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23.4: ECOLOGY OF PROTISTS

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- Topic hierarchy

23.4A: Protists as Primary Producers, Food Sources, and Symbionts
23.4B: Protists as Human Pathogens
23.4C: Protists as Plant Pathogens

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23.4A: Protists as Primary Producers, Food Sources, and Symbionts

Learning Objectives

- Give examples of how protists act as primary producers

Primary Producers/Food Sources

Protists function in various ecological niches. Some protist species are essential components of the food chain and are generators of biomass.

Protists are essential sources of nutrition for many other organisms. In some cases, as in plankton, protists are consumed directly. Alternatively, photosynthetic protists serve as producers of nutrition for other organisms. For instance, photosynthetic dinoflagellates called zooxanthellae use sunlight to fix inorganic carbon. In this symbiotic relationship, these protists provide nutrients for the coral polyps that house them, giving corals a boost of energy to secrete a calcium carbonate skeleton. In turn, the corals provide the protists with a protected environment and the compounds needed for photosynthesis. This type of symbiotic relationship is important in nutrient-poor environments. Without dinoflagellate symbionts, corals lose algal pigments in a process called coral bleaching and they eventually die. This explains why reef-building corals do not reside in waters deeper than 20 meters: insufficient light reaches those depths for dinoflagellates to photosynthesize.



Figure 23.4A.1: Corals and dinoflagellates: Coral polyps obtain nutrition through a symbiotic relationship with dinoflagellates.

The protists themselves and their products of photosynthesis are essential, directly or indirectly, to the survival of organisms ranging from bacteria to mammals. As primary producers, protists feed a large proportion of the world's aquatic species. (On land, terrestrial plants serve as primary producers.) In fact, approximately one-quarter of the world's photosynthesis is conducted by protists, particularly dinoflagellates, diatoms, and multicellular algae.

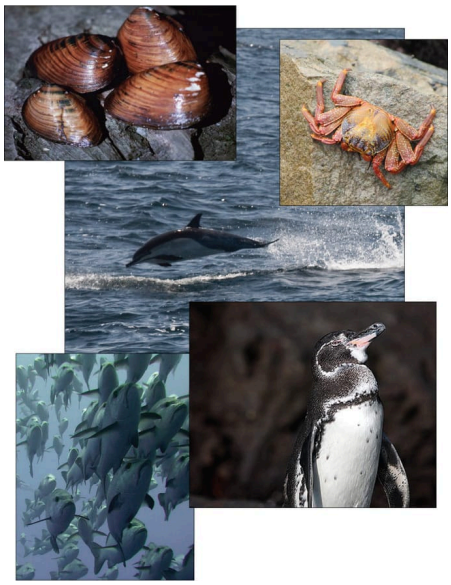


Figure 23.4A.1: Protists and aquatic organisms: Virtually all aquatic organisms depend directly or indirectly on protists for food.

Protists do not only create food sources for sea-dwelling organisms. Certain anaerobic parabasalid species exist in the digestive tracts of termites and wood-eating cockroaches where they contribute an essential step in the digestion of cellulose ingested by these insects as they bore through wood.

Key Points

- Photosynthetic protists serve as producers of nutrition for other organisms.
- Protists like zooxanthellae have a symbiotic relationship with coral reefs; the protists act as a food source for coral and the coral provides shelter and compounds for photosynthesis for the protists.
- Protists feed a large portion of the world's aquatic species and conduct a quarter of the world's photosynthesis.
- Protists help land-dwelling animals such as cockroaches and termites digest cellulose.

Key Terms

- **zooxanthella**: an animal of the genus Symbiodinium, a yellow dinoflagellate, notably found in coral reefs
- **primary producer**: an autotroph organism that produces complex organic matter using photosynthesis or chemosynthesis

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23.4B: Protists as Human Pathogens

Learning Objectives

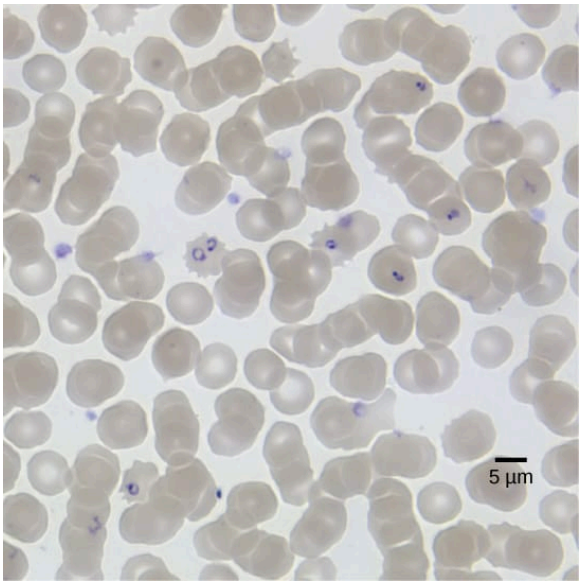
- Identify the effects on humans of protist pathogens

Human Pathogens

A pathogen is anything that causes disease. Parasites live in or on an organism and harm that organism. A significant number of protists are pathogenic parasites that must infect other organisms to survive and propagate. Protist parasites include the causative agents of malaria, African sleeping sickness, and waterborne gastroenteritis in humans.

Plasmodium Species

Members of the genus *Plasmodium* must colonize both a mosquito and a vertebrate to complete their life cycle. In vertebrates, the parasite develops in liver cells and goes on to infect red blood cells, bursting from and destroying the blood cells with each asexual replication cycle. Of the four *Plasmodium* species known to infect humans, *P. falciparum* accounts for 50 percent of all malaria cases and is the primary cause of disease-related fatalities in tropical regions of the world. In 2010, it was estimated that malaria caused between one and one-half million deaths, mostly in African children. During the course of malaria, *P. falciparum* can infect and destroy more than one-half of a human's circulating blood cells, leading to severe anemia. In response to waste products released as the parasites burst from infected blood cells, the host immune system mounts a massive inflammatory response with episodes of delirium-inducing fever as parasites lyse red blood cells, spilling parasitic waste into the bloodstream. *P. falciparum* is transmitted to humans by the African malaria mosquito, *Anopheles gambiae*. Techniques to kill, sterilize, or avoid exposure to this highly-aggressive mosquito species are crucial to malaria control.



Plasmodium

Red blood cells are shown to be infected with *P. falciparum*, the causative agent of malaria. In this light microscopic image taken using a 100× oil immersion lens, the ring-shaped *P. falciparum*stains purple.

Trypanosomes

Trypanosoma brucei, the parasite that is responsible for African sleeping sickness, confounds the human immune system by changing its thick layer of surface glycoproteins with each infectious cycle. The glycoproteins are identified by the immune system as foreign antigens and a specific antibody defense is mounted against the parasite. However, *T. brucei* has thousands of possible antigens; with each subsequent generation, the protist switches to a glycoprotein coating of a different molecular structure. In this way, *T. brucei* is capable of replicating continuously without the immune system ever succeeding in clearing the parasite. Without treatment, *T. brucei* attacks red blood cells, causing the patient to lapse into a coma and eventually die. During epidemic periods, mortality from the disease can be high. Greater surveillance and control measures lead to a reduction in reported cases; some of the lowest numbers reported in 50 years (fewer than 10,000 cases in all of sub-Saharan Africa) have happened since 2009.

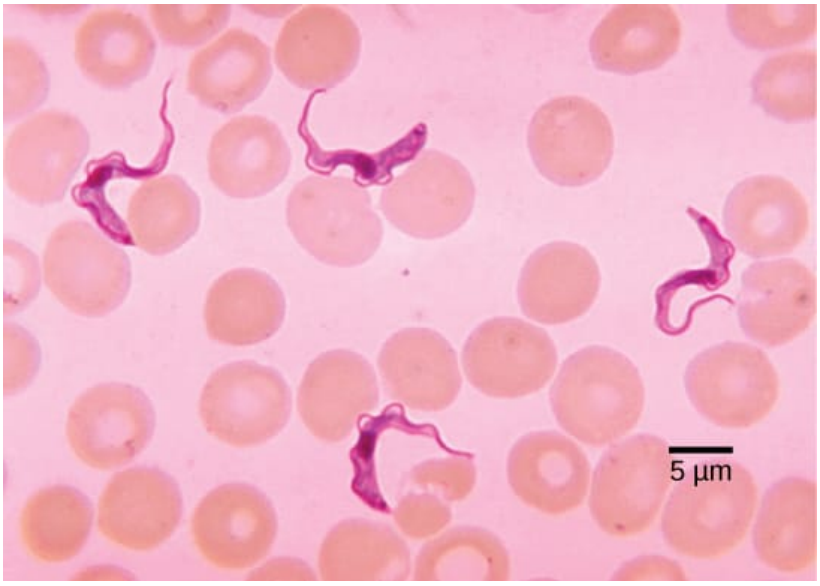


Figure $23.4B.1$: Trypanosomes: Trypanosomes are shown among red blood cells.

In Latin America, another species, *T. cruzi*, is responsible for Chagas disease. *T. cruzi* infections are mainly caused by a blood-sucking bug. The parasite inhabits heart and digestive system tissues in the chronic phase of infection, leading to malnutrition and heart failure due to abnormal heart rhythms. An estimated 10 million people are infected with Chagas disease; it caused 10,000 deaths in 2008.

Key Points

- The protist parasite *Plasmodium* must colonize both a mosquito and a vertebrate; *P. falciparum*, which is responsible for 50 percent of malaria cases, is transmitted to humans by the African malaria mosquito, *Anopheles gambiae*.
- When *P. falciparum* infects and destroys red blood cells, they burst, and parasitic waste leaks into the blood stream, causing deliruim, fever, and anemia in patients.
- *Trypanosoma brucei* is responsible for African sleeping sickness which the human immune system is unable to guard against since it has thousands of possible antigens and changes surface glycoproteins with each infectious cycle.
- Another *Trypanosoma* species, *T. cruzi*, inhabits the heart and digestive system tissues, causing malnutrition and heart failure.

Key Terms

- **Trypanosoma**: infects a variety of hosts and cause various diseases, including the fatal African sleeping sickness in humans
- **plasmodium**: parasitic protozoa that must colonize a mosquito and a vertebrate to complete its life cycle
- **pathogen**: any organism or substance, especially a microorganism, capable of causing disease, such as bacteria, viruses, protozoa, or fungi

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23.4C: Protists as Plant Pathogens

Learning Objectives

- Describe the ways in which protists act as decomposers and the actions of parasitic protists on plants

Plant Parasites

Protist parasites prey on terrestrial plants and include agents that cause massive destruction to food crops. The oomycete *Plasmopara viticola* parasitizes grape plants, which causes a disease called downy mildew. Grape plants infected with *P. viticola* appear stunted and have discolored, withered leaves. The spread of downy mildew nearly collapsed the French wine industry in the nineteenth century. They are easily controlled once discovered, so careful monitoring of susceptible hosts is key because if left unaddressed, the organism can quickly spread and completely overwhelm the host species

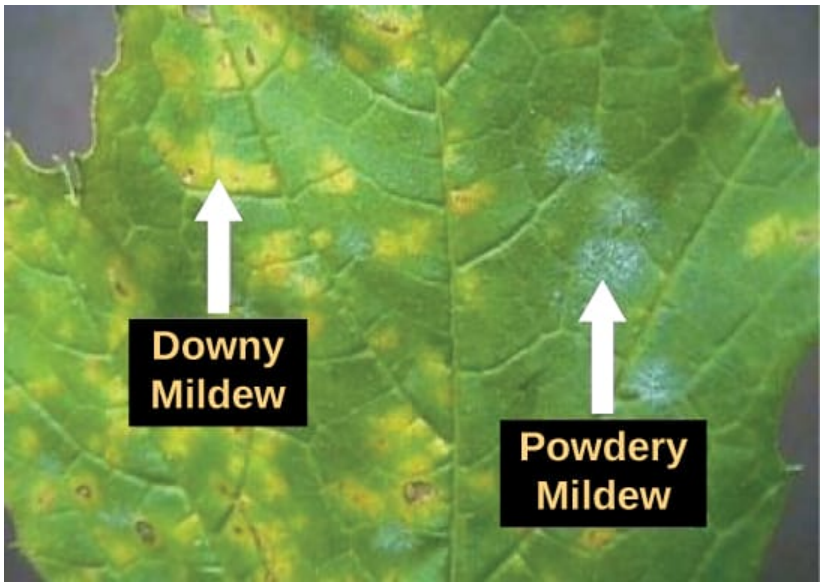


Figure $23.4C.1$: Downy mildew: Both downy and powdery mildews on this grape leaf are caused by an infection of P. viticola.

Because the downy mildew pathogen does not overwinter in midwestern fields, crop rotations and tillage practices do not affect disease development. The pathogen tends to become established in late summer. Therefore, planting early season varieties may further reduce the threat posed by downy mildew. Fungicides can also be applied to control downy mildew. Broad spectrum protectant fungicides such as chlorothalonil, mancozeb, and fixed copper are somewhat effective in protecting against downy mildew infection.

Phytophthora infestans is an oomycete responsible for potato late blight. This disease causes potato stalks and stems to decay into black slime. Widespread potato blight caused by *P. infestans* led to the well-known Irish potato famine in the nineteenth century that claimed the lives of approximately one million people and resulted in the emigration of at least one million more from Ireland. Late blight continues to plague potato crops in certain parts of the United States and Russia, wiping out as much as 70 percent of crops when no pesticides are applied.



Figure 23.4C.1: Potato Late Blight: These unappetizing remnants result from an infection with P. infestans, the causative agent of potato late blight.

Agents of Decomposition

The fungus-like protist saprobes are specialized to absorb nutrients from non-living organic matter, such as dead organisms or their wastes. For instance, many types of oomycetes grow on dead animals or algae. Saprobic protists have the essential function of returning inorganic nutrients to the soil and water. This process allows for new plant growth, which in turn generates sustenance for other organisms along the food chain. Indeed, without saprobe species, such as protists, fungi, and bacteria, life would cease to exist as all organic carbon became "tied up" in dead organisms.

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Key Points

- *Plasmopara viticola* causes downy mildew in grape plants, resulting in stunted growth and withered, discolored leaves.
- Since downy mildew has a higher incidence in the late summer, planting early in the season can reduce the threat of downy mildew; fungicides are also somewhat effective at preventing downy mildew.
- *Phytophthora infestans* causes potato late blight (potato stalks and stems decay into black slime) and was responsible for the Irish potato famine in the nineteenth century.
- Protist saprobes feed on dead organisms, which returns inorganic nutrients to soil and water.

Key Terms

- **saprobe**: an organism that lives off of dead or decaying organic material
- **oomycete**: fungus-like filamentous unicellular protists; the water molds
- **downy mildew**: plant disease caused by oomycetes; causes stunted growth in plants as well as discolored, withered leaves

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24: FUNGI

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24.5A: Importance of Fungi in Human Life

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24.1: CHARACTERISTICS OF FUNGI

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- Topic hierarchy

24.1A: Characteristics of Fungi
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24.1A: Characteristics of Fungi

Learning Objectives

- Describe the role of fungi in the ecosystem

Introduction to Fungi

The word fungus comes from the Latin word for mushrooms. Indeed, the familiar mushroom is a reproductive structure used by many types of fungi. However, there are also many fungi species that don't produce mushrooms at all. Being eukaryotes, a typical fungal cell contains a true nucleus and many membrane-bound organelles. The kingdom Fungi includes an enormous variety of living organisms collectively referred to as Ascomycota, or true Fungi. While scientists have identified about 100,000 species of fungi, this is only a fraction of the 1.5 million species of fungus probably present on earth. Edible mushrooms, yeasts, black mold, and the producer of the antibiotic penicillin, *Penicillium notatum*, are all members of the kingdom Fungi, which belongs to the domain Eukarya.



Figure 24.1A.1: Examples of fungi: Many species of fungus produce the familiar mushroom (a) which is a reproductive structure. This (b) coral fungus displays brightly-colored fruiting bodies. This electron micrograph shows (c) the spore-bearing structures of Aspergillus, a type of toxic fungi found mostly in soil and plants.

Fungi, once considered plant-like organisms, are more closely related to animals than plants. Fungi are not capable of photosynthesis: they are heterotrophic because they use complex organic compounds as sources of energy and carbon. Some fungal organisms multiply only asexually, whereas others undergo both asexual reproduction and sexual reproduction with alternation of generations. Most fungi produce a large number of spores, which are haploid cells that can undergo mitosis to form multicellular, haploid individuals. Like bacteria, fungi play an essential role in ecosystems because they are decomposers and participate in the cycling of nutrients by breaking down organic and inorganic materials to simple molecules.

Fungi often interact with other organisms, forming beneficial or mutualistic associations. For example most terrestrial plants form symbiotic relationships with fungi. The roots of the plant connect with the underground parts of the fungus forming mycorrhizae. Through mycorrhizae, the fungus and plant exchange nutrients and water, greatly aiding the survival of both species Alternatively, lichens are an association between a fungus and its photosynthetic partner (usually an alga). Fungi also cause serious infections in plants and animals. For example, Dutch elm disease, which is caused by the fungus *Ophiostoma ulmi*, is a particularly devastating type of fungal infestation that destroys many native species of elm (*Ulmus* sp.) by infecting the tree's vascular system. The elm bark beetle acts as a vector, transmitting the disease from tree to tree. Accidentally introduced in the 1900s, the fungus decimated elm trees across the continent. Many European and Asiatic elms are less susceptible to Dutch elm disease than

American elms.

In humans, fungal infections are generally considered challenging to treat. Unlike bacteria, fungi do not respond to traditional antibiotic therapy because they are eukaryotes. Fungal infections may prove deadly for individuals with compromised immune systems.

Fungi have many commercial applications. The food industry uses yeasts in baking, brewing, and cheese and wine making. Many industrial compounds are byproducts of fungal fermentation. Fungi are the source of many commercial enzymes and antibiotics.

Key Points

- Fungi are more closely related to animals than plants.
- Fungi are heterotrophic: they use complex organic compounds as sources of energy and carbon, not photosynthesis.
- Fungi multiply either asexually, sexually, or both.
- The majority of fungi produce spores, which are defined as haploid cells that can undergo mitosis to form multicellular, haploid individuals.
- Fungi interact with other organisms by either forming beneficial or mutualistic associations (mycorrhizae and lichens) or by causing serious infections.

Key Terms

- **mycorrhiza**: a symbiotic association between a fungus and the roots of a vascular plant
- **spore**: a reproductive particle, usually a single cell, released by a fungus, alga, or plant that may germinate into another
- **lichen**: any of many symbiotic organisms, being associations of fungi and algae; often found as white or yellow patches on old walls, etc.
- **Ascomycota**: a taxonomic division within the kingdom Fungi; those fungi that produce spores in a microscopic sporangium called an ascus
- **heterotrophic**: organisms that use complex organic compounds as sources of energy and carbon

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24.1B: Fungi Cell Structure and Function

Learning Objectives

- Describe the physical structures associated with fungi

Cell Structure and Function

Fungi are eukaryotes and have a complex cellular organization. As eukaryotes, fungal cells contain a membrane-bound nucleus where the DNA is wrapped around histone proteins. A few types of fungi have structures comparable to bacterial plasmids (loops of DNA). Fungal cells also contain mitochondria and a complex system of internal membranes, including the endoplasmic reticulum and Golgi apparatus.

Unlike plant cells, fungal cells do not have chloroplasts or chlorophyll. Many fungi display bright colors arising from other cellular pigments, ranging from red to green to black. The poisonous *Amanita muscaria* (fly agaric) is recognizable by its bright red cap with white patches. Pigments in fungi are associated with the cell wall. They play a protective role against ultraviolet radiation and can be toxic.



Figure $24.1B.1$: The poisonous *Amanita muscaria*: The poisonous *Amanita muscaria* is native to temperate and boreal regions of North America.

The rigid layers of fungal cell walls contain complex polysaccharides called chitin and glucans. Chitin, also found in the exoskeleton of insects, gives structural strength to the cell walls of fungi. The wall protects the cell from desiccation and predators. Fungi have plasma membranes similar to other eukaryotes, except that the structure is stabilized by ergosterol: a steroid molecule that replaces the cholesterol found in animal cell membranes. Most members of the kingdom Fungi are nonmotile.

Growth

The vegetative body of a fungus is a unicellular or multicellular thallus. Dimorphic fungi can change from the unicellular to multicellular state depending on environmental conditions. Unicellular fungi are generally referred to as yeasts. *Saccharomyces cerevisiae* (baker's yeast) and *Candida* species (the agents of thrush, a common fungal infection) are examples of unicellular fungi.

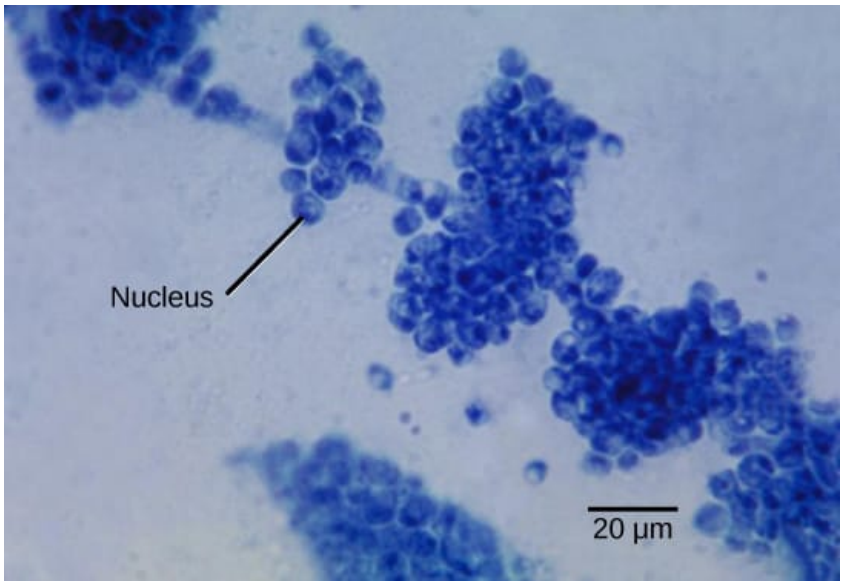


Figure 24.1B.1: Example of a unicellular fungus: *Candida albicans* is a yeast cell and the agent of candidiasis and thrush. This organism has a similar morphology to coccus bacteria; however, yeast is a eukaryotic organism (note the nucleus).

Most fungi are multicellular organisms. They display two distinct morphological stages: the vegetative and reproductive. The vegetative stage consists of a tangle of slender thread-like structures called hyphae (singular, hypha), whereas the reproductive stage can be more conspicuous. The mass of hyphae is a mycelium. It can grow on a surface, in soil or decaying material, in a liquid, or even on living tissue. Although individual hyphae must be observed under a microscope, the mycelium of a fungus can be very large, with some species truly being “the fungus humongous.” The giant *Armillaria solidipe*s (honey mushroom) is considered the largest organism on Earth, spreading across more than 2,000 acres of underground soil in eastern Oregon; it is estimated to be at least 2,400 years old.

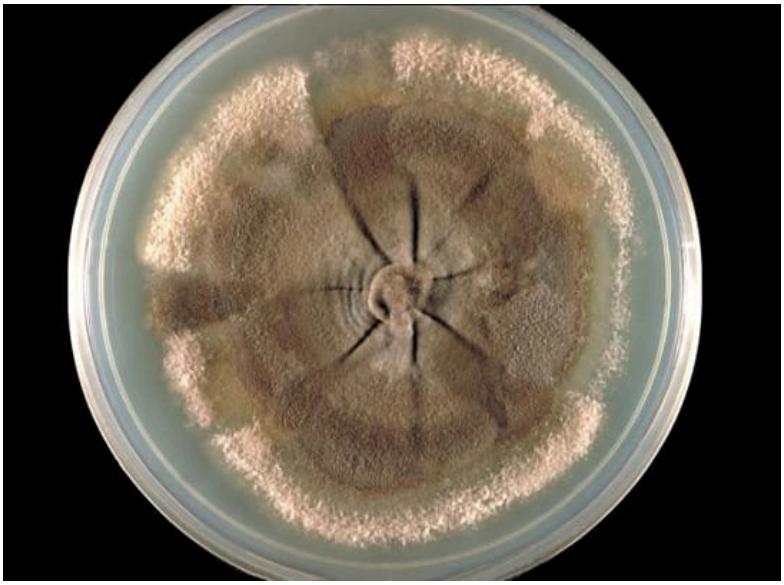


Figure 24.1B.1: Example of a mycelium of a fungus: The mycelium of the fungus *Neotestudina rosati* can be pathogenic to humans. The fungus enters through a cut or scrape and develops a mycetoma, a chronic subcutaneous infection.

Most fungal hyphae are divided into separate cells by endwalls called septa (singular, septum) (a, c). In most phyla of fungi, tiny holes in the septa allow for the rapid flow of nutrients and small molecules from cell to cell along the hypha. They are described as perforated septa. The hyphae in bread molds (which belong to the Phylum Zygomycota) are not separated by septa. Instead, they are formed by large cells containing many nuclei, an arrangement described as coenocytic hyphae (b). Fungi thrive in environments that are moist and slightly acidic; they can grow with or without light.

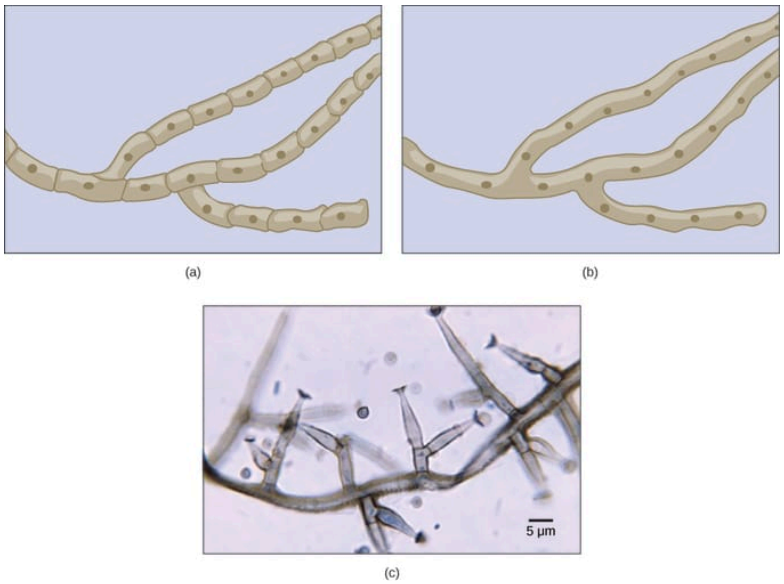


Figure 24.1B.1: Division of hyphae into separate cells: Fungal hyphae may be (a) septated or (b) coenocytic (coeno- = "common"; -cytic = "cell") with many nuclei present in a single hypha. A bright field light micrograph of (c) *Phialophora richardsiae* shows septa that divide the hyphae.

Nutrition

Like animals, fungi are heterotrophs: they use complex organic compounds as a source of carbon, rather than fix carbon dioxide from the atmosphere as do some bacteria and most plants. In addition, fungi do not fix nitrogen from the atmosphere. Like animals, they must obtain it from their diet. However, unlike most animals, which ingest food and then digest it internally in specialized organs, fungi perform these steps in the reverse order: digestion precedes ingestion. First, exoenzymes are transported out of the hyphae, where they process nutrients in the environment. Then, the smaller molecules produced by this external digestion are absorbed through the large surface area of the mycelium. As with animal cells, the polysaccharide of storage is glycogen rather than the starch found in plants.

Fungi are mostly saprobes (saprophyte is an equivalent term): organisms that derive nutrients from decaying organic matter. They obtain their nutrients from dead or decomposing organic matter, mainly plant material. Fungal exoenzymes are able to break down insoluble polysaccharides, such as the cellulose and lignin of dead wood, into readily-absorbable glucose molecules. The carbon, nitrogen, and other elements are thus released into the environment. Because of their varied metabolic pathways, fungi fulfill an important ecological role and are being investigated as potential tools in bioremediation.

Some fungi are parasitic, infecting either plants or animals. Smut and Dutch elm disease affect plants, whereas athlete's foot and candidiasis (thrush) are medically important fungal infections in humans.

Key Points

- Fungal cell walls are rigid and contain complex polysaccharides called chitin (adds structural strength) and glucans.
- Ergosterol is the steroid molecule in the cell membranes that replaces the cholesterol found in animal cell membranes.
- Fungi can be unicellular, multicellular, or dimorphic, which is when the fungi is unicellular or multicellular depending on environmental conditions.
- Fungi in the morphological vegetative stage consist of a tangle of slender, thread-like hyphae, whereas the reproductive stage is usually more obvious.
- Fungi like to be in a moist and slightly acidic environment; they can grow with or without light or oxygen.
- Fungi are saprophyte heterotrophs in that they use dead or decomposing organic matter as a source of carbon.

Key Terms

- **glucan**: any polysaccharide that is a polymer of glucose

- **ergosterol**: the functional equivalent of cholesterol found in cell membranes of fungi and some protists, as well as, the steroid precursor of vitamin D2
- **mycelium**: the vegetative part of any fungus, consisting of a mass of branching, threadlike hyphae, often underground
- **hypha**: a long, branching, filamentous structure of a fungus that is the main mode of vegetative growth
- **septum**: cell wall division between hyphae of a fungus
- **thallus**: vegetative body of a fungus
- **saprophyte**: any organism that lives on dead organic matter, as certain fungi and bacteria
- **chitin**: a complex polysaccharide, a polymer of N-acetylglucosamine, found in the exoskeletons of arthropods and in the cell walls of fungi; thought to be responsible for some forms of asthma in humans

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24.1C: Fungi Reproduction

Learning Objectives

- Describe the mechanisms of sexual and asexual reproduction in fungi

Reproduction

Fungi reproduce sexually and/or asexually. Perfect fungi reproduce both sexually and asexually, while imperfect fungi reproduce only asexually (by mitosis).

In both sexual and asexual reproduction, fungi produce spores that disperse from the parent organism by either floating on the wind or hitching a ride on an animal. Fungal spores are smaller and lighter than plant seeds. The giant puffball mushroom bursts open and releases trillions of spores. The huge number of spores released increases the likelihood of landing in an environment that will support growth.



Figure $24.1C.1$: The release of fungal spores: The (a) giant puff ball mushroom releases (b) a cloud of spores when it reaches maturity.

Asexual Reproduction

Fungi reproduce asexually by fragmentation, budding, or producing spores. Fragments of hyphae can grow new colonies. Mycelial fragmentation occurs when a fungal mycelium separates into pieces with each component growing into a separate mycelium. Somatic cells in yeast form buds. During budding (a type of cytokinesis), a bulge forms on the side of the cell, the nucleus divides mitotically, and the bud ultimately detaches itself from the mother cell.

The most common mode of asexual reproduction is through the formation of asexual spores, which are produced by one parent only (through mitosis) and are genetically identical to that parent. Spores allow fungi to expand their distribution and colonize new environments. They may be released from the parent thallus, either outside or within a special reproductive sac called a sporangium.

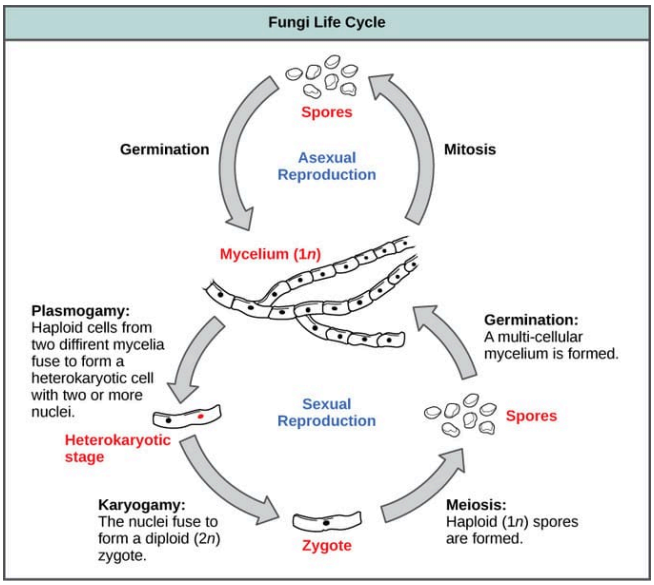


Figure $24.1C.1$: Types of fungal reproduction: Fungi may utilize both asexual and sexual stages of reproduction; sexual reproduction often occurs in response to adverse environmental conditions.

There are many types of asexual spores. Conidiospores are unicellular or multicellular spores that are released directly from the tip or side of the hypha. Other asexual spores originate in the fragmentation of a hypha to form single cells that are released as spores; some of these have a thick wall surrounding the fragment. Yet others bud off the vegetative parent cell. Sporangiospores are produced in a sporangium.

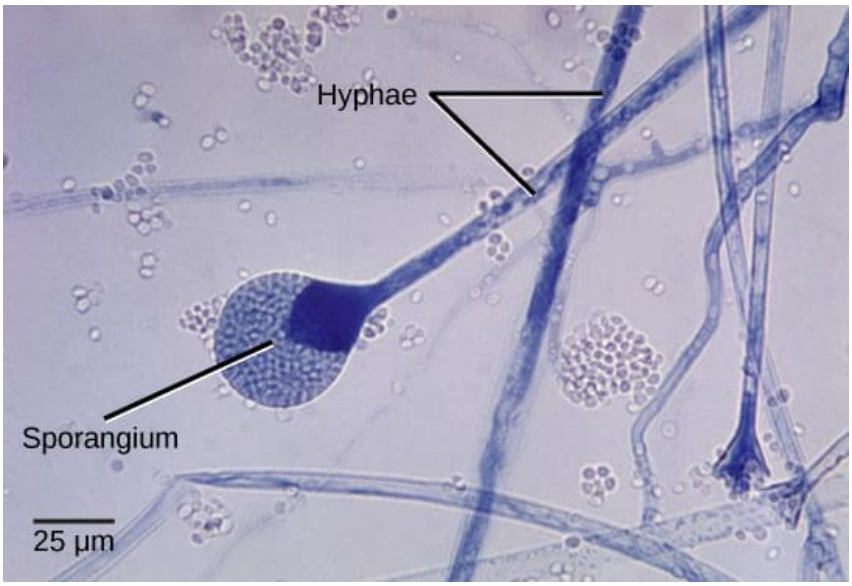


Figure $24.1C.1$: Release of spores from a sporangium: This bright field light micrograph shows the release of spores from a sporangium at the end of a hypha called a sporangiophore. The organism depicted is a Mucor sp. fungus: a mold often found indoors.

Sexual Reproduction

Sexual reproduction introduces genetic variation into a population of fungi. In fungi, sexual reproduction often occurs in response to adverse environmental conditions. Two mating types are produced. When both mating types are present in the same mycelium, it is called homothallic, or self-fertile. Heterothallic mycelia require two different, but compatible, mycelia to reproduce sexually.

Although there are many variations in fungal sexual reproduction, all include the following three stages. First, during plasmogamy (literally, “marriage or union of cytoplasm”), two haploid cells fuse, leading to a dikaryotic stage where two haploid nuclei coexist in a single cell. During karyogamy (“nuclear marriage”), the haploid nuclei fuse to form a diploid zygote nucleus. Finally, meiosis

takes place in the gametangia (singular, gametangium) organs, in which gametes of different mating types are generated. At this stage, spores are disseminated into the environment.

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Key Points

- New colonies of fungi can grow from the fragmentation of hyphae.
- During budding, a bulge forms on the side of the cell; the bud ultimately detaches after the nucleus divides mitotically.
- Asexual spores are genetically identical to the parent and may be released either outside or within a special reproductive sac called a sporangium.
- Adverse environmental conditions often cause sexual reproduction in fungi.
- Mycelium can either be homothallic or heterothallic when reproducing sexually.
- Fungal sexual reproduction includes the following three stages: plasmogamy, karyogamy, and gametangia.

Key Terms

- **homothallic**: male and female reproductive structures are present in the same plant or fungal mycelium
- **gametangium**: an organ or cell in which gametes are produced that is found in many multicellular protists, algae, fungi, and the gametophytes of plants
- **spore**: a reproductive particle, usually a single cell, released by a fungus, alga, or plant that may germinate into another
- **sporangium**: a case, capsule, or container in which spores are produced by an organism
- **karyogamy**: the fusion of two nuclei within a cell
- **plasmogamy**: stage of sexual reproduction joining the cytoplasm of two parent mycelia without the fusion of nuclei

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24.2: ECOLOGY OF FUNGI

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24.2A: Fungi Habitat, Decomposition, and Recycling

24.2B: Mutualistic Relationships with Fungi and Fungivores

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24.2A: Fungi Habitat, Decomposition, and Recycling

Learning Objectives

- Explain the roles played by fungi in decomposition and recycling

Fungi & Their Roles as Decomposers and Recyclers

Fungi play a crucial role in the balance of ecosystems. They colonize most habitats on earth, preferring dark, moist conditions. They can thrive in seemingly-hostile environments, such as the tundra. However, most members of the Kingdom Fungi grow on the forest floor where the dark and damp environment is rich in decaying debris from plants and animals. In these environments, fungi play a major role as decomposers and recyclers, making it possible for members of the other kingdoms to be supplied with nutrients and to live.

The food web would be incomplete without organisms that decompose organic matter. Some elements, such as nitrogen and phosphorus, are required in large quantities by biological systems; yet, they are not abundant in the environment. The action of fungi releases these elements from decaying matter, making them available to other living organisms. Trace elements present in low amounts in many habitats are essential for growth, but would remain tied up in rotting organic matter if fungi and bacteria did not return them to the environment via their metabolic activity.



Figure 24.2A.1: Fungi as decomposers: Fungi are an important part of ecosystem nutrient cycles. These bracket fungi growing on the side of a tree are the fruiting structures of a basidiomycete. They receive their nutrients through their hyphae, which invade and decay the tree trunk.

The ability of fungi to degrade many large and insoluble molecules is due to their mode of nutrition. As seen earlier, digestion precedes ingestion. Fungi produce a variety of exoenzymes to digest nutrients. These enzymes are either released into the substrate or remain bound to the outside of the fungal cell wall. Large molecules are broken down into small molecules, which are transported into the cell by a system of protein carriers embedded in the cell membrane. Because the movement of small molecules and enzymes is dependent on the presence of water, active growth depends on a relatively-high percentage of moisture in the environment.

As saprobes, fungi help maintain a sustainable ecosystem for the animals and plants that share the same habitat. In addition to replenishing the environment with nutrients, fungi interact directly with other organisms in beneficial, but sometimes damaging, ways.



Figure 24.2A.1: Fungi: beneficial & pathogenic: Shelf fungi, so called because they grow on trees in a stack, attack and digest the trunk or branches of a tree. While some shelf fungi are found only on dead trees, others can parasitize living trees, causing eventual death. They are considered serious tree pathogens.

Key Points

- Aiding the survival of species from other kingdoms through the supply of nutrients, fungi play a major role as decomposers and recyclers in the wide variety of habitats in which they exist.
- Fungi provide a vital role in releasing scarce, yet biologically-essential elements, such as nitrogen and phosphorus, from decaying matter.
- Their mode of nutrition, which involves digestion before ingestion, allows fungi to degrade many large and insoluble molecules that would otherwise remain trapped in a habitat.

Key Terms

- **decomposer**: any organism that feeds off decomposing organic material, especially bacterium or fungi
- **exoenzyme**: any enzyme, generated by a cell, that functions outside of that cell
- **saprobe**: an organism that lives off of dead or decaying organic material

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24.2B: Mutualistic Relationships with Fungi and Fungivores

Learning Objectives

- Describe mutualistic relationships with fungi

Mutualistic Relationships

Symbiosis is the ecological interaction between two organisms that live together. However, the definition does not describe the quality of the interaction. When both members of the association benefit, the symbiotic relationship is called mutualistic. Fungi form mutualistic associations with many types of organisms, including cyanobacteria, plants, and animals.

Fungi & Plant Mutualism

Mycorrhiza, which comes from the Greek words “myco” meaning fungus and “rhizo” meaning root, refers to the association between vascular plant roots and their symbiotic fungi. About 90 percent of all plant species have mycorrhizal partners. In a mycorrhizal association, the fungal mycelia use their extensive network of hyphae and large surface area in contact with the soil to channel water and minerals from the soil into the plant, thereby increasing a plant’s nutrient uptake. In exchange, the plant supplies the products of photosynthesis to fuel the metabolism of the fungus.

Mycorrhizae display many characteristics of primitive fungi: they produce simple spores, show little diversification, do not have a sexual reproductive cycle, and cannot live outside of a mycorrhizal association. There are a number of types of mycorrhizae. Ectomycorrhizae (“outside” mycorrhiza) depend on fungi enveloping the roots in a sheath (called a mantle) and a Hartig net of hyphae that extends into the roots between cells. The fungal partner can belong to the Ascomycota, Basidiomycota, or Zygomycota. In a second type, the Glomeromycete fungi form vesicular–arbuscular interactions with arbuscular mycorrhiza (sometimes called endomycorrhizae). In these mycorrhiza, the fungi form arbuscules that penetrate root cells and are the site of the metabolic exchanges between the fungus and the host plant. The arbuscules (from the Latin for “little trees”) have a shrub-like appearance. Orchids rely on a third type of mycorrhiza. Orchids are epiphytes that form small seeds without much storage to sustain germination and growth. Their seeds will not germinate without a mycorrhizal partner (usually a Basidiomycete). After nutrients in the seed are depleted, fungal symbionts support the growth of the orchid by providing necessary carbohydrates and minerals. Some orchids continue to be mycorrhizal throughout their lifecycle.

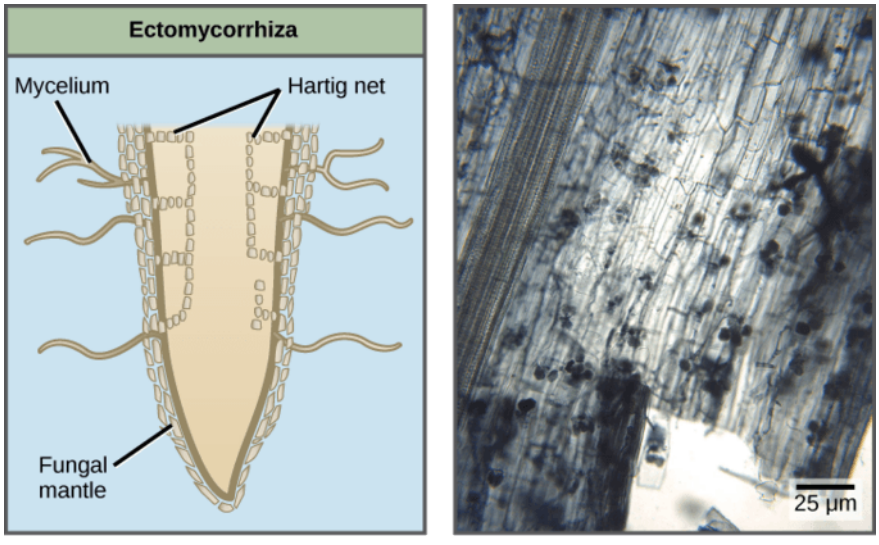


Figure $24.2B.1$: Mycorrhizal fungi: (a) Ectomycorrhiza and (b) arbuscular mycorrhiza have different mechanisms for interacting with the roots of plants.

Lichens

Lichens display a range of colors and textures. They can survive in the most unusual and hostile habitats. They cover rocks, gravestones, tree bark, and the ground in the tundra where plant roots cannot penetrate. Lichens can survive extended periods of drought: they become completely desiccated and then rapidly become active once water is available again. Lichens fulfill many ecological roles, including acting as indicator species, which allow scientists to track the health of a habitat because of their sensitivity to air pollution.



Figure $24.2B.1$: Lichen: fungi and cyanobateria: Lichens have many forms. They may be (a) crust-like, (b) hair-like, or (c) leaf-like.

Lichens are not a single organism, but, rather, an example of a mutualism in which a fungus (usually a member of the Ascomycota or Basidiomycota phyla) lives in close contact with a photosynthetic organism (a eukaryotic alga or a prokaryotic cyanobacterium). Generally, neither the fungus nor the photosynthetic organism can survive alone outside of the symbiotic relationship. The body of a lichen, referred to as a thallus, is formed of hyphae wrapped around the photosynthetic partner. The photosynthetic organism provides carbon and energy in the form of carbohydrates. Some cyanobacteria fix nitrogen from the atmosphere, contributing nitrogenous compounds to the association. In return, the fungus supplies minerals and protection from dryness and excessive light by encasing the algae in its mycelium. The fungus also attaches the symbiotic organism to the substrate.

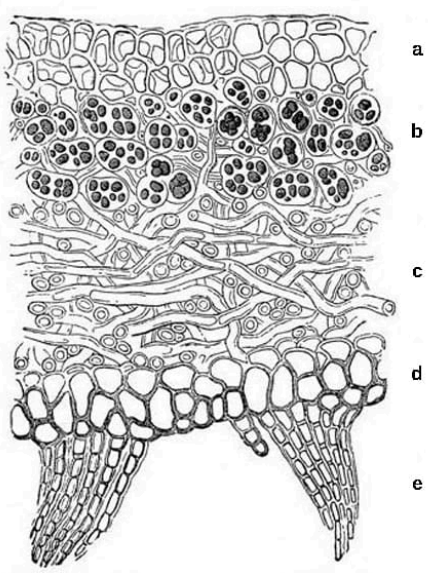


Figure $24.2B.1$: Thallus of lichen: This cross-section of a lichen thallus shows the (a) upper cortex of fungal hyphae, which provides protection; the (b) algal zone where photosynthesis occurs, the (c) medulla of fungal hyphae, and the (d) lower cortex, which also provides protection and may have (e) rhizines to anchor the thallus to the substrate.

The thallus of lichens grows very slowly, expanding its diameter a few millimeters per year. Both the fungus and the alga participate in the formation of dispersal units for reproduction. Lichens produce soredia, clusters of algal cells surrounded by mycelia. Soredia are dispersed by wind and water and form new lichens.

Fungi & Animal Mutualism

Fungi have evolved mutualisms with numerous insects. Arthropods (jointed, legged invertebrates, such as insects) depend on the fungus for protection from predators and pathogens, while the fungus obtains nutrients and a way to disseminate spores into new environments. The association between species of Basidiomycota and scale insects is one example. The fungal mycelium covers and protects the insect colonies. The scale insects foster a flow of nutrients from the parasitized plant to the fungus. In a second example, leaf-cutting ants of Central and South America literally farm fungi. They cut disks of leaves from plants and pile them up in gardens. Fungi are cultivated in these disk gardens, digesting the cellulose in the leaves that the ants cannot break down. Once smaller sugar molecules are produced and consumed by the fungi, the fungi in turn become a meal for the ants. The insects also patrol their garden, preying on competing fungi. Both ants and fungi benefit from the association. The fungus receives a steady supply of leaves and freedom from competition, while the ants feed on the fungi they cultivate.

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Key Points

- Mutualistic relationships are those where both members of an association benefit; Fungi form these types of relationships with various other Kingdoms of life.
- Mycorrhiza, formed from an association between plant roots and primitive fungi, help increase a plant's nutrient uptake; in return, the plant supplies the fungi with photosynthesis products for their metabolic use.
- In lichen, fungi live in close proximity with photosynthetic cyanobateria; the algae provide fungi with carbon and energy while the fungi supplies minerals and protection to the algae.

- Mutualistic relationships between fungi and animals involves numerous insects; Arthropods depend on fungi for protection, while fungi receive nutrients in return and ensure a way to disseminate the spores into new environments.

Key Terms

- **mycorrhiza**: a symbiotic association between a fungus and the roots of a vascular plant
- **lichen**: any of many symbiotic organisms, being associations of fungi and algae; often found as white or yellow patches on old walls, etc.
- **thallus**: vegetative body of a fungus

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24.3: CLASSIFICATIONS OF FUNGI

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- Topic hierarchy

24.3A: Chytridiomycota- The Chytrids

24.3B: Zygomycota - The Conjugated Fungi

24.3C: Ascomycota - The Sac Fungi

24.3D: Basidiomycota- The Club Fungi

24.3E: Deuteromycota - The Imperfect Fungi

24.3F: Glomeromycota

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24.3A: Chytridiomycota- The Chytrids

Learning Objectives

- Describe the ecology and reproduction of chytrids

Chytridiomycota: The Chytrids

The kingdom Fungi contains five major phyla, which were established according to their mode of sexual reproduction or use of molecular data. The Phylum Chytridiomycota (chytrids) is one of the five true phyla of fungi. There is only one class in the Phylum Chytridiomycota, the Chytridiomycetes. The chytrids are the simplest and most primitive Eumycota, or true fungi. The evolutionary record shows that the first, recognizable chytrids appeared during the late pre-Cambrian period, more than 500 million years ago. Like all fungi, chytrids have chitin in their cell walls, but one group of chytrids has both cellulose and chitin in the cell wall. Most chytrids are unicellular; a few form multicellular organisms and hyphae, which have no septa between cells (coenocytic). They reproduce both sexually and asexually; the asexual spores are called diploid zoospores. Their gametes are the only fungal cells known to have a flagellum.

The ecological habitat and cell structure of chytrids have much in common with protists. Chytrids usually live in aquatic environments, although some species live on land. Some species thrive as parasites on plants, insects, or amphibians, while others are saprobes. Some chytrids cause diseases in many species of amphibians, resulting in species decline and extinction. An example of a harmful parasitic chytrid is *Batrachochytrium dendrobatidis*, which is known to cause skin disease. Another chytrid species, *Allomyces*, is well characterized as an experimental organism. Its reproductive cycle includes both asexual and sexual phases. *Allomyces* produces diploid or haploid flagellated zoospores in a sporangium.

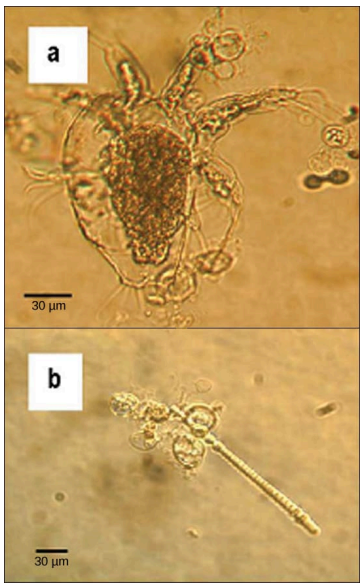


Figure 24.3A.1: Parasitic chytrids: The chytrid *Batrachochytrium dendrobatidis* is seen in these light micrographs as transparent spheres growing on (a) a freshwater arthropod and (b) algae. This chytrid causes skin diseases in many species of amphibians, resulting in species decline and extinction.

Key Points

- The first recognizable chytrids appeared more than 500 million years ago during the late pre-Cambrian period.
- Like protists, chytrids usually live in aquatic environments, but some species live on land.
- Some chytrids are saprobes while others are parasites that may be harmful to amphibians and other animals.
- Chytrids reproduce both sexually and asexually, which leads to the production of zoospores.

- Chytrids have chitin in their cell walls; one unique group also has cellulose along with chitin.
- Chytrids are mostly unicellular, but multicellular organisms do exist.

Key Terms

- **chytridiomycete**: an organism of the phylum Chytridiomycota
- **zoospore**: an asexual spore of some algae and fungi
- **flagellum**: a flagellum is a lash-like appendage that protrudes from the cell body of certain prokaryotic and eukaryotic cells
- **coenocytic**: a multinucleate cell that can result from multiple nuclear divisions without their accompanying cytokinesis

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24.3B: Zygomycota - The Conjugated Fungi

Learning Objectives

- Describe the ecology and reproduction of Zygomycetes

The zygomycetes are a relatively small group in the fungi kingdom and belong to the Phylum Zygomycota. They include the familiar bread mold, *Rhizopus stolonifer,* which rapidly propagates on the surfaces of breads, fruits, and vegetables. They are mostly terrestrial in habitat, living in soil or on plants and animals. Most species are saprobes meaning they live off decaying organic material. Some are parasites of plants, insects, and small animals, while others form symbiotic relationships with plants. Zygomycetes play a considerable commercial role. The metabolic products of other species of *Rhizopus* are intermediates in the synthesis of semi-synthetic steroid hormones.

Zygomycetes have a thallus of coenocytic hyphae in which the nuclei are haploid when the organism is in the vegetative stage. The fungi usually reproduce asexually by producing sporangiospores. The black tips of bread mold, *Rhizopus stolonifer*, are the swollen sporangia packed with black spores. When spores land on a suitable substrate, they germinate and produce a new mycelium.

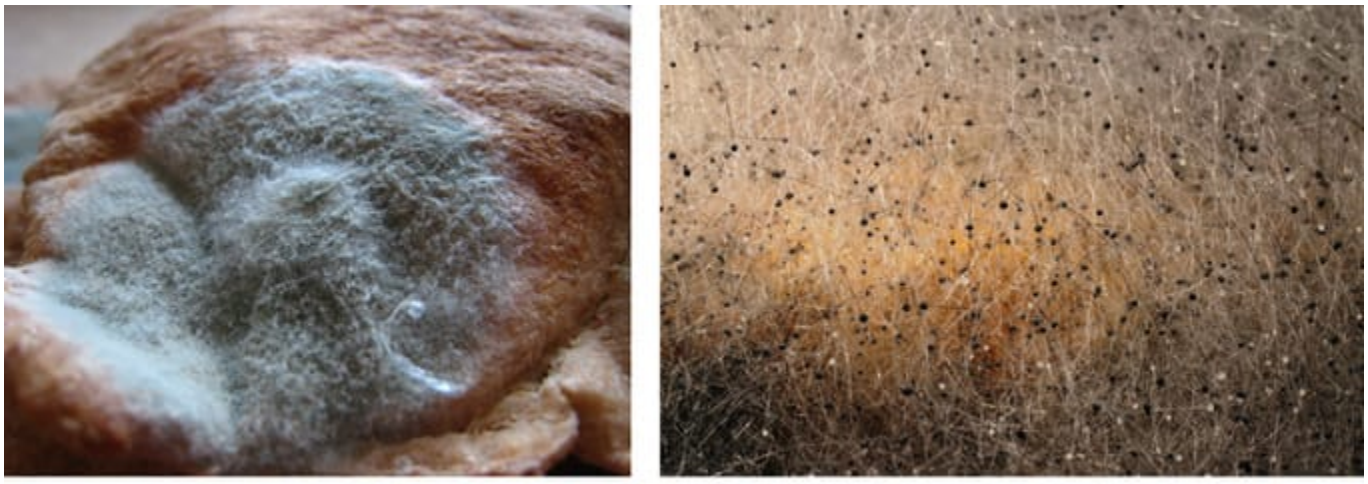


Figure $24.3B.1$: Sporangia of bread mold: Sporangia grow at the end of stalks, which appear as (a) white fuzz seen on this bread mold, *Rhizopus stolonifer*. The (b) tips of bread mold are the spore-containing sporangia.

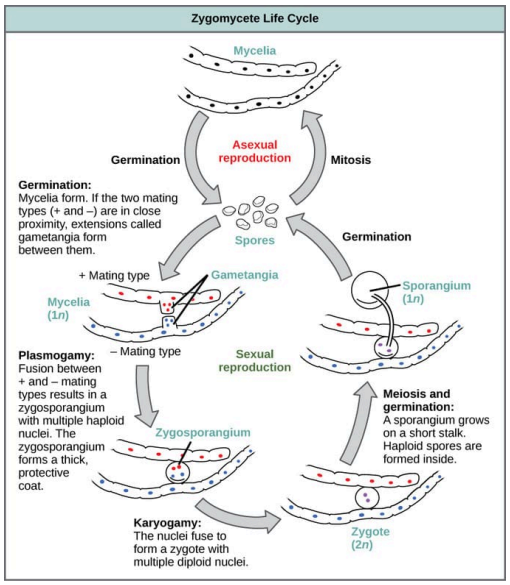


Figure $24.3B.1$: Zygomycete life cycle: Zygomycetes have asexual and sexual life cycles. In the sexual life cycle, plus and minus mating types conjugate to form a zygosporangium.

Sexual reproduction starts when conditions become unfavorable. Two opposing mating strains (type + and type –) must be in close proximity for gametangia (singular: gametangium) from the hyphae to be produced and fuse, leading to karyogamy. The developing diploid zygospores have thick coats that protect them from desiccation and other hazards. They may remain dormant until environmental conditions become favorable. When the zygospore germinates, it undergoes meiosis and produces haploid spores, which will, in turn, grow into a new organism. This form of sexual reproduction in fungi is called conjugation (although it differs markedly from conjugation in bacteria and protists), giving rise to the name “conjugated fungi”.

Key Points

- Most zygomycota are saprobes, while a few species are parasites.
- Zygomycota usually reproduce asexually by producing sporangiospores.
- Zygomycota reproduce sexually when environmental conditions become unfavorable.
- To reproduce sexually, two opposing mating strains must fuse or conjugate, thereby, sharing genetic content and creating zygospores.
- The resulting diploid zygospores remain dormant and protected by thick coats until environmental conditions have improved.
- When conditions become favorable, zygospores undergo meiosis to produce haploid spores, which will eventually grow into a new organism.

Key Terms

- **zygomycete**: an organism of the phylum Zygomycota
- **karyogamy**: the fusion of two nuclei within a cell
- **zygospore**: a spore formed by the union of several zoospores
- **conjugation**: the temporary fusion of organisms, especially as part of sexual reproduction

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24.3C: Ascomycota - The Sac Fungi

Learning Objectives

- Describe the ecology and the reproduction of Ascomycetes

The majority of known fungi belong to the Phylum Ascomycota, which is characterized by the formation of an ascus (plural, asci), a sac-like structure that contains haploid ascospores. Many ascomycetes are of commercial importance. Some play a beneficial role, such as the yeasts used in baking, brewing, and wine fermentation, plus truffles and morels, which are held as gourmet delicacies. *Aspergillus oryzae* is used in the fermentation of rice to produce sake. Other ascomycetes parasitize plants and animals, including humans. For example, fungal pneumonia poses a significant threat to AIDS patients who have a compromised immune system. Ascomycetes not only infest and destroy crops directly, they also produce poisonous secondary metabolites that make crops unfit for consumption. Filamentous ascomycetes produce hyphae divided by perforated septa, allowing streaming of cytoplasm from one cell to the other. Conidia and asci, which are used respectively for asexual and sexual reproductions, are usually separated from the vegetative hyphae by blocked (non-perforated) septa.

Asexual reproduction is frequent and involves the production of conidiophores that release haploid conidiospores. Sexual reproduction starts with the development of special hyphae from either one of two types of mating strains. The “male” strain produces an antheridium (plural: antheridia) and the “female” strain develops an ascogonium (plural: ascogonia). At fertilization, the antheridium and the ascogonium combine in plasmogamy without nuclear fusion. Special ascogenous hyphae arise, in which pairs of nuclei migrate: one from the “male” strain and one from the “female” strain. In each ascus, two or more haploid ascospores fuse their nuclei in karyogamy. During sexual reproduction, thousands of asci fill a fruiting body called the ascocarp. The diploid nucleus gives rise to haploid nuclei by meiosis. The ascospores are then released, germinate, and form hyphae that are disseminated in the environment and start new mycelia.

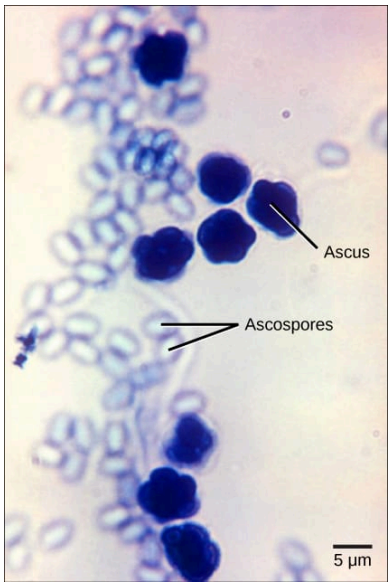


Figure $24.3C.1$: Release of ascospores: The bright field light micrograph shows ascospores being released from asci in the fungus Talaromyces flavus var. flavus.

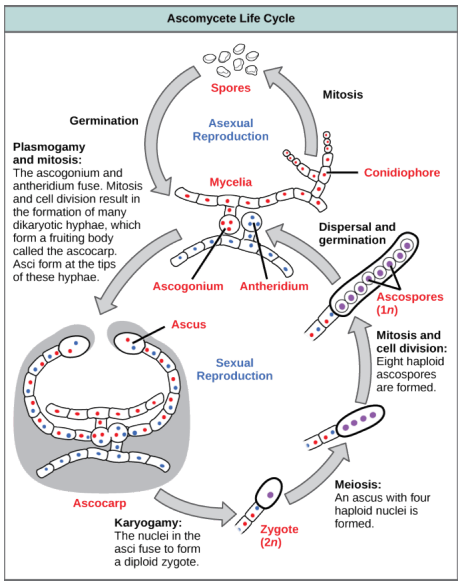


Figure $24.3C.1$: Lifecycle of an ascomycete: The lifecycle of an ascomycete is characterized by the production of asci during the sexual phase. The haploid phase is the predominant phase of the life cycle.

Key Points

- Ascomycota fungi are the yeasts used in baking, brewing, and wine fermentation, plus delicacies such as truffles and morels.
- Ascomycetes are filamentous and produce hyphae divided by perforated septa.
- Ascomycetes frequently reproduce asexually which leads to the production of conidiophores that release haploid conidiospores.
- Two types of mating strains, a “male” strain which produces an antheridium and a “female” strain which develops an ascogonium, are required for sexual reproduction.
- The antheridium and the ascogonium combine in plasmogamy at the time of fertilization, followed by nuclei fusion in the asci.
- In the ascocarp, a fruiting body, thousands of asci undergo meiosis to generate haploid ascospores ready to be released to the world.

Key Terms

- **plasmogamy**: stage of sexual reproduction joining the cytoplasm of two parent mycelia without the fusion of nuclei
- **Ascomycota**: a taxonomic division within the kingdom Fungi; those fungi that produce spores in a microscopic sporangium called an ascus
- **ascus**: a sac-shaped cell present in ascomycete fungi; it is a reproductive cell in which meiosis and an additional cell division produce eight spores
- **ascospore**: a sexually-produced spore from the ascus of an Ascomycetes fungus
- **conidia**: asexual, non-motile spores of a fungus, named after the Greek word for dust, conia; also known as conidiospores and mitospores
- **antheridia**: a haploid structure or organ producing and containing male gametes (called antherozoids or sperm) present in lower plants like mosses and ferns, primitive vascular psilotophytes, and fungi
- **ascogonium**: a haploid structure or organ producing and containing female gametes in certain Ascomycota fungi
- **ascocarp**: the sporocarp of an ascomycete, typically bowl-shaped
- **ascomycete**: any fungus of the phylum Ascomycota, characterized by the production of a sac, or ascus, which contains non-motile spores

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24.3D: Basidiomycota- The Club Fungi

Learning Objectives

- Describe the ecology and reproduction of the Basidiomycota

Basidiomycota: The Club Fungi

The fungi in the Phylum Basidiomycota are easily recognizable under a light microscope by their club-shaped fruiting bodies called basidia (singular, basidium), which are the swollen terminal cell of a hypha. The basidia, which are the reproductive organs of these fungi, are often contained within the familiar mushroom, commonly seen in fields after rain, on the supermarket shelves, and growing on your lawn. These mushroom-producing basidiomyces are sometimes referred to as “gill fungi” because of the presence of gill-like structures on the underside of the cap. The “gills” are actually compacted hyphae on which the basidia are borne. This group also includes shelf fungus, which cling to the bark of trees like small shelves. In addition, the basidiomycota includes smuts and rusts, which are important plant pathogens, and toadstools. Most edible fungi belong to the Phylum Basidiomycota; however, some basidiomycetes produce deadly toxins. For example, *Cryptococcus neoformans* causes severe respiratory illness.



Figure $24.3D.1$: Fruiting bodies of a basidiomycete: The fruiting bodies of a basidiomycete form a ring in a meadow, commonly called “fairy ring.” The best-known fairy ring fungus has the scientific name *Marasmius oreades*. The body of this fungus, its mycelium, is underground and grows outward in a circle. As it grows, the mycelium depletes the soil of nitrogen, causing the mycelia to grow away from the center, leading to the “fairy ring” of fruiting bodies where there is adequate soil nitrogen.

The lifecycle of basidiomycetes includes alternation of generations. Spores are generally produced through sexual reproduction, rather than asexual reproduction. The club-shaped basidium carries spores called basidiospores. In the basidium, nuclei of two different mating strains fuse (karyogamy), giving rise to a diploid zygote that then undergoes meiosis. The haploid nuclei migrate into basidiospores, which germinate and generate monokaryotic hyphae. The mycelium that results is called a primary mycelium. Mycelia of different mating strains can combine and produce a secondary mycelium that contains haploid nuclei of two different mating strains. This is the dikaryotic stage of the basidiomyces lifecyle and it is the dominant stage. Eventually, the secondary mycelium generates a basidiocarp, which is a fruiting body that protrudes from the ground; this is what we think of as a mushroom. The basidiocarp bears the developing basidia on the gills under its cap.

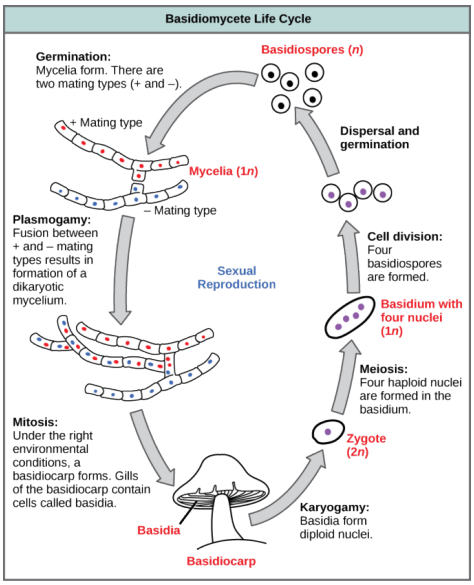


Figure $24.3D.1$: Lifecycle of a basidiomycete: The lifecycle of a basidiomycete alternates generation with a prolonged stage in which two nuclei (dikaryon) are present in the hyphae.

Key Points

- The majority of edible fungi belong to the Phylum Basidiomycota.
- The basidiomycota includes shelf fungus, toadstools, and smuts and rusts.
- Unlike most fungi, basidiomycota reproduce sexually as opposed to asexually.
- Two different mating strains are required for the fusion of genetic material in the basidium which is followed by meiosis producing haploid basidiospores.
- Mycelia of different mating strains combine to produce a secondary mycelium that contains haploid basidiospores in what is called the dikaryotic stage, where the fungi remains until a basidiocarp (mushroom) is generated with the developing basidia on the gills under its cap.

Key Terms

- **basidiocarp**: a fruiting body that protrudes from the ground, known as a mushroom, which has a developing basidia on the gills under its cap
- **basidiomycete**: a fungus of the phylum Basidiomycota, which produces sexual spores on a basidium
- **Basidiomycota**: a taxonomic division within the kingdom Fungi: 30,000 species of fungi that produce spores from a basidium
- **basidium**: a small structure, shaped like a club, found in the Basidiomycota phylum of fungi, that bears four spores at the tips of small projections
- **basidiospore**: a sexually-reproductive spore produced by fungi of the phylum Basidiomycota

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24.3E: Deuteromycota - The Imperfect Fungi

Learning Objectives

- Describe the ecology and reproduction of the Deuteromycota

Imperfect fungi are those that do not display a sexual phase. They are classified as belonging to the form Phylum Deuteromycota. Deuteromycota is a polyphyletic group where many species are more closely related to organisms in other phyla than to each other; hence it cannot be called a true phylum and must, instead, be given the name form phylum. Since they do not possess the sexual structures that are used to classify other fungi, they are less well described in comparison to other divisions. Most members live on land, with a few aquatic exceptions. They form visible mycelia with a fuzzy appearance and are commonly known as mold. Molecular analysis shows that the closest group to the deuteromycetes is the ascomycetes. In fact, some species, such as *Aspergillus*, which were once classified as imperfect fungi, are now classified as ascomycetes.

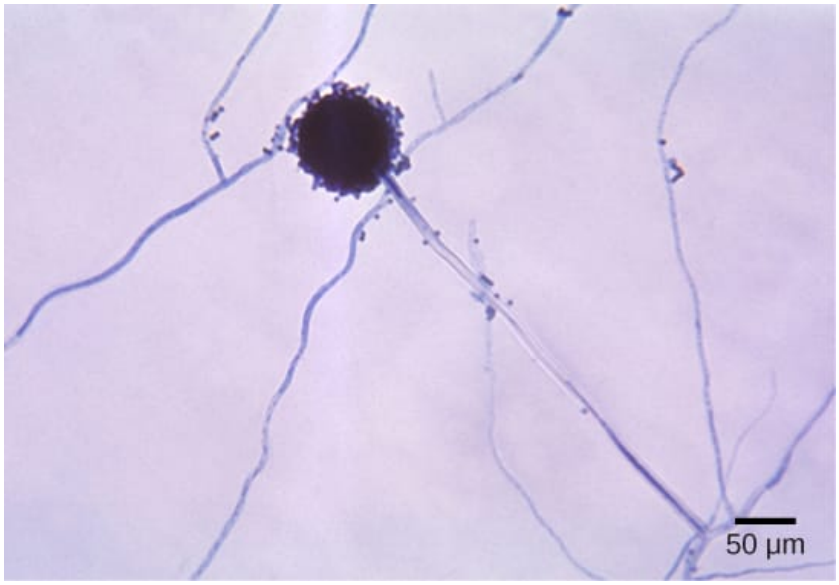


Figure $24.3E.1$: Example of an imperfect fungus: Aspergillus niger is an imperfect fungus commonly found as a food contaminant. The spherical structure in this light micrograph is a conidiophore.

Reproduction of Deuteromycota is strictly asexual, occuring mainly by production of asexual conidiospores. Some hyphae may recombine and form heterokaryotic hyphae. Genetic recombination is known to take place between the different nuclei.

Imperfect fungi have a large impact on everyday human life. The food industry relies on them for ripening some cheeses. The blue veins in Roquefort cheese and the white crust on Camembert are the result of fungal growth. The antibiotic penicillin was originally discovered on an overgrown Petri plate on which a colony of *Penicillium* fungi killed the bacterial growth surrounding it. Many imperfect fungi cause serious diseases, either directly as parasites (which infect both plants and humans), or as producers of potent toxic compounds, as seen in the aflatoxins released by fungi of the genus *Aspergillus*.

Key Points

- Deuteromycota do not possess the sexual structures that are used to classify other fungi.
- Most deuteromycota live on land; they form visible mycelia with a fuzzy appearance called mold.
- Recombination of genetic material is known to take place between the different nuclei after some hyphae recombine.

Key Terms

- **deuteromycete**: an organism of the phylum Deuteromycota
- **Deuteromycota**: a taxonomic morphological group within the kingdom Fungi; the fungi have no sexual reproduction
- **polyphyletic**: having multiple ancestral sources; referring to a taxon that does not contain the most recent common ancestor of its members
- **conidiospore**: a unicellular spore produced asexually by a fungus

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24.3F: Glomeromycota

Learning Objectives

- Describe the ecology and reproduction of Glomeromycetes

In the kingdom Fungi, the Glomeromycota is a newly-established phylum comprised of about 230 species that live in close association with the roots of trees and plants. Fossil records indicate that trees and their root symbionts share a long evolutionary history. It appears that most members of this family form arbuscular mycorrhizae: the hyphae interact with the root cells forming a mutually-beneficial association where the plants supply the carbon source and energy in the form of carbohydrates to the fungus while the fungus supplies essential minerals from the soil to the plant. This association is termed biotrophic. The Glomeromycota species that have arbuscular mycorrhizal are terrestrial and widely distributed in soils worldwide where they form symbioses with the roots of the majority of plant species. They can also be found in wetlands, including salt-marshes, and are associated with epiphytic plants.



Figure $24.3F.1$: Glyomeromycetes and tree roots: This image illustrates the bitrophic relationship between a glomeromycota (Gigaspora margarita) and the roots of a plant (Lotus corniculatus).

The glomeromycetes do not reproduce sexually and cannot survive without the presence of plant roots. They have coenocytic hyphae and reproduce asexually, producing glomerospores. The biochemical and genetic characterization of the Glomeromycota has been hindered by their biotrophic nature, which impedes laboratory culturing. This obstacle was eventually surpassed with the use of root cultures. With the advent of molecular techniques, such as gene sequencing, the phylogenetic classification of Glomeromycota has become clearer. The first mycorrhizal gene to be sequenced was the small-subunit ribosomal RNA (SSU rRNA). This gene is highly conserved and commonly used in phylogenetic studies so it was isolated from spores of each taxonomic group. Using a molecular clock approach based on the substitution rates of SSU sequences, scientists were able to estimate the time of divergence of the fungi. This analysis shows that all glomeromycetes probably descended from a common ancestor 462 and 353 million years ago, making them a monophyletic lineage. A long-held theory is that Glomeromycota were instrumental in the colonization of land by plants.

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Key Points

- Most glomeromycetes form arbuscular mycorrhizae, a type of symbiotic relationship between a fungus and plant roots; the plants supply a source of energy to the fungus while the fungus supplies essential minerals to the plant.
- Glomeromycota that have arbuscular mycorrhizal are mostly terrestrial, but can also be found in wetlands.
- The glomeromycetes reproduce asexually by producing glomerospores and cannot survive without the presence of plant roots.
- DNA analysis shows that all glomeromycetes probably descended from a common ancestor 462 and 353 million years ago.
- The classification of fungi as Glomeromycota has been redefined with adoption of molecular techniques.

Key Terms

- **biotrophic**: describing a parasite that needs its host to stay alive
- **arbuscular mycorrhizae**: a type of symbiotic relationship between a fungus and the roots of a plant where the plants supply a source of energy to the fungus while the fungus supplies essential minerals to the plant
- **glomeromycete**: an organism of the phylum Glomeromycota

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24.4: FUNGAL PARASITES AND PATHOGENS

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24.4A: Fungi as Plant, Animal, and Human Pathogens

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24.4A: Fungi as Plant, Animal, and Human Pathogens

Learning Objectives

- Give examples of fungi that are plant and animal parasites and pathogens

Fungal Parasites and Pathogens

The production of sufficient good-quality crops is essential to human existence. Plant diseases have ruined crops, bringing widespread famine. Many plant pathogens are fungi that cause tissue decay and eventual death of the host. In addition to destroying plant tissue directly, some plant pathogens spoil crops by producing potent toxins. Fungi are also responsible for food spoilage and the rotting of stored crops. For example, the fungus *Claviceps purpurea* causes ergot, a disease of cereal crops (especially of rye). Although the fungus reduces the yield of cereals, the effects of the ergot's alkaloid toxins on humans and animals are of much greater significance. In animals, the disease is referred to as ergotism. The most common signs and symptoms are convulsions, hallucinations, gangrene, and loss of milk in cattle. The active ingredient of ergot is lysergic acid, which is a precursor of the drug LSD. Smuts, rusts, and powdery or downy mildew are other examples of common fungal pathogens that affect crops.



Figure 24.4A.1: Fungal pathogens: Some fungal pathogens include (a) green mold on grapefruit, (b) powdery mildew on a zinnia, (c) stem rust on a sheaf of barley, and (d) grey rot on grapes.

Aflatoxins are toxic, carcinogenic compounds released by fungi of the genus *Aspergillus*. Periodically, harvests of nuts and grains are tainted by aflatoxins, leading to massive recall of produce. This sometimes ruins producers and causes food shortages in developing countries.

Animal and Human Parasites and Pathogens

Fungi can affect animals, including humans, in several ways. A mycosis is a fungal disease that results from infection and direct damage. Fungi attack animals directly by colonizing and destroying tissues. Mycotoxicosis is the poisoning of humans (and other animals) by foods contaminated by fungal toxins (mycotoxins). Mycetismus describes the ingestion of preformed toxins in poisonous mushrooms. In addition, individuals who display hypersensitivity to molds and spores develop strong and dangerous allergic reactions. Fungal infections are generally very difficult to treat because, unlike bacteria, fungi are eukaryotes. Antibiotics only target prokaryotic cells, whereas compounds that kill fungi also harm the eukaryotic animal host.

Many fungal infections are superficial; that is, they occur on the animal's skin. Termed cutaneous ("skin") mycoses, they can have devastating effects. For example, the decline of the world's frog population in recent years may be caused by the fungus *Batrachochytrium dendrobatidis*, which infects the skin of frogs and presumably interferes with gaseous exchange. Similarly, more than a million bats in the United States have been killed by white-nose syndrome, which appears as a white ring around the mouth of the bat. It is caused by the cold-loving fungus *Geomyces destructans*, which disseminates its deadly spores in caves where bats hibernate. Mycologists are researching the transmission, mechanism, and control of *G. destructans* to stop its spread.

Fungi that cause the superficial mycoses of the epidermis, hair, and nails rarely spread to the underlying tissue. These fungi are often misnamed "dermatophytes", from the Greek words dermis meaning skin and phyte meaning plant, although they are not plants. Dermatophytes are also called "ringworms" because of the red ring they cause on skin. They secrete extracellular enzymes that break down keratin (a protein found in hair, skin, and nails), causing conditions such as athlete's foot and jock itch. These conditions are usually treated with over-the-counter topical creams and powders; they are easily cleared. More persistent superficial mycoses may require prescription oral medications.

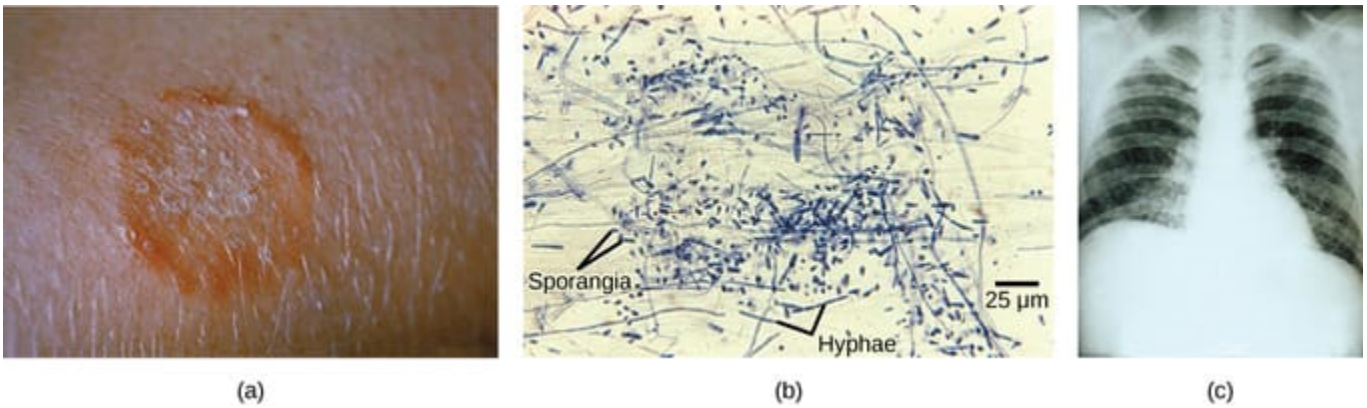


Figure 24.4A.1: Mycosis infection: (a) Ringworm presents as a red ring on skin; (b) *Trichophyton violaceum*, shown in this bright field light micrograph, causes superficial mycoses on the scalp; (c) *Histoplasma capsulatum* is an ascomycete that infects airways and causes symptoms similar to influenza.

Systemic mycoses spread to internal organs, most commonly entering the body through the respiratory system. For example, coccidioidomycosis (valley fever) is commonly found in the southwestern United States where the fungus resides in the dust. Once inhaled, the spores develop in the lungs and cause symptoms similar to those of tuberculosis. Histoplasmosis is caused by the dimorphic fungus *Histoplasma capsulatum*. It also causes pulmonary infections. In rarer cases, it causes swelling of the membranes of the brain and spinal cord. Treatment of these and many other fungal diseases requires the use of antifungal medications that have serious side effects.

Opportunistic mycoses are fungal infections that are either common in all environments or are part of the normal biota. They mainly affect individuals who have a compromised immune system. Patients in the late stages of AIDS suffer from opportunistic mycoses that can be life threatening. The yeast *Candida sp.*, a common member of the natural biota, can grow unchecked and infect the vagina or mouth (oral thrush) if the pH of the surrounding environment, the person's immune defenses, or the normal population of bacteria are altered.

Mycetismus can occur when poisonous mushrooms are eaten. It causes a number of human fatalities during mushroom-picking season. Many edible fruiting bodies of fungi resemble highly-poisonous relatives. Amateur mushroom hunters are cautioned to carefully inspect their harvest and avoid eating mushrooms of doubtful origin.

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Key Points

- In plants, fungi can destroy plant tissue directly or through the production of potent toxins, which usually ends in host death and can even lead to ergotism in animals like humans.
- During mycosis, fungi, like dermatophytes, successfully attack hosts directly by colonizing and destroying their tissues.
- Examples of fungal parasites and pathogens in animals that cause mycoses include *Batrachochytrium dendrobatidis*, *Geomyces destructans*, and *Histoplasma capsulatum*.
- Systemic mycoses, such as valley fever, Histoplasmosis, or pulmonary disease, are fungal diseases that spread to internal organs and commonly enter the body through the respiratory system.
- Opportunistic mycoses, fungal infections that are common in all environments, mainly take advantage of individuals who have a compromised immune system, such as AIDS patients.
- Fungi can also cause mycetismus, a disease caused by the ingestion of toxic mushrooms that leads to poisoning.

Key Terms

- **mycosis**: a fungal disease caused by infection and direct damage
- **dermatophyte**: a parasitic fungus that secretes extracellular enzymes that break down keratin, causing infections the skin, such as jock itch and athlete's foot
- **aflatoxin**: toxic, carcinogenic compounds released by fungi of the genus Aspergillus; contaminate nut and grain harvests
- **ergot**: any fungus in the genus Claviceps which are parasitic on grasses

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24.5: IMPORTANCE OF FUNGI IN HUMAN LIFE

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24.5A: Importance of Fungi in Human Life

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24.5A: Importance of Fungi in Human Life

Learning Objectives

- Explain the important roles fungi play in human life

Importance of Fungi in Human Life

Although we often think of fungi as organisms that cause disease and rot food, fungi are important to human life on many levels. They influence the well-being of human populations on a large scale because they are part of the nutrient cycle in ecosystems. They also have other ecosystem uses, such as pesticides.

Biological Insecticides

As animal pathogens, fungi help to control the population of damaging pests. These fungi are very specific to the insects they attack; they do not infect animals or plants. Fungi are currently under investigation as potential microbial insecticides, with several already on the market. For example, the fungus *Beauveria bassiana* is a pesticide being tested as a possible biological control agent for the recent spread of emerald ash borer.



Figure 24.5A.1: Fungal Insecticides: The emerald ash borer is an insect that attacks ash trees. It is in turn parasitized by a pathogenic fungus that holds promise as a biological insecticide. The parasitic fungus appears as white fuzz on the body of the insect.

Farming

The mycorrhizal relationship between fungi and plant roots is essential for the productivity of farm land. Without the fungal partner in root systems, 80–90 percent of trees and grasses would not survive. Mycorrhizal fungal inoculants are available as soil additives from gardening supply stores and are promoted by supporters of organic agriculture.

Food

Fungi figure prominently in the human diet. Morels, shiitake mushrooms, chanterelles, and truffles are considered delicacies. The meadow mushroom, *Agaricus campestris*, appears in many dishes. Molds of the genus *Penicillium*ripen many cheeses. They

originate in the natural environment such as the caves of Roquefort, France, where wheels of sheep milk cheese are stacked to capture the molds responsible for the blue veins and pungent taste of the cheese.



Figure 24.5A.1: Morel mushroom: The morel mushroom is an ascomycete much appreciated for its delicate taste.

Fermentation of grains to produce beer and of fruits to produce wine is an ancient art that humans in most cultures have practiced for millennia. Ancient humans acquired wild yeasts from the environment and used them to ferment sugars into CO_2 and ethanol under anaerobic conditions. It is now possible to purchase isolated strains of wild yeasts from different wine-making regions. Louis Pasteur was instrumental in developing a reliable strain of brewer's yeast, *Saccharomyces cerevisiae*, for the French brewing industry in the late 1850s.

Saccharomyces cerevisiae, also know as baker's yeast, is an important ingredient in bread, a food that has been considered a staple of human life for thousands of years. Before isolated yeast became available in modern times, humans simply let the dough collect yeast from the air and rise over a period of hours or days. A small piece of this leavened dough was saved and used as a starter (source of the same yeast) for the next batch, much in the same way sourdough bread is made today.

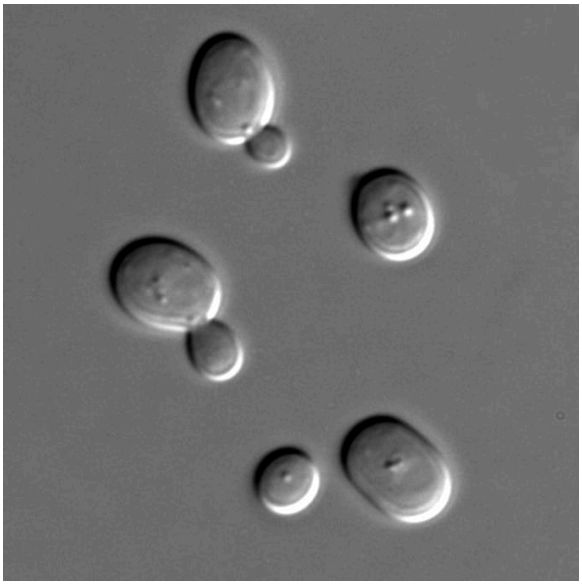


Figure 24.5A.1: Saccharomyces cerevisiae: The yeast Saccharomyces cerevisiae is approximately 5 µm in diameter and is important for the production of wine, beer, and bread. The yeast also has many applications in medical research.

Medicine

Many secondary metabolites of fungi are of great commercial importance. Fungi naturally produce antibiotics to kill or inhibit the growth of bacteria, limiting their competition in the natural environment. Important antibiotics, such as penicillin and the cephalosporins, can be isolated from fungi. Valuable drugs isolated from fungi include the immunosuppressant drug cyclosporine (which reduces the risk of rejection after organ transplant), the precursors of steroid hormones, and ergot alkaloids used to stop bleeding. Psilocybin is a compound found in fungi such as *Psilocybe semilanceata* and *Gymnopilus junonius*, which have been used for their hallucinogenic properties by various cultures for thousands of years.

As simple eukaryotic organisms, fungi are important model research organisms. Many advances in modern genetics were achieved by the use of the red bread mold *Neurospora crassa*. Additionally, many important genes originally discovered in *S. cerevisiae* served as a starting point in discovering analogous human genes. As a eukaryotic organism, the yeast cell produces and modifies proteins in a manner similar to human cells, as opposed to the bacterium *Escherichia coli*, which lacks the internal membrane structures and enzymes to tag proteins for export. This makes yeast a much better organism for use in recombinant DNA technology experiments. Like bacteria, yeasts grow easily in culture, have a short generation time, and are amenable to genetic modification.

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Key Points

- The majority of grasses and trees require a mycorrhizal relationship with fungi to survive.
- Yeasts have been used for thousands of years in the production of beer, wine, and bread.
- Fungi not only directly produce substances that humans use as medicine, but they are also versatile tools in the vast field of medical research.
- Some fungi attack insects and, therefore, can be used as natural pesticides.

Key Terms

- **inoculant**: the active material used in an inoculation
- **ergot**: any fungus in the genus Claviceps which are parasitic on grasses
- **immunosuppressant**: capable of immunosuppression, or the reduction of immune system efficacy

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25: SEEDLESS PLANTS

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25.1: EARLY PLANT LIFE

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25.1A: Early Plant Life

Learning Objectives

- Describe the pervasiveness of seedless plants during the history of the kingdom Plantae

Introduction to Early Plant Life

An incredible variety of seedless plants populates the terrestrial landscape. Mosses may grow on a tree trunk and horsetails may display their jointed stems and spindly leaves across the forest floor. Today, however, seedless plants represent only a small fraction of the plants in our environment. The kingdom Plantae constitutes a large and varied group of organisms with more than 300,000 species of cataloged plants. Of these, more than 260,000 are seed plants. However, three hundred million years ago, seedless plants dominated the landscape and grew in the enormous swampy forests of the Carboniferous period. Their decomposition created large deposits of coal that we mine today.



Figure 25.1A.1: Horsetails are seedless plants: Seedless plants, like these horsetails (*Equisetum* sp.), thrive in damp, shaded environments under a tree canopy where dryness is rare.

Current evolutionary thought holds that all plants, green algae as well as land dwellers, are monophyletic; that is, they are descendants of a single common ancestor. The evolutionary transition from water to land imposed severe constraints on plants. They had to develop strategies: to avoid drying out, to disperse reproductive cells in air, for structural support, and for capturing and filtering sunlight. While seed plants developed adaptations that allowed them to populate even the most arid habitats on Earth, full independence from water did not happen in all plants. Most seedless plants still require a moist environment.

Seedless plants are classified into three main categories: green algae, seedless non-vascular plants, and seedless vascular plants. Seedless non-vascular plants (bryophytes), such as mosses, are the group of plants that are the closest extant relative of early terrestrial plants. Seedless vascular plants include horsetails and ferns.

Key Points

- Non-vascular seedless plants, or bryophytes, are the group of plants that are the closest extant relative of early terrestrial plants.
- The vast majority of terrestrial plants today are seed plants, which tend to be better adapted to the arid land environment.
- Seedless plants are classified into three main catagories: green algae, seedless non- vascular plants, and seedless vascular

plants.

Key Terms

- **vascular plant**: any plant possessing vascular tissue (xylem and phloem), including ferns, conifers, and flowering plants
- **bryophyte**: seedless, nonvascular plants that are the closest extant relative of early terrestrial plants

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25.1B: Evolution of Land Plants

Learning Objectives

- Summarize the development of adaptations in land plants

Evolution of Land Plants

No discussion of the evolution of plants on land can be undertaken without a brief review of the timeline of the geological eras. The early era, known as the Paleozoic, is divided into six periods. It starts with the Cambrian period, followed by the Ordovician, Silurian, Devonian, Carboniferous, and Permian. The major event to mark the Ordovician, more than 500 million years ago, was the colonization of land by the ancestors of modern land plants. Fossilized cells, cuticles, and spores of early land plants have been dated as far back as the Ordovician period in the early Paleozoic era. The evolution of plants occurred by a gradual development of novel structures and reproduction mechanisms. Embryo protection developed prior to the development of vascular plants which, in turn, evolved before seed plants and flowering plants. The oldest-known vascular plants have been identified in deposits from the Devonian. One of the richest sources of information is the Rhynie chert, a sedimentary rock deposit found in Rhynie, Scotland, where embedded fossils of some of the earliest vascular plants have been identified.



Figure $25.1B.1$: The Rhynie chert sedimentary rock deposit: This Rhynie chert contains fossilized material from vascular plants. The area inside the circle contains bulbous underground stems called corms and root-like structures called rhizoids.

image

Gradual evolution of land plants: The adaptation of plants to life on land occurred gradually through the stepwise development of physical structures and reproduction mechanisms

How organisms acquired traits that allow them to colonize new environments, and how the contemporary ecosystem is shaped, are fundamental questions of evolution. Paleobotany (the study of extinct plants) addresses these questions through the analysis of fossilized specimens retrieved from field studies, reconstituting the morphology of organisms that disappeared long ago. Paleobotanists trace the evolution of plants by following the modifications in plant morphology, which sheds light on the connection between existing plants by identifying common ancestors that display the same traits. This field seeks to find transitional species that bridge gaps in the path to the development of modern organisms. Paleobotanists collect fossil specimens in the field and place them in the context of the geological sediments and other fossilized organisms surrounding them.

Paleobotanists distinguish between extinct species, as fossils, and extant species, which are still living. The extinct vascular plants, classified as zosterophylls and trimerophytes, most probably lacked true leaves and roots, forming low vegetation mats similar in size to modern-day mosses, although some trimetophytes could reach one meter in height. The later genus *Cooksonia*, which flourished during the Silurian, has been extensively studied from well-preserved examples. Imprints of *Cooksonia* show slender, branching stems ending in what appear to be sporangia. From the recovered specimens, it is not possible to establish for certain whether *Cooksonia*possessed vascular tissues. Fossils indicate that by the end of the Devonian period, ferns, horsetails, and seed plants populated the landscape, giving rising to trees and forests. This luxuriant vegetation helped enrich the atmosphere in oxygen, making it easier for air-breathing animals to colonize dry land. Plants also established early symbiotic relationships with fungi, creating mycorrhizae: a relationship in which the fungal network of filaments increases the efficiency of the plant root system. The plants provide the fungi with byproducts of photosynthesis.

Key Points

- Land plants first appeared during the Ordovician period, more than 500 million years ago.
- The evolution of plants occurred by a stepwise development of physical structures and reproductive mechanisms such as vascular tissue, seed production, and flowering.
- Paleobotonists trace the evolution of plant morphology through a study of the fossil record in the context of the surrounding geological sediments.

Key Terms

- **Paleobotany**: the branch of paleontology or paleobiology dealing with the recovery and identification of plant remains from geological contexts
- **mycorrhiza**: a symbiotic association between a fungus and the roots of a vascular plant

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25.1C: Plant Adaptations to Life on Land

Learning Objectives

- Discuss how lack of water in the terrestrial environment led to significant adaptations in plants

Plant Adaptations to Life on Land

As organisms adapted to life on land, they had to contend with several challenges in the terrestrial environment. The cell ‘s interior is mostly water: in this medium, small molecules dissolve and diffuse and the majority of the chemical reactions of metabolism take place. Desiccation, or drying out, is a constant danger for organisms exposed to air. Even when parts of a plant are close to a source of water, the aerial structures are prone to desiccation. Water also provides buoyancy to organisms. On land, plants need to develop structural support in a medium that does not give the same lift as water. The organism is also subject to bombardment by mutagenic radiation because air does not filter out the ultraviolet rays of sunlight. Additionally, the male gametes must reach the female gametes using new strategies because swimming is no longer possible. As such, both gametes and zygotes must be protected from desiccation. Successful land plants have developed strategies to face all of these challenges. Not all adaptations appeared at once; some species never moved very far from the aquatic environment, although others went on to conquer the driest environments on Earth.

Despite these survival challenges, life on land does offer several advantages. First, sunlight is abundant. Water acts as a filter, altering the spectral quality of light absorbed by the photosynthetic pigment chlorophyll. Second, carbon dioxide is more readily available in air than water since it diffuses faster in air. Third, land plants evolved before land animals; therefore, until dry land was also colonized by animals, no predators threatened plant life. This situation changed as animals emerged from the water and fed on the abundant sources of nutrients in the established flora. In turn, plants developed strategies to deter predation: from spines and thorns to toxic chemicals.

Early land plants, like the early land animals, did not live far from an abundant source of water and developed survival strategies to combat dryness. One of these strategies is called desiccation tolerance. Many mosses can dry out to a brown and brittle mat, but as soon as rain or a flood makes water available, mosses will absorb it and are restored to their healthy green appearance. Another strategy is to colonize environments where droughts are uncommon. Ferns, which are considered an early lineage of plants, thrive in damp and cool places such as the understory of temperate forests. Later, plants moved away from moist or aquatic environments and developed resistance to desiccation, rather than tolerance. These plants, like cacti, minimize the loss of water to such an extent they can survive in extremely dry environments.

The most successful adaptation solution was the development of new structures that gave plants the advantage when colonizing new and dry environments. Four major adaptations are found in all terrestrial plants: the alternation of generations, a sporangium in which the spores are formed, a gametangium that produces haploid cells, and apical meristem tissue in roots and shoots. The evolution of a waxy cuticle and a cell wall with lignin also contributed to the success of land plants. These adaptations are noticeably lacking in the closely-related green algae, which gives reason for the debate over their placement in the plant kingdom.

Alternation of Generations

Alternation of generations describes a life cycle in which an organism has both haploid and diploid multicellular stages (n represents the number of copies of chromosomes). Haplontic refers to a lifecycle in which there is a dominant haploid stage (1n), while diplontic refers to a lifecycle in which the diploid (2n) is the dominant life stage. Humans are diplontic. Most plants exhibit alternation of generations, which is described as haplodiplodontic. The haploid multicellular form, known as a gametophyte, is followed in the development sequence by a multicellular diploid organism: the sporophyte. The gametophyte gives rise to the gametes (reproductive cells) by mitosis. This can be the most obvious phase of the life cycle of the plant, as in the mosses. In fact, the sporophyte stage is barely noticeable in lower plants (the collective term for the plant groups of mosses, liverworts, and lichens). Alternatively, the gametophyte stage can occur in a microscopic structure, such as a pollen grain, in the higher plants (a common collective term for the vascular plants). Towering trees are the diplontic phase in the life cycles of plants such as sequoias and pines.

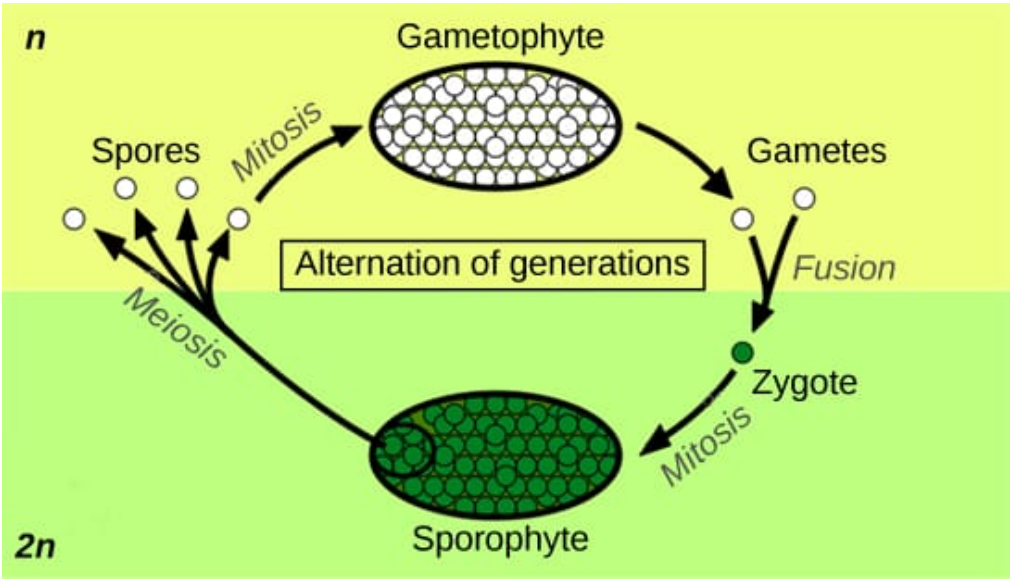


Figure $25.1C.1$: Alternation of generations of plants: Plants exhibit an alternation of generations between a 1n gametophyte and 2n sporophyte.

Protection of the embryo is a major requirement for land plants. The vulnerable embryo must be sheltered from desiccation and other environmental hazards. In both seedless and seed plants, the female gametophyte provides protection and nutrients to the embryo as it develops into the new generation of sporophyte. This distinguishing feature of land plants gave the group its alternate name of embryophytes.

Key Points

- While some plants remain dependent on a moist and humid environment, many have adapted to a more arid climate by developing tolerance or resistance to drought conditions.
- Alternation of generations describes a life cycle in which an organism has both haploid (1n) and diploid (2n) multicellular stages, although in different species the haploid or diploid stage can be dominant.
- The life on land presents significant challenges for plants, including the potential for desiccation, mutagenic radiation from the sun, and a lack of buoyancy from the water.

Key Terms

- **desiccation tolerance**: the ability of an organism to withstand or endure extreme dryness, or drought-like condition
- **alternation of generation**: the life cycle of plants with a multicellular sporophyte, which is diploid, that alternates with a multicellular gametophyte, which is haploid

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25.1D: Sporophytes and Gametophytes in Seedless Plants

Learning Objectives

- Describe the role of the sporophyte and gametophyte in plant reproduction

Sporangia in Seedless Plants

The sporophyte of seedless plants is diploid and results from syngamy (fusion) of two gametes. The sporophyte bears the sporangia (singular, sporangium): organs that first appeared in the land plants. The term “sporangia” literally means “spore in a vessel”: it is a reproductive sac that contains spores. Inside the multicellular sporangia, the diploid sporocytes, or mother cells, produce haploid spores by meiosis, where the 2n chromosome number is reduced to 1n (note that many plant sporophytes are polyploid: for example, durum wheat is tetraploid, bread wheat is hexaploid, and some ferns are 1000-ploid). The spores are later released by the sporangia and disperse in the environment.



Figure $25.1D.1$: Sporangia: Spore-producing sacs called sporangia grow at the ends of long, thin stalks in this photo of the moss Esporangios bryum.

Two different spore-forming methods are used in land plants, resulting in the separation of sexes at different points in the lifecycle. Seedless, non- vascular plants produce only one kind of spore and are called homosporous. The gametophyte phase (1n) is dominant in these plants. After germinating from a spore, the resulting gametophyte produces both male and female gametangia, usually on the same individual. In contrast, heterosporous plants produce two morphologically different types of spores. The male spores are called microspores, because of their smaller size, and develop into the male gametophyte; the comparatively larger megaspores develop into the female gametophyte. Heterospory is observed in a few seedless vascular plants and in all seed plants.

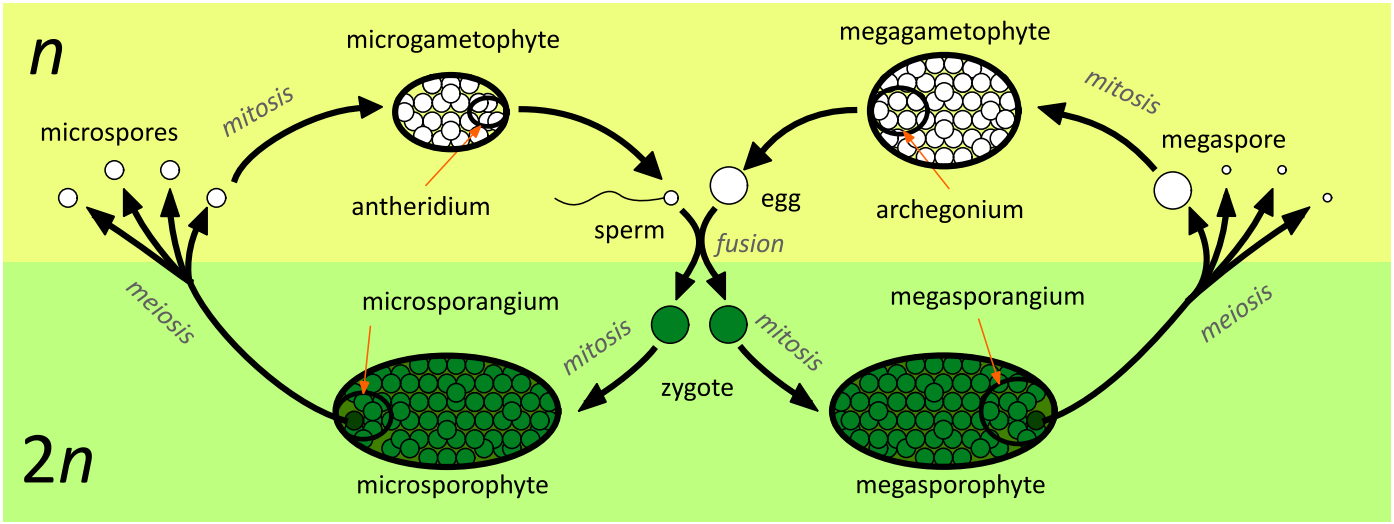


Figure $25.1D.1$: Lifecycle of heterosporous plants: Heterosporous plants produce two morphologically different types of spores: microspores, which develop into the male gametophyte, and megaspores, which develop into the female gametophyte.

When the haploid spore germinates in a hospitable environment, it generates a multicellular gametophyte by mitosis. The gametophyte supports the zygote formed from the fusion of gametes and the resulting young sporophyte (vegetative form). The cycle then begins anew.

The spores of seedless plants are surrounded by thick cell walls containing a tough polymer known as sporopollenin. This complex substance is characterized by long chains of organic molecules related to fatty acids and carotenoids: hence the yellow color of most pollen. Sporopollenin is unusually resistant to chemical and biological degradation. In seed plants, which use pollen to transfer the male sperm to the female egg, the toughness of sporopollenin explains the existence of well-preserved pollen fossils. Sporopollenin was once thought to be an innovation of land plants; however, the green algae, Coleochaetes, also forms spores that contain sporopollenin.

Gametangia in Seedless Plants

Gametangia (singular, gametangium) are organs observed on multicellular haploid gametophytes. In the gametangia, precursor cells give rise to gametes by mitosis. The male gametangium (antheridium) releases sperm. Many seedless plants produce sperm equipped with flagella that enable them to swim in a moist environment to the archegonia: the female gametangium. The embryo develops inside the archegonium as the sporophyte. Gametangia are prominent in seedless plants, but are replaced by pollen grains in seed-producing plants.

Key Points

- The diploid stage of a plant (2n), the sporophyte, bears a sporangium, an organ that produces spores during meiosis.
- Homosporous plants produce one type of spore which develops into a gametophyte (1n) with both male and female organs.
- Heterosporous plants produce separate male and female gametophytes, which produce sperm and eggs, respectively.
- In seedless plants, male gametangia (antheridium) release sperm, which can then swim to and fertilize an egg at the female gametangia (archegonia); this mode of reproduction is replaced by pollen production in seed plants.

Key Terms

- **gametophyte**: a plant (or the haploid phase in its life cycle) that produces gametes by mitosis in order to produce a zygote
- **gametangium**: an organ or cell in which gametes are produced that is found in many multicellular protists, algae, fungi, and the gametophytes of plants
- **sporopollenin**: a combination of biopolymers observed in the tough outer layer of the spore and pollen wall
- **syngamy**: the fusion of two gametes to form a zygote
- **sporophyte**: a plant (or the diploid phase in its life cycle) that produces spores by meiosis in order to produce gametophytes

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25.1E: Structural Adaptations for Land in Seedless Plants

Learning Objectives

- Discuss the primary structural adaptations made by plants to living on land

Land Plant Adaptations

As plants adapted to dry land and became independent from the constant presence of water in damp habitats, new organs and structures made their appearance. Early land plants did not grow more than a few inches off the ground, competing for light on these low mats. By developing a shoot and growing taller, individual plants captured more light. Because air offers substantially less support than water, land plants incorporated more rigid molecules in their stems (and later, tree trunks).

Apical Meristems

Shoots and roots of plants increase in length through rapid cell division in a tissue called the apical meristem, which is a small zone of cells found at the shoot tip or root tip. The apical meristem is made of undifferentiated cells that continue to proliferate throughout the life of the plant. Meristematic cells give rise to all the specialized tissues of the organism. Elongation of the shoots and roots allows a plant to access additional space and resources: light, in the case of the shoot, and water and minerals, in the case of roots. A separate meristem, called the lateral meristem, produces cells that increase the diameter of tree trunks.

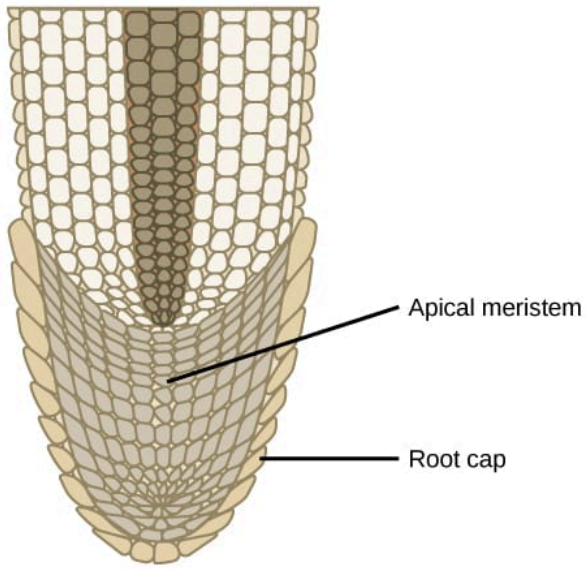


Figure $25.1E.1$: Apical meristem: Addition of new cells in a root occurs at the apical meristem. Subsequent enlargement of these cells causes the organ to grow and elongate. The root cap protects the fragile apical meristem as the root tip is pushed through the soil by cell elongation.

Vascular structures

In small plants such as single-celled algae, simple diffusion suffices to distribute water and nutrients throughout the organism. However, for plants to develop larger forms, the evolution of vascular tissue for the distribution of water and solutes was a prerequisite. The vascular system contains xylem and phloem tissues. Xylem conducts water and minerals absorbed from the soil up to the shoot, while phloem transports food derived from photosynthesis throughout the entire plant. A root system evolved to take up water and minerals from the soil, while anchoring the increasingly taller shoot in the soil.

Additional land plant adaptations

In land plants, a waxy, waterproof cover called a cuticle protects the leaves and stems from desiccation. However, the cuticle also prevents intake of carbon dioxide needed for the synthesis of carbohydrates through photosynthesis. To overcome this, stomata, or pores, that open and close to regulate traffic of gases and water vapor, appeared in plants as they moved away from moist environments into drier habitats.

Water filters ultraviolet-B (UVB) light, which is harmful to all organisms, especially those that must absorb light to survive. This filtering does not occur for land plants. This presented an additional challenge to land colonization, which was met by the evolution of biosynthetic pathways for the synthesis of protective flavonoids and other compounds: pigments that absorb UV wavelengths of light and protect the aerial parts of plants from photodynamic damage.

Plants cannot avoid being eaten by animals. Instead, they synthesize a large range of poisonous secondary metabolites: complex organic molecules such as alkaloids, whose noxious smells and unpleasant taste deter animals. These toxic compounds can also cause severe diseases and even death, thus discouraging predation. Humans have used many of these compounds for centuries as drugs, medications, or spices. In contrast, as plants co-evolved with animals, the development of sweet and nutritious metabolites lured animals into providing valuable assistance in dispersing pollen grains, fruit, or seeds. Plants have been enlisting animals to be their helpers in this way for hundreds of millions of years.

Key Points

- Many plants developed a vascular system: to distribute water from the roots (via the xylem) and sugars from the shoots (via the phloem) throughout the entire plant.
- An apical meristem enables elongation of the shoots and roots, allowing a plant to access additional space and resources.
- Because of the waxy cuticle covering leaves to prevent water loss, plants evolved stomata, or pores on the leaves, which open and close to regulate traffic of gases and water vapor.
- Plants evolved pathways for the synthesis of complex organic molecules, called secondary metabolites, for protection from both UV lights and predators.

Key Terms

- **phloem**: a vascular tissue in land plants primarily responsible for the distribution of sugars and nutrients manufactured in the shoot
- **stoma**: a pore found in the leaf and stem epidermis used for gaseous exchange
- **xylem**: a vascular tissue in land plants primarily responsible for the distribution of water and minerals taken up by the roots; also the primary component of wood
- **meristem**: the plant tissue composed of totipotent cells that allows plant growth

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25.1F: The Major Divisions of Land Plants

Learning Objectives

- Identify the major divisions of land plants

The Major Divisions of Land Plants

The green algae, known as the charophytes, and land plants are grouped together into a subphylum called the Streptophytina and are, therefore, called Streptophytes. Land plants, which are called embryophytes, are classified into two major groups according to the absence or presence of vascular tissue. Plants that lack vascular tissue, which is formed of specialized cells for the transport of water and nutrients, are referred to as non-vascular plants or bryophytes. Non-vascular embryophytes probably appeared early in land plant evolution and are all seedless. These plants include liverworts, mosses, and hornworts.

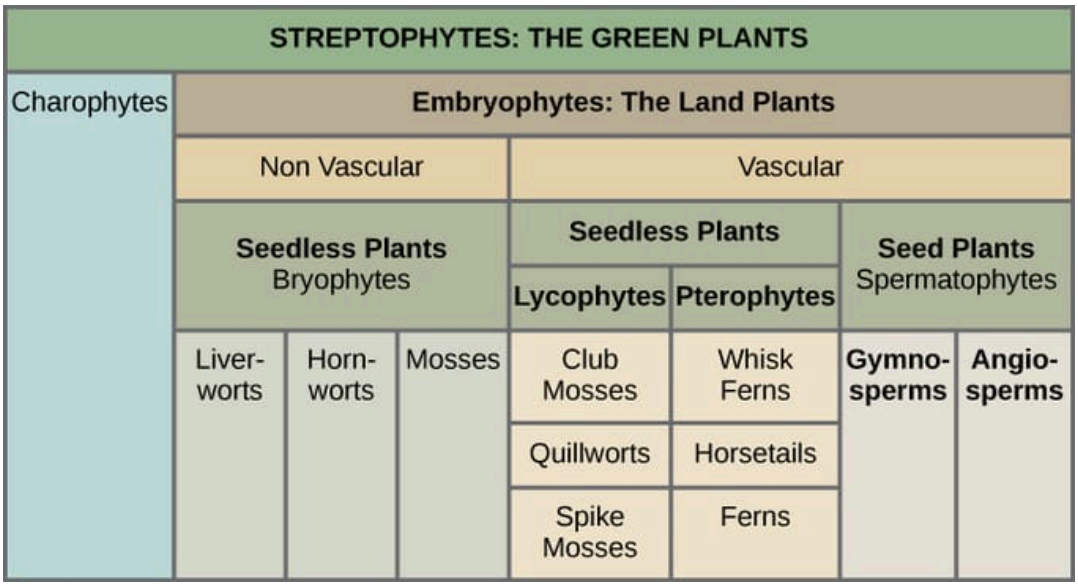


Figure 25.1F.1: Major divisions of land plants: Land plants are categorized by presence or absence of vascular tissue and their reproduction with or without the use of seeds.

In contrast, vascular plants developed a network of cells, called xylem and phloem, that conduct water and solutes throughout the plant. The first vascular plants appeared in the late Ordovician period of the Paleozoic Era (approximately 440-485 million years ago). These early plants were probably most similar to modern day lycophytes, which include club mosses (not to be confused with the mosses), and pterophytes, which include ferns, horsetails, and whisk ferns. Lycophytes and pterophytes are both referred to as seedless vascular plants because they do not produce any seeds.

The seed producing plants, or spermatophytes, form the largest group of all existing plants, dominating the landscape. Seed-producing plants include gymnosperms, most notably conifers, which produce “naked seeds,” and the most successful of all modern-day plants, angiosperms, which are the flowering plants. Angiosperms protect their seeds inside chambers at the center of a flower; the walls of the chamber later develop into a fruit.

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Key Points

- Non- vascular plants, or bryophytes, appeared early in plant evolution and reproduce without seeds; they include mosses, liverworts, and hornworts.
- Vascular plants are subdivided into two classes: seedless plants, which probably evolved first (including lycophytes and pterophytes), and seed plants.
- Seed-producing plants include gymnosperms, which produce “naked” seeds, and angiosperms, which reproduce by flowering.

Key Terms

- **spermatophyte**: any plant that bears seeds rather than spores
- **embryophyte**: any member of the subkingdom Embryophyta; most land plants
- **bryophyte**: seedless, nonvascular plants that are the closest extant relative of early terrestrial plants

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25.2: GREEN ALGAE- PRECURSORS OF LAND PLANTS

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- Topic hierarchy

25.2A: Streptophytes and Reproduction of Green Algae
25.2B: Charales

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25.2A: Streptophytes and Reproduction of Green Algae

Learning Objectives

- Discuss the general similarities of green algae and land plants

Streptophytes

Until recently, all photosynthetic eukaryotes were considered members of the kingdom Plantae. The brown, red, and gold algae, however, have been reassigned to the Protista kingdom. This is because, apart from their ability to capture light energy and fix CO_2, they lack many structural and biochemical traits that distinguish plants from protists. The position of green algae is more ambiguous. Green algae include unicellular and colonial flagellates, most with two flagella per cell, as well as various colonial, coccoid, and filamentous forms, along with macroscopic seaweeds, all of which add to the ambiguity of green algae classification since plants are multicellular.

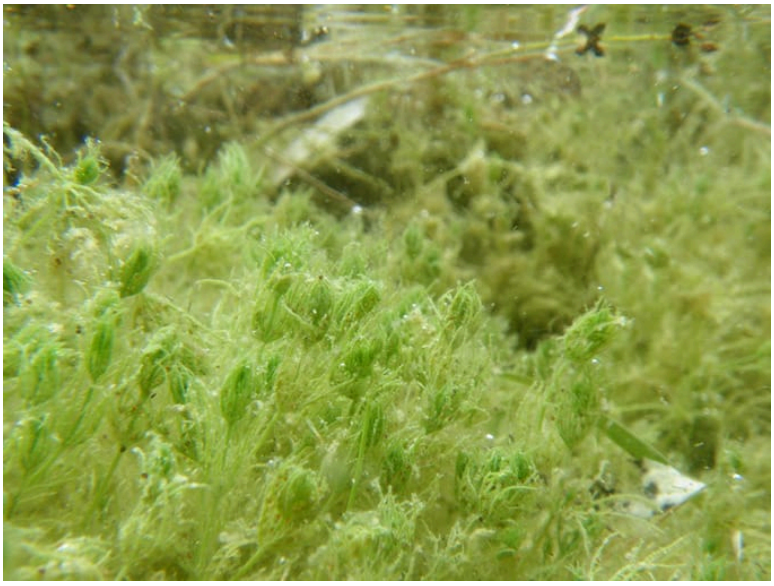


Figure 25.2A.1: Chara vulgaris: A representative charophyte alga is Chara vulgris, or common stonewort, which is a multicellular branching species that can grow up to 120m long.

Green algae contain the same carotenoids and chlorophyll a and b as land plants, whereas other algae have different accessory pigments and types of chlorophyll molecules in addition to chlorophyll a. Both green algae and land plants also store carbohydrates as starch. Cells in green algae divide along cell plates called phragmoplasts and their cell walls are layered with cellulose in the same manner as the cell walls of embryophytes. Consequently, land plants (embryophytes) and closely-related green algae (Charophyta) are now part of a new monophyletic group called Streptophyta. The remaining green algae, which are more distantly related to plants, belong to a group called Chlorophyta that includes more than 7000 different species that live in fresh or brackish water, in seawater, or in snow patches.

The Charophyta are a division of green algae that includes the closest relatives of the embryophyte plants. Charophyta are a small but important group of plants which show marked differences from both the Thallophyta and the Bryophyta. They are all specialized water plants. The reproductive organs consist of antheridia and oogonia, although the structure of these organs differs considerably from the corresponding organs in the Algae.

Key Points

- There is a diverse array of green algae including single-celled or multicellular species, which can reproduce both sexually or

asexually.
- The classification of green algae is challenging because they bear many of the structural and biochemical traits of plants.
- Species of green algae that are closely related to embryophytes are classified as charophytes while the remaining green algae are classified as chlorophytes.
- Like plants, charophytes have chlorophyll a and b, store carbohydrates as starch, have cell walls consisting of cellulose, and undergo similar cell-division processes.
- Charophytes have unique reproductive organs that differ considerably from that of other algae.

Key Terms

- **streptophytes**: a subphylum consisting of several orders of green algae and embryophytes
- **Charophyta**: a division of green algae that includes the closest relatives of the embryophyte plants
- **Chlorophyta**: a division of green algae that are considered more distantly related to plants

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25.2B: Charales

Learning Objectives

- Identify the principle features of charophyte algae

Charales

Green algae in the order Charales, and the coleochaetes, microscopic green algae that enclose their spores in sporopollenin, are considered the closest-living relatives of embryophytes. The Charales can be traced as far back as 420 million years. They live in a range of fresh water habitats and vary in size from as small as a few millimeters to as large as a meter in length. A representative species of Charales is Chara, which is often called muskgrass or skunkweed because of its unpleasant smell.



Figure $25.2B.1$: Charophyte algae: A representative charophyte alga, Chara, is a noxious weed in Florida, where it clogs waterways.

In Charales, large cells form the thallus: the main stem of the alga. Branches arising from the nodes are made of smaller cells. Male and female reproductive structures are found on the nodes; the sperm have flagella. Unlike land plants, Charales do not undergo alternation of generations in their lifecycle. Like embryophytes, Charales exhibit a number of traits that are significant in their adaptation to land life. They produce the compounds lignin and sporopollenin. They form plasmodesmata, which are microscopic channels that connect the cytoplasm of adjacent cells. The egg and, later, the zygote, form in a protected chamber on the parent plant.

New information from recent, extensive DNA sequence analysis of green algae indicates that the Zygnematales are more closely-related to the embryophytes than the Charales. The Zygnematales include the familiar genus Spirogyra. As techniques in DNA analysis improve and new information on comparative genomics arises, the phylogenetic connections between species will probably continue to change. Clearly, plant biologists have yet to solve the mystery of the origin of land plants.

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Key Points

- The structure of charophyte algae consists of a thallus, which is the main stem, and branches that arise from nodes which bear both male and female reproductive structures.
- Although charophyte algae do not exhibit alteration of generations, they share a number of adaptations to life on land with embryophytes, including the encasement of eggs in protective enclosures.
- As new DNA sequence analysis techniques develop, revisions may need to be made in our understanding of plant evolution, such as indications that green algae in the order of Zygnematales may be more-closely related to embryophytes than is Charales.

Key Terms

- **Charales**: green algae in the division Charophyta which are green plants believed to be the closest relatives of the green land plants
- **sporopollenin**: a combination of biopolymers observed in the tough outer layer of the spore and pollen wall

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25.3: BRYOPHYTES

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- Topic hierarchy

25.3A: Bryophytes

25.3B: Liverworts and Hornworts

25.3C: Mosses

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25.3A: Bryophytes

Learning Objectives

- Describe the characteristics of bryophytes

Bryophytes

Bryophytes are the group of seedles plants that are the closest-extant relative of early terrestrial plants. The first bryophytes (liverworts) probably appeared in the Ordovician period, about 450 million years ago. However, because they lack of lignin and other resistant structures, bryophyte fossil formation is improbable and the fossil record is poor. Some spores protected by sporopollenin have survived and are attributed to early bryophytes. By the Silurian period, however, vascular plants had spread through the continents. This compelling fact is used as evidence that non-vascular plants must have preceded the Silurian period.

More than 25,000 species of bryophytes thrive in mostly-damp habitats, although some live in deserts. They constitute the major flora of inhospitable environments like the tundra where their small size and tolerance to desiccation offer distinct advantages. They generally lack lignin and do not have actual tracheids (xylem cells specialized for water conduction). Rather, water and nutrients circulate inside specialized conducting cells. Although the term non-tracheophyte is more accurate, bryophytes are commonly called non-vascular plants.

In a bryophyte, all the conspicuous vegetative organs, including the photosynthetic leaf-like structures, the thallus, stem, and the rhizoid that anchors the plant to its substrate, belong to the haploid organism, or gametophyte. The sporophyte is barely noticeable. Thus, the gametophyte is the dominant and most familiar form; the sporophyte appears for only a short period. The gametes formed by bryophytes swim with a flagellum. The sporangium, the multicellular sexual reproductive structure, is present in bryophytes and absent in the majority of algae. The sporophyte embryo also remains attached to the parent plant, which protects and nourishes it. This is a characteristic of land plants. The bryophytes are divided into three phyla: the liverworts (Hepaticophyta), the hornworts (Anthocerotophyta), and the mosses (true Bryophyta).



Figure $25.3A.1$: Moss: Mosses (true bryophyta) are one of the three kinds of bryophytes (along with liverworts and hornworts). This image shows a moss growing on a dry stone wall.

Key Points

- Bryophytes are the closest-living relative of early terrestrial plants; liverworts were the first Bryophytes, probably appearing

during the Ordovician period.
- Bryophytes fossil formation is improbable since they do not possess lignin.
- Bryophytes thrive in mostly-damp habitats; however, some species can live in deserts while others can inhabit hostile environments such as the tundra.
- Bryophytes are nonvascular because they do not have tracheids; instead, water and nutrients circulate inside specialized conducting cells.
- In a bryophyte, all the vegetative organs belong to the gametophyte, which is the dominant and most familiar form; the sporophyte appears for only a short period.
- The sporophyte is dependent on the gametophyte and remains permanently attached to it in order to gain nutrition and protection.

Key Terms

- **bryophyte**: seedless, nonvascular plants that are the closest extant relative of early terrestrial plants
- **tracheid**: elongated cells in the xylem of vascular plants that serve in the transport of water and mineral salts
- **sporangium**: a case, capsule, or container in which spores are produced by an organism

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25.3B: Liverworts and Hornworts

Learning Objectives

- Describe the distinguishing traits of hornworts and liverworts

Liverworts and Hornworts

Liverworts

Liverworts (Hepaticophyta) are viewed as the plants most closely related to the ancestor that moved to land. Liverworts have colonized every terrestrial habitat on earth and diversified to more than 7000 existing species. Liverwort gametophytes (the dominant stage of the life cycle) form lobate green structures. The shape of these leaves are similar to the lobes of the liver; hence, providing the origin of the name given to the phylum. Openings that allow the movement of gases may be observed in liverworts. However, these are not stomata because they do not actively open and close. The plant takes up water over its entire surface and has no cuticle to prevent desiccation.



Figure $25.3B.1$: Liverworts: A liverwort, *Lunularia cruciata*, displays its lobate, flat thallus. The organism in the photograph is in the dominant gametophyte stage.

The liverwort's life cycle begins with the release of haploid spores from the sporangium that developed on the sporophyte. Spores disseminated by wind or water germinate into flattened thalli gametophytes attached to the substrate by thin, single-celled filaments. Male and female gametangia develop on separate, individual plants. Once released, male gametes swim with the aid of their flagella to the female gametangium (the archegonium), and fertilization ensues. The zygote grows into a small sporophyte still attached to the parent gametophyte and develops spore-producing cells and elaters. The spore-producing cells undergo meiosis to form spores, which disperse (with the help of elaters), giving rise to new gametophytes. Thus, the life cycle of liverworts follows the pattern of alternation of generations.

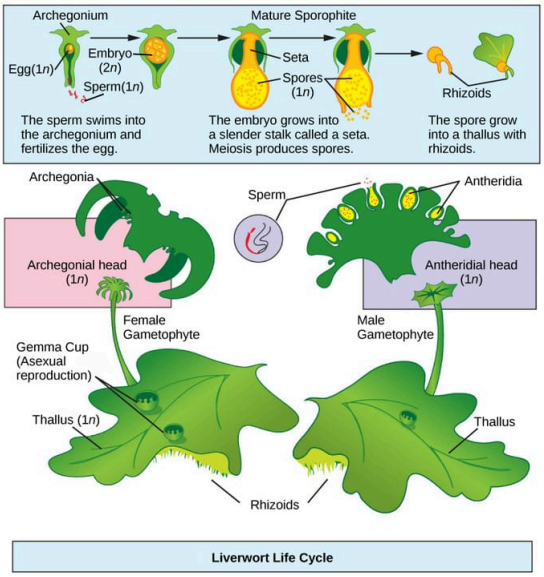


Figure $25.3B.1$: Liverwort Life Cycle: The life cycle of a typical liverwort follows the pattern of alternation of generations. Spores are released from sporophytes and form the gametophyte. Male gametes fertilize female gametes to form a zygote, which grows into a sporophyte. This sporophyte disperses spores with the help of elaters; the process begins again.

Liverwort plants can also reproduce asexually by the breaking of branches or the spreading of leaf fragments called gemmae. In this latter type of reproduction, the gemmae (small, intact, complete pieces of plant that are produced in a cup on the surface of the thallus) are splashed out of the cup by raindrops. The gemmae then land nearby and develop into gametophytes.

Hornworts

The hornworts (Anthocerotophyta) belong to the broad bryophyte group that have colonized a variety of habitats on land, although they are never far from a source of moisture. The short, blue-green gametophyte is the dominant phase of the lifecycle of a hornwort. The narrow, pipe-like sporophyte is the defining characteristic of the group. The sporophytes emerge from the parent gametophyte and continue to grow throughout the life of the plant. Stomata appear in the hornworts and are abundant on the sporophyte. Photosynthetic cells in the thallus contain a single chloroplast. Meristem cells at the base of the plant keep dividing and adding to its height. Many hornworts establish symbiotic relationships with cyanobacteria that fix nitrogen from the environment.



Figure $25.3B.1$: Hornworts: Unlike liverworts, hornworts grow a tall and slender sporophyte.

The life cycle of hornworts also follows the general pattern of alternation of generations and has a similar life cycle to liverworts. The gametophytes grow as flat thalli on the soil with embedded gametangia. Flagellated sperm swim to the archegonia and fertilize eggs. However, unlike liverworts, the zygote develops into a long and slender sporophyte that eventually splits open, releasing spores. Additionally, thin cells called pseudoelaters surround the spores and help propel them further in the environment. Unlike the elaters observed in liverworts, the hornwort pseudoelaters are single-celled structures. The haploid spores germinate and produce the next generation of gametophytes. Like liverworts, some hornworts may also produce asexually through fragmentation.

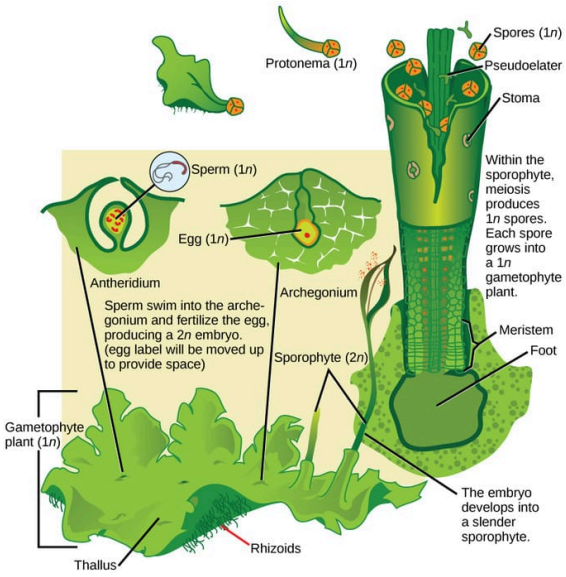


Figure 25.3B.1: Life Cycle of Hornworts: The life cycle of hornworts is similar to that of liverworts. Both follow the pattern of alternation of generations. However, liverworts develop a small sporophyte, whereas hornworts develop a long, slender sporophyte. Liverworts also disperse their spores with the help of elaters, while hornworts utilize pseudoelaters to aid in spore dispersal.

Key Points

- The leaves of liverworts are lobate green structures similar to the lobes of the liver, while hornworts have narrow, pipe-like structures.
- The gametophyte stage is the dominant stage in both liverworts and hornworts; however, liverwort sporophytes do not contain stomata, while hornwort sporophytes do.
- The life cycle of liverworts and hornworts follows alternation of generations: spores germinate into gametophytes, the zygote develops into a sporophyte that releases spores, and then spores produce new gametophytes.
- Liverworts develop short, small sporophytes, whereas hornworts develop long, slender sporophytes.
- To aid in spore dispersal, liverworts utilize elaters, whereas hornworts utilize pseudoelaters.
- Liverworts and hornworts can reproduce asexually through the fragmentation of leaves into gemmae that disperse and develop into gametophytes.

Key Terms

- **alternation of generation**: the life cycle of plants with a multicellular sporophyte, which is diploid, that alternates with a multicellular gametophyte, which is haploid
- **pseudoelater**: single-celled structure that aids in spore dispersal
- **gemmae**: small, intact, complete pieces of plant that are produced in a cup on the surface of the thallus and develop into gametophytes through asexual reproduction

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25.3C: Mosses

Learning Objectives

- Describe the distinguishing traits of mosses

Mosses

More than 10,000 species of mosses have been cataloged. Their habitats vary from the tundra, where they are the main vegetation, to the understory of tropical forests. In the tundra, the mosses' shallow rhizoids allow them to fasten to a substrate without penetrating the frozen soil. Mosses slow down erosion, store moisture and soil nutrients, and provide shelter for small animals as well as food for larger herbivores, such as the musk ox. Mosses are very sensitive to air pollution and are used to monitor air quality. They are also sensitive to copper salts. Such salts are a common ingredient of compounds marketed to eliminate mosses from lawns.

Mosses form diminutive gametophytes, which are the dominant phase of the life cycle. Green, flat structures resembling true leaves, but lacking vascular tissue are attached in a spiral to a central stalk or seta. The plants absorb water and nutrients directly through these leaf-like structures. The seta (plural, setae) contains tubular cells that transfer nutrients from the base of the sporophyte (the foot) to the sporangium. Some mosses have small branches. Some primitive traits of green algae, such as flagellated sperm, are still present in mosses that are dependent on water for reproduction. Other features of mosses are adaptations to dry land. For example, stomata are present on the stems of the sporophyte and a primitive vascular system runs up the sporophyte's stalk. Additionally, mosses are anchored to the substrate, whether it is soil, rock, or roof tiles, by multicellular rhizoids. These structures are precursors of roots. They originate from the base of the gametophyte, but are not the major route for the absorption of water and minerals. The lack of a true root system explains why it is so easy to rip moss mats from a tree trunk.



Figure $25.3C.1$: Setae: This photograph shows the long slender stems, called setae, connected to capsules of the moss Thamnobryum alopecurum.

The moss life cycle follows the pattern of alternation of generations. The most familiar structure is the haploid gametophyte, which germinates from a haploid spore and forms first a protonema: usually, a tangle of single-celled filaments that hug the ground. Cells akin to an apical meristem actively divide and give rise to a gametophore, consisting of a photosynthetic stem and foliage-like structures. Rhizoids form at the base of the gametophore. Gametangia of both sexes develop on separate gametophores. The male organ (the antheridium) produces many sperm, whereas the archegonium (the female organ) forms a single egg. At fertilization, the sperm swims down the neck to the venter and unites with the egg inside the archegonium. The zygote, protected

by the archegonium, divides and grows into a sporophyte, still attached by its foot to the gametophyte.

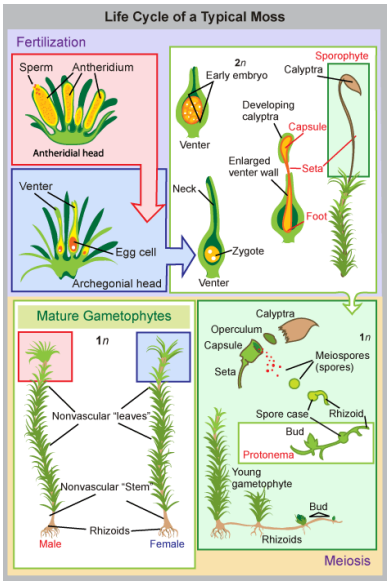


Figure $25.3C.1$: Life cycle of mosses: The alternation of generations cycle begins when the gametophyte germinates from a haploid spore and forms a protonema. Apical meristem-like cells divide and give rise to the gametophores. The archegonium (female organ) and antheridium (male organ) develop on separate gametophores. After fertilization, the zygote divides and grows into a sporophyte, which stays attached to the gametophyte. Spores released from the sporophyte germinate and produce gametophytes; the process begins again.

A structure called a peristome increases the spread of spores after the tip of the capsule falls off at dispersal. The concentric tissue around the mouth of the capsule is made of triangular, close-fitting units, a little like “teeth”; these open and close depending on moisture levels, periodically releasing spores.

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Key Points

- Mosses slow down erosion, store moisture and soil nutrients, and provide shelter for small animals and food for larger herbivores.
- Mosses have green, flat structures that resemble true leaves, which absorb water and nutrients; some mosses have small branches.
- Mosses have traits that are adaptations to dry land, such as stomata present on the stems of the sporophyte.
- Mosses are anchored to the substrate by rhizoids, which originate from the base of the gametophyte.
- The moss life cycle follows the pattern of alternation of generations where gametophytes form male and female gametophores, which fertilize to form the sporophyte; spores are released from the sporophyte to produce new gametophytes.
- The concentric tissue around the mouth of the capsule is made of triangular, close-fitting units that open and close to release spores, and the peristome increases the spread of spores after the tip of the capsule falls off at dispersal.

Key Terms

- **peristome**: one or two rings of tooth-like appendages surrounding the opening of the capsule of many mosses that aid in spreading spores
- **rhizoid**: a rootlike structure that acts as support and anchors the plant to its substrate
- **seta**: the stalk of a moss sporangium, or occasionally in a liverwort

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25.4: SEEDLESS VASCULAR PLANTS

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- Topic hierarchy

25.4A: Seedless Vascular Plants
25.4B: Vascular Tissue- Xylem and Phloem
25.4C: The Evolution of Roots in Seedless Plants
25.4D: Ferns and Other Seedless Vascular Plants
25.4E: The Importance of Seedless Vascular Plants

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25.4A: Seedless Vascular Plants

Learning Objectives

- Evaluate the evolution of seedless vascular plants

Seedless Vascular Plants

The vascular plants, or tracheophytes, are the dominant and most conspicuous group of land plants. They contain tissue that transports water and other substances throughout the plant. More than 260,000 species of tracheophytes represent more than 90 percent of the earth's vegetation. By the late Devonian period, plants had evolved vascular tissue, well-defined leaves, and root systems. With these advantages, plants increased in height and size and were able to spread to all habitats.

Seedless vascular plants are plants that contain vascular tissue, but do not produce flowers or seeds. In seedless vascular plants, such as ferns and horsetails, the plants reproduce using haploid, unicellular spores instead of seeds. The spores are very lightweight (unlike many seeds), which allows for their easy dispersion in the wind and for the plants to spread to new habitats. Although seedless vascular plants have evolved to spread to all types of habitats, they still depend on water during fertilization, as the sperm must swim on a layer of moisture to reach the egg. This step in reproduction explains why ferns and their relatives are more abundant in damp environments, including marshes and rainforests. The life cycle of seedless vascular plants is an alternation of generations, where the diploid sporophyte alternates with the haploid gametophyte phase. The diploid sporophyte is the dominant phase of the life cycle, while the gametophyte is an inconspicuous, but still-independent, organism. Throughout plant evolution, there is a clear reversal of roles in the dominant phase of the life cycle.

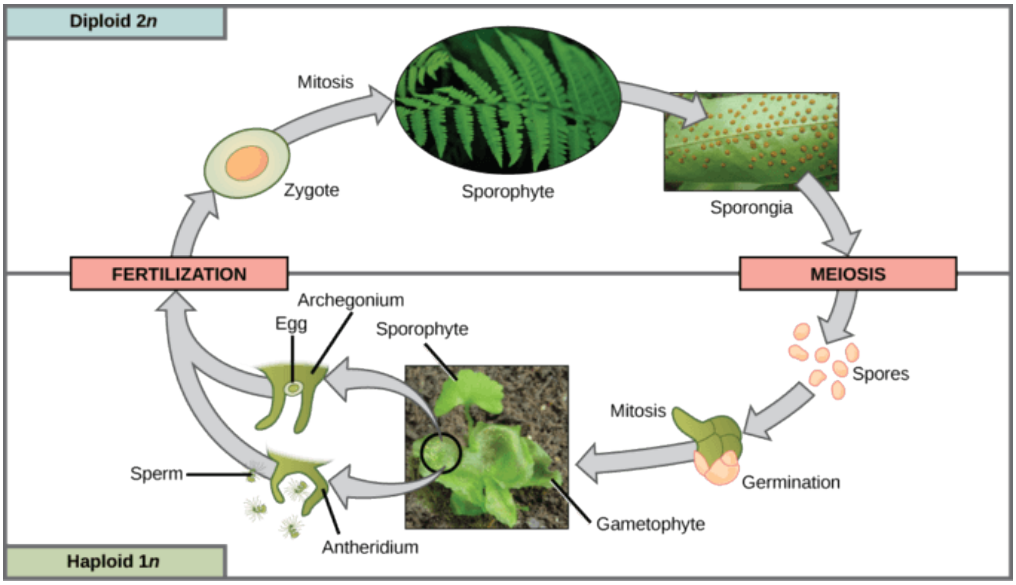


Figure 25.4A.1: Life cycle of a fern: This life cycle of a fern shows alternation of generations with a dominant sporophyte stage.

Key Points

- The life cycle of seedless vascular plants alternates between a diploid sporophyte and a haploid gametophyte phase.
- Seedless vascular plants reproduce through unicellular, haploid spores instead of seeds; the lightweight spores allow for easy dispersion in the wind.
- Seedless vascular plants require water for sperm motility during reproduction and, thus, are often found in moist environments.

Key Terms

- **gametophyte**: a plant (or the haploid phase in its life cycle) that produces gametes by mitosis in order to produce a zygote
- **sporophyte**: a plant (or the diploid phase in its life cycle) that produces spores by meiosis in order to produce gametophytes
- **tracheophyte**: any plant possessing vascular tissue (xylem and phloem), including ferns, conifers, and flowering plants

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25.4B: Vascular Tissue- Xylem and Phloem

Learning Objectives

- Describe the functions of plant vascular tissue

Vascular Tissue: Xylem and Phloem

The first fossils that show the presence of vascular tissue date to the Silurian period, about 430 million years ago. The simplest arrangement of conductive cells shows a pattern of xylem at the center surrounded by phloem. Together, xylem and phloem tissues form the vascular system of plants.

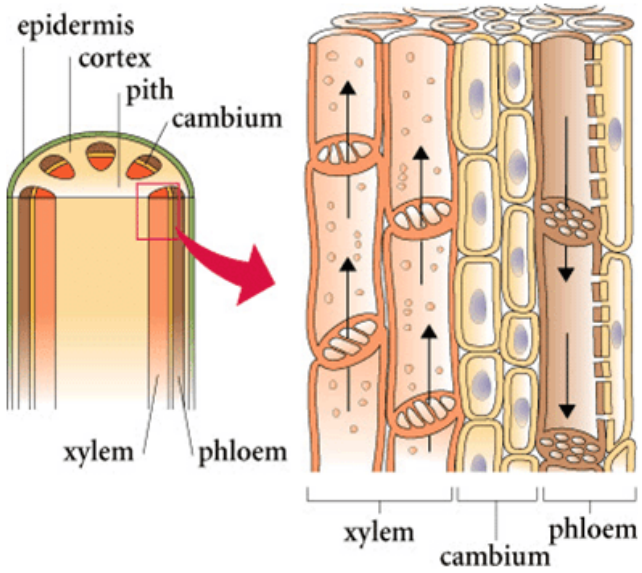


Figure $25.4B.1$: Xylem and phloem: Xylem and phloem tissue make up the transport cells of stems. The direction of water and sugar transportation through each tissue is shown by the arrows.

Xylem is the tissue responsible for supporting the plant as well as for the storage and long-distance transport of water and nutrients, including the transfer of water-soluble growth factors from the organs of synthesis to the target organs. The tissue consists of vessel elements, conducting cells, known as tracheids, and supportive filler tissue, called parenchyma. These cells are joined end-to-end to form long tubes. Vessels and tracheids are dead at maturity. Tracheids have thick secondary cell walls and are tapered at the ends. It is the thick walls of the tracheids that provide support for the plant and allow it to achieve impressive heights. Tall plants have a selective advantage by being able to reach unfiltered sunlight and disperse their spores or seeds further away, thus expanding their range. By growing higher than other plants, tall trees cast their shadow on shorter plants and limit competition for water and precious nutrients in the soil. The tracheids do not have end openings like the vessels do, but their ends overlap with each other, with pairs of pits present. The pit pairs allow water to pass horizontally from cell to cell.

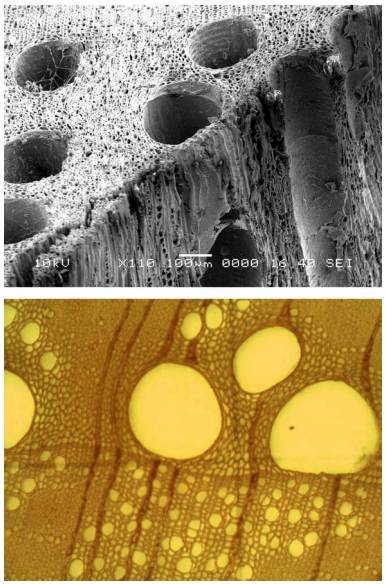


Figure $25.4B.1$: Tracheids and vessel elements: Tracheids (top) and vessel elements (bottom) are the water conducting cells of xylem tissue.

Phloem tissue is responsible for translocation, which is the transport of soluble organic substances, for example, sugar. The substances travel along sieve elements, but other types of cells are also present: the companion cells, parenchyma cells, and fibers. The end walls, unlike vessel members in xylem, do not have large openings. The end walls, however, are full of small pores where cytoplasm extends from cell to cell. These porous connections are called sieve plates. Despite the fact that their cytoplasm is actively involved in the conduction of food materials, sieve-tube members do not have nuclei at maturity. The activity of the sieve tubes is controlled by companion cells through plasmadesmata.

Key Points

- Xylem transports and stores water and water-soluble nutrients in vascular plants.
- Phloem is responsible for transporting sugars, proteins, and other organic molecules in plants.
- Vascular plants are able to grow higher than other plants due to the rigidity of xylem cells, which support the plant.

Key Terms

- **xylem**: a vascular tissue in land plants primarily responsible for the distribution of water and minerals taken up by the roots; also the primary component of wood
- **phloem**: a vascular tissue in land plants primarily responsible for the distribution of sugars and nutrients manufactured in the shoot
- **tracheid**: elongated cells in the xylem of vascular plants that serve in the transport of water and mineral salts

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25.4C: The Evolution of Roots in Seedless Plants

Learning Objectives

- Explain how roots provide support for plants

Roots: Support for the Plant

Roots are not well preserved in the fossil record. Nevertheless, it seems that roots appeared later in evolution than vascular tissue. The development of an extensive network of roots represented a significant new feature of vascular plants. Roots provided seed plants with three major functions: anchoring the plant to the soil, absorbing water and minerals and transporting them upwards, and storing the products of photosynthesis. Importantly, roots are modified to absorb moisture and exchange gases. In addition, while most roots are underground, some plants have adventitious roots, which emerge above the ground from the shoot.

Types of Root Systems

There are mainly two types of root systems. Dicots (flowering plants with two embryonic seed leaves) have a tap root system while monocots (flowering plants with one embryonic seed leaf) have a fibrous root system. A tap root system has a main root that grows down vertically from which many smaller lateral roots arise. Dandelions are a good example; their tap roots usually break off when trying to pull these weeds; they can regrow another shoot from the remaining root.



Figure $25.4C.1$: Root types: (a) Tap root systems have a main root that grows down, while (b) fibrous root systems consist of many small roots.

A tap root system penetrates deep into the soil. In contrast, a fibrous root system is located closer to the soil surface, forming a dense network of roots that also helps prevent soil erosion (lawn grasses are a good example, as are wheat, rice, and corn). In addition, some plants actually have a combination of tap root and fibrous roots. Plants that grow in dry areas often have deep root systems, whereas plants growing in areas with abundant water tend to have shallower root systems.

Root Growth and Anatomy

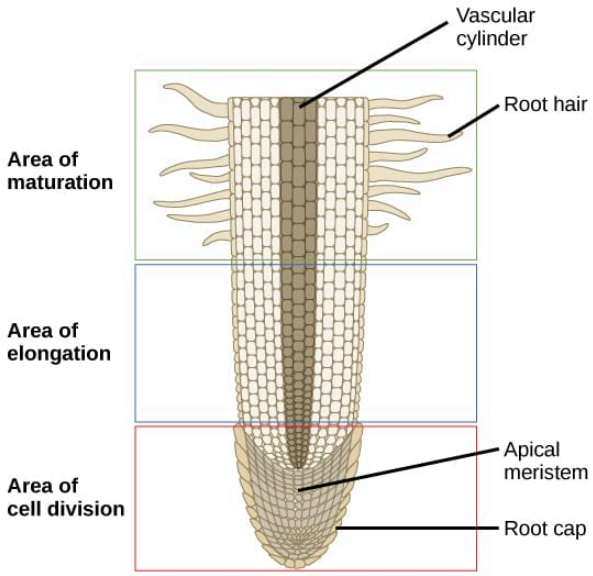


Figure $25.4C.1$: Zones on a root tip: A longitudinal view of the root reveals the zones of cell division, elongation, and maturation. Cell division occurs in the apical meristem.

Root growth begins with seed germination. When the plant embryo emerges from the seed, the radicle of the embryo forms the root system. The tip of the root is protected by the root cap, a structure exclusive to roots and unlike any other plant structure. The root cap is continuously replaced because it gets damaged easily as the root pushes through soil. The root tip can be divided into three zones: a zone of cell division, a zone of elongation, and a zone of maturation and differentiation. The zone of cell division is closest to the root tip; it is made up of the actively-dividing cells of the root meristem. The zone of elongation is where the newly-formed cells increase in length, thereby lengthening the root. Beginning at the first root hair is the zone of cell maturation where the root cells begin to differentiate into special cell types. All three zones are in the first centimeter or so of the root tip.



Figure $25.4C.1$: Modified roots: Many vegetables are modified roots, such as radishes and carrots, which store energy in the form of starches and sugars.

The vascular tissue in the root is arranged in the inner portion of the root, which is called the vascular cylinder. A layer of cells, known as the endodermis, separates the vascular tissue from the ground tissue in the outer portion of the root. The endodermis is exclusive to roots, serving as a checkpoint for materials entering the root's vascular system. A waxy substance called suberin is present on the walls of the endodermal cells. This waxy region, known as the Casparian strip, forces water and solutes to cross the plasma membranes of endodermal cells instead of slipping between the cells. This ensures that only materials required by

the root pass through the endodermis, while toxic substances and pathogens are generally excluded. The outermost cell layer of the root's vascular tissue is the pericycle, an area that can give rise to lateral roots. In dicot roots, the xylem and phloem of the stele are arranged alternately in an X shape, whereas in monocot roots, the vascular tissue is arranged in a ring around the pith.

Root Modifications

Root structures may be modified for specific purposes. For example, some roots are bulbous and store starch. Aerial roots and prop roots are two forms of aboveground roots that provide additional support to anchor the plant. Tap roots, such as carrots, turnips, and beets, are examples of roots that are modified for food storage.

Key Points

- There are two main types of root systems: tap root systems consist of one main root that grows down vertically with smaller lateral roots growing off of the main root, while fibrous root systems form a dense network of roots near the soil surface.
- Roots can be modified to store food or starches and to provide additional support for plants; many vegetables, such as carrots, are modified roots.
- A zone of cell division, a zone of elongation, and a zone of maturation and differentiation make up a root tip, where the root cells divide, grow, and differentiate into specialized cells.
- The vascular system of roots is surrounded by an epidermis, which regulates materials that enter the root's vascular system.

Key Terms

- **endodermis**: in a plant stem or root, a cylinder of cells that separates the outer cortex from the central core and controls the flow of water and minerals within the plant
- **suberin**: a waxy material found in bark that can repel water
- **pericycle**: in a plant root, the cylinder of plant tissue between the endodermis and phloem

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25.4D: Ferns and Other Seedless Vascular Plants

Learning Objectives

- Identify types of seedless vascular plants

Ferns and Other Seedless Vascular Plants

Water is required for fertilization of seedless vascular plants; most favor a moist environment. Modern-day seedless tracheophytes include lycophytes and monilophytes.

Phylum Lycopodiophyta: Club Mosses

The club mosses, or phylum Lycopodiophyta, are the earliest group of seedless vascular plants. They dominated the landscape of the Carboniferous, growing into tall trees and forming large swamp forests. Today's club mosses are diminutive, evergreen plants consisting of a stem (which may be branched) and microphylls (leaves with a single unbranched vein). The phylum Lycopodiophyta consists of close to 1,200 species, including the quillworts (Isoetales), the club mosses (Lycopodiales), and spike mosses (Selaginellales), none of which are true mosses or bryophytes.

Lycophytes follow the pattern of alternation of generations seen in the bryophytes, except that the sporophyte is the major stage of the life cycle. The gametophytes do not depend on the sporophyte for nutrients. Some gametophytes develop underground and form mycorrhizal associations with fungi. In club mosses, the sporophyte gives rise to sporophylls arranged in strobili, cone-like structures that give the class its name. Lycophytes can be homosporous or heterosporous.



Figure $25.4D.1$: Strobili of club mosses: In some club mosses such as *Lycopodium clavatum*, sporangia are arranged in clusters called strobili.

Phylum Monilophyta: Class Equisetopsida (Horsetails)

Horsetails, whisk ferns, and ferns belong to the phylum Monilophyta, with horsetails placed in the Class Equisetopsida. The single extant genus *Equisetum* is the survivor of a large group of plants, which produced large trees, shrubs, and vines in the swamp forests in the Carboniferous. The plants are usually found in damp environments and marshes.

The stem of a horsetail is characterized by the presence of joints or nodes, hence the old name Arthrophyta (arthro- = "joint";

-phyta = “plant”). Leaves and branches come out as whorls from the evenly-spaced joints. The needle-shaped leaves do not contribute greatly to photosynthesis, the majority of which takes place in the green stem.



Figure $25.4D.1$: Leaves of a horsetail: The whorls of green structures at the joints are actually stems. The leaves are barely noticeable as brown rings just above each joint. Horsetails were once used as scrubbing brushes and so were called scouring rushes.

Silica collects in the epidermal cells, contributing to the stiffness of horsetail plants. Underground stems known as rhizomes anchor the plants to the ground. Modern-day horsetails are homosporous and produce bisexual gametophytes.

Phylum Monilophyta: Class Psilotopsida (Whisk Ferns)

While most ferns form large leaves and branching roots, the whisk ferns, Class Psilotopsida, lack both roots and leaves, which were probably lost by reduction. Photosynthesis takes place in their green stems; small yellow knobs form at the tip of the branch stem and contain the sporangia. Whisk ferns were considered an early pterophytes. However, recent comparative DNA analysis suggests that this group may have lost both leaves and roots through evolution and is more closely related to ferns.

Phylum Monilophyta: Class Polypodiopsida (Ferns)

With their large fronds, ferns are the most-readily recognizable seedless vascular plants. More than 20,000 species of ferns live in environments ranging from tropics to temperate forests. Although some species survive in dry environments, most ferns are restricted to moist, shaded places. Ferns made their appearance in the fossil record during the Devonian period and expanded during the Carboniferous.

The dominant stage of the life cycle of a fern is the sporophyte, which typically consists of large compound leaves called fronds. Fronds fulfill a double role; they are photosynthetic organs that also carry reproductive structure. The stem may be buried underground as a rhizome from which adventitious roots grow to absorb water and nutrients from the soil, or they may grow above ground as a trunk in tree ferns. Adventitious organs are those that grow in unusual places, such as roots growing from the side of a stem. Most ferns produce the same type of spores and are, therefore, homosporous. The diploid sporophyte is the most conspicuous stage of the life cycle. On the underside of its mature fronds, sori (singular, sorus) form as small clusters where sporangia develop. Sporangia in a sorus produce spores by meiosis and release them into the air. Those that land on a suitable substrate germinate and form a heart-shaped gametophyte, which is attached to the ground by thin filamentous rhizoids. The inconspicuous gametophyte harbors both sex gametangia. Flagellated sperm are released and swim on a wet surface to where the egg is fertilized. The newly-formed zygote grows into a sporophyte that emerges from the gametophyte, growing by mitosis into the next generation sporophyte.



Figure $25.4D.1$: Sori on a fern frond: Sori appear as small bumps on the underside of a fern frond.

Key Points

- Club mosses, which are the earliest form of seedless vascular plants, are lycophytes that contain a stem and microphylls.
- Horsetails are often found in marshes and are characterized by jointed hollow stems with whorled leaves.
- Photosynthesis occurs in the stems of whisk ferns, which lack roots and leaves.
- Most ferns have branching roots and form large compound leaves, or fronds, that perform photosynthesis and carry the reproductive organs of the plant.

Key Terms

- **sorus**: a cluster of sporangia associated with a fern leaf
- **lycophyte**: a tracheophyte subdivision of the Kingdom Plantae; the oldest extant (living) vascular plant division at around 410 million years old
- **sporangia**: enclosures in which spores are formed

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25.4E: The Importance of Seedless Vascular Plants

Learning Objectives

- Explain the beneficial roles of seedless vascular plants

The Importance of Seedless Vascular Plants

Mosses and liverworts are often the first macroscopic organisms to colonize an area, both in a primary succession (where bare land is settled for the first time by living organisms) or in a secondary succession (where soil remains intact after a catastrophic event wipes out many existing species). Their spores are carried by the wind, birds, or insects. Once mosses and liverworts are established, they provide food and shelter for other species. In a hostile environment, such as the tundra where the soil is frozen, bryophytes grow well because they do not have roots and can dry and rehydrate rapidly once water is again available. Mosses are at the base of the food chain in the tundra biome. Many species, from small insects to musk oxen and reindeer, depend on mosses for food. In turn, predators feed on the herbivores, which are the primary consumers. Some reports indicate that bryophytes make the soil more amenable to colonization by other plants. Because they establish symbiotic relationships with nitrogen-fixing cyanobacteria, mosses replenish the soil with nitrogen.

At the end of the nineteenth century, scientists observed that lichens and mosses were becoming increasingly rare in urban and suburban areas. Since bryophytes have neither a root system for absorption of water and nutrients, nor a cuticle layer that protects them from desiccation, pollutants in rainwater readily penetrate their tissues; they absorb moisture and nutrients through their entire exposed surfaces. Therefore, pollutants dissolved in rainwater penetrate plant tissues readily and have a larger impact on mosses than on other plants. The disappearance of mosses can be considered a bioindicator for the level of pollution in the environment.

Ferns contribute to the environment by promoting the weathering of rock, accelerating the formation of topsoil, and slowing down erosion by spreading rhizomes in the soil. The water ferns of the genus *Azolla* harbor nitrogen-fixing cyanobacteria and restore this important nutrient to aquatic habitats.

Seedless plants have historically played a role in human life through uses as tools, fuel, and medicine. Dried peat moss, *Sphagnum*, is commonly used as fuel in some parts of Europe and is considered a renewable resource. *Sphagnum* bogs are cultivated with cranberry and blueberry bushes. The ability of Sphagnum to hold moisture makes the moss a common soil conditioner. Florists use blocks of Sphagnum to maintain moisture for floral arrangements.



Figure $25.4E.1$: Plants as a renewable resource for fuel: Sphagnum acutifolium is dried peat moss and can be used as fuel.

The attractive fronds of ferns make them a favorite ornamental plant. Because they thrive in low light, they are well suited as house plants. More importantly, fiddleheads are a traditional spring food of Native Americans in the Pacific Northwest and are popular as a side dish in French cuisine. The licorice fern, *Polypodium glycyrrhiza*, is part of the diet of the Pacific Northwest coastal tribes, owing in part to the sweetness of its rhizomes. It has a faint licorice taste and serves as a sweetener. The rhizome also figures in the pharmacopoeia of Native Americans for its medicinal properties and is used as a remedy for sore throat.



Figure $25.4E.1$: Fiddlehead ferns as food: A chicken dish with fiddlehead ferns as a side is shown. Native Americans traditionally cook fiddleheads with meals during the spring.

By far the greatest impact of seedless vascular plants on human life, however, comes from their extinct progenitors. The tall club mosses, horsetails, and tree-like ferns that flourished in the swampy forests of the Carboniferous period gave rise to large deposits of coal throughout the world. Coal provided an abundant source of energy during the Industrial Revolution, which had tremendous consequences on human societies, including rapid technological progress and growth of large cities, as well as the degradation of the environment. Coal is still a prime source of energy and also a major contributor to global warming.



Figure $25.4E.1$: Carboniferous period plants: This drawing depicts the tall mosses and tree-like ferns of the Carboniferous period that deposited the large amounts of coal throughout the world.

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Key Points

- Mosses and liverworts provide food and shelter for other organisms in otherwise barren or hostile environments.
- The level of pollution in an environment can be determined by the disappearance of mosses, which absorb the pollutants with moisture through their entire surfaces.

- Dried peat moss is used as a renewable resource for fuel.
- Ferns prevent soil erosion, promote topsoil formation, restore nitrogen to aquatic habitats by harboring cyanobacteria, make good house plants, and have been used as food and for medicinal remedies.
- Coal, a major fuel source and contributor to global warming, was deposited by the seedless vascular plants of the Carboniferous period.

Key Terms

- **bioindicator**: any species that acts as a biological indicator of the health of an environment
- **pharmacopoeia**: an official book describing medicines or other pharmacological substances, especially their use, preparation, and regulation
- **sphagnum**: any of various widely-distributed mosses, of the genus Sphagnum, which slowly decompose to form peat; often used for fuel

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26: SEED PLANTS

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26.1: EVOLUTION OF SEED PLANTS

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- Topic hierarchy

26.1A: The Evolution of Seed Plants and Adaptations for Land

26.1B: Evolution of Gymnosperms

26.1C: Evolution of Angiosperms

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26.1A: The Evolution of Seed Plants and Adaptations for Land

Learning Objectives

- Recognize the significance of seed plant evolution

Evolution of Seed Plants

The lush palms on tropical shorelines do not depend upon water for the dispersal of their pollen, fertilization, or the survival of the zygote, unlike mosses, liverworts, and ferns of the terrain. Seed plants, such as palms, have broken free from the need to rely on water for their reproductive needs. They play an integral role in all aspects of life on the planet, shaping the physical terrain, influencing the climate, and maintaining life as we know it. For millennia, human societies have depended upon seed plants for nutrition and medicinal compounds; and more recently, for industrial by-products, such as timber and paper, dyes, and textiles. Palms provide materials including rattans, oils, and dates. Wheat is grown to feed both human and animal populations. The fruit of the cotton boll flower is harvested as a boll, with its fibers transformed into clothing or pulp for paper. The showy opium poppy is valued both as an ornamental flower and as a source of potent opiate compounds.

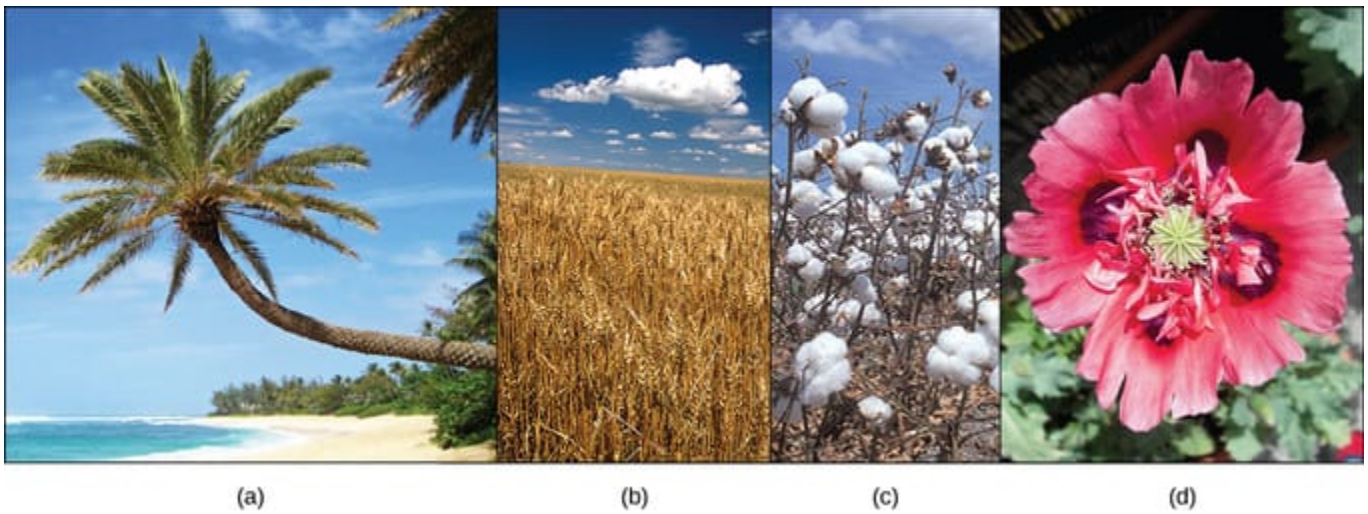


Figure 26.1A.1: Seed plants dominate the landscape: Seed plants dominate the landscape and play an integral role in human societies. (a) Palm trees grow along the shoreline; (b) wheat is a crop grown in most of the world; (c) the flower of the cotton plant produces fibers that are woven into fabric; (d) the potent alkaloids of the beautiful opium poppy have influenced human life both as a medicinal remedy and as a dangerously-addictive drug.

Seeds and Pollen as an Evolutionary Adaptation to Dry Land

Unlike bryophyte and fern spores (which are haploid cells dependent on moisture for rapid development of gametophytes), seeds contain a diploid embryo that will germinate into a sporophyte. Storage tissue to sustain growth and a protective coat give seeds their superior evolutionary advantage. Several layers of hardened tissue prevent desiccation, freeing reproduction from the need for a constant supply of water. Furthermore, seeds remain in a state of dormancy induced by desiccation and the hormone abscisic acid until conditions for growth become favorable. Whether blown by the wind, floating on water, or carried away by animals, seeds are scattered in an expanding geographic range, thus avoiding competition with the parent plant.

Pollen grains are male gametophytes carried by wind, water, or a pollinator. The whole structure is protected from desiccation and can reach the female organs without dependence on water. Male gametes reach female gametophyte and the egg cell gamete though a pollen tube: an extension of a cell within the pollen grain. The sperm of modern gymnosperms lack flagella, but in cycads

and the Gingko, the sperm still possess flagella that allow them to swim down the pollen tube to the female gamete; however, they are enclosed in a pollen grain.

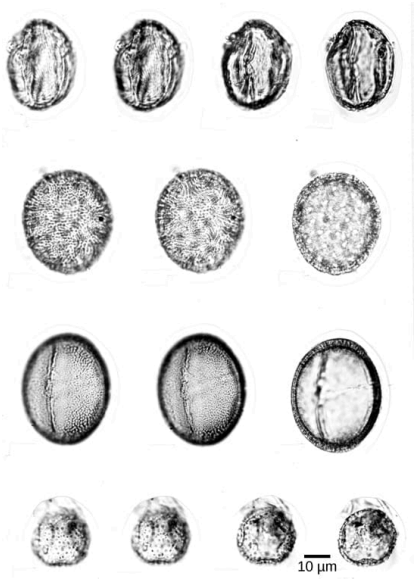


Figure 26.1A.1: Fossilized pollen grains: This fossilized pollen is from a Buckbean fen core found in Yellowstone National Park, Wyoming. The pollen is magnified 1,000 times.

Key Points

- Plants are used for food, textiles, medicines, building materials, and many other products that are important to humans.
- The evolution of seeds allowed plants to decrease their dependency upon water for reproduction.
- Seeds contain an embryo that can remain dormant until conditions are favorable when it grows into a diploid sporophyte.
- Seeds are transported by the wind, water, or by animals to encourage reproduction and reduce competition with the parent plant.

Key Terms

- **seed**: a fertilized ovule, containing an embryonic plant
- **sporophyte**: a plant (or the diploid phase in its life cycle) that produces spores by meiosis in order to produce gametophytes
- **pollen**: microspores produced in the anthers of flowering plants

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26.1B: Evolution of Gymnosperms

Learning Objectives

- Explain how and why gymnosperms became the dominant plant group during the Permian period

Evolution of Gymnosperms

The fossil plant *Elkinsia polymorpha*, a "seed fern" from the Devonian period (about 400 million years ago) is considered the earliest seed plant known to date. Seed ferns produced their seeds along their branches without specialized structures. What makes them the first true seed plants is that they developed structures called cupules to enclose and protect the ovule (the female gametophyte and associated tissues) which develops into a seed upon fertilization. Seed plants resembling modern tree ferns became more numerous and diverse in the coal swamps of the Carboniferous period. This appears to have been the result of a whole genome duplication event around 319 million years ago.



Figure 26.1B.1: Seed ferns: This fossilized leaf is from *Glossopteris*, a seed fern that thrived during the Permian age (290–240 million years ago).

Fossil records indicate the first gymnosperms (progymnosperms) most likely originated in the Paleozoic era, during the middle Devonian period about 390 million years ago. Following the wet Mississippian and Pennsylvanian periods, which were dominated by giant fern trees, the Permian period was dry. This gave a reproductive edge to seed plants, which are better adapted to survive dry spells. The Ginkgoales, a group of gymnosperms with only one surviving species, the Gingko biloba, were the first gymnosperms to appear during the lower Jurassic. Gymnosperms expanded in the Mesozoic era (about 240 million years ago), supplanting ferns in the landscape, and reaching their greatest diversity during this time. It has been suggested that during the mid-Mesozoic era, pollination of some extinct groups of gymnosperms was performed by extinct species of scorpionflies that had a specialized proboscis for feeding on pollination drops. The scorpionflies probably engaged in pollination mutualisms with gymnosperms, long before the similar and independent coevolution of nectar-feeding insects on angiosperms.



Figure 26.1B.2: Gymnosperms of the taiga: This boreal forest (taiga) has low-lying plants and conifer trees, as these plants are better suited to the colder, dryer conditions.

The Jurassic period was as much the age of the cycads (palm-tree-like gymnosperms) as the age of the dinosaurs. Gingkoales and the more familiar conifers also dotted the landscape. Although angiosperms (flowering plants) are the major form of plant life in most biomes, gymnosperms still dominate some ecosystems, such as the taiga (boreal forests) and the alpine forests at higher mountain elevations because of their adaptation to cold and dry growth conditions.

Key Points

- Seed ferns were the first seed plants, protecting their reproductive parts in structures called cupules.
- Seed ferns gave rise to the gymnosperms during the Paleozoic Era, about 390 million years ago.
- Gymnosperms include the gingkoes and conifers and inhabit many ecosystems, such as the taiga and the alpine forests, because they are well adapted for cold weather.
- True seed plants became more numerous and diverse during the Carboniferous period around 319 million years ago; an explosion that appears to be due to a whole genome duplication event.

Key Terms

- **cupule**: any small structure shaped like a cup
- **gymnosperm**: any plant, such as a conifer, whose seeds are not enclosed in an ovary
- **mutualism**: any interaction between two species that benefits both

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26.1C: Evolution of Angiosperms

Learning Objectives

- Discuss the evolution and adaptations of angiosperms

Evolution of Angiosperms

Undisputed fossil records place the massive appearance and diversification of angiosperms in the middle to late Mesozoic era. Angiosperms ("seed in a vessel") produce a flower containing male and/or female reproductive structures. Fossil evidence indicates that flowering plants first appeared in the Lower Cretaceous, about 125 million years ago, and were rapidly diversifying by the Middle Cretaceous, about 100 million years ago. Earlier traces of angiosperms are scarce. Fossilized pollen recovered from Jurassic geological material has been attributed to angiosperms. A few early Cretaceous rocks show clear imprints of leaves resembling angiosperm leaves. By the mid-Cretaceous, a staggering number of diverse, flowering plants crowd the fossil record. The same geological period is also marked by the appearance of many modern groups of insects, including pollinating insects that played a key role in ecology and the evolution of flowering plants.



Figure $26.1C.1$: Fossil evidence of angiosperms: This leaf imprint shows a Ficus speciosissima, an angiosperm that flourished during the Cretaceous period. A large number of pollinating insects also appeared during this same time.

Although several hypotheses have been offered to explain this sudden profusion and variety of flowering plants, none have garnered the consensus of paleobotanists (scientists who study ancient plants). New data in comparative genomics and paleobotany have, however, shed some light on the evolution of angiosperms. Rather than being derived from gymnosperms, angiosperms form a sister clade (a species and its descendents) that developed in parallel with the gymnosperms. The two innovative structures of flowers and fruit represent an improved reproductive strategy that served to protect the embryo, while increasing genetic variability and range. Paleobotanists debate whether angiosperms evolved from small woody bushes, or were basal angiosperms related to tropical grasses. Both views draw support from cladistic studies. The so-called woody magnoliid hypothesis (which proposes that the early ancestors of angiosperms were shrubs) also offers molecular biological evidence.

The most primitive living angiosperm is considered to be *Amborellatrichopoda*, a small plant native to the rainforest of New Caledonia, an island in the South Pacific. Analysis of the genome of *A. trichopoda* has shown that it is related to all existing flowering plants and belongs to the oldest confirmed branch of the angiosperm family tree. A few other angiosperm groups, known as basal angiosperms, are viewed as primitive because they branched off early from the phylogenetic tree. Most modern angiosperms are classified as either monocots or eudicots based on the structure of their leaves and embryos. Basal angiosperms, such as water lilies, are considered more primitive because they share morphological traits with both monocots and

eudicots.

Flowers and Fruits as an Evolutionary Adaptation

Angiosperms produce their gametes in separate organs, which are usually housed in a flower. Both fertilization and embryo development take place inside an anatomical structure that provides a stable system of sexual reproduction largely sheltered from environmental fluctuations. Flowering plants are the most diverse phylum on Earth after insects; flowers come in a bewildering array of sizes, shapes, colors, smells, and arrangements. Most flowers have a mutualistic pollinator, with the distinctive features of flowers reflecting the nature of the pollination agent. The relationship between pollinator and flower characteristics is one of the great examples of coevolution.



Figure 26.1C.2: Coevolution of flowers and pollinators: Many flowers have coevolved with particular pollinators, such that the flower is uniquely structured for the mouthparts of the pollinator. It often has features considered attractive to its particular pollinator.

Following fertilization of the egg, the ovule grows into a seed. The surrounding tissues of the ovary thicken, developing into a fruit that will protect the seed and often ensure its dispersal over a wide geographic range. Not all fruits develop from an ovary; such structures are “false fruits.” Like flowers, fruit can vary tremendously in appearance, size, smell, and taste. Tomatoes, walnut shells and avocados are all examples of fruit. As with pollen and seeds, fruits also act as agents of dispersal. Some may be carried away by the wind. Many attract animals that will eat the fruit and pass the seeds through their digestive systems, then deposit the seeds in another location. Cockleburs are covered with stiff, hooked spines that can hook into fur (or clothing) and hitch a ride on an animal for long distances. The cockleburs that clung to the velvet trousers of an enterprising Swiss hiker, George de Mestral, inspired his invention of the loop and hook fastener he named Velcro.

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Key Points

- Angiosperms evolved during the late Cretaceous Period, about 125-100 million years ago.
- Angiosperms have developed flowers and fruit as ways to attract pollinators and protect their seeds, respectively.
- Flowers have a wide array of colors, shapes, and smells, all of which are for the purpose of attracting pollinators.
- Once the egg is fertilized, it grows into a seed that is protected by a fleshy fruit.
- As angiosperms evolved in the Cretaceous period, many modern groups of insects also appeared, including pollinating insects that drove the evolution of angiosperms; in many instances, flowers and their pollinators have coevolved.
- Angiosperms did not evolve from gymnosperms, but instead evolved in parallel with the gymnosperms; however, it is unclear as to what type of plant actually gave rise to angiosperms.

Key Terms

- **clade**: a group of animals or other organisms derived from a common ancestor species
- **angiosperm**: a plant whose ovules are enclosed in an ovary
- **basal angiosperm**: the first flowering plants to diverge from the ancestral angiosperm, including a single species of shrub from New Caledonia, water lilies and some other aquatic plants, and woody aromatic plants

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26.2: GYMNOSPERMS

26.2A: Characteristics of Gymnosperms
26.2B: Life Cycle of a Conifer
26.2C: Diversity of Gymnosperms

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26.2A: Characteristics of Gymnosperms

Learning Objectives

- Discuss the type of seeds produced by gymnosperms

Characteristics of Gymnosperms

Gymnosperms are seed plants adapted to life on land; thus, they are autotrophic, photosynthetic organisms that tend to conserve water. They have a vascular system (used for the transportation of water and nutrients) that includes roots, xylem, and phloem. The name gymnosperm means “naked seed,” which is the major distinguishing factor between gymnosperms and angiosperms, the two distinct subgroups of seed plants. This term comes from the fact that the ovules and seeds of gymnosperms develop on the scales of cones rather than in enclosed chambers called ovaries.

Gymnosperms are older than angiosperms on the evolutionary scale. They are found far earlier in the fossil record than angiosperms. As will be discussed in subsequent sections, the various environmental adaptations gymnosperms have represent a step on the path to the most successful (diversity-wise) clade (monophyletic branch).



Figure 26.2A.1: Female cone of Tamarack pine: The female cone of *Pinus tontorta*, the Tamarack Pine, showing the rough scales. This is the cone that produces ovules.

Gymnosperm Reproduction and Seeds

Gymnosperms are sporophytes (a plant with two copies of its genetic material, capable of producing spores). Their sporangia (receptacle in which sexual spores are formed) are found on sporophylls, plated scale-like structures that together make up cones. The female gametophyte develops from the haploid (meaning one set of genetic material) spores that are contained within the sporangia. Like all seed plants, gymnosperms are heterosporous: both sexes of gametophytes develop from different types of spores produced by separate cones. One type of cone is the small pollen cone, which produces microspores that subsequently develop into pollen grains. The other type of cones, the larger “ovulate” cones, make megaspores that develop into female gametophytes called ovules. Incredibly, this whole sexual process can take three years: from the production of the two sexes of gametophytes, to bringing the gametophytes together in the process of pollination, and finally to forming mature seeds from fertilized ovules. After this process is completed, the individual sporophylls separate (the cone breaks apart) and float in the wind to a habitable place. This is concluded with germination and the formation of a seedling. Conifers have sperm that do not have flagella, but instead are conveyed to the egg via a pollen tube. It is important to note that the seeds of gymnosperms are not

enclosed in their final state upon the cone.



Figure 26.2A.2: Male cone of Tamarack pine: The male cone of *Pinus tontorta*, the Tamarack pine, showing the close proximity of the scales. This is the cone that produces pollen.

Key Points

- Gymnosperms produce both male and female cones, each making the gametes needed for fertilization; this makes them heterosporous.
- Megaspores made in cones develop into the female gametophytes inside the ovules of gymnosperms, while pollen grains develop from cones that produce microspores.
- Conifer sperm do not have flagella but rather move by way of a pollen tube once in contact with the ovule.

Key Terms

- **ovule**: the structure in a plant that develops into a seed after fertilization; the megasporangium of a seed plant with its enclosing integuments
- **sporophyll**: the equivalent to a leaf in ferns and mosses that bears the sporangia
- **heterosporous**: producing both male and female gametophytes

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26.2B: Life Cycle of a Conifer

Learning Objectives

- Describe the life cycle of a gymnosperm

Life Cycle of a Conifer

Pine trees are conifers (cone bearing) and carry both male and female sporophylls on the same mature sporophyte. Therefore, they are monoecious plants. Like all gymnosperms, pines are heterosporous, generating two different types of spores: male microspores and female megaspores. In the male cones (staminate cones), the microsporocytes give rise to pollen grains by meiosis. In the spring, large amounts of yellow pollen are released and carried by the wind. Some gametophytes will land on a female cone. Pollination is defined as the initiation of pollen tube growth. The pollen tube develops slowly as the generative cell in the pollen grain divides into two haploid sperm cells by mitosis. At fertilization, one of the sperm cells will finally unite its haploid nucleus with the haploid nucleus of an egg cell.

Female cones (ovulate cones) contain two ovules per scale. One megaspore mother cell (megasporocyte) undergoes meiosis in each ovule. Three of the four cells break down leaving only a single surviving cell which will develop into a female multicellular gametophyte. It encloses archegonia (an archegonium is a reproductive organ that contains a single large egg). Upon fertilization, the diploid egg will give rise to the embryo, which is enclosed in a seed coat of tissue from the parent plant. Fertilization and seed development is a long process in pine trees: it may take up to two years after pollination. The seed that is formed contains three generations of tissues: the seed coat that originates from the sporophyte tissue, the gametophyte that will provide nutrients, and the embryo itself.

In the life cycle of a conifer, the sporophyte (2n) phase is the longest phase. The gametophytes (1n), microspores and megaspores, are reduced in size. This phase may take more than one year between pollination and fertilization while the pollen tube grows towards the megasporocyte (2n), which undergoes meiosis into megaspores. The megaspores will mature into eggs (1n).

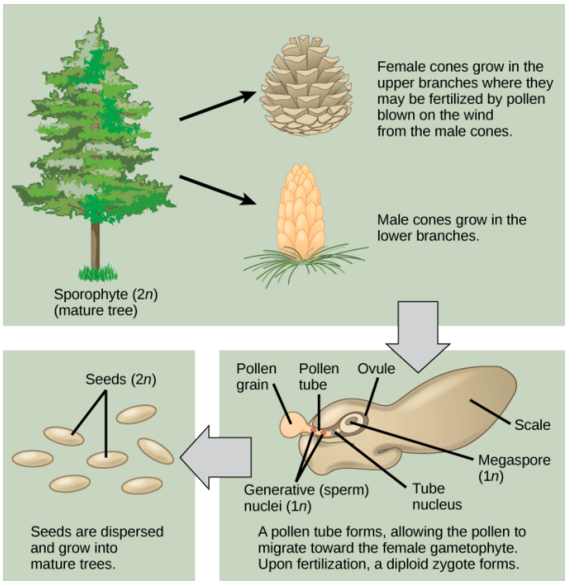


Figure $26.2B.1$: Life cycle of a conifer: This image shows the life cycle of a conifer. Pollen from male cones moves up into upper branches where it fertilizes female cones.

Key Points

- Male cones give rise to microspores, which produce pollen grains, while female cones give rise to megaspores, which

produce ovules.
- The pollen tube develops from the pollen grain to initiate fertilization; the pollen grain divides into two sperm cells by mitosis; one of the sperm cells unites with the egg cell during fertilization.
- Once the ovule is fertilized, a diploid sporophyte is produced, which gives rise to the embryo enclosed in a seed coat of tissue from the parent plant.
- Fertilization and seed development can take years; the seed that is formed is made up of three tissues: the seed coat, the gametophyte, and the embryo.

Key Terms

- **megaspore**: the larger spore of a heterosporous plant, typically producing a female gametophyte
- **microspore**: a small spore, as contrasted to the larger megaspore, which develops into male gametophytes
- **monoecious**: having the male (stamen) and female (carpel) reproductive organs on the same plant rather than on separate plants

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26.2C: Diversity of Gymnosperms

Learning Objectives

- Give examples showing the diversity of gymnosperms

Diversity of Gymnosperms

Modern gymnosperms are classified into four phyla. The first three (the Coniferophyta, Cycadophyta, and Gingkophyta) are similar in their production of secondary cambium (cells that generate the vascular system of the trunk or stem and are partially specialized for water transportation) and their pattern of seed development. However, these three phyla are not closely related phylogenetically to each other. The fourth phylum (the Gnetophyta) are considered the closest group to angiosperms because they produce true xylem tissue.

Coniferophytes

Conifers are the dominant phylum of gymnosperms, with the most variety of species. They are typically tall trees that usually bear scale-like or needle-like leaves. Water evaporation from leaves is reduced by their thin shape and the thick cuticle. Snow slides easily off needle-shaped leaves, keeping the load light and decreasing breaking of branches. Adaptations to cold and dry weather explain the predominance of conifers at high altitudes and in cold climates. Conifers include familiar evergreen trees such as pines, spruces, firs, cedars, sequoias, and yews. A few species are deciduous, losing their leaves in fall. The European larch and the tamarack are examples of deciduous conifers. Many coniferous trees are harvested for paper pulp and timber. The wood of conifers is more primitive than the wood of angiosperms; it contains tracheids, but no vessel elements, and is, therefore, referred to as “soft wood.”



Figure $26.2C.1$: Diversity of conifers: Conifers are the dominant form of vegetation in cold or arid environments and at high altitudes. Shown here are the (a) evergreen spruce Picea sp., (b) juniper Juniperus sp., (c) sequoia Sequoia Semervirens, which is a deciduous gymnosperm, and (d) the tamarack Larix larcinia. Notice the yellow leaves of the tamarack.

Cycads

Cycads thrive in mild climates. They are often mistaken for palms because of the shape of their large, compound leaves. Cycads bear large cones and may be pollinated by beetles rather than wind, which is unusual for a gymnosperm (). They dominated the

landscape during the age of dinosaurs in the Mesozoic, but only a hundred or so species persisted to modern times. Cycads face possible extinction; several species are protected through international conventions. Because of their attractive shape, they are often used as ornamental plants in gardens in the tropics and subtropics.



Figure 26.2C.2: Cycad leaves: This *Encephalartos ferox* cycad has large cones and broad, fern-like leaves.

Gingkophytes

The single surviving species of the gingkophytes group is the *Gingko biloba*. Its fan-shaped leaves, unique among seed plants because they feature a dichotomous venation pattern, turn yellow in autumn and fall from the tree. For centuries, *G. biloba* was cultivated by Chinese Buddhist monks in monasteries, which ensured its preservation. It is planted in public spaces because it is unusually resistant to pollution. Male and female organs are produced on separate plants. Typically, gardeners plant only male trees because the seeds produced by the female plant have an off-putting smell of rancid butter.



Gingko biloba

Gingko biloba is the only surviving species of the phylum Gingkophyta. This plate from the 1870 book Flora Japonica, Sectio Prima (Tafelband) depicts the leaves and fruit of Gingko biloba, as drawn by Philipp Franz von Siebold and Joseph Gerhard Zuccarini.

Gnetophytes

Gnetophytes are the closest relative to modern angiosperms and include three dissimilar genera of plants: *Ephedra*, *Gnetum*, and *Welwitschia*. Like angiosperms, they have broad leaves. In tropical and subtropical zones, gnetophytes are vines or small shrubs. *Ephedra* occurs in dry areas of the West Coast of the United States and Mexico. *Ephedra's* small, scale-like leaves are the source of the compound ephedrine, which is used in medicine as a potent decongestant. Because ephedrine is similar to amphetamines, both in chemical structure and neurological effects, its use is restricted to prescription drugs. Like angiosperms, but unlike other gymnosperms, all gnetophytes possess vessel elements in their xylem.



(a) *Ephedra* (b) *Gnetum* (c) *Welwitschia*

Figure 26.2C.3: Gnetophytes: (a) *Ephedra viridis*, known by the common name Mormon tea, grows on the West Coast of the United States and Mexico. (b) *Gnetum gnemon* grows in Malaysia. (c) The large *Welwitschia mirabilis* can be found in the Namibian desert.

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Key Points

- Gymnosperms consist of four main phyla: the Coniferophyta, Cycadophyta, Gingkophyta and Gnetophyta.
- Conifers are the dominant plant of the gymnosperms, having needle-like leaves and living in areas where the weather is cold and dry.
- Cycads live in warm climates, have large, compound leaves, and are unusual in that they are pollinated by beetles rather than wind.
- *Gingko biloba* is the only remaining species of the Gingkophyta and is usually resistant to pollution.
- Gnetophytes are the gymnosperms believed to be most closely related to the angiosperms because of the presence of vessel elements within their stems.

Key Terms

- **tracheid**: elongated cells in the xylem of vascular plants that serve in the transport of water and mineral salts
- **angiosperm**: a plant whose ovules are enclosed in an ovary
- **conifer**: a plant belonging to the conifers; a cone-bearing seed plant with vascular tissue, usually a tree

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26.3: ANGIOSPERMS

26.3A: Angiosperm Flowers

26.3B: Angsiosperm Fruit

26.3C: The Life Cycle of an Angiosperm

26.3D: Diversity of Angiosperms

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26.3A: Angiosperm Flowers

Learning Objectives

- Describe the main parts of a flower and their purposes

Flowers

Flowers are modified leaves, or sporophylls, organized around a central stalk. Although they vary greatly in appearance, all flowers contain the same structures: sepals, petals, carpels, and stamens. The peduncle attaches the flower to the plant. A whorl of sepals (collectively called the calyx) is located at the base of the peduncle and encloses the unopened floral bud. Sepals are usually photosynthetic organs, although there are some exceptions. For example, the corolla in lilies and tulips consists of three sepals and three petals that look virtually identical. Petals, collectively the corolla, are located inside the whorl of sepals and often display vivid colors to attract pollinators. Flowers pollinated by wind are usually small, feathery, and visually inconspicuous. Sepals and petals together form the perianth. The sexual organs (carpels and stamens) are located at the center of the flower.

Styles, stigmas, and ovules constitute the female organ: the gynoecium or carpel. Flower structure is very diverse. Carpels may be singular, multiple, or fused. Multiple fused carpels comprise a pistil. The megaspores and the female gametophytes are produced and protected by the thick tissues of the carpel. A long, thin structure called a style leads from the sticky stigma, where pollen is deposited, to the ovary, enclosed in the carpel. The ovary houses one or more ovules, each of which will develop into a seed upon fertilization. The male reproductive organs, the stamens (collectively called the androecium), surround the central carpel. Stamens are composed of a thin stalk called a filament and a sac-like structure called the anther. The filament supports the anther, where the microspores are produced by meiosis and develop into pollen grains.

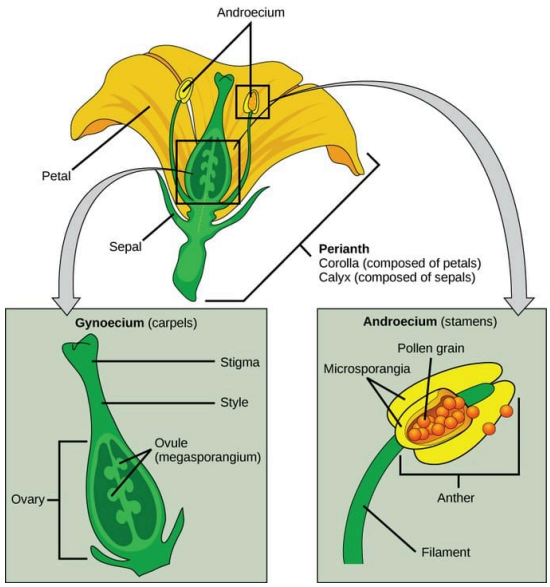


Figure 26.3A.1: Structure of flowers: This image depicts the structure of a flower. Perfect flowers produce both male and female floral organs. The flower shown has only one carpel, but some flowers have a cluster of carpels. Together, all the carpels make up the gynoecium.

Key Points

- Sepals, petals, carpels, and stamens are structures found in all flowers.
- To attract pollinators, petals usually exhibit vibrant colors; however, plants that depend on wind pollination contain flowers that are small and light.
- Carpels protect the female gametophytes and megaspores.
- The stigma is the structure where pollen is deposited and is connected to the ovary through the style.

- The anther, which comprises the stamen, is the site of microspore production and their development into pollen.

Key Terms

- **sepal**: a part of an angiosperm, and one of the component parts of the calyx; collectively the sepals are called the calyx (plural calyces), the outermost whorl of parts that form a flower
- **corolla**: an outermost-but-one whorl of a flower, composed of petals, when it is not the same in appearance as the outermost whorl (the calyx); it usually comprises the petal, which may be fused
- **stamen**: in flowering plants, the structure in a flower that produces pollen, typically consisting of an anther and a filament
- **carpel**: one of the individual female reproductive organs in a flower composed of an ovary, a style, and a stigma; also known as the gynoecium

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26.3B: Angsiosperm Fruit

Learning Objectives

- Recall the evolutionary advantage of fruits

Fruit

In botany, a fertilized, fully-grown, and ripened ovary is a fruit. As the seed develops, the walls of the ovary in which it forms thicken and form the fruit, enlarging as the seeds grow. Many foods commonly-called vegetables are actually fruit. Eggplants, zucchini, string beans, and bell peppers are all technically fruit because they contain seeds and are derived from the thick ovary tissue. Acorns are nuts and winged, maple whirligigs (whose botanical name is samara) are also fruit. Botanists classify fruit into more than two dozen different categories, only a few of which are actually fleshy and sweet.

Mature fruit can be fleshy or dry. Fleshy fruit include the familiar berries, peaches, apples, grapes, and tomatoes. Rice, wheat, and nuts are examples of dry fruit. Another distinction is that not all fruits are derived from the ovary. For instance, strawberries are derived from the receptacle, while apples are derived from the pericarp, or hypanthium. Some fruits are derived from separate ovaries in a single flower, such as the raspberry. Other fruits, such as the pineapple, form from clusters of flowers. Additionally, some fruits, like watermelon and oranges, have rinds.

Regardless of how they are formed, fruits are an agent of seed dispersal. The variety of shapes and characteristics reflect the mode of dispersal, whether it be wind, water, or animals. Wind carries the light dry fruit of trees and dandelions. Water transports floating coconuts. Some fruits attract herbivores with color or perfume, or as food. Once eaten, tough, undigested seeds are dispersed through the herbivore's feces. Other fruits have burs and hooks to cling to fur and hitch rides on animals.



Figure $26.3B.1$: Wind dispersal: The winged shape of *Alsomitra macrocarpa's* seeds allow them to use wind for dispersal. They can, therefore, glide for great distances.



Figure $26.3B.1$: Fruit dispersal: A fruit's distinctive shape and specialized characteristics will determine its dispersal mechanism.

Key Points

- Scientists classify fruit in many different categories that include descriptions, such as mature, fleshy, and dry; only a few are actually classified as being fleshy and sweet.
- Some fruit are developed from ovaries, while others develop from the pericarp, from clusters of flowers, or from separate ovaries in a single flower.
- Fruit are vital dispersal agents for plants; their unique shapes and features evolved to take advantage of specific dispersal modes.
- Dispersal methods of seeds within fruit include wind, water, herbivores, and animal fur.

Key Terms

- **fruit**: the seed-bearing part of a plant, often edible, colorful, and fragrant, produced from a floral ovary after fertilization
- **pericarp**: the outermost layer, or skin, of a ripe fruit or ovary
- **hypanthium**: the bowl-shaped part of a flower on which the sepals, petals, and stamens are borne

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26.3C: The Life Cycle of an Angiosperm

Learning Objectives

- Explain the life cycle of an angiosperm, including cross-pollination and the ways in which it takes place

The Life Cycle of an Angiosperm

The adult, or sporophyte, phase is the main phase of an angiosperm's life cycle. As with gymnosperms, angiosperms are heterosporous. Therefore, they generate microspores, which will produce pollen grains as the male gametophytes, and megaspores, which will form an ovule that contains female gametophytes. Inside the anthers' microsporangia, male gametophytes divide by meiosis to generate haploid microspores, which, in turn, undergo mitosis and give rise to pollen grains. Each pollen grain contains two cells: one generative cell that will divide into two sperm and a second cell that will become the pollen tube cell.

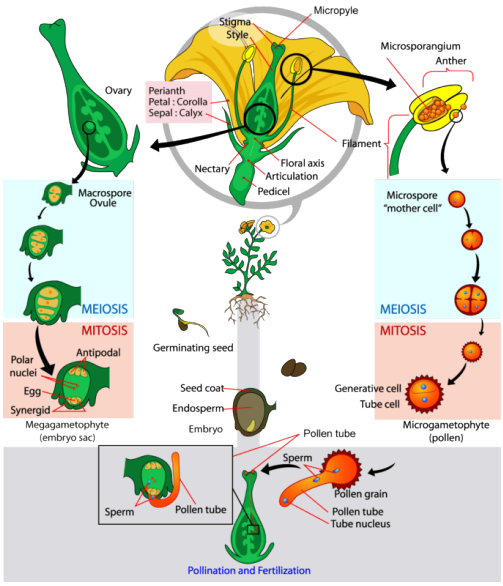


Figure $26.3C.1$: Life cycle of angiosperms: The life cycle of an angiosperm is shown. Anthers and carpels are structures that shelter the actual gametophytes: the pollen grain and embryo sac. Double fertilization is a process unique to angiosperms.

The ovule, sheltered within the ovary of the carpel, contains the megasporangium protected by two layers of integuments and the ovary wall. Within each megasporangium, a megasporocyte undergoes meiosis, generating four megaspores: three small and one large. Only the large megaspore survives; it produces the female gametophyte referred to as the embryo sac. The megaspore divides three times to form an eight-cell stage. Four of these cells migrate to each pole of the embryo sac; two come to the equator and will eventually fuse to form a 2n polar nucleus. The three cells away from the egg form antipodals while the two cells closest to the egg become the synergids.

The mature embryo sac contains one egg cell, two synergids ("helper" cells), three antipodal cells, and two polar nuclei in a central cell. When a pollen grain reaches the stigma, a pollen tube extends from the grain, grows down the style, and enters through the micropyle, an opening in the integuments of the ovule. The two sperm cells are deposited in the embryo sac.

A double fertilization event then occurs. One sperm and the egg combine, forming a diploid zygote, the future embryo. The other sperm fuses with the 2n polar nuclei, forming a triploid cell that will develop into the endosperm, which is tissue that serves as a food reserve. The zygote develops into an embryo with a radicle, or small root, and one (monocot) or two (dicot) leaf-like organs called cotyledons. This difference in the number of embryonic leaves is the basis for the two major groups of angiosperms: the monocots and the eudicots. Seed food reserves are stored outside the embryo in the form of complex carbohydrates, lipids, or proteins. The cotyledons serve as conduits to transmit the broken-down food reserves from their storage site inside the seed to the developing embryo. The seed consists of a toughened layer of integuments forming the coat, the endosperm with food

reserves, and the well-protected embryo at the center.



Figure $26.3C.1$: The fruit of the Aesculus or Horse Chestnut tree: These seeds are enclosed a protective outer covering called the seed coat, usually with some stored food. After fertilization and some growth in the angiosperm, the ripened ovule is produced. The formation of the seed completes the process of reproduction in seed plants (started with the development of flowers and pollination), with the embryo developed from the zygote and the seed coat from the integuments of the ovule.

Some species of angiosperms are hermaphroditic (stamens and pistils are contained on a single flower), some species are monoecious (stamens and pistils occur on separate flowers, but the same plant), and some are dioecious (staminate and pistillate flowers occur on separate plants). Both anatomical and environmental barriers promote cross-pollination mediated by a physical agent (wind or water) or an animal, such as an insect or bird. Cross-pollination increases genetic diversity in a species.

Key Points

- Microspores develop into pollen grains, which are the male gametophytes, while megaspores form an ovule that contains the female gametophytes.
- In the ovule, the megasporocyte undergoes meiosis, generating four megaspores; three small and one large; only the large megaspore survives and produces the female gametophyte (embryo sac).
- When the pollen grain reaches the stigma, it extends its pollen tube to enter the ovule and deposits two sperm cells in the embryo sac.
- The two available sperm cells allow for double fertilization to occur, which results in a diploid zygote (the future embryo) and a triploid cell (the future endosperm), which acts as a food store.
- Some species are hermaphroditic (stamens and pistils are contained on a single flower), some species are monoecious (stamens and pistils occur on separate flowers, but the same plant), and some are dioecious (staminate and pistillate flowers occur on separate plants).

Key Terms

- **cotyledon**: the leaf of the embryo of a seed-bearing plant; after germination it becomes the first leaves of the seedling
- **heterosporous**: producing both male and female gametophytes
- **synergid**: either of two nucleated cells at the top of the embryo sac that aid in the production of the embryo; helper cells

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26.3D: Diversity of Angiosperms

Learning Objectives

- Explain how angiosperm diversity is classified

Diversity of Angiosperms

Angiosperms are classified in a single phylum: the Anthophyta. Modern angiosperms appear to be a monophyletic group, which means that they originated from a single ancestor. Flowering plants are divided into two major groups according to the structure of the cotyledons and pollen grains, among others. Monocots include grasses and lilies while eudicots or dicots form a polyphyletic group. However, many species exhibit characteristics that belong to either group; as such, the classification of a plant as a monocot or a eudicot is not always clearly evident. Basal angiosperms are a group of plants that are believed to have branched off before the separation into monocots and eudicots because they exhibit traits from both groups. They are categorized separately in many classification schemes. The Magnoliidae (magnolia trees, laurels, and water lilies) and the Piperaceae (peppers) belong to the basal angiosperm group.

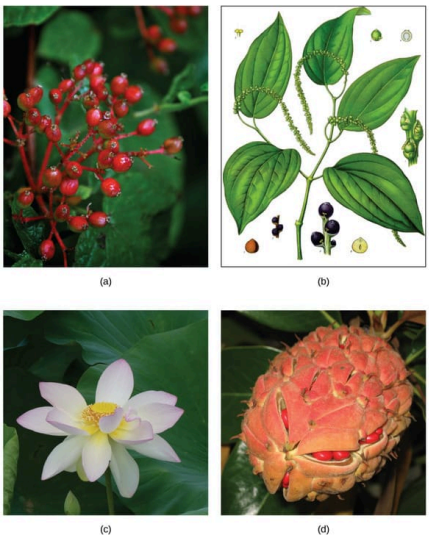


Figure $26.3D.1$: Examples of basal angiosperms: The (a) common spicebush belongs to the Laurales, the same family as cinnamon and bay laurel. The fruit of (b) the *Piper nigrum* plant is black pepper, the main product that was traded along spice routes. Notice the small, unobtrusive, clustered flowers. (c) Lotus flowers, *Nelumbo nucifera*, have been cultivated since ancient times for their ornamental value; the root of the lotus flower is eaten as a vegetable. The red seeds of (d) a magnolia tree, characteristic of the final stage, are just starting to appear.

Basal Angiosperms

Examples of basal angiosperms include the Magnoliidae, Laurales, Nymphaeales, and the Piperales. Members in these groups all share traits from both monocot and dicot groups. The Magnoliidae are represented by the magnolias: tall trees bearing large, fragrant flowers that have many parts and are considered archaic. Laurel trees produce fragrant leaves and small, inconspicuous flowers. The Laurales grow mostly in warmer climates and are small trees and shrubs. Familiar plants in this group include the bay laurel, cinnamon, spice bush, and avocado tree. The Nymphaeales are comprised of the water lilies, lotus, and similar plants; all species thrive in freshwater biomes and have leaves that float on the water surface or grow underwater. Water lilies are particularly prized by gardeners and have graced ponds and pools for thousands of years. The Piperales are a group of herbs, shrubs, and small trees that grow in the tropical climates. They have small flowers without petals that are tightly arranged in long spikes. Many species are the source of prized fragrance or spices; for example, the berries of *Piper nigrum* are the familiar black peppercorns

that are used to flavor many dishes.

Monocots

Plants in the monocot group are primarily identified as such by the presence of a single cotyledon in the seedling. Other anatomical features shared by monocots include veins that run parallel to the length of the leaves and flower parts that are arranged in a three- or six-fold symmetry. True woody tissue is rarely found in monocots. In palm trees, vascular and parenchyma tissues produced by the primary and secondary thickening of meristems form the trunk. The pollen from the first angiosperms was monosulcate, containing a single furrow or pore through the outer layer. This feature is still seen in the modern monocots. Vascular tissue of the stem is not arranged in any particular pattern. The root system is mostly adventitious and unusually positioned, with no major tap root. The monocots include familiar plants such as the true lilies (which are the origin of their alternate name: Liliopsida), orchids, grasses, and palms. Many important crops are monocots, such as rice and other cereals, corn, sugar cane, and tropical fruits like bananas and pineapples.



Figure $26.3D.1$: Monocots and Dicots: major crops of the world: The world's major crops are flowering plants. (a) Rice, (b) wheat, and (c) bananas are monocots, while (d) cabbage, (e) beans, and (f) peaches are dicots.

Eudicots

Eudicots, or true dicots, are characterized by the presence of two cotyledons in the developing shoot. Veins form a network in leaves, while flower parts come in four, five, or many whorls. Vascular tissue forms a ring in the stem whereas in monocots, vascular tissue is scattered in the stem. Eudicots can be herbaceous (like grasses), or produce woody tissues. Most eudicots produce pollen that is trisulcate or triporate, with three furrows or pores. The root system is usually anchored by one main root developed from the embryonic radicle. Eudicots comprise two-thirds of all flowering plants.

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Key Points

- Angiosperm are flowering plants that are classified based on characteristics that include (but are not limited to) cotyledon structure, pollen grains, as well as flower and vascular tissue arrangement.
- Basal angiosperms, classified separately, contain features found in both monocots and dicots, as they are believed to have originated before the separation of these two main groups.
- Monocots contain a single cotyledon and have veins that run parallel to the length of their leaves; their flowers are arranged in three to six-fold symmetry.
- Dicots have flowers arranged in whorls, two cotyledons, and a vein arrangement that forms networks within their leaves.
- Monocots do not contain any true woody tissue while dicots can be herbacious or woody and have vascular tissue that forms a ring in the stem.

Key Terms

- **dicot**: a plant whose seedlings have two cotyledons; a dicotyledon
- **angiosperm**: a plant whose ovules are enclosed in an ovary
- **monocot**: one of two major groups of flowering plants (or angiosperms) that are traditionally recognized; seedlings typically have one cotyledon (seed-leaf)
- **cotyledon**: the leaf of the embryo of a seed-bearing plant; after germination it becomes the first leaves of the seedling
- **basal angiosperm**: the first flowering plants to diverge from the ancestral angiosperm, including a single species of shrub from New Caledonia, water lilies and some other aquatic plants, and woody aromatic plants

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26.4: THE ROLE OF SEED PLANTS

26.4A: Herbivory and Pollination

26.4B: The Importance of Seed Plants in Human Life

26.4C: Biodiversity of Plants

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26.4A: Herbivory and Pollination

The diversity of plants can be attributed to pollination and herbivory, both examples of coevolution between animals and plants.

Learning Objectives

- Describe the interaction of plants and animals in achieving pollination

Animal & Plant Interactions

Angiosperm diversity is due in part to multiple interactions with animals. Herbivory has favored the development of defense mechanisms in plants and avoidance of those defense mechanisms in animals. Pollination (the transfer of pollen to a carpel) is mainly carried out by wind and animals; therefore, angiosperms have evolved numerous adaptations to capture the wind or attract specific classes of animals.

Coevolution of flowering plants and insects is a hypothesis that has received much attention and support, especially because both angiosperms and insects diversified at about the same time in the middle Mesozoic. Many authors have attributed the diversity of plants and insects to pollination and herbivory, which is the consumption of plants by insects and other animals. This is believed to have been as much a driving force as pollination.

Herbivory

Coevolution of herbivores and plant defenses is observed in nature. Unlike animals, most plants cannot outrun predators or use mimicry to hide from hungry animals. A sort of arms race exists between plants and herbivores. To “combat” herbivores, some plant seeds (such as acorn and unripened persimmon) are high in alkaloids and, therefore, unsavory to some animals. Other plants are protected by bark, although some animals have developed specialized mouth pieces to tear and chew vegetal material. Spines and thorns deter most animals, except for mammals with thick fur; some birds have specialized beaks to get past such defenses.



Figure 26.4A.1: Plant defenses from herbivory: (a) Spines and (b) thorns are examples of plant defenses.

Herbivory has been used by seed plants for their own benefit in a display of mutualistic relationships. The dispersal of fruit by animals is the most striking example. The plant offers to the herbivore a nutritious source of food in return for spreading the plant’s genetic material to a wider area.

An extreme example of collaboration between an animal and a plant is the case of acacia trees and ants. The trees support the insects with shelter and food. In return, ants discourage herbivores, both invertebrates and vertebrates, by stinging and attacking leaf-eating organisms.

Pollination

Grasses are a successful group of flowering plants that are wind pollinated. They produce large amounts of powdery pollen carried over large distances by the wind. The flowers are small and wisp-like. Large trees such as oaks, maples, and birches are also wind pollinated.

More than 80 percent of angiosperms depend on animals for pollination: the transfer of pollen from the anther to the stigma. Consequently, plants have developed many adaptations to attract pollinators. The specificity of specialized plant structures that target animals can be very surprising. It is possible, for example, to determine the type of pollinator favored by a plant just from the flower's characteristics. Many bird or insect-pollinated flowers secrete nectar, a sugary liquid. They also produce both fertile pollen for reproduction and sterile pollen rich in nutrients for birds and insects. Butterflies and bees can detect ultraviolet light. Flowers that attract these pollinators usually display a pattern of low ultraviolet reflectance that helps them quickly locate the flower's center to collect nectar while being dusted with pollen. Large, red flowers with little smell and a long funnel shape are preferred by hummingbirds who have good color perception, a poor sense of smell, and need a strong perch. White flowers that open at night attract moths. Other animals (such as bats, lemurs, and lizards) can also act as pollinating agents. Any disruption to these interactions, such as the disappearance of bees as a consequence of colony collapse disorders, can lead to disaster for agricultural industries that depend heavily on pollinated crops.



Figure 26.4A.2: Animal-aided pollination: As a bee collects nectar from a flower, it is dusted by pollen, which it then disperses to other flowers.

Key Points

- Herbivory is believed to have been as much a driving force in the evolution of plant diversity as pollination.
- Coevolution between herbivores and plants is commonly seen in nature; for example, plants have developed unique ways to fight off herbivores while, in turn, herbivores have developed specialized features to get around these defenses.
- Plants have developed unique pollination adaptations, such as the ability to capture the wind or attract specific classes of animals.
- Birds, insects, bats, lemurs, and lizards can act as pollinators; each is attracted to a specific plant adaptation, which has been developed to attract a suitable pollinator.
- Any disruption between pollinator and plant interactions, such as the extinction of a species, can lead to the collapse of an ecosystem and/or the demise of an agricultural industry.

Key Terms

- **coevolution**: the evolution of organisms of two or more species in which each adapts to changes in the other
- **pollination**: the transfer of pollen from an anther to a stigma that is carried out by insects, birds, bats, and the wind
- **herbivory**: the consumption of living plant tissue by animals

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26.4B: The Importance of Seed Plants in Human Life

Learning Objectives

- Explain the importance of seed plants to humans

The Importance of Seed Plants in Human Life

Seed plants are cultivated for their beauty and smells, as well as their importance in the development of medicines. Plants are also the foundation of human diets across the world. Many societies eat, almost exclusively, vegetarian fare and depend solely on seed plants for their nutritional needs. A few crops (rice, wheat, and potatoes) dominate the agricultural landscape. Many crops were developed during the agricultural revolution when human societies made the transition from nomadic hunter–gatherers to horticulture and agriculture. Cereals, rich in carbohydrates, provide the staple of many human diets. In addition, beans and nuts supply proteins. Fats are derived from crushed seeds, as is the case for peanut and rapeseed (canola) oils, or fruits such as olives. Animal husbandry also requires large amounts of crops.



Figure $26.4B.1$: Importance of plants to humans: Humans rely on plants for a variety of reasons. (a) Cacao beans were introduced in Europe from the New World, where they were used by Mesoamerican civilizations. Combined with sugar, another plant product, chocolate is a popular food. (b) Flowers like the tulip are cultivated for their beauty. (c) Quinine, extracted from cinchona trees, is used to treat malaria, to reduce fever, and to alleviate pain. (d) This violin is made of wood.

Staple crops are not the only food derived from seed plants. Fruits and vegetables provide nutrients, vitamins, and fiber. Sugar, to sweeten dishes, is produced from the monocot sugarcane and the eudicot sugar beet. Drinks are made from infusions of tea leaves, chamomile flowers, crushed coffee beans, or powdered cocoa beans. Spices come from many different plant parts: saffron and cloves are stamens and buds, black pepper and vanilla are seeds, the bark of a bush in the Laurales family supplies cinnamon, and the herbs that flavor many dishes come from dried leaves and fruit, such as the pungent red chili pepper. The volatile oils of flowers and bark provide the scent of perfumes. Additionally, no discussion of seed plant contribution to human diet would be complete without the mention of alcohol. Fermentation of plant-derived sugars and starches is used to produce alcoholic beverages in all societies. In some cases, the beverages are derived from the fermentation of sugars from fruit, as with wines, and, in other cases, from the fermentation of carbohydrates derived from seeds, as with beers.

Seed plants have many other uses, including providing wood as a source of timber for construction, fuel, and material to build furniture. Most paper is derived from the pulp of coniferous trees. Fibers of seed plants, such as cotton, flax, and hemp, are woven into cloth. Textile dyes, such as indigo, were mostly of plant origin until the advent of synthetic chemical dyes. Lastly, it is more difficult to quantify the benefits of ornamental seed plants. These grace private and public spaces, adding beauty and serenity to

human lives and inspiring painters and poets alike.

The medicinal properties of plants have been known to human societies since ancient times. There are references to the use of plants' curative properties in Egyptian, Babylonian, and Chinese writings from 5,000 years ago. Many modern synthetic therapeutic drugs are derived or synthesized de novo from plant secondary metabolites. It is important to note that the same plant extract can be a therapeutic remedy at low concentrations, become an addictive drug at higher doses, and can potentially kill at high concentrations.

Ethnobotany

The relatively new field of ethnobotany studies the interaction between a particular culture and the plants native to the region. Seed plants have a large influence on day-to-day human life. Not only are plants the major source of food and medicine, they also influence many other aspects of society, from clothing to industry. The medicinal properties of plants were recognized early on in human cultures. From the mid-1900s, synthetic chemicals began to supplant plant-based remedies.

Pharmacognosy is the branch of pharmacology that focuses on medicines derived from natural sources. With massive globalization and industrialization, there is a concern that much human knowledge of plants and their medicinal purposes will disappear with the cultures that fostered them. This is where ethnobotanists come in. To learn about and understand the use of plants in a particular culture, an ethnobotanist must bring in knowledge of plant life and an understanding and appreciation of diverse cultures and traditions. The Amazon forest is home to an incredible diversity of vegetation and is considered an untapped resource of medicinal plants; yet, both the ecosystem and its indigenous cultures are threatened with extinction.

To become an ethnobotanist, a person must acquire a broad knowledge of plant biology, ecology, and sociology. Not only are the plant specimens studied and collected, but also the stories, recipes, and traditions that are linked to them. For ethnobotanists, plants are not viewed solely as biological organisms to be studied in a laboratory; they are seen as an integral part of human culture. The convergence of molecular biology, anthropology, and ecology make the field of ethnobotany a truly multidisciplinary science.

Key Points

- Providing much of the nutritional values that humans need, seed plants are the foundation of human diets across the world.
- Wood, paper, textiles, and dyes are just a few examples of plant uses in everyday human life.
- Traditionally, humans have also used plants as ornamental species through their use as decorations and as inspiration in the arts.
- As medicinal sources, plants are vital to humans, as many modern drugs have been derived from secondary plant metabolites; ancient societies also depended on them for their curative properties.
- The important relationship that human cultures have developed with plants can be studied through the field of ethnobotany.

Key Terms

- **ethnobotany**: the scientific study of the relationships between people and plants
- **pharmacognosy**: the branch of pharmacology that studies medical substances that are extracted from natural sources, including drugs derived from plants and herbs used for medicinal purposes
- **husbandry**: the raising of livestock and the cultivation of crops; agriculture

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26.4C: Biodiversity of Plants

Learning Objectives

- Discuss the threats to plant biodiversity

Threats to Plant Biodiversity

Plants play a key role in ecosystems. They are a source of food and medicinal compounds while also providing raw materials for many industries. Rapid deforestation and industrialization, however, threaten plant biodiversity. In turn, this threatens the ecosystem.

Biodiversity of plants ensures a resource for new food crops and medicines. Plant life balances ecosystems, protects watersheds, mitigates erosion, moderates climate, and provides shelter for many animal species. Threats to plant diversity, however, come from many angles. The explosion of the human population, especially in tropical countries where birth rates are highest and economic development is in full swing, is leading to human encroachment into forested areas. To feed the larger population, humans need to obtain arable land which leads to massive clearing of trees. The need for more energy to power larger cities and economic growth results in the construction of dams, the consequent flooding of ecosystems, and increased emissions of pollutants. Other threats to tropical forests come from poachers who log trees for their precious wood. Ebony and Brazilian rosewood, both on the endangered list, are examples of tree species driven almost to extinction by indiscriminate logging.



Figure $26.4C.1$: Indiscriminate logging: Indiscriminate logging, which leads to the clearing of whole habitats, has become a severe threat to plant biodiversity and has led to species extinction.

The number of plant species becoming extinct is increasing at an alarming rate. Because ecosystems are in a delicate balance and because seed plants maintain close symbiotic relationships with animals, whether predators or pollinators, the disappearance of a single plant can lead to the extinction of connected animal species. A real and pressing issue is that many plant species have not yet been cataloged; their place in the ecosystem is unknown. These unknown species are threatened by logging, habitat destruction, and loss of pollinators. They may become extinct before we have the chance to begin to understand the possible impacts resulting from their disappearance. Efforts to preserve biodiversity take several lines of action, from preserving heirloom seeds to barcoding species. Heirloom seeds come from plants that were traditionally grown in human populations, as opposed to the seeds used for large-scale agricultural production. Barcoding is a technique in which one or more short gene sequences, taken from a well-characterized portion of the genome, are used to identify a species through DNA analysis.

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Key Points

- Plant biodiversity is invaluable because it balances ecosystems, protects watersheds, mitigates erosion, moderates climate, and provides shelter for animals.
- Threats to plant biodiversity include the increasing human population, pollution, deforestation, and species extinction.
- Plant extinction is progressing at an alarming rate; this, in turn, affects other species, which also become extinct because they depend on the delicate ecological balance.Efforts to preserve plant biodiversity currently include heirloom seed collections and barcoding DNA analysis.

Key Terms

- **biodiversity**: the diversity (number and variety of species) of plant and animal life within a region
- **barcoding**: a taxonomic method that uses a short genetic marker in an organism's DNA to identify it as belonging to a particular species
- **heirloom seed**: seeds which are not of agricultural importance yet hold traditional importance; these seeds are kept in seed banks and are still maintained by some gardeners and farmers

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27: INTRODUCTION TO ANIMAL DIVERSITY

- Topic hierarchy

27.1: Features of the Animal Kingdom

27.1A: Characteristics of the Animal Kingdom

27.1B: Complex Tissue Structure

27.1C: Animal Reproduction and Development

27.2: Features Used to Classify Animals

27.2A: Animal Characterization Based on Body Symmetry

27.2B: Animal Characterization Based on Features of Embryological Development

27.3: Animal Phylogeny

27.3A: Constructing an Animal Phylogenetic Tree

27.3B: Molecular Analyses and Modern Phylogenetic Trees

27.4: The Evolutionary History of the Animal Kingdom

27.4A: Pre-Cambrian Animal Life

27.4B: The Cambrian Explosion of Animal Life

27.4C: Post-Cambrian Evolution and Mass Extinctions

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27.1: FEATURES OF THE ANIMAL KINGDOM

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- Topic hierarchy

27.1A: Characteristics of the Animal Kingdom
27.1B: Complex Tissue Structure
27.1C: Animal Reproduction and Development

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27.1A: Characteristics of the Animal Kingdom

Learning Objectives

- Describe the methods used to classify animals

Introduction: Features of the Animal Kingdom

Animal evolution began in the ocean over 600 million years ago with tiny creatures that probably do not resemble any living organism today. Since then, animals have evolved into a highly-diverse kingdom. Although over one million extant (currently living) species of animals have been identified, scientists are continually discovering more species as they explore ecosystems around the world. The number of extant species is estimated to be between 3 and 30 million.

But what is an animal? While we can easily identify dogs, birds, fish, spiders, and worms as animals, other organisms, such as corals and sponges, are not as easy to classify. Animals vary in complexity, from sea sponges to crickets to chimpanzees, and scientists are faced with the difficult task of classifying them within a unified system. They must identify traits that are common to all animals as well as traits that can be used to distinguish among related groups of animals. The animal classification system characterizes animals based on their anatomy, morphology, evolutionary history, features of embryological development, and genetic makeup. This classification scheme is constantly developing as new information about species arises. Understanding and classifying the great variety of living species help us better understand how to conserve the diversity of life on earth.

Even though members of the animal kingdom are incredibly diverse, most animals share certain features that distinguish them from organisms in other kingdoms. All animals are eukaryotic, multicellular organisms, and almost all animals have a complex tissue structure with differentiated and specialized tissues. Most animals are motile, at least during certain life stages. All animals require a source of food and are, therefore, heterotrophic: ingesting other living or dead organisms. This feature distinguishes them from autotrophic organisms, such as most plants, which synthesize their own nutrients through photosynthesis. As heterotrophs, animals may be carnivores, herbivores, omnivores, or parasites. Most animals reproduce sexually with the offspring passing through a series of developmental stages that establish a fixed body plan. The body plan refers to the morphology of an animal, determined by developmental cues.



Figure 27.1A.1: Heterotrophs: All animals are heterotrophs that derive energy from food. 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 mosquitoes and its adult stage infesting the heart of dogs and other mammals.

Key Points

- Animals vary in complexity and are classified based on anatomy, morphology, genetic makeup, and evolutionary history.
- All animals are eukaryotic, multicellular organisms, and most animals have complex tissue structure with differentiated and specialized tissue.
- Animals are heterotrophs; they must consume living or dead organisms since they cannot synthesize their own food and can be carnivores, herbivores, omnivores, or parasites.
- Most animals are motile for at least some stages of their lives, and most animals reproduce sexually.

Key Terms

- **body plan**: an assemblage of morphological features shared among many members of a phylum-level group
- **heterotroph**: an organism that requires an external supply of energy in the form of food, as it cannot synthesize its own
- **extant**: still in existence; not extinct

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27.1B: Complex Tissue Structure

Learning Objectives

- List the various specialized tissue types found in animals and describe their functions

Complex Tissue Structure

As multicellular organisms, animals differ from plants and fungi because their cells don't have cell walls; their cells may be embedded in an extracellular matrix (such as bone, skin, or connective tissue); and their cells have unique structures for intercellular communication (such as gap junctions). In addition, animals possess unique tissues, absent in fungi and plants, which allow coordination (nerve tissue) and motility (muscle tissue). Animals are also characterized by specialized connective tissues that provide structural support for cells and organs. This connective tissue constitutes the extracellular surroundings of cells and is made up of organic and inorganic materials. In vertebrates, bone tissue is a type of connective tissue that supports the entire body structure. The complex bodies and activities of vertebrates demand such supportive tissues. Epithelial tissues cover, line, protect, and secrete; these tissues include the epidermis of the integument: the lining of the digestive tract and trachea. They also make up the ducts of the liver and glands of advanced animals.

The animal kingdom is divided into Parazoa (sponges) and Eumetazoa (all other animals). As very simple animals, the organisms in group Parazoa ("beside animal") do not contain true specialized tissues. Although they do possess specialized cells that perform different functions, those cells are not organized into tissues. These organisms are considered animals since they lack the ability to make their own food. Animals with true tissues are in the group Eumetazoa ("true animals"). When we think of animals, we usually think of Eumetazoans, since most animals fall into this category.

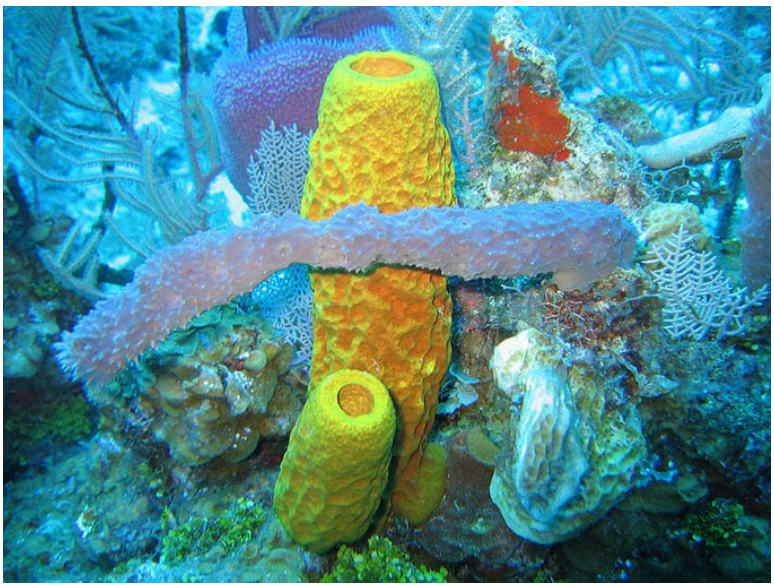


Figure $27.1B.1$: Sponges: Sponges, such as those in the Caribbean Sea, are classified as Parazoans because they are very simple animals that do not contain true specialized tissues.

The different types of tissues in true animals are responsible for carrying out specific functions for the organism. This differentiation and specialization of tissues is part of what allows for such incredible animal diversity. For example, the evolution of nerve tissues and muscle tissues has resulted in animals' unique ability to rapidly sense and respond to changes in their environment. This allows animals to survive in environments where they must compete with other species to meet their nutritional demands.

Key Points

- Animal cells don't have cell walls; their cells may be embedded in an extracellular matrix and have unique structures for intercellular communication.
- Animals have nerve and muscle tissues, which provide coordination and movement; these are not present in plants and fungi.
- Complex animal bodies demand connective tissues made up of organic and inorganic materials that provide support and structure.
- Animals are also characterized by epithelial tissues, like the epidermis, which function in secretion and protection.
- The animal kingdom is divided into Parazoa (sponges), which do not contain true specialized tissues, and Eumetazoa (all other animals), which do contain true specialized tissues.

Key Terms

- **Parazoa**: a taxonomic subkingdom within the kingdom Animalia; the sponges
- **Eumetazoa**: a taxonomic subkingdom, within kingdom Animalia; all animals except the sponges
- **epithelial tissue**: one of the four basic types of animal tissue, which line the cavities and surfaces of structures throughout the body, and also form many glands

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27.1C: Animal Reproduction and Development

Learning Objectives

- Explain the processes of animal reproduction and embryonic development

Animal Reproduction and Development

Most animals are diploid organisms (their body, or somatic, cells are diploid) with haploid reproductive (gamete) cells produced through meiosis. The majority of animals undergo sexual reproduction. This fact distinguishes animals from fungi, protists, and bacteria where asexual reproduction is common or exclusive. However, a few groups, such as cnidarians, flatworms, and roundworms, undergo asexual reproduction, although nearly all of those animals also have a sexual phase to their life cycle.

Processes of Animal Reproduction and Embryonic Development

During sexual reproduction, the haploid gametes of the male and female individuals of a species combine in a process called fertilization. Typically, the small, motile male sperm fertilizes the much larger, sessile female egg. This process produces a diploid fertilized egg called a zygote.

Some animal species (including sea stars and sea anemones, as well as some insects, reptiles, and fish) are capable of asexual reproduction. The most common forms of asexual reproduction for stationary aquatic animals include budding and fragmentation where part of a parent individual can separate and grow into a new individual. In contrast, a form of asexual reproduction found in certain insects and vertebrates is called parthenogenesis where unfertilized eggs can develop into new offspring. This type of parthenogenesis in insects is called haplodiploidy and results in male offspring. These types of asexual reproduction produce genetically identical offspring, which is disadvantageous from the perspective of evolutionary adaptability because of the potential buildup of deleterious mutations. However, for animals that are limited in their capacity to attract mates, asexual reproduction can ensure genetic propagation.

After fertilization, a series of developmental stages occur during which primary germ layers are established and reorganize to form an embryo. During this process, animal tissues begin to specialize and organize into organs and organ systems, determining their future morphology and physiology. Some animals, such as grasshoppers, undergo incomplete metamorphosis, in which the young resemble the adult. Other animals, such as some insects, undergo complete metamorphosis where individuals enter one or more larval stages that may differ in structure and function from the adult. In complete metamorphosis, the young and the adult may have different diets, limiting competition for food between them. Regardless of whether a species undergoes complete or incomplete metamorphosis, the series of developmental stages of the embryo remains largely the same for most members of the animal kingdom.

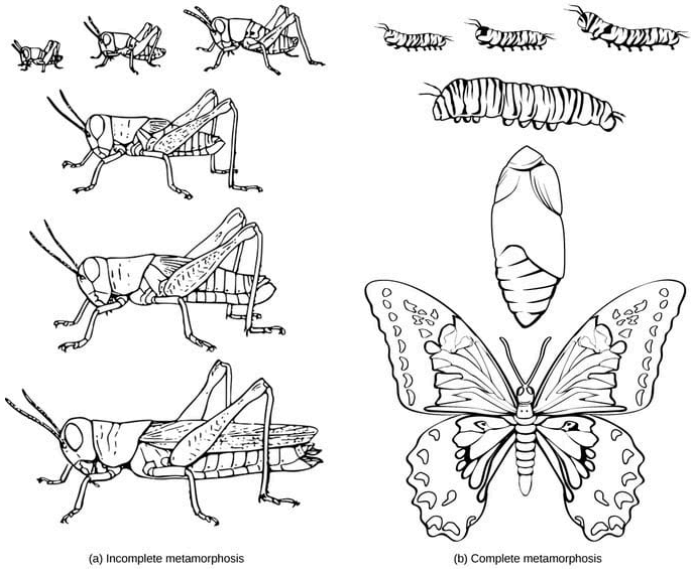


Figure $27.1C.1$: Incomplete and complete metamorphosis: (a) The grasshopper undergoes incomplete metamorphosis. (b) The butterfly undergoes complete metamorphosis.

The process of animal development begins with the cleavage, or series of mitotic cell divisions, of the zygote. Three cell divisions transform the single-celled zygote into an eight-celled structure. After further cell division and rearrangement of existing cells, a 6–32-celled hollow structure called a blastula is formed. Next, the blastula undergoes further cell division and cellular rearrangement during a process called gastrulation. This leads to the formation of the next developmental stage, the gastrula, in which the future digestive cavity is formed. Different cell layers (called germ layers) are formed during gastrulation. These germ layers are programed to develop into certain tissue types, organs, and organ systems during a process called organogenesis.

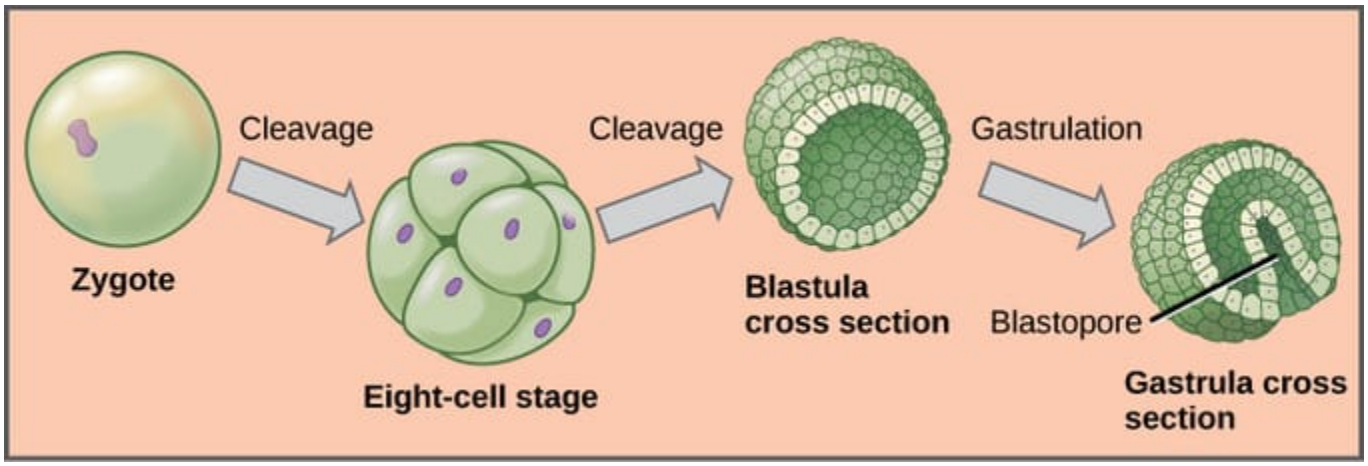


Figure $27.1C.1$: Embryonic development: During embryonic development, the zygote undergoes a series of mitotic cell divisions, or cleavages, to form an eight-cell stage, then a hollow blastula. During a process called gastrulation, the blastula folds inward to form a cavity in the gastrula.

The Role of Homeobox (Hox) Genes in Animal Development

Since the early 19th century, scientists have observed that many animals, from the very simple to the complex, shared similar embryonic morphology and development. Surprisingly, a human embryo and a frog embryo, at a certain stage of embryonic development, appear remarkably similar. For a long time, scientists did not understand why so many animal species looked similar during embryonic development, but were very different as adults. Near the end of the 20th century, a particular class of genes that dictate developmental direction was discovered. These genes that determine animal structure are called “homeotic genes.” They contain DNA sequences called homeoboxes, with specific sequences referred to as Hox genes. This family of genes is responsible for determining the general body plan: the number of body segments of an animal, the number and placement of appendages,

and animal head-tail directionality. The first Hox genes to be sequenced were those from the fruit fly (*Drosophila melanogaster*). A single Hox mutation in the fruit fly can result in an extra pair of wings or even appendages growing from the "wrong" body part.

There are many genes that play roles in the morphological development of an animal, but Hox genes are so powerful because they can turn on or off large numbers of other genes. Hox genes do this by coding transcription factors that control the expression of numerous other genes. Hox genes are homologous in the animal kingdom: the genetic sequences and their positions on chromosomes are remarkably similar across most animals (e.g., worms, flies, mice, humans) because of their presence in a common ancestor. Hox genes have undergone at least two duplication events during animal evolution: the additional genes allowed more complex body types to evolve.

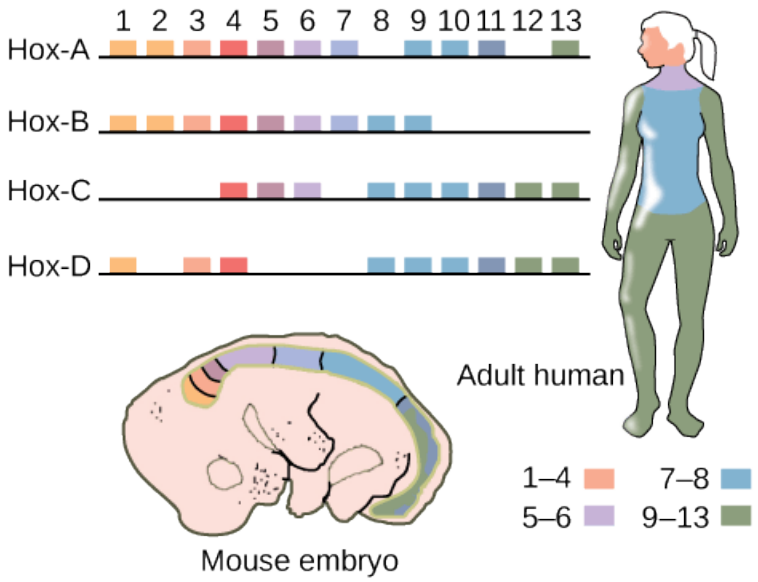


Figure $27.1C.1$: Hox genes: Hox genes are highly-conserved genes encoding transcription factors that determine the course of embryonic development in animals. In vertebrates, the genes have been duplicated into four clusters: Hox-A, Hox-B, Hox-C, and Hox-D. Genes within these clusters are expressed in certain body segments at certain stages of development. Shown here is the homology between Hox genes in mice and humans. Note how Hox gene expression, as indicated with orange, pink, blue, and green shading, occurs in the same body segments in both the mouse and the human.

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Key Points

- Most animals reproduce through sexual reproduction, but some animals are capable of asexual reproduction through parthenogenesis, budding, or fragmentation.
- Following fertilization, an embryo is formed, and animal tissues organize into organ systems; some animals may also undergo incomplete or complete metamorphosis.
- Cleavage of the zygote leads to the formation of a blastula, which undergoes further cell division and cellular rearrangement during a process called gastrulation, which leads to the formation of the gastrula.
- During gastrulation, the digestive cavity and germ layers are formed; these will later develop into certain tissue types, organs, and organ systems during a process called organogenesis.
- Hox genes are responsible for determining the general body plan, such as the number of body segments of an animal, the number and placement of appendages, and animal head-tail directionality.
- Hox genes, similar across most animals, can turn on or off other genes by coding transcription factors that control the expression of numerous other genes.

Key Terms

- **metamorphosis**: a change in the form and often habits of an animal after the embryonic stage during normal development
- **Hox gene**: genes responsible for determining the general body plan, such as the number of body segments of an animal, the number and placement of appendages, and animal head-tail directionality
- **blastula**: a 6-32-celled hollow structure that is formed after a zygote undergoes cell division

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27.2: FEATURES USED TO CLASSIFY ANIMALS

27.2A: Animal Characterization Based on Body Symmetry

27.2B: Animal Characterization Based on Features of Embryological Development

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27.2A: Animal Characterization Based on Body Symmetry

Learning Objectives

- Differentiate among the ways in which animals can be characterized by body symmetry

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. Only a few animal groups display radial symmetry, while asymmetry is a unique feature of phyla Porifera (sponges). All types of symmetry are well suited to meet the unique demands of a particular animal's lifestyle.

Radial Symmetry

Radial symmetry is the arrangement of body parts around a central axis, like rays on a sun or pieces in a pie. Radially symmetrical animals have top and bottom surfaces, but no left and right sides, or front and back. The two halves of a radially symmetrical animal may be described as the side with a mouth ("oral side") and the side without a mouth ("aboral side"). This form of symmetry marks the body plans of animals in the phyla Ctenophora (comb jellies) and Cnidaria (corals, sea anemones, and other jellies). Radial symmetry enables these sea creatures, which may be sedentary or only capable of slow movement or floating, to experience the environment equally from all directions.



Figure 27.2A.1: Radial symmetry: Some organisms, like sea anemones (phylum Cnidaria), have radial symmetry.

Bilateral Symmetry

Bilateral symmetry involves the division of the animal through a sagittal plane, resulting in two mirror-image, right and left halves, such as those of a butterfly, 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. All true animals, except those with radial symmetry, are bilaterally symmetrical. The evolution of bilateral symmetry and, therefore, 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 mobility and

increased sophistication of resource-seeking and predator-prey relationships.



Figure 27.2A.2: Bilateral symmetry: This monarch butterfly demonstrates bilateral symmetry down the sagittal plane, with the line of symmetry running from ventral to dorsal and dividing the body into two left and right halves.

Animals in the phylum Echinodermata (such as sea stars, sand dollars, and sea urchins) display radial symmetry as adults, but their larval stages exhibit bilateral symmetry. This is termed secondary radial symmetry. They are believed to have evolved from bilaterally symmetrical animals; thus, they are classified as bilaterally symmetrical.



Figure 27.2A.3: Secondary radial symmetry in echinoderms: The larvae of echinoderms (sea stars, sand dollars, and sea urchins) have bilateral symmetry as larvae, but develop radial symmetry as full adults.

Asymmetry

Only members of the phylum Porifera (sponges) have no body plan symmetry. There are some fish species, such as flounder, that lack symmetry as adults. However, the larval fish are bilaterally symmetrical.

Key Points

- Animals with radial symmetry have no right or left sides, only a top or bottom; these species are usually marine organisms like jellyfish and corals.
- Most animals are bilaterally symmetrical with a line of symmetry dividing their body into left and right sides along with a “head” and “tail” in addition to a top and bottom.
- Only sponges (phylum Porifera) have asymmetrical body plans.
- Some animals start life with one type of body symmetry, but develop a different type as adults; for example, sea stars are classified as bilaterally symmetrical even though their adult forms are radially symmetrical.

Key Terms

- **sagittal plane**: divides the body into right and left halves
- **radial symmetry**: a form of symmetry wherein identical parts are arranged in a circular fashion around a central axis
- **bilateral symmetry**: having equal arrangement of parts (symmetry) about a vertical plane running from head to tail

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27.2B: Animal Characterization Based on Features of Embryological Development

Learning Objectives

- Explain the ways in which animals can be characterized by features of embryological development

Animal Characterization Based on Features of Embryological Development

Most animal species undergo a separation of tissues into germ layers during embryonic development. These germ layers are formed during gastrulation, developing into the animal's specialized tissues and organs. Animals develop either two or three embryonic germs layers. Radially-symmetrical animals are diploblasts, developing two germ layers: an inner layer (endoderm) and an outer layer (ectoderm). Diploblasts have a non-living layer between the endoderm and ectoderm. Bilaterally-symmetrical animals are called triploblasts, developing three tissue layers: an inner layer (endoderm), an outer layer (ectoderm), and a middle layer (mesoderm).

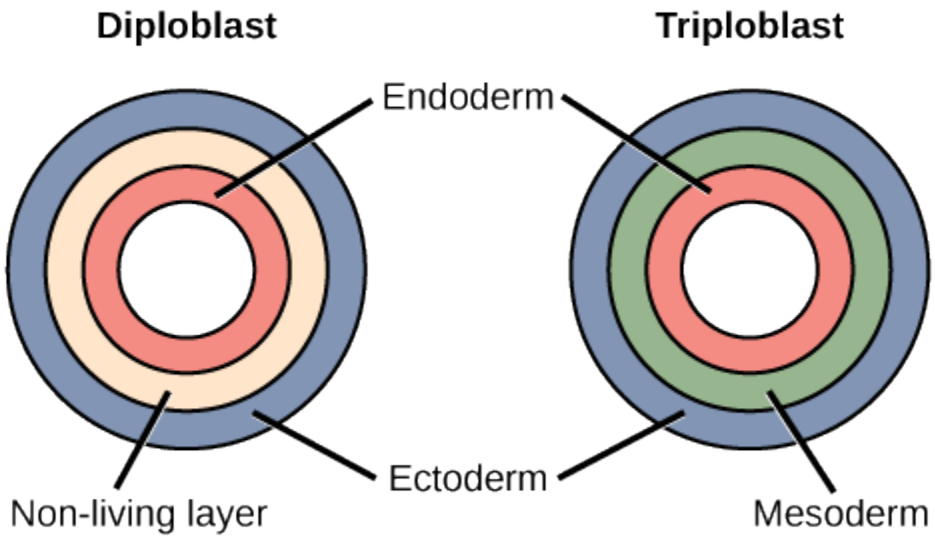


Figure $27.2B.1$: Germ development in embryogenesis: During embryogenesis, diploblasts develop two embryonic germ layers: an ectoderm and an endoderm. Triploblasts develop a third layer, the mesoderm, between the endoderm and ectoderm

Germ Layers

Each of the three germ layers in a blastula, or developing ball of cells, becomes particular body tissues and organs. The endoderm gives rise to the stomach, intestines, liver, pancreas, and the lining of the digestive tract, as well as to the lining of the trachea, bronchi, and lungs of the respiratory tract. The ectoderm develops into the outer epithelial covering of the body surface and the central nervous system. The mesoderm, the third germ layer forming between the endoderm and ectoderm in triploblasts, gives rise to all 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.

Presence or Absence of a Coelom

Triploblasts can be differentiated into three categories: those that do not develop an internal body cavity called a coelom (acoelomates), those with a true coelom (eucoelomates), and those with "false" coeloms (pseudocoelomates).

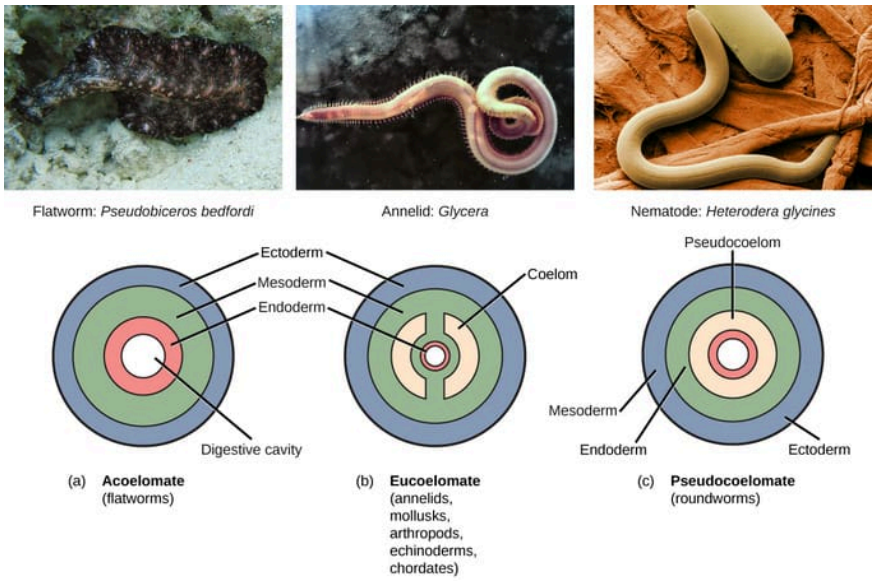


Figure $27.2B.1$: Differentiation in triploblasts: Triploblasts may be (a) acoelomates, (b) eucoelomates, or (c) pseudocoelomates. Acoelomates have no body cavity. Eucoelomates have a body cavity within the mesoderm, called a coelom, which is lined with mesoderm. Pseudocoelomates also have a body cavity, but it is sandwiched between the endoderm and mesoderm.

Acoelomates

Triploblasts that do not develop a coelom are called acoelomates: their mesoderm region is completely filled with tissue. Flatworms in the phylum Platyhelminthes are acoelomates.

Eucoelomates

Eucoelomates (or coelomates) have a true coelom that arises entirely within the mesoderm germ layer and is lined by an epithelial membrane. This coelomic cavity represents a fluid-filled space that lies between the visceral organs and the body wall. It houses the digestive system, kidneys, reproductive organs, and heart, and it contains the circulatory system. The epithelial membrane also lines the organs within the coelom, connecting and holding them in position while allowing them some free motion. Annelids, mollusks, arthropods, echinoderms, and chordates are all eucoelomates. The coelom also provides space for the diffusion of gases and nutrients, as well as body flexibility and improved animal motility. The coelom also provides cushioning and shock absorption for the major organ systems, while allowing organs to move freely for optimal development and placement.

Pseudocoelomates

The pseudocoelomates have a coelom derived partly from mesoderm and partly from endoderm. Although still functional, these are considered false coeloms. The phylum Nematoda (roundworms) is an example of a pseudocoelomate.

Embryonic Development of the Mouth

Bilaterally symmetrical, tribloblastic eucoelomates can be further divided into two groups based on differences in their early embryonic development. These two groups are separated based on which opening of the digestive cavity develops first: mouth (protostomes) or anus (deuterostomes). The word protostome comes from the Greek word meaning “mouth first. ” The protostomes include arthropods, mollusks, and annelids. Deuterostome originates from the word meaning “mouth second. ” Deuterostomes include more complex animals such as chordates, but also some simple animals such as echinoderms.

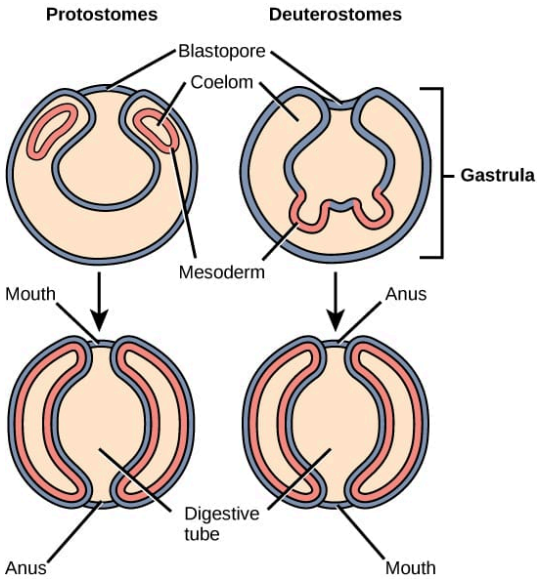


Figure $27.2B.1$: Early embryonic development in eucoelomates: Eucoelomates can be divided into two groups based on their early embryonic development. In protostomes, part of the mesoderm separates to form the coelom in a process called schizocoely. In deuterostomes, the mesoderm pinches off to form the coelom in a process called enterocoely.

Development of the Coelom

The coelom of most protostomes is formed through a process called schizocoely, when a solid mass of the mesoderm splits apart and forms the hollow opening of the coelom. Deuterostomes differ in that their coelom forms through a process called enterocoely, when the mesoderm develops as pouches that are pinched off from the endoderm tissue. These pouches eventually fuse to form the mesoderm, which then gives rise to the coelom.

Embryonic Cleavage

Protostomes undergo spiral cleavage: the cells of one pole of the embryo are rotated and, thus, misaligned with respect to the cells of the opposite pole. This spiral cleavage is due to the oblique angle of the cleavage. Protostomes also undergo determinate cleavage: the developmental fate of each embryonic cell is pre-determined. Deuterostomes undergo radial cleavage where the cleavage axes are either parallel or perpendicular to the polar axis, resulting in the alignment of the cells between the two poles. Unlike protostomes, deuterostomes undergo indeterminate cleavage: cells remain undifferentiated until a later developmental stage. This characteristic of deuterostomes is reflected in the existence of familiar embryonic stem cells, which have the ability to develop into any cell type.

Key Points

- Diploblasts contain two germ layers (inner endoderm and outer ectoderm), while triploblasts contain three germ layers (endoderm, mesoderm, and ectoderm).
- The endoderm becomes the digestive and respiratory tracts; the ectoderm becomes the outer epithelial covering of the body surface and the central nervous system; and the mesoderm becomes all muscle tissues, connective tissues, and most other organs.
- Triploblasts can be further categorized into those without a coelom (acoelomates), those with a true coelom (eucoelomates), and those with “false” coeloms (pseudocoelomates).
- Bilaterally symmetrical, tribloblastic eucoelomates can be divided into protostomes, those animals that develop a mouth first, and deuterstomes, those animals that develop an anus first and a mouth second.
- In protostomes, the coelom forms when the mesoderm splits through the process of schizocoely, while in deuterostomes, the coelom forms when the mesoderm pinches off through the process of enterocoely.
- Protostomes undergo spiral cleavage, while deuterostomes undergo radial cleavage.

Key Terms

- **protostome**: any animal in which the mouth is derived first from the embryonic blastopore (“mouth first”)
- **deuterostome**: Any animal in which the initial pore formed during gastrulation becomes the anus, and the second pore becomes the mouth
- **diploblast**: a blastula in which there are two primary germ layers: the ectoderm and endoderm
- **triploblast**: a blastula in which there are three primary germ layers: the ectoderm, mesoderm, and endoderm; formed during gastrulation of the blastula
- **acoelomate**: any animal without a coelom, or body cavity
- **coelomate**: any animal possessing a fluid-filled cavity within which the digestive system is suspended.
- **schizocoely**: the process by which protostome animal embryos develop; it occurs when a coelom (body cavity) is formed by splitting the mesodermal embryonic tissue
- **enterocoely**: the process by which deuterostome animal embryos develop; the coelom forms from pouches “pinched” off of the digestive tract

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27.3: ANIMAL PHYLOGENY

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- Topic hierarchy

27.3A: Constructing an Animal Phylogenetic Tree

27.3B: Molecular Analyses and Modern Phylogenetic Trees

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27.3A: Constructing an Animal Phylogenetic Tree

Learning Objectives

- Describe the information needed to construct a phylogenetic tree of animals

Constructing an Animal Phylogenetic Tree

Evolutionary trees, or phylogeny, is the formal study of organisms and their evolutionary history with respect to each other. Phylogenetic trees are most-commonly used to depict the relationships that exist between species. In particular, they clarify whether certain traits are homologous (found in the common ancestor as a result of divergent evolution) or homoplasy (sometimes referred to as analogous: a character that is not found in a common ancestor, but whose function developed independently in two or more organisms through convergent evolution). Evolutionary trees are diagrams that show various biological species and their evolutionary relationships. They consist of branches that flow from lower forms of life to the higher forms of life.

Evolutionary trees differ from taxonomy which is an ordered division of organisms into categories based on a set of characteristics used to assess similarities and differences. Evolutionary trees involve biological classification and use morphology to show relationships. Phylogeny is evolutionary history shown by the relationships found when comparing polymeric molecules such as RNA, DNA, or proteins of various organisms. The evolutionary pathway is analyzed by the sequence similarity of these polymeric molecules. This is based on the assumption that the similarities of sequence result from having fewer evolutionary divergences than others. The evolutionary tree is constructed by aligning the sequences; the length of the branch is proportional to the amount of amino acid differences between the sequences.

Phylogenetic systematics informs the construction of phylogenetic trees based on shared characters. Comparing nucleic acids or other molecules to infer relationships is a valuable tool for tracing an organism's evolutionary history. The ability of molecular trees to encompass both short and long periods of time is hinged on the ability of genes to evolve at different rates, even in the same evolutionary lineage. For example, the DNA that codes for rRNA changes relatively slowly, so comparisons of DNA sequences in these genes are useful for investigating relationships between taxa that diverged a long time ago. Interestingly, 99% of the genes in humans and mice are detectably orthologous, and 50% of our genes are orthologous with those of yeast. The hemoglobin B genes in humans and in mice are orthologous. These genes serve similar functions, but their sequences have diverged since the time that humans and mice had a common ancestor.

Evolutionary pathways relating the members of a family of proteins may be deduced by examination of sequence similarity. This approach is based on the notion that sequences that are more similar to one another have had less evolutionary time to diverge than have sequences that are less similar. Evolutionary trees are used today for DNA hybridization, which determines the percentage difference of genetic material between two similar species. If there is a high resemblance of DNA between the two species, then the species are closely related. If only a small percentage is identical, then they are distantly related.

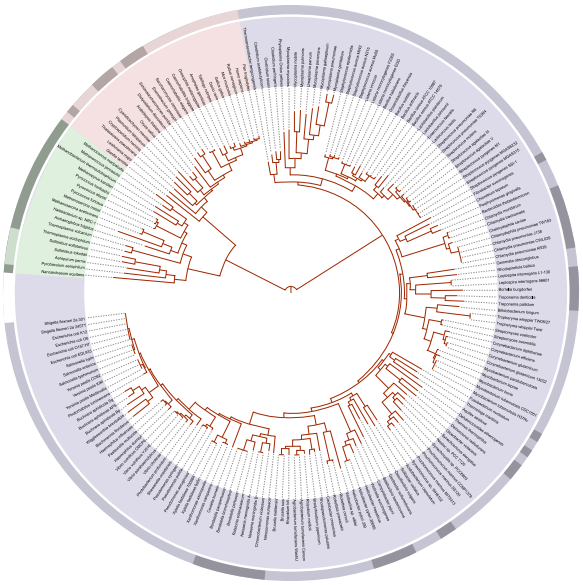


Figure 27.3A.1: Phylogenetic tree of life: A phylogenetic tree of life, showing the relationship between species whose genomes had been sequenced as of 2006. The very center represents the last universal ancestor of all life on earth. The different colors represent the three domains of life: pink represents eukaryota (animals, plants, and fungi); blue represents bacteria; and green represents archaea.

Animal Phyla

The current understanding of evolutionary relationships between animal, or Metazoa, phyla begins with the distinction between "true" animals with true differentiated tissues, called Eumetazoa, and animal phyla that do not have true differentiated tissues (such as the sponges), called Parazoa. Both Parazoa and Eumetazoa evolved from a common ancestral organism that resembles the modern-day protists called choanoflagellates. These protist cells strongly resemble sponge choanocyte cells.

Eumetazoa are subdivided into radially-symmetrical animals and bilaterally-symmetrical animals and are classified into clade Radiata or Bilateria, respectively. The cnidarians and ctenophores are animal phyla with true radial 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). Ecdysozoa includes nematodes and arthropods; named for a commonly-found characteristic among the group: exoskeletal molting (termed 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.

Key Points

- Phylogenetic trees are constructed using various data derived from studies on homologous traits, analagous traits, and molecular evidence that can be used to establish relationships using polymeric molecules (DNA, RNA, and proteins).
- Evolutionary relationships between animal phyla, or Metazoa, are based on the the presence or absence of differentiated tissues, referred to as Eumetazoa or Parazoa, respectively.
- Eumetazoa can be further classified into categories that are based on whether they have radial or bilateral symmetry, referred to as Radiata or Bilateria, respectively.

Key Terms

- **orthologous**: having been separated by a speciation event
- **homoplasy**: a correspondence between the parts or organs of different species acquired as the result of parallel evolution or convergence

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27.3B: Molecular Analyses and Modern Phylogenetic Trees

Learning Objectives

- Distinguish between morphological and molecular data in creating phylogenetic trees of animals

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. Previously, phylogenetic trees were constructed based on homologous and analogous morphology; however, with the advances in molecular biology, construction of phylogenetic trees is increasingly performed using data derived from molecular analyses.

Many evolutionary relationships in the modern tree have only recently been determined due to molecular evidence. Nucleic acid and protein analyses have informed the construction of 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. Evolutionary trees can be made by the determination of sequence information of similar genes in different organisms. Sequences that are similar to each other frequently are considered to have less time to diverge, while less similar sequences have more evolutionary time to diverge. The evolutionary tree is created by aligning sequences and having each branch length proportional to the amino acid differences of the sequences. Furthermore, by assigning a constant mutation rate to a sequence and performing a sequence alignment, it is possible to calculate the approximate time when the sequence of interest diverged into monophyletic groups.

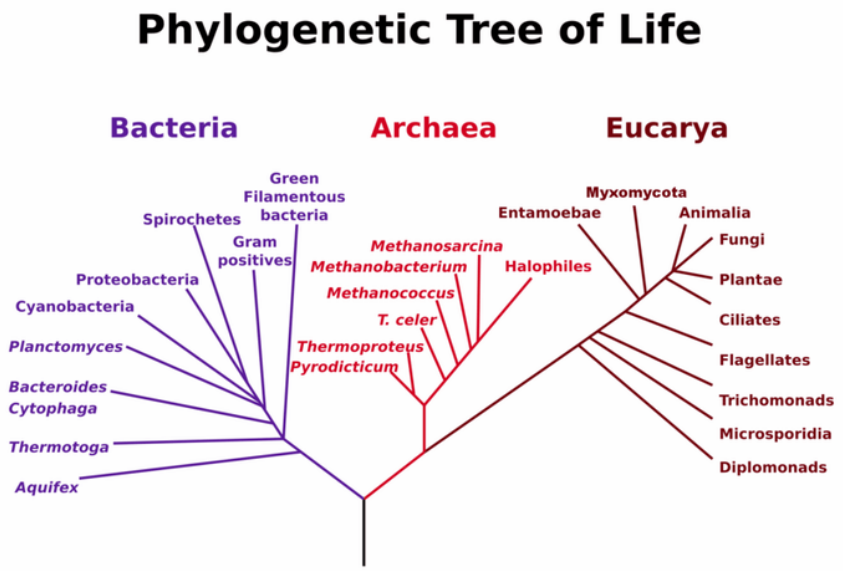


Figure $27.3B.1$: Phlyogenetic tree of life: Advances in molecular biology and analysis of polymeric molecules such as DNA, RNA, and proteins have contributed to the development of phylogenetic trees.

Sequence alignments can be performed on a variety of sequences. For constructing an evolutionary tree from proteins, for example, the sequences are aligned and then compared. rRNA (ribosomal RNA) is typically used to compare organisms since rRNA has a slower mutation rate and is a better source for evolutionary tree construction. This is best supported by research of Dr. Carl Woese that was conducted in the late 1970s. Since the ribosomes are critical to the function of living organisms, they are not easily changed through the process of evolution. Taking advantage of this fact, Dr. Woese compared the minuscule differences in the sequences of ribosomes among a great array of bacteria and showed that they were not all related.

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 to be protostomes, more closely related to annelids and mollusks. This discovery allowed for the distinction of the protostome clade: the lophotrochozoans. Molecular data have also shed light on some differences within the lophotrochozoan group. Some scientists believe that the phyla Platyhelminthes and Rotifera within this group should actually belong to their own group 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; 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 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 a closer relationship with deuterostomes. The placement of this new phylum remains disputed, but scientists agree that with sufficient molecular data, their true phylogeny will be determined.

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Key Points

- The construction of phylogenetic trees is now based on similarities and differences within the molecular sources used for analysis which include DNA, RNA, and proteins.
- The ability to use molecular sources as a basis of phylogenetic tree construction has allowed for determination of previously-unknown evolutionary relationships between organisms.
- In addition to the establishment of new relationships within phylogenetic trees, the ability to use molecular sources for analysis has also created an emergence of new phlyums that were previously classified in larger groups.
- Besides identifying molecular similarities and differences between organisms, by assigning a constant mutation rate to a sequence and performing a sequence alignment, it is possible to determine when two organisms diverged from one another.

Key Terms

- **monophyletic**: of, pertaining to, or affecting a single phylum (or other taxon) of organisms

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27.4: THE EVOLUTIONARY HISTORY OF THE ANIMAL KINGDOM

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- Topic hierarchy

27.4A: Pre-Cambrian Animal Life
27.4B: The Cambrian Explosion of Animal Life
27.4C: Post-Cambrian Evolution and Mass Extinctions

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27.4A: Pre-Cambrian Animal Life

Learning Objectives

- Describe the types of animals found in the Ediacaran period

Pre-Cambrian Animal Life

The time before the Cambrian period is known as the Ediacaran period (between 635-543 million years ago), the final period of the late Proterozoic Neoproterozoic Era. It is believed that early animal life, termed Ediacaran biota, evolved from protists at this time. Some protist species called choanoflagellates closely resemble the choanocyte cells in the simplest animals, sponges. In addition to their morphological similarity, molecular analyses have revealed similar sequence homologies in their DNA.

EON	ERA	PERIOD	MILLIONS OF YEARS AGO
Phanerozoic	Cenozoic	Quaternary	1.6
		Tertiary	66
	Mesozoic	Cretaceous	138
		Jurassic	205
		Triassic	240
	Paleozoic	Permian	290
		Pennsylvanian	330
		Mississippian	360
		Devonian	410
		Silurian	435
		Ordovician	500
		Cambrian	540
Proterozoic	Late Proterozoic Middle Proterozoic Early Proterozoic	Ediacaran 635-543 MYA	2500
Archean	Late Archean Middle Archean Early Archean		3800?
Pre-Archean			

(a)



(b)

Figure 27.4A.1: Earth's history: (a) Earth's history is divided into eons, eras, and periods. The Ediacaran period was the final period of the Proterozoic Era which ended in the Cambrian period of the Phanerozoic Era. (b) Stages on the geological time scale are represented as a spiral.

The earliest life comprising Ediacaran biota was long believed to include only tiny, sessile, soft-bodied sea creatures. However, recently there has been increasing scientific evidence suggesting that more varied and complex animal species lived during this time, and possibly even before the Ediacaran period.

Fossils believed to represent the oldest animals with hard body parts were recently discovered in South Australia. These sponge-like fossils, named *Coronacollina acula*, date back as far as 560 million years. They are believed to show the existence of hard body parts and spicules that extended 20–40 cm from the main body (estimated about 5 cm long). Other organisms, such as *Cyclomedusa* and *Dickinsonia*, also evolved during the Ediacaran period.

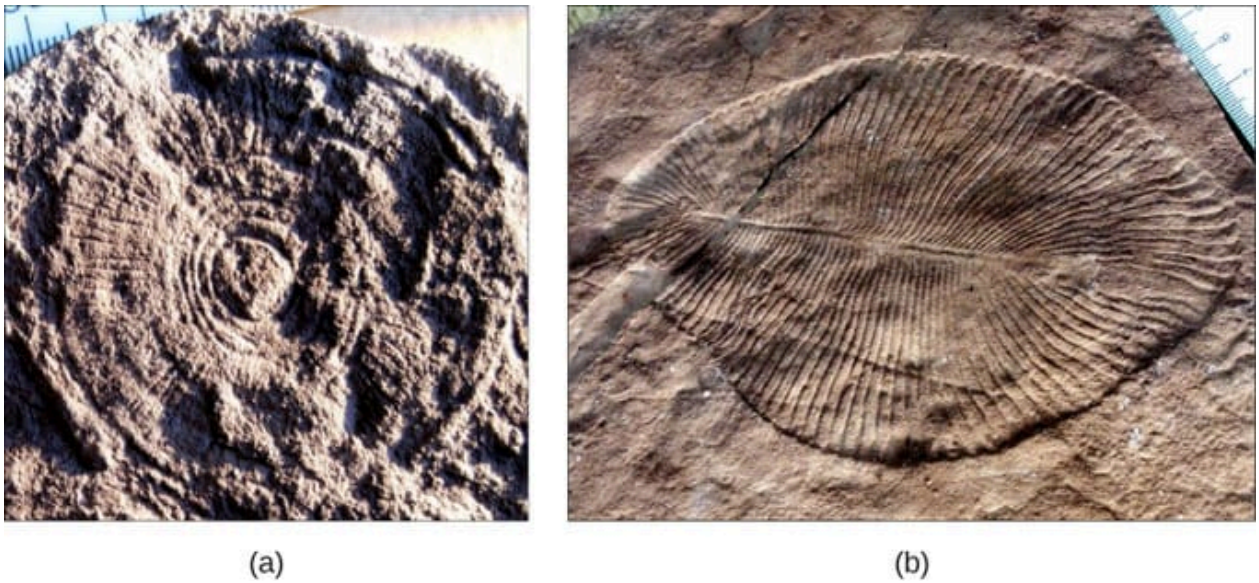


Figure 27.4A.1: Fossils from Ediacaran period: Fossils of (a) *Cyclomedusa* and (b) *Dickinsonia* that evolved during the Ediacaran period.

Another recent fossil discovery may represent the earliest animal species ever found. While the validity of this claim is still under investigation, these primitive fossils appear to be small, one-centimeter long, sponge-like creatures. These fossils from South Australia date back 650 million years, actually placing the putative animal before the great ice age extinction event that marked the transition between the Cryogenian period and the Ediacaran period. Until this discovery, most scientists believed that there was no animal life prior to the Ediacaran period. Many scientists now believe that animals may, in fact, have evolved during the Cryogenian period.

Key Points

- The pre-Cambrian period (Ediacaran period) took place between 635-543 million years ago.
- Early animal life, called Ediacaran biota, evolved from protists; it was previously believed early animal life included only tiny, sessile, soft-bodied sea creatures, but scientific evidence suggests more complex animals lived during this time.
- Sponge-like fossils believed to represent the oldest animals with hard body parts, named *Coronacollina acula*, date back as far as 560 million years.
- The fossils of the earliest animal species ever found were small, one-centimeter long, sponge-like creatures, dating before 650 million years, which predates the Ediacaran period.
- The discovery of the fossils of the earliest animal species provided evidence that animals may have evolved before the Ediacaran period during the Cryogenian period.

Key Terms

- **Ediacaran period**: period from about 635-543 million years ago; the final period of the late Proterozoic Neoproterozoic Era
- **choanoflagellate**: any of a group of flagellate protozoa thought to be the closest unicellular ancestors of animals
- **Coronacollina acula**: sponge-like fossils believed to represent the oldest animals with hard body parts that date back as far as 560 million years

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27.4B: The Cambrian Explosion of Animal Life

Learning Objectives

- Compare the theories that attempt to explain the Cambrian Explosion

The Cambrian Explosion of Animal Life

The Cambrian period, occurring between approximately 542–488 million years ago, marks the most rapid evolution of new animal phyla and animal diversity in earth's history. It is believed that most of the animal phyla in existence today had their origins during this time, often referred to as the Cambrian explosion. Echinoderms, mollusks, worms, arthropods, and chordates arose during this period. One of the most dominant species during the Cambrian period was the trilobite, an arthropod that was among the first animals to exhibit a sense of vision.

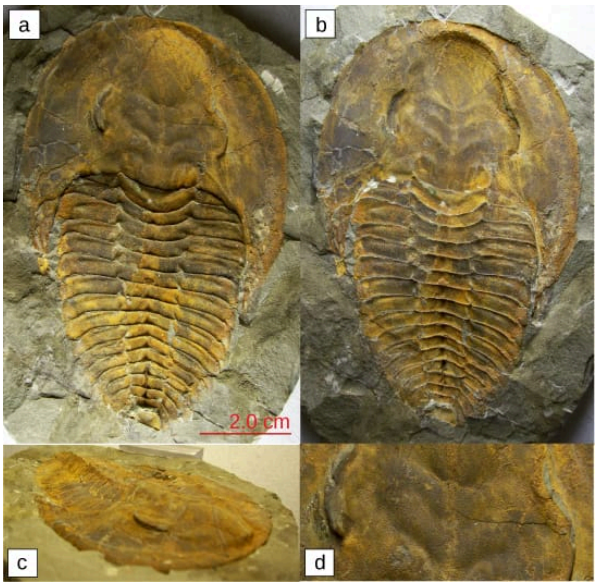


Figure 27.4B.1: Trilobites: These fossils (a–d) belong to trilobites, extinct arthropods that appeared in the early Cambrian period 525 million years ago and disappeared from the fossil record during a mass extinction at the end of the Permian period about 250 million years ago.



Figure $27.4B.1$: Cambrian period: An artist's rendition depicts some organisms from the Cambrian period.

The causes of the Cambrian explosion are still debated. There are many theories that attempt to answer this question. Environmental changes may have created a more suitable environment for animal life. Examples of these changes include rising atmospheric oxygen levels and large increases in oceanic calcium concentrations that preceded the Cambrian period. Some scientists believe that an expansive, continental shelf with numerous shallow lagoons or pools provided the necessary living space for larger numbers of different types of animals to co-exist. There is also support for theories that argue that ecological relationships between species, such as changes in the food web, competition for food and space, and predator-prey relationships, were primed to promote a sudden, massive coevolution of species. Yet other theories claim genetic and developmental reasons for the Cambrian explosion. The morphological flexibility and complexity of animal development afforded by the evolution of Hox control genes may have provided the necessary opportunities for increases in possible animal morphologies at the time of the Cambrian period. Theories that attempt to explain why the Cambrian explosion happened must be able to provide valid reasons for the massive animal diversification, as well as explain why it happened when it did. There is evidence that both supports and refutes each of the theories described above. The answer may very well be a combination of these and other theories.

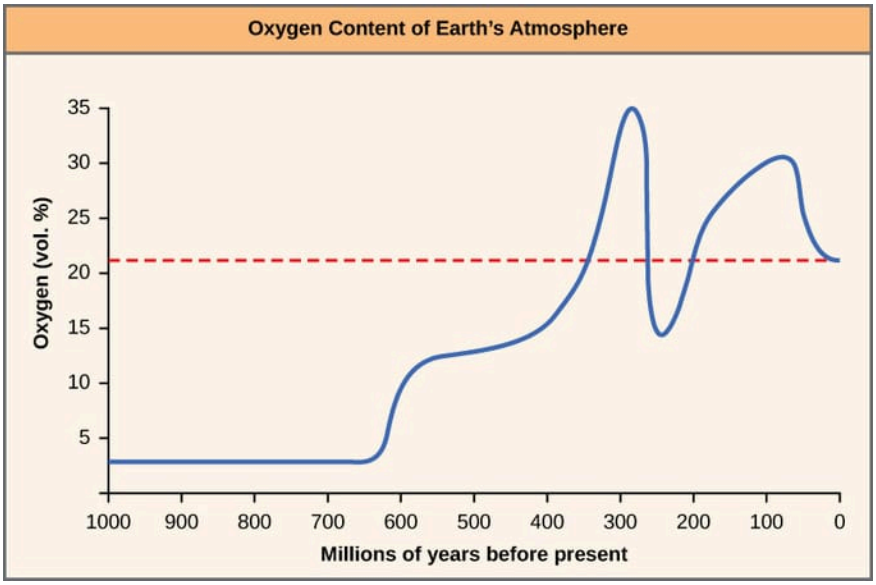


Figure $27.4B.1$: Earth's oxygen concentration: The oxygen concentration in earth's atmosphere rose sharply around 300 million years ago.

Unresolved questions about the animal diversification that took place during the Cambrian period remain. For example, we do not understand how the evolution of so many species occurred in such a short period of time. Was there really an "explosion" of life at this particular time? Some scientists question the validity of this idea because there is increasing evidence to suggest that more animal life existed prior to the Cambrian period and that other similar species' so-called explosions (or radiations) occurred later

in history as well. Furthermore, the vast diversification of animal species that appears to have begun during the Cambrian period continued well into the following Ordovician period. Despite some of these arguments, most scientists agree that the Cambrian period marked a time of impressively-rapid animal evolution and diversification that is unmatched elsewhere during history.

Key Points

- Echinoderms, mollusks, worms, chordates, and arthropods (including arthropods called trilobites which were the one of the first species to exhibit a sense of vision) developed during the Cambrian period.
- Environmental changes such as rising levels of atmospheric oxygen and an increase in oceanic calcium concentrations may have caused The Cambrian Explosion.
- A continental shelf with numerous shallow pools that provided the necessary living space for larger numbers of different types of animals to co-exist may have caused the Cambrian Explosion.
- The Cambrian Explosion may have been a result of ecological relationships between species, such as changes in the food web, competition for food and space, and predator-prey relationships.
- The evolution of Hox control genes resulting in animal complexity and flexibility may have provided the necessary opportunities for increases in possible animal morphologies.

Key Terms

- **Ordovician period**: covers the time between 485-443 million years ago; followed the Cambrian period
- **Cambrian explosion**: the relatively rapid appearance (over a period of many millions of years), around 530 million years ago, of most major animal phyla as demonstrated in the fossil record

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27.4C: Post-Cambrian Evolution and Mass Extinctions

Learning Objectives

- Differentiate among the causes of mass extinctions and their effects on animal life

Post-Cambrian Evolution and Mass Extinctions

The periods that followed the Cambrian during the Paleozoic Era were marked by further animal evolution and the emergence of many new orders, families, and species. As animal phyla continued to diversify, new species adapted to new ecological niches. During the Ordovician period, which followed the Cambrian period, plant life first appeared on land. This change allowed formerly-aquatic animal species to invade land, feeding directly on plants or decaying vegetation. Continual changes in temperature and moisture throughout the remainder of the Paleozoic Era due to continental plate movements encouraged the development of new adaptations to terrestrial existence in animals, such as limbs in amphibians and epidermal scales in reptiles.

Changes in the environment often create new niches (living spaces) that contribute to rapid speciation and increased diversity. On the other hand, cataclysmic events, such as volcanic eruptions and meteor strikes that obliterate life, can result in devastating losses of diversity. Such periods of mass extinction have occurred repeatedly in the evolutionary record of life, erasing some genetic lines while creating room for others to evolve into the empty niches left behind. The end of the Permian period (and the Paleozoic Era) was marked by the largest mass extinction event in Earth's history, a loss of roughly 95 percent of the extant species at that time. Some of the dominant phyla in the world's oceans, such as the trilobites, disappeared completely. On land, the disappearance of some dominant species of Permian reptiles made it possible for a new line of reptiles to emerge: the dinosaurs. The warm and stable climatic conditions of the ensuing Mesozoic Era promoted an explosive diversification of dinosaurs into every conceivable niche in land, air, and water. Plants, too, radiated into new landscapes and empty niches, creating complex communities of producers and consumers, some of which became extremely large on the abundant food available.

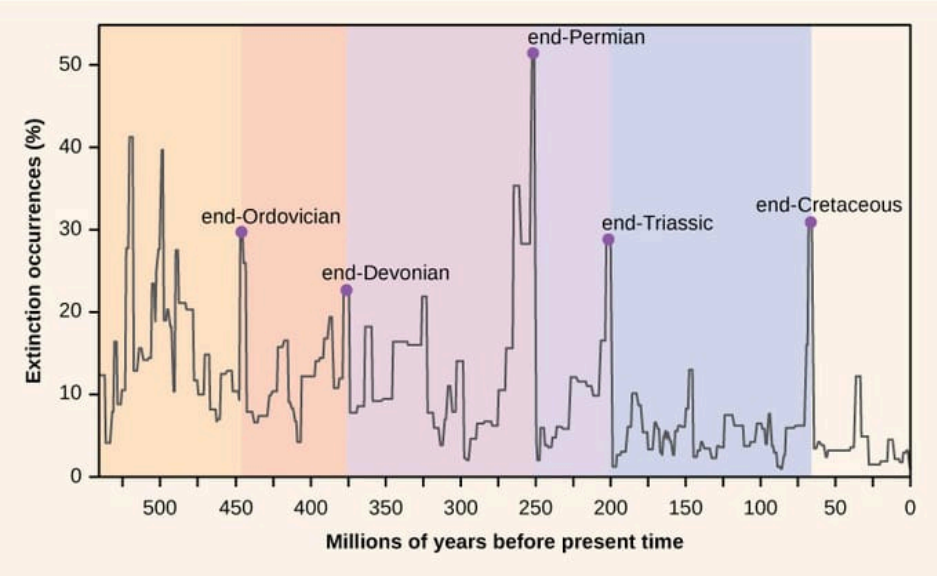


Figure $27.4C.1$: Mass extinctions: Mass extinctions have occurred repeatedly over geological time.

Another mass extinction event occurred at the end of the Cretaceous period, bringing the Mesozoic Era to an end. Skies darkened and temperatures fell as a large meteor impact expelled tons of volcanic ash, blocking incoming sunlight. Plants died, herbivores and carnivores starved, and the mostly cold-blooded dinosaurs ceded their dominance of the landscape to more warm-blooded mammals. In the following Cenozoic Era, mammals radiated into terrestrial and aquatic niches once occupied by dinosaurs. Birds, the warm-blooded offshoots of one line of the ruling reptiles, became aerial specialists. The appearance and dominance of flowering plants in the Cenozoic Era created new niches for insects, as well as for birds and mammals. Changes in animal species diversity during the late Cretaceous and early Cenozoic were also promoted by a dramatic shift in earth's geography, as

continental plates slid over the crust into their current positions, leaving some animal groups isolated on islands and continents or separated by mountain ranges or inland seas from other competitors. Early in the Cenozoic, new ecosystems appeared, with the evolution of grasses and coral reefs. Late in the Cenozoic, further extinctions followed by speciation occurred during ice ages that covered high latitudes with ice and then retreated, leaving new open spaces for colonization.

Key Points

- During the Ordovician period, plant life first appeared on land, which allowed aquatic animals to move on to land.
- Periods of mass extinction caused by cataclysmic events like volcanic eruptions and meteor strikes have erased many genetic lines and created room for new species.
- The largest mass extinction event in earth's history, which occurred at the end of the Permian period, resulted in a loss of roughly 95 percent of the existing species at that time.
- The disappearance of some dominant species of Permian reptiles and the warm and stable climate that followed made it possible for the dinosaurs to emerge and diversify.
- Another mass extinction event caused by a meteor strike and volcanic ash eruption occurred at the end of the Cretaceous period, bringing the Mesozoic Era to an end and pushing dinosaurs into extinction.
- The disappearance of dinosaurs led to the dominance of plants, which created new niches for birds, insects, and mammals; animal diversity was also brought on by the creation of continents, islands, and mountains.

Key Terms

- **Cenozoic**: a geologic era about between 65 million years ago to the present when the continents moved to their current position and modern plants and animals evolved
- **mass extinction**: a sharp decrease in the total number of species in a relatively short period of time
- **Cretaceous**: the last geologic period within the Mesozoic era from about 146 to 65 million years ago; ended with a large mass extinction

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28: INVERTEBRATES

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28.1: PHYLUM PORIFERA

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28.1A: Phylum Porifera

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28.1A: Phylum Porifera

Learning Objectives

- Explain the position of the phylum Porifera in the phylogenetic tree of invertebrates

Introduction

The invertebrates, or Invertebrata, are animals that do not contain bony structures such as the cranium and vertebrae. The simplest of all the invertebrates are the Parazoans, which include only the phylum Porifera. Phylum Porifera ("pori" = pores, "fera" = bearers) are popularly known as sponges. Sponge larvae are able to swim; however, adults are non-motile and spend their life attached to a substratum through a holdfast. The majority of sponges are marine, living in seas and oceans. There is, however, one family of fresh water sponges (Family Spongillidae). The great majority of the marine species can be found in ocean habitats ranging from tidal zones to depths exceeding 8,800 m (5.5 mi).

Sponges are classified within four classes: calcareous sponges (Calcarea), glass sponges (Hexactinellida), demosponges (Demospongiae), and the recently-recognized, encrusting sponges (Homoscleromorpha). The presence and composition of spicules and spongin are the differentiating characteristics between the classes of sponges. Demosponges, which contain spongin and may or may not have spicules, constitute about 90% of all known sponge species, including all freshwater ones, and have the widest range of habitats. Calcareous sponges, which have calcium carbonate spicules and, in some species, calcium carbonate exoskeletons, are restricted to relatively shallow marine waters where production of calcium carbonate is easiest. They contain no spongin. Hemoscleromorpha sponges tend to be massive or encrusting in form and have a very simple structure with very little variation in spicule form (all spicules tend to be very small). Hexactinellid sponges have sturdy lattice-like internal skeletons made up of fused spicules of silica; they tend to be more-or-less cup-shaped.

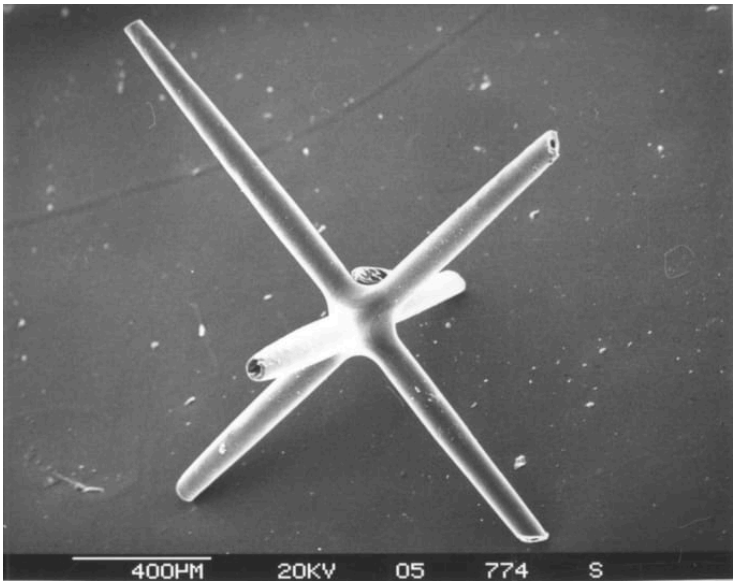


Figure 28.1A.1: Sponge Spicule: Sponges are classified based on the presence and types of spicules they contain.



Figure 28.1A.1: Types 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.

Unlike Protozoans, the Poriferans are multicellular. However, unlike higher metazoans, the cells that make up a sponge are not organized into tissues. Therefore, sponges lack true tissues and organs; in addition, they have no body symmetry. Sponges do, however, have specialized cells that perform specific functions. The shapes of their bodies are adapted for maximal efficiency of water flow through the central cavity, where nutrients are deposited, and leaves through a hole called the osculum. Many sponges have internal skeletons of spongin and/or spicules of calcium carbonate or silica. Primarily, their body consists of a thin sheet of cells over a frame (skeleton). As their name suggests, Poriferans are characterized by the presence of minute pores called ostia on their body.

Since water is vital to sponges for excretion, feeding, and gas exchange, their body structure facilitates the movement of water through the sponge. Structures such as canals, chambers, and cavities enable water to move through the sponge to nearly all body cells.

Most species use sexual reproduction, releasing sperm cells into the water to fertilize ova that in some species are released and in others are retained by the “mother. ” The fertilized eggs form larvae which swim off in search of places to settle. Sponges are also known for regenerating from fragments that are broken off, although this only works if the fragments include the right types of cells. A few species reproduce by budding. When conditions deteriorate, such as when temperatures drop, many freshwater species and a few marine ones produce gemmules: “survival pods” of unspecialized cells that remain dormant until conditions improve. They then either form completely new sponges or recolonize the skeletons of their parents.

Most of the approximately 5,000–10,000 known species of sponges are filter-feeders, feeding on bacteria and other food particles in the water. However, a few species of sponge that live in food-poor environments have become carnivores that prey mainly on small crustaceans. Other species host photosynthesizing micro-organisms as endosymbionts; these alliances often produce more food and oxygen than they consume.

Key Points

- As larvae, sponges are able to swim, but as adults, they are sessile, spending their life attached to a substrate.
- Although the majority of sponges live in marine habitats, one family, the Spongillidae, is found in fresh water.
- Calcarea, Hexactinellida, Demospongiae, and Homoscleromorpha make up the four classes of sponges; each type is classified based on the presence or composition of its spicules or spongin.
- Most sponges reproduce sexually; however, some can reproduce through budding and the regeneration of fragments.
- The majority of sponges are filter-feeders, but a few species are carnivorous due to the nutrient -poor environment in which they are found.

Key Terms

- **parazoan**: include only one phylum known as the sponges
- **endosymbiont**: an organism that lives within the body or cells of another organism
- **spongin**: a horny, sulfur-containing protein related to keratin that forms the skeletal structure of certain classes of sponges
- **spicule**: a sharp, needle-like piece
- **holdfast**: a root-like structure that anchors aquatic sessile organisms, such as seaweed, other sessile algae, stalked crinoids,

benthic cnidarians, and sponges, to the substrate

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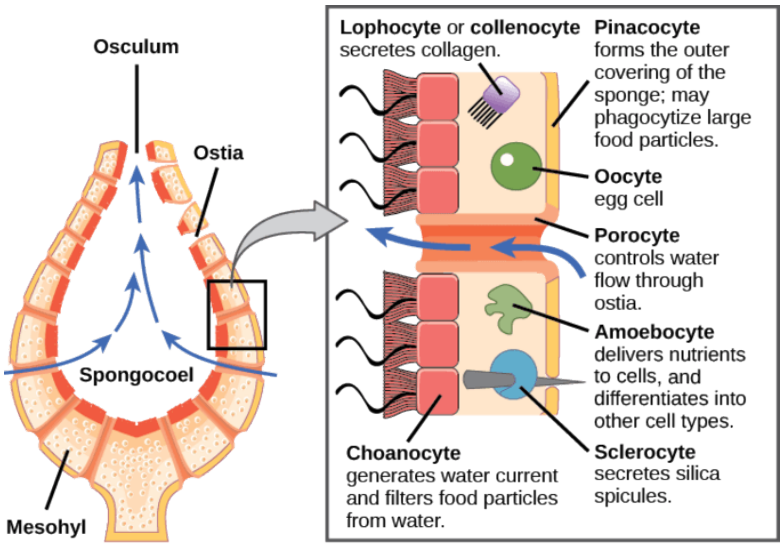
28.1B: Morphology of Sponges

Learning Objectives

- Explain the various cell forms and bodily functions of sponges

Morphology of Sponges

The morphology of the simplest sponges takes the shape of a cylinder with a large central cavity, the spongocoel, occupying the inside of the cylinder. Water can enter into the spongocoel from numerous pores in the body wall. Water entering the spongocoel is extruded via a large, common opening called the osculum. However, sponges exhibit a range of diversity in body forms, including variations in the size of the spongocoel, the number of osculi, and where the cells that filter food from the water are located.



(a) Basic sponge body plan (b) Some sponge cell types

Figure $28.1B.1$: Sponge morphology: The sponge's (a) basic body plan is a cylinder shape with a large central cavity. The specialized cell types in sponges (b) each perform a distinct function.

While sponges (excluding the Hexactinellids) do not exhibit tissue-layer organization, they do have different cell types that perform distinct functions. Pinacocytes, which are epithelial-like cells, form the outermost layer of sponges, enclosing a jelly-like substance called mesohyl. Mesohyl is an extracellular matrix consisting of a collagen -like gel with suspended cells that perform various functions. The gel-like consistency of mesohyl acts as an endoskeleton, maintaining the tubular morphology of sponges. In addition to the osculum, sponges have multiple pores called ostia on their bodies that allow water to enter the sponge. 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.

Choanocytes ("collar cells") are present at various locations, depending on the type of sponge; however, they always line the inner portions of some space through which water flows: the spongocoel in simple sponges; canals within the body wall in more complex sponges; and chambers scattered throughout the body in the most complex sponges. Whereas pinacocytes line the outside of the sponge, choanocytes tend to line certain inner portions of the sponge body that surround the mesohyl. The structure of a choanocyte is critical to its function, which is to generate a water current through the sponge and to trap and ingest food particles by phagocytosis. Note that there is a similarity in appearance between the sponge choanocyte and choanoflagellates (Protista). This similarity suggests that sponges and choanoflagellates are closely related and probably share a recent, common ancestry.

The cell body is embedded in mesohyl. It contains all organelles required for normal cell function, but protruding into the "open space" inside of the sponge is a mesh-like collar composed of microvilli with a single flagellum in the center of the column. The

cumulative effect of the flagella from all choanocytes aids the movement of water through the sponge: drawing water into the sponge through the numerous ostia, into the spaces lined by choanocytes, and eventually out through the osculum (or osculi). Meanwhile, food particles, including waterborne bacteria and algae, are trapped by the sieve-like collar of the choanocytes, slide down into the body of the cell, are ingested by phagocytosis, and become encased in a food vacuole. Finally, choanocytes will differentiate into sperm for sexual reproduction; they will become dislodged from the mesohyl, leaving the sponge with expelled water through the osculum.

The second crucial cells in sponges are called amoebocytes (or archaeocytes), named for the fact that they move throughout the mesohyl in an amoeba-like fashion. Amoebocytes have a variety of functions: delivering nutrients from choanocytes to other cells within the sponge; giving rise to eggs for sexual reproduction (which remain in the mesohyl); delivering phagocytized sperm from choanocytes to eggs; and differentiating into more-specific cell types. Some of these more-specific cell types include collencytes and lophocytes, which produce the collagen-like protein to maintain the mesohyl; sclerocytes, which produce spicules in some sponges; and spongocytes, which produce the protein spongin in the majority of sponges. These cells produce collagen to maintain the consistency of the mesohyl.

Key Points

- Although sponges do not have organized tissue, they depend on specialized cells, such as choanocytes, porocytes, amoebocytes, and pinacocytes, for specialized functions within their bodies.
- The mesohyl acts as a type of endoskeleton, helping to maintain the tubular shape of sponges.
- Porocytes control the amount of water that enters pores into the spongocoel, while choanocytes, which are flagellated cells, aid the movement of water through the sponge, thereby helping the sponge to trap and ingest food particles.
- Amoebocytes carry out several special functions: they deliver nutrients from choanocytes to other cells, give rise to eggs for sexual reproduction, deliver phagocytized sperm from choanocytes to eggs, and can transform into other cell types.
- Collencytes, lophocytes, sclerocytes, and spongocytes are examples of cells that are derived from amoebocytes; these cells manage other vital functions in the body of sponges.

Key Terms

- **choanocyte**: any of the cells in sponges that contain a flagellum and are used to control the movement of water
- **spongocoel**: the large, central cavity of sponges
- **osculum**: an opening in a sponge from which water is expelled
- **mesohyl**: the gelatinous matrix within a sponge

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28.1C: Physiological Processes in Sponges

Learning Objectives

- Summarize the physiological processes of sponges

Physiological Processes in Sponges

Sponges, despite being simple organisms, regulate their different physiological processes through a variety of mechanisms. These mechanisms regulate metabolism, reproduction, and locomotion.

Metabolism

Sponges lack complex digestive, respiratory, circulatory, reproductive, and nervous systems. Their food is trapped when 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 nutrition, and are ingested by phagocytosis. Particles that are larger than the ostia may be phagocytized by pinacocytes. In some sponges, amoebocytes transport food from cells that have ingested food particles to those that do not. For this type of digestion, in which food particles are digested within individual cells, the sponge draws water through diffusion. The limit of this type of digestion is that food particles must be smaller than individual 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 by-product of protein metabolism is excreted via diffusion by individual cells into the water as it passes through the sponge.

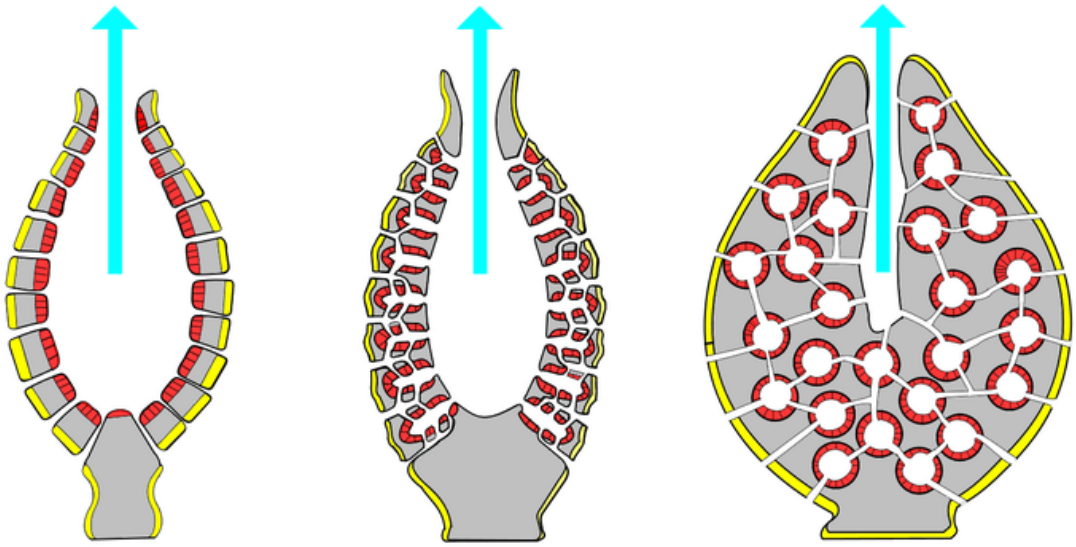


Figure $28.1C.1$: Water flow in a sponge: In a sponge, water enters through the body pores and exits in the direction of the osculum (direction of blue arrow). This diffusion of water through the body supports major functions in the sponge.

Reproduction

Sponges reproduce by sexual, as well as, asexual methods. The typical means of asexual reproduction is either fragmentation (where a piece of the sponge breaks off, settles on a new substrate, and develops into a new individual) or budding (a genetically-

identical outgrowth from the parent eventually detaches or remains attached to form a colony). An atypical type of asexual reproduction is found only in freshwater sponges, occurring through the formation of gemmules. Gemmules are environmentally-resistant structures produced by adult sponges wherein the typical sponge morphology is inverted. In gemmules, an inner layer of amoebocytes is surrounded by a layer of collagen (spongin) that may be reinforced by spicules. The collagen that is normally found in the mesohyl becomes the outer protective layer. In freshwater sponges, gemmules may survive hostile environmental conditions such as changes in temperature. They serve to recolonize the habitat once environmental conditions 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. 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. 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. Ejection of spermatozoa may be a timed and coordinated event, as seen in certain species. Spermatozoa carried along by water currents can fertilize the oocytes borne in the mesohyl of other sponges. Early larval development occurs within the sponge; free-swimming larvae 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 as do free-swimming marine invertebrates. However, sponge cells are capable of creeping along substrata via organizational plasticity. 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, but it remains to be observed in natural sponge habitats.

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Key Points

- Choanocytes trap bacteria and other food particles from water flowing within the sponge: in through the ostia and out through the osculum; particles are ingested by phagocytosis.
- Sponges reproduce by sexual and asexual methods, which include fragmentation or budding; the production of gemmules is another asexual reproduction method, but is found only in freshwater sponges.
- Sponges are monoecious; depending on the species, production of gametes may be continuous through the year or dependent on water temperature.
- In nature, sponges are sessile as adults; however, under laboratory conditions, sponge cells are capable of localized creeping movements through organizational plasticity.
- Gas exchange, circulation, and excretion are other major body functions in the sponge; these are achieved through the diffusion of water through the sponge body.

Key Terms

- **oocyte**: a cell that develops into an egg or ovum; a female gametocyte
- **gemmule**: a small gemma or bud of dormant embryonic cells produced by some freshwater sponges
- **phagocytosis**: the process where a cell incorporates a particle by extending pseudopodia and drawing the particle into a vacuole of its cytoplasm

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28.2: PHYLUM CNIDARIA

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- Topic hierarchy

28.2A: Phylum Cnidaria

28.2B: Class Anthozoa

28.2C: Class Scyphozoa

28.2D: Class Cubozoa and Class Hydrozoa

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28.2A: Phylum Cnidaria

Learning Objectives

- Describe the fundamental anatomy of a Cnidarian

Introduction to Phylum Cnidaria

Phylum Cnidaria includes animals that show radial or biradial symmetry and are diploblastic: they develop from two embryonic layers. Nearly all (about 99 percent) cnidarians are marine species.

Cnidarians contain specialized cells known as cnidocytes (“stinging cells”), which contain organelles called nematocysts (stingers). These cells are present around the mouth and tentacles, serving to immobilize prey with toxins contained within the cells. Nematocysts contain coiled threads that may bear barbs. The outer wall of the cell has hairlike projections called cnidocils, which are sensitive to touch. When touched, the cells are known to fire coiled threads that can either penetrate the flesh of the prey or predators of cnidarians, or ensnare it. These coiled threads release toxins into the target that can often immobilize prey or scare away predators ().

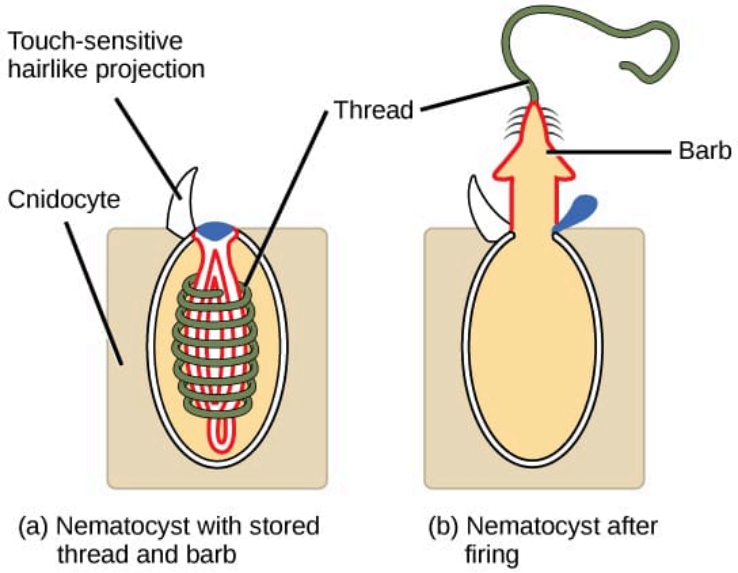


Figure 28.2A.1: Cnidocytes: Animals from the phylum Cnidaria have stinging cells called cnidocytes. Cnidocytes contain large organelles called (a) nematocysts that store a coiled thread and barb. When hairlike projections on the cell surface are touched, (b) the thread, barb, and a toxin are fired from the organelle.

Animals in this phylum display two distinct morphological body plans: polyp or “stalk” and medusa or “bell”. An example of the polyp form is *Hydra* spp.; perhaps the most well-known medusoid animals are the jellies (jellyfish). Polyp forms are sessile as adults, with a single opening to the digestive system (the mouth) facing up with tentacles surrounding it. Medusa forms are motile, with the mouth and tentacles hanging down from an umbrella-shaped bell.

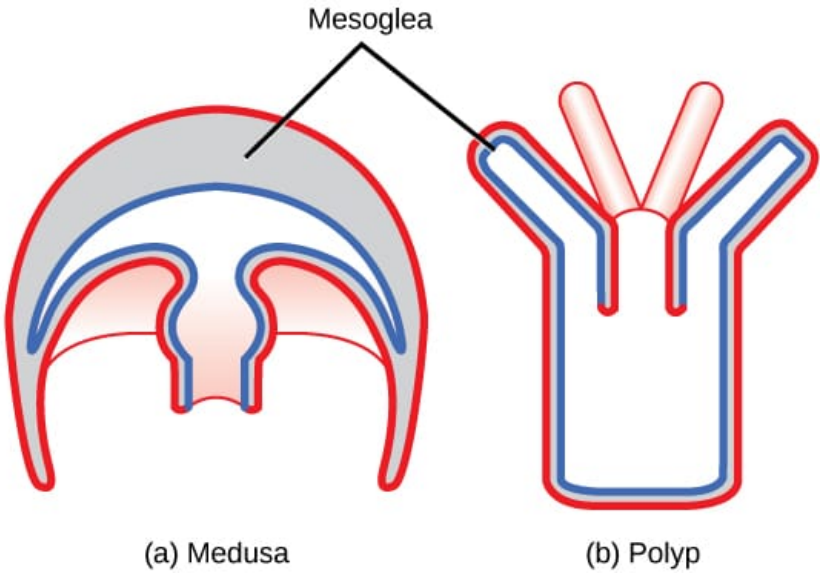


Figure 28.2A.1: Cnidarian morphology: Cnidarians have two distinct body plans, the medusa (a) and the polyp (b). All cnidarians have two membrane layers, with a jelly-like mesoglea between them.

Some cnidarians are polymorphic, having two body plans during their life cycle. An example is the colonial hydroid called an *Obelia*. The sessile polyp form has, in fact, two types of polyps. The first is the gastrozooid, which is adapted for capturing prey and feeding; the other type of polyp is the gonozooid, adapted for the asexual budding of medusa. When the reproductive buds mature, they break off and become free-swimming medusa, which are either male or female (dioecious). The male medusa makes sperm, whereas the female medusa makes eggs. After fertilization, the zygote develops into a blastula and then into a planula larva. The larva is free swimming for a while, but eventually attaches and a new colonial reproductive polyp is formed.

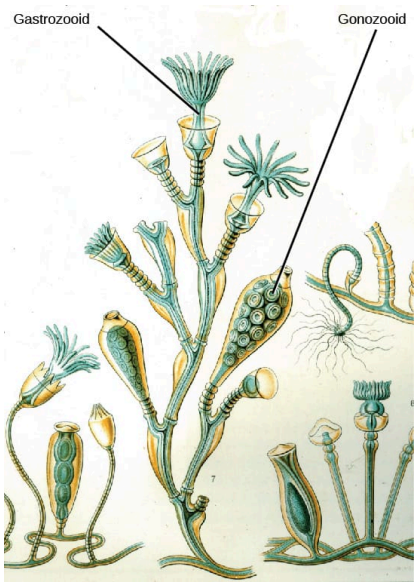


Figure 28.2A.1: Types of polyps in *Obelia*: The sessile form of *Obelia geniculate* has two types of polyps: gastrozooids, which are adapted for capturing prey, and gonozooids, which bud to produce medusae asexually.

All cnidarians show the presence of two membrane 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. Between these two membrane layers is a non-living, jelly-like mesoglea connective layer. In terms of cellular complexity, cnidarians show the presence of differentiated cell types in each tissue layer: nerve cells, contractile epithelial cells, enzyme-secreting cells, and nutrient-absorbing cells, as well as the presence of intercellular connections. However, the development of organs or organ systems is not advanced in this phylum.

The nervous system is primitive, with nerve cells scattered across the body. This nerve net may show the presence of groups of

cells in the form of nerve plexi (singular: plexus) or nerve cords. The nerve cells show mixed characteristics of motor as well as sensory neurons. The predominant signaling molecules in these primitive nervous systems are chemical peptides, which perform both excitatory and inhibitory functions. Despite the simplicity of the nervous system, it coordinates the movement of tentacles, the drawing of captured prey to the mouth, the digestion of food, and the expulsion of waste.

The cnidarians perform extracellular digestion in which the food is taken into the gastrovascular cavity, enzymes are secreted into the cavity, and the cells lining the cavity absorb nutrients. The gastrovascular cavity has only one opening that serves as both a mouth and an anus; this is termed an incomplete digestive system. Cnidarian cells exchange oxygen and carbon dioxide by diffusion between cells in the epidermis with water in the environment, and between cells in the gastrodermis with water in the gastrovascular cavity. The lack of a circulatory system to move dissolved gases limits the thickness of the body wall, necessitating a non-living mesoglea between the layers. There is no excretory system or organs; nitrogenous wastes simply diffuse from the cells into the water outside the animal or in the gastrovascular cavity. There is also no circulatory system, so nutrients must move from the cells that absorb them in the lining of the gastrovascular cavity through the mesoglea to other cells.

The phylum Cnidaria contains about 10,000 described species divided into four classes: Anthozoa, Scyphozoa, Cubozoa, and Hydrozoa. The anthozoans, the sea anemones and corals, are all sessile species, whereas the scyphozoans (jellyfish) and cubozoans (box jellies) are swimming forms. The hydrozoans contain sessile forms and swimming colonial forms like the Portuguese Man O' War.

Key Points

- Cnidarians have two distinct morphological body plans known as polyp, which are sessile as adults, and medusa, which are mobile; some species exhibit both body plans in their lifecycle.
- All cnidarians have two membrane layers in the body: the epidermis and the gastrodermis; between both layers they have the mesoglea, which is a connective layer.
- Cnidarians carry out extracellular digestion, where enzymes break down the food particles and cells lining the gastrovascular cavity absorb the nutrients.
- Cnidarians have an incomplete digestive system with only one opening; the gastrovascular cavity serves as both a mouth and an anus.
- The nervous system of cnidarians, responsible for tentacle movement, drawing of captured prey to the mouth, digestion of food, and expulsion of waste, is composed of nerve cells scattered across the body.
- Anthozoa, Scyphozoa, Cubozoa, and Hydrozoa make up the four different classes of Cnidarians.

Key Terms

- **diploblastic**: having two embryonic germ layers (the ectoderm and the endoderm)
- **cnidocyte**: a capsule, in certain cnidarians, containing a barbed, threadlike tube that delivers a paralyzing sting

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28.2B: Class Anthozoa

Learning Objectives

- Identify the adaptive features of anthozoa

Class Anthozoa

The class Anthozoa includes all cnidarians that exhibit a polyp body plan only; in other words, there is no medusa stage within their life cycle. Examples include sea anemones, 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. These animals are usually cylindrical in shape and are attached to a substrate.

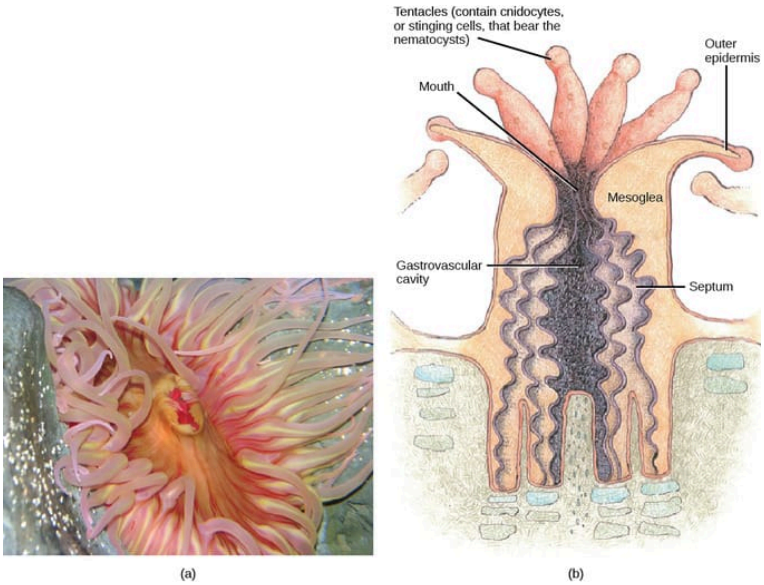


Figure $28.2B.1$: Anthozoans: The sea anemone (a), like all anthozoans, has only a polyp body plan (b).

The mouth of a sea anemone is surrounded by tentacles that bear cnidocytes. They have slit-like mouth openings and a pharynx, which is the muscular part of the digestive system that serves to ingest as well as egest food. It 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 one ectodermal and one endodermal cell layer with the mesoglea sandwiched in between. Mesenteries do not divide the gastrovascular cavity completely; 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.

Sea anemones feed on small fish and shrimp, usually by immobilizing their prey using the cnidocytes. Some sea anemones establish a mutualistic relationship with hermit crabs by attaching to the crab's shell. In this relationship, the anemone gets food particles from prey caught by the crab, while the crab is protected from the predators by the stinging cells of the anemone. Anemone fish, or clownfish, are able to live in the anemone since they are immune to the toxins contained within the nematocysts. Another type of anthozoan that forms an important mutualistic relationship is reef building coral. These hermatypic corals rely on a symbiotic relationship with zooxanthellae. The coral gains photosynthetic capability, while the zooxanthellae benefit by using nitrogenous waste and carbon dioxide produced by the cnidarian host.

Anthozoans remain polypoid throughout their lives. They can reproduce asexually by budding or fragmentation, or sexually by producing gametes. Both gametes are produced by the polyp, which can fuse to give rise to a free-swimming planula larva. The larva settles on a suitable substratum and develops into a sessile polyp.

Key Points

- Anthozoans include sea anemones, sea pens, and corals.
- The pharynx of anthozoans (ingesting as well as egesting food) leads to the gastrovascular cavity, which is divided by mesenteries.
- In Anthozoans, gametes are produced by the polyp; if they fuse, they will give rise to a free-swimming planula larva, which will become sessile once it finds an optimal substrate.
- Sea anemonies and coral are examples of anthozoans that form unique mutualistic relationships with other animal species; both sea anemonies and coral benefit from food availability provided by their partners.

Key Terms

- **mesentery**: in invertebrates, it describes any tissue that divides the body cavity into partitions
- **cnidocyte**: a capsule, in certain cnidarians, containing a barbed, threadlike tube that delivers a paralyzing sting
- **hermatypic**: of a coral that is a species that builds coral reefs

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28.2C: Class Scyphozoa

Learning Objectives

- Explain the key features of scyphozoa

Class Scyphozoa

Class Scyphozoa, an exclusively marine class of animals with about 200 known species, includes all the jellies. The defining characteristic of this class is that the medusa is the prominent stage in the life cycle, although there is a polyp stage present. Members of this species range from 2 to 40 cm in length, but the largest scyphozoan species, *Cyanea capillata*, can reach a size of 2 m across. Scyphozoans display a characteristic bell-like morphology.

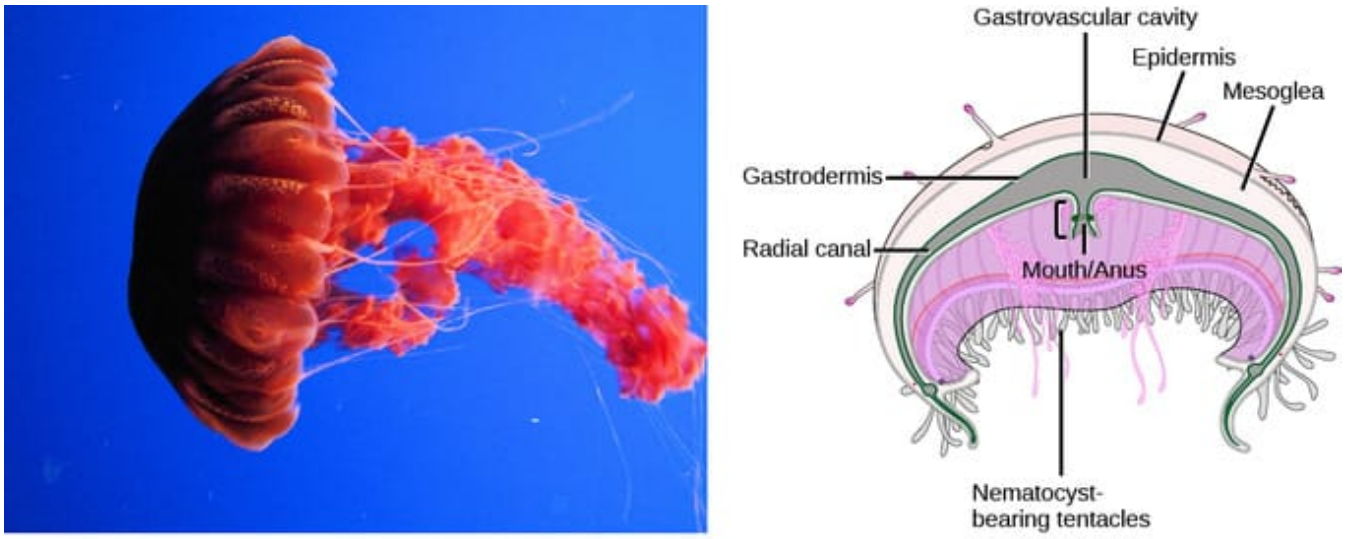


Figure $28.2C.1$: Scyphozoans: For jellyfish (a), and all other scyphozoans, the medusa (b) is the most prominent of the two life stages.

In the jellyfish, a mouth opening, surrounded by tentacles bearing nematocysts, is present on the underside of the animal. 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 be further branched into radial canals. Like the septa in anthozoans, the branched gastrovascular cells serves to increase the surface area for nutrient absorption and diffusion; thus, more cells are in direct contact with the nutrients in the gastrovascular cavity.

In scyphozoans, nerve cells are scattered over the entire body. Neurons may even be present in clusters called rhopalia. These animals possess a ring of muscles lining the dome of the body, which provides the contractile force required to swim through water. Scyphozoans are dioecious animals, having separate sexes. The gonads are formed from the gastrodermis with gametes expelled through the mouth. Planula larvae are formed by external fertilization; they settle on a substratum in a polypoid form known as scyphistoma. These forms may produce additional polyps by budding or may transform into the medusoid form. The life cycle of these animals can be described as polymorphic because they exhibit both a medusal and polypoid body plan at some point.

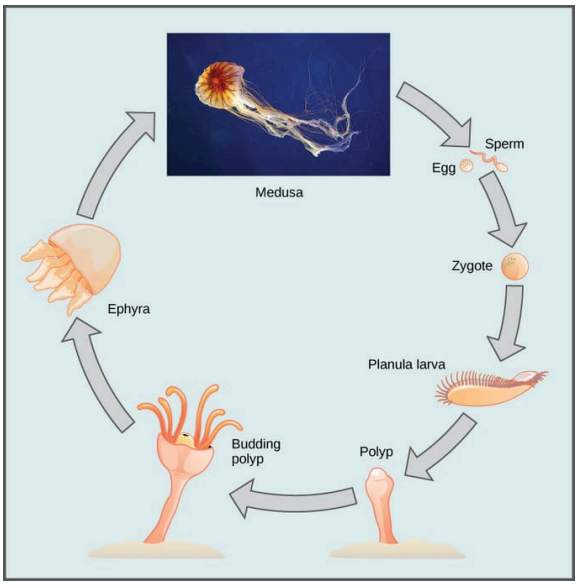


Figure $28.2C.1$: Lifecycle of a jellyfish: The lifecycle of a jellyfish includes two stages: the medusa stage and the polyp stage. The polyp reproduces asexually by budding,while the medusa reproduces sexually.

Key Points

- Scyphozoans have a ring of muscles that lines the dome of their bodies; these structures provide them with the contractile force they need to swim through water.
- Scyphozoans have separate sexes and form planula larvae through external fertilization.
- Jellies exhibit the polyp form, known as a scyphistoma, after their larvae settle on a substrate; these forms will later bud-off and transform into their more prominenent medusa forms.

Key Terms

- **dioecious**: having the male and female reproductive organs on separate parts (of the same species)
- **rhopalia**: small sensory structures found within Scyphozoa that are characterized by clusters of neurons that can be used to sense light
- **scyphistoma**: the polypoid form of scyphozoans
- **nematocyst**: a capsule, in certain cnidarians, containing a barbed, threadlike tube that delivers a paralyzing sting

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28.2D: Class Cubozoa and Class Hydrozoa

Learning Objectives

- Distinguish between cubozoa and hydrozoa cnidarians

Class Cubozoa

Class Cubozoa includes jellies that have a box-shaped medusa: a bell that is square in cross-section; hence, they are colloquially known as “box jellyfish.” These species may achieve sizes of 15–25 cm. 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. This is the most venomous group of all the cnidarians.

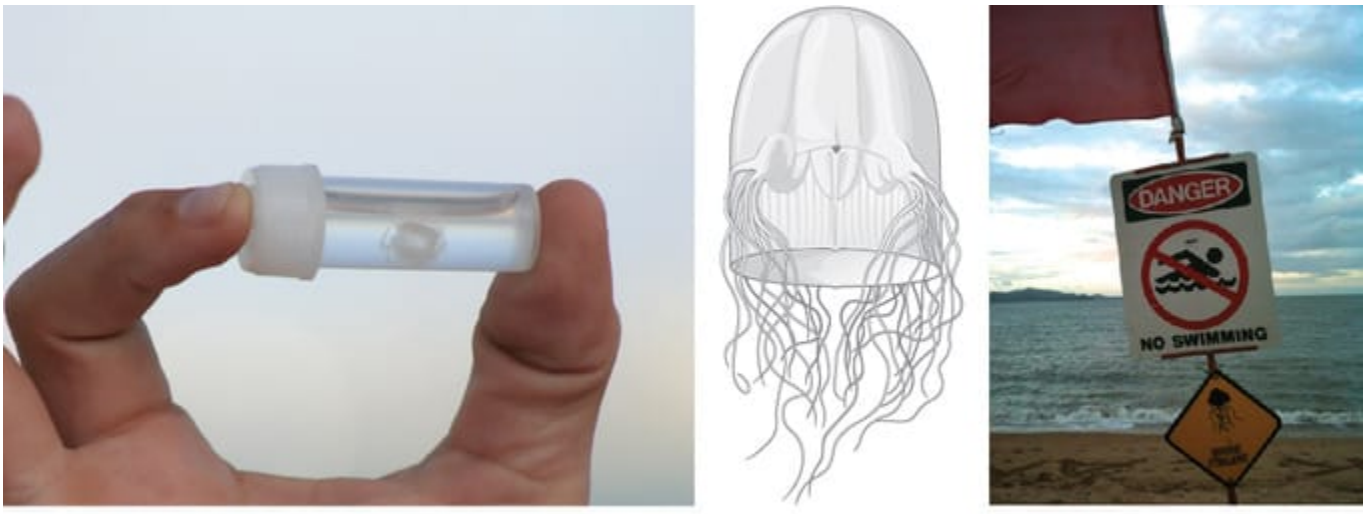


Figure 28.2D.1: Cubozoans: The (a) tiny cubazoan jelly *Malo kingi* is thimble shaped and, like all cubozoan jellies, (b) has four muscular pedalia to which the tentacles attach. *M. kingi* is one of two species of jellies known to cause Irukandji syndrome, a condition characterized by excruciating muscle 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.

The cubozoans contain muscular pads called pedalia at the corners of the square bell canopy, with one or more tentacles attached to each pedalium. These animals are further classified into orders based on the presence of single or multiple tentacles per 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 exist in a polypoid form that develops from a planula larva. These polyps show limited mobility along the substratum. As with scyphozoans, they may bud to form more polyps to colonize a habitat. Polyp forms then transform into the medusoid forms.

Class Hydrozoa

Hydrozoa includes nearly 3,200 species; most are marine, although some freshwater species are known. Animals in this class are polymorphs: most exhibit both polypoid and medusoid forms in their lifecycle, although this is variable.

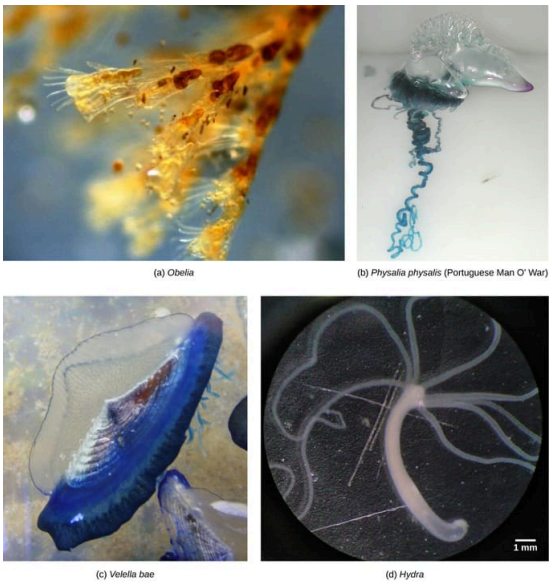


Figure 28.2D.1: Hydrozoans: (a) *Obelia*, (b) *Physalia physalis*, known as the Portuguese Man O‘ War, (c) *Velella bae*, and (d) *Hydra* have different body shapes, but all belong to the family Hydrozoa.

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 colonies that are composed of a branched colony of specialized polyps that share a gastrovascular cavity, such as in the colonial hydroid *Obelia*. Colonies may also be free-floating and contain medusoid and polypoid individuals in the colony as in *Physalia* (the Portuguese Man O’ War) or *Velella* (By-the-wind sailor). Other species are solitary polyps (*Hydra*) or solitary medusae (*Gonionemus*). The true characteristic shared by all these diverse species is that their gonads for sexual reproduction are derived from epidermal tissue, whereas in all other cnidarians they are derived from gastrodermal tissue.

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Key Points

- Cubozoans differ from Scyphozoans in their arrangement of tentacles; they are also known for their box-shaped medusa.
- Out of all cnidarians, cubozoans are the most venomous.
- Hydrozoans are polymorphs, existing as solitary polyps, solitary medusae, or as colonies.

- Hydrozoans are unique from all other cnidarians in that their gonads are derived from epidermal tissue.

Key Terms

- **hydroid**: any of many colonial coelenterates that exist mainly as a polyp; a hydrozoan

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28.3: SUPERPHYLUM LOPHOTROCHOZOA

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28.3B: Phylum Platyhelminthes

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28.3D: Phylum Nemertea

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28.3F: Classification of Phylum Mollusca

28.3G: Phylum Annelida

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28.3A: Superphylum Lophotrochozoa

Learning Objectives

- Describe the phylogenetic position and basic features of lophotrochozoa

Lophotrochozoans

Animals belonging to superphylum Lophotrochozoa are protostomes: the blastopore (or the point of involution of the ectoderm or outer germ layer) becomes the mouth opening to the alimentary canal. This is called protostomy or "first mouth." In protostomy, solid groups of cells split from the endoderm or inner germ layer to form a central mesodermal layer of cells. This layer multiplies into a band which then splits internally to form the coelom; this protostomic coelom is termed schizocoelom.

As lophotrochozoans, the organisms in this superphylum possess either lophophore or trochophore larvae. The exact relationships between the different phyla are not entirely certain. The lophophores include groups that are united by the presence of the lophophore, a set of ciliated tentacles surrounding the mouth. Lophophorata include the flatworms and several other phyla, including the Bryozoa, Entoprocta, Phoronida, and Brachiopoda. These clades are upheld when RNA sequences are compared. Trochophore larvae are characterized by two bands of cilia around the body. Previously, these were treated together as the Trochozoa, together with the arthropods, which do not produce trochophore larvae, but were considered close relatives of the annelids because they are both segmented. However, they show a number of important differences. Arthropods are now placed separately among the Ecdysozoa. The Trochozoa include the Nemertea, Mollusca, Sipuncula, and Annelida.

The lophotrochozoans are triploblastic, possessing an embryonic mesoderm sandwiched between the ectoderm and endoderm found in the diploblastic cnidarians. These phyla are also bilaterally symmetrical: a longitudinal section will divide them into right and left sides that are symmetrical. They also show the beginning of cephalization: the evolution of a concentration of nervous tissues and sensory organs in the head of the organism, which is where it first encounters its environment.

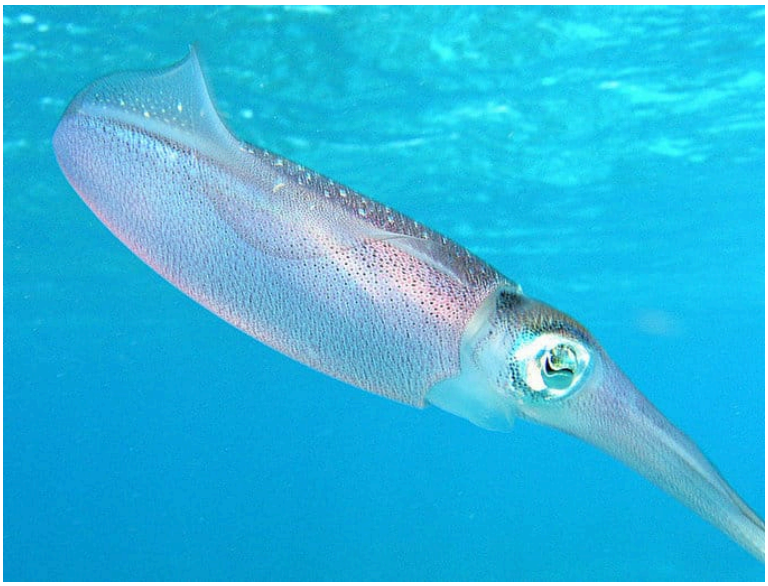


Figure 28.3A.1: Lophotrochozoans: The Caribbean Reef Squid or Sepioteuthis sepioidea is a complex lophotrochozoan. Species in this group have bilateral symmetry.

Key Points

- Lophotrochozoa have a blastopore, which is an involution of the ectoderm that forms a rudimentary mouth opening to the alimentary canal, a condition called protostomy or "first mouth".

- The Lophotrochozoa are comprised of the trochozoans and the lophophorata, although the exact relationships between the different phyla are not clearly determined.
- Lophophores are characterized by the presence of the lophophore, a set of ciliated tentacles surrounding the mouth; they include the flatworms and several other phyla whose relationships are upheld by genetic evidence.
- Trochophore larvae are distinguished from the lophophores by two bands of cilia around the body; they include the Nemertea, Mollusca, Sipuncula, and Annelida.
- The lophotrochozoans have a mesoderm layer positioned between the ectoderm and endoderm and are bilaterally symmetrical, which signals the beginning of cephalization, the concentration of nervous tissues and sensory organs in the head of the organism.

Key Terms

- **blastopore**: the opening into the archenteron
- **lophophore**: a feeding organ of brachiopods, bryozoans, and phoronids
- **cephalization**: an evolutionary trend in which the neural and sense organs become centralized at one end (the head) of an animal

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28.3B: Phylum Platyhelminthes

Learning Objectives

- Differentiate among the classes of platyhelminthes

Phylum Platyhelminthes

Phylum Platyhelminthes is composed of the flatworms: acoelomate organisms that include many free-living and parasitic forms. Most of the flatworms are classified in the superphylum Lophotrochozoa, which also includes the mollusks and annelids. The Platyhelminthes consist of two 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; therefore, they resemble a chain. The remaining flatworms discussed here are part of the Rhabditophora.

Many flatworms are parasitic, including important parasites of humans. Flatworms have three embryonic tissue layers that give rise to surfaces that cover tissues (from ectoderm), internal tissues (from mesoderm), and line the digestive system (from endoderm). The epidermal tissue is a single layer cells or a layer of fused cells (syncytium) that covers a layer of circular muscle above a layer of longitudinal muscle. The mesodermal tissues include mesenchymal cells that contain collagen and support secretory cells that secrete mucus and other materials at the surface. The flatworms are acoelomates: their bodies are solid between the outer 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 on the tissues of their hosts. Most flatworms have a gastrovascular cavity rather than a complete digestive system; in such animals, the "mouth" is also used to expel waste materials from the digestive system. Some species also have an anal opening. The gut may be a simple sac or highly branched. Digestion is extracellular, with digested materials taken in to the cells of the gut lining by phagocytosis. One group, the cestodes, lacks a digestive system. Flatworms have an excretory system with a network of tubules throughout the body with openings to the environment and nearby flame cells, whose cilia beat to direct waste fluids concentrated in the tubules out of the body. The system is responsible for the regulation of dissolved salts and the excretion of nitrogenous wastes. The nervous system consists of a pair of nerve cords running the length of the body with connections between them and a large ganglion or concentration of nerves at the anterior end of the worm, where there may also be a concentration of photosensory and chemosensory cells.

There is neither a circulatory nor respiratory system, with gas and nutrient exchange dependent on diffusion and cell-cell junctions. This necessarily limits the thickness of the body in these organisms, constraining them to be "flat" worms. In addition, most flatworm species are monoecious; typically, fertilization is internal. Asexual reproduction is common in some groups.

Diversity of Flatworms

Platyhelminthes are traditionally divided into four classes: Turbellaria, Monogenea, Trematoda, and Cestoda. The class Turbellaria includes mainly free-living, marine species, although some species live in freshwater or moist terrestrial environments. The ventral epidermis of turbellarians is ciliated which facilitates their locomotion. Some turbellarians are capable of remarkable feats of regeneration: they may regrow the entire body from a small fragment.



Figure $28.3B.1$: Turbellaria: Pseudobiceros bedfordi (Bedford's Flatworm), a member of the Turbellaria, is a marine species which uses the epidermis of its belly for locomotion.

The monogeneans are ectoparasites, mostly of fish, with simple life cycles that consist of a free-swimming larva that attaches to a fish to begin transformation to the parasitic adult form. The worms may produce enzymes that digest the host tissues or simply graze on surface mucus and skin particles.

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 almost always a mollusk. Trematodes are responsible for serious human diseases including schistosomiasis, a blood fluke.



Figure $28.3B.1$: Trematodes: Botulus microporus is a trematode that lives only in the intestinal tract of Lancetfish, *Alepisaurus ferox*.

The cestodes, or tapeworms, are also internal parasites, mainly of vertebrates. Tapeworms live in the intestinal tract of the primary host, remaining fixed by using a sucker on the anterior end, or scolex, of the tapeworm body. The remainder of the tapeworm is composed of a long series of units called proglottids. Each may contain an excretory system with flame cells and both female and male reproductive structures. Tapeworms do not possess a digestive system; instead, they absorb nutrients from the food matter passing through them in the host's intestine.

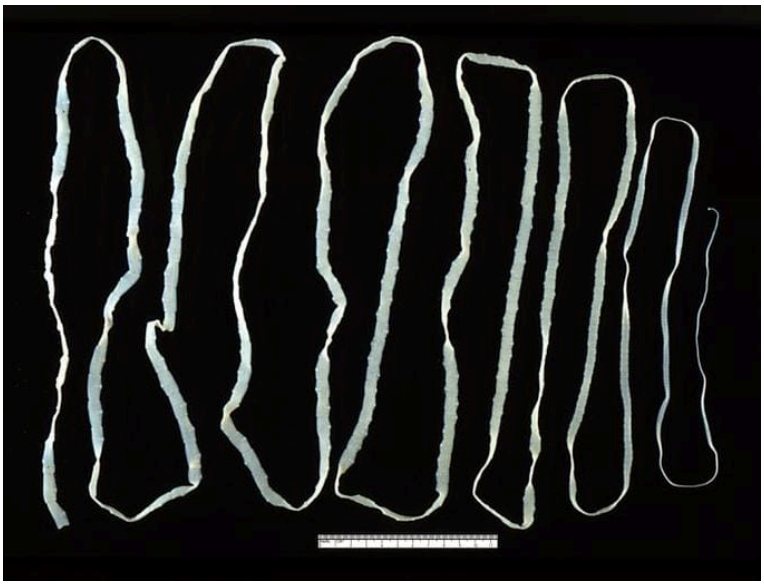


Figure $28.3B.1$: Cestodes: Taenia saginata, also known as Taeniarhynchus saginata or the beef tapeworm, is a parasite of both cattle and humans. It displays the long series of proglottid subunits characteristic of the species.

Key Points

- The Platyhelminthes are acoelomate flatworms: their bodies are solid between the outer surface and the cavity of the digestive system.
- Most flatworms have a gastrovascular cavity rather than a complete digestive system; the same cavity used to bring in food is used to expel waste materials.
- Platyhelminthes are either predators or scavengers; many are parasites that feed on the tissues of their hosts.
- Flatworms posses a simple nervous system, no circulatory or respiratory system, and most produce both eggs and sperm, with internal fertilization.
- Platyhelminthes are divided into four classes: Turbellaria, free-living marine species; Monogenea, ectoparasites of fish; Trematoda, internal parasites of humans and other species; and Cestoda (tapeworms), which are internal parasites of many vertebrates.
- In flatworms, digested materials are taken into the cells of the gut lining by phagocytosis, rather than being processed internally.

Key Terms

- **acoelomate**: any animal without a coelom, or body cavity
- **ectoparasite**: a parasite that lives on the surface of a host organism
- **scolex**: the structure at the rear end of a tapeworm which, in the adult, has suckers and hooks by which it attaches itself to a host
- **proglottid**: any of the segments of a tapeworm; they contain both male and female reproductive organs

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28.3C: Phylum Rotifera

Learning Objectives

- Identify the features of rotifers involved in movement and feeding

Phylum Rotifera

The rotifers are a microscopic (about 100 µm to 30 mm) group of mostly-aquatic organisms that get their name from the corona: a rotating, wheel-like structure that is covered with cilia at their anterior end. Although their taxonomy is currently in flux, one treatment places the rotifers in three classes: Bdelloidea, Monogononta, and Seisonidea. The classification of the group is currently under revision, however, as more phylogenetic evidence becomes available. It is possible that the "spiny headed worms" currently in phylum Acanthocephala will be incorporated into this group in the future.



Figure 28.3C.1: Rotifers: A bdelloid rotifer is a member of a class of rotifers found in fresh water and moist soil. The rotifer body consists of a head, a truck, and a foot. They eat by filtering food into the mouth by creating currents with the corona.

The rotifer body form consists of a head (which contains the corona), a trunk (which contains the organs), and the foot. Rotifers are typically free-swimming and truly planktonic organisms, but the toes or extensions of the foot can secrete a sticky material forming a holdfast to help them adhere to surfaces. The head contains sensory organs in the form of a bi-lobed brain and small eyespots near the corona.

The rotifers are filter feeders that will eat dead material, algae, and other microscopic living organisms. Therefore, they are very important components of aquatic food webs. Rotifers obtain food that is directed toward the mouth by the current created from the movement of the corona. The food particles enter the mouth and travel to the mastax (pharynx with jaw-like structures). Food passes by digestive and salivary glands into the stomach and then into the intestines. Digestive and excretory wastes are collected in a cloacal bladder before being released out the anus.

Rotifers are pseudocoelomates commonly found in fresh water and some salt water environments throughout the world. About 2,200 species of rotifers have been identified. Rotifers are dioecious organisms (having either male or female genitalia) and exhibit sexual dimorphism (males and females have different forms). Many species are parthenogenic and exhibit haplodiploidy, a method of gender determination in which a fertilized egg develops into a female and an unfertilized egg develops into a male. In many dioecious species, males are short-lived and smaller, with no digestive system and a single testis. Females can produce eggs that are capable of dormancy, which protects eggs during harsh environmental conditions.

Key Points

- The rotifer body form consists of a head (containing the sensory organs in the form of a bi-lobed brain and small eyespots near the corona), the trunk (containing organs), and the foot (which can hold fast).
- The foot of the rotifer secretes a sticky material to help it adhere to surfaces.
- Rotifers are filter feeders that generate a current using the corona to pass food into the mouth, which then passes by digestive and salivary glands into the stomach and intestines.
- Rotifers exhibit sexual dimorphism; the gender of many species is determined by whether the egg is fertilized (and develops into a female) or unfertilized (and develops into a male).

Key Terms

- **pseudocoelomate**: any invertebrate animal with a three-layered body and a pseudocoel
- **mastax**: the pharynx of a rotifer which usually contains four horny pieces that work to crush the food

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28.3D: Phylum Nemertea

Learning Objectives

- Identify the key features of the Phylum Nemertea

Phylum Nemertea

The Nemertea are colloquially known as ribbon worms. Most species of phylum Nemertea are marine (predominantly benthic or bottom dwellers) with an estimated 900 species known. However, nemertini have been recorded in freshwater and terrestrial habitats as well. Most nemerteans are carnivores, feeding on worms, clams, and crustaceans. Some species are scavengers, while other nemertini species, such as *Malacobdella grossa*, have also evolved commensalistic relationships with some mollusks. Interestingly, nemerteans have almost no predators, two species are sold as fish bait, and some species have devastated commercial fishing of clams and crabs.

Morphology

Ribbon worms 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 also show a flattened morphology: they are flat from front to back, like a flattened tube. In addition, nemertea are soft, unsegmented animals.



Figure $28.3D.1$: Morphology of Nemertea: A terrestrial Geonemertes, a Nemertean, displaying the flat, ribbon-like body of the organism that is unsegmented.

A unique characteristic of this phylum is the presence of a proboscis enclosed in a rhynchocoel. The proboscis serves to capture food and may be ornamented with barbs in some species. 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. The proboscis may be extended or retracted by the retractor muscle attached to the wall of the rhynchocoel.

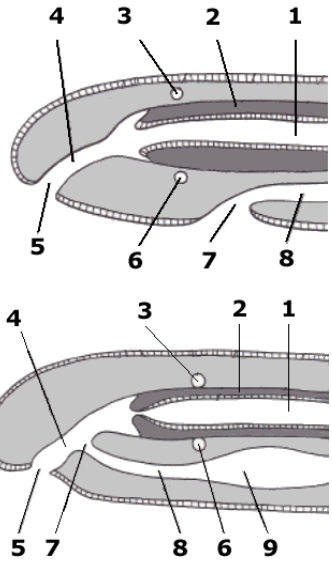


Figure $28.3D.1$: Internal structures of the Nemertini: This image shows the internal structures of a basic nemertean, including the proboscis and the rhynchocoel: 1: Proboscis 2: Rhynchocoel 3: Dorsal commissure of brain 4: Rhynchodeum 5: Proboscis pore 6: Ventral commissure of brain 7: Mouth 8: Foregut 9: Stomach

Metabolism

The nemertini show a very 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 which ends in a rectum that opens via an anus. Gonads are interspersed with the intestinal diverticular pouches, opening outwards via genital pores. A circulatory system consists of a closed loop of a pair of lateral blood vessels. The circulatory system is derived from the coelomic cavity of the embryo. Some animals may also have cross-connecting vessels in addition to lateral ones. Although these are called blood vessels, since they are of coelomic origin, the circulatory fluid is colorless. Some species bear hemoglobin as well as yellow or green pigments. The blood vessels are connected to the rhynchocoel. The flow of fluid in these vessels is facilitated by the contraction of muscles in the body wall. A pair of protonephridia, or primitive kidneys, is present in these animals to facilitate osmoregulation. Gaseous exchange occurs through the skin in the nemertini.

Nervous System

Nemertini have a ganglion or “brain” situated at the anterior end between the mouth and the foregut, surrounding the digestive system as well as the rhynchocoel. A ring of four nerve masses called “ganglia” comprises the brain in these animals. Paired longitudinal nerve cords emerge from the brain ganglia, extending to the posterior end. 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

Animals in phylum Nemertea show sexual dimorphism, although freshwater species may be hermaphroditic. Eggs and sperm are released into the water; fertilization occurs externally. The zygote develops into a special kind of nemertean larvae called a planuliform larva. In some nemertine species, another larva specific to the nemertinis, a pilidium, may develop inside the young worm from a series of imaginal discs. This larval form, characteristically shaped like a deerstalker cap, devours tissues from the young worm for survival before metamorphosing into the adult-like morphology.

Key Points

- The Nemertini are mostly bottom-dwelling marine organisms, although some are found in freshwater and terrestrial habitats.
- Most nemerteans are carnivores, some are scavengers, and others have evolved relationships with some mollusks that are

benefit the Nemertean but do not harm the mollusk.
- Nemerteans vary greatly in size and are bilaterally symmetrical; they are unsegmented and resemble a flat tube which can change morphological presentation in response to environmental cues.
- Nemertini have a simple nervous system comprised of a ring of four nerve masses called “ganglia” at the anterior end between the mouth and the foregut from which paired longitudinal nerve cords emerge and extend to the posterior end.
- Nemertini are mostly sexually dimorphic, fertilizing eggs externally by releasing both eggs and sperm into the water; a larva may develop inside the resulting young worm and devour its tissues before metamorphosing into the adult.

Key Terms

- **protonephridia**: an invertebrate organ which occurs in pairs and removes metabolic wastes from an animal’s body
- **rhynchocoel**: a cavity which mostly runs above the midline and ends a little short of the rear of the body of a nemertean and extends or retracts the proboscis
- **proboscis**: an elongated tube from the head or connected to the mouth, of an animal

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28.3E: Phylum Mollusca

Learning Objectives

- Describe the unique anatomical and morphological features of molluscs

Phylum Mollusca

Phylum Mollusca is the predominant phylum in marine environments. It is estimated that 23 percent of all known marine species are mollusks; there are around 85,000 described species, making them the second most diverse phylum of animals. The name “mollusca” signifies a soft body; the earliest descriptions of mollusks came from observations of unshelled cuttlefish. Mollusks are predominantly a marine group of animals; however, they are known to inhabit freshwater as well as terrestrial habitats. Mollusks display a wide range of morphologies in each class and subclass. They range from large predatory squids and octopus, some of which show a high degree of intelligence, to grazing forms with elaborately-sculpted and colored shells. In spite of their tremendous diversity, however, they also share a few key characteristics, including a muscular foot, a visceral mass containing internal organs, and a mantle that may or may not secrete a shell of calcium carbonate.



Figure $28.3E.1$: Mollusk shells: Helix aspersa, a common land snail, has a calcium carbonate shell.

Mollusks have a muscular foot used for locomotion and anchorage that varies in shape and function, depending on the type of mollusk under study. In shelled mollusks, this foot is usually the same size as the opening of the shell. The foot is a retractable as well as an extendable organ. It is the ventral-most organ, whereas the mantle is the limiting dorsal organ. Mollusks are eucoelomate, but the cavity is restricted to a region around the heart in adult animals. The mantle cavity develops independently of the coelomic cavity.

The visceral mass is present above the foot in the visceral hump. This includes digestive, nervous, excretory, reproductive, and respiratory systems. Mollusk species that are exclusively aquatic have gills for respiration, whereas some terrestrial species have lungs for respiration. Additionally, a tongue-like organ called a radula, which bears chitinous tooth-like ornamentation, is present in many species, serving to shred or scrape food. The mantle (also known as the pallium) is the dorsal epidermis in mollusks; shelled mollusks are specialized to secrete a chitinous and hard calcareous shell.

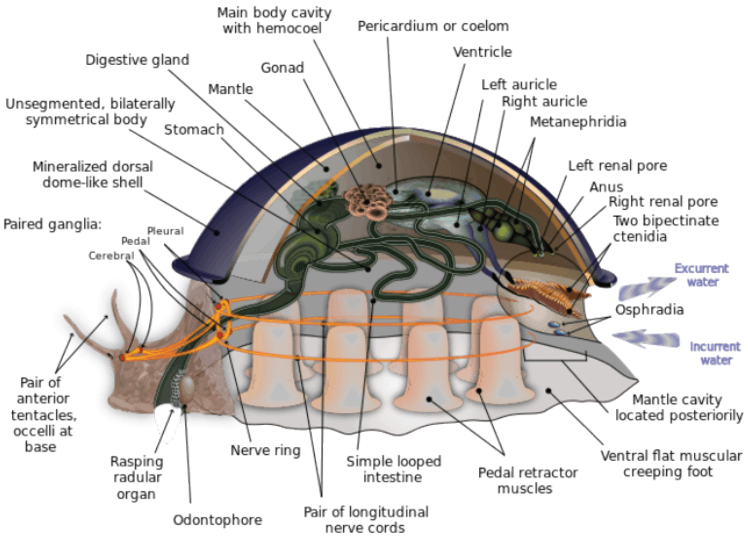


Figure $28.3E.1$: A "generalized mollusk": An anatomical diagram of a hypothetical ancestral mollusk, showing features common to many mollusk types.

Most mollusks are dioecious animals where fertilization occurs externally, although this is not the case in terrestrial mollusks, such as snails and slugs, or in cephalopods. In some mollusks, the zygote hatches and undergoes two larval stages, trochophore and veliger, before becoming a young adult; bivalves may exhibit a third larval stage, glochidia.

Key Points

- A mollusk's muscular foot is used for locomotion and anchorage, varies in shape and function, and can both extend and retract.
- The visceral mass inside the mollusk includes digestive, nervous, excretory, reproductive, and respiratory systems.
- Most mollusks possess a radula, which is similar to a tongue with teeth-like projections, serving to shred or scrape food.
- The mantle is the dorsal epidermis in mollusks; in some mollusks it secretes a chitinous and hard calcareous shell.

Key Terms

- **visceral mass**: the soft, non-muscular metabolic region of the mollusc that contains the body organs
- **mantle**: the body wall of a mollusc, from which the shell is secreted
- **radula**: the rasping tongue of snails and most other mollusks

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28.3F: Classification of Phylum Mollusca

Learning Objectives

- Differentiate among the classes in the phylum mollusca

Classes in Phylum Mollusca

Phylum Mollusca is a very diverse (85,000 species) group of mostly marine species, with a dramatic variety of form. This phylum can be segregated into seven classes: Aplacophora, Monoplacophora, Polyplacophora, Bivalvia, Gastropoda, Cephalopoda, and Scaphopoda.

Class Aplacophora

Class Aplacophora (“bearing no plates”) includes worm-like animals primarily found in benthic marine habitats. These animals lack a calcareous shell, but possess aragonite spicules on their epidermis. They have a rudimentary mantle cavity and lack eyes, tentacles, and nephridia (excretory organs).

Class Monoplacophora

Members of class Monoplacophora (“bearing one plate”) posses a single, cap-like shell that encloses the body. The morphology of the shell and the underlying animal can vary from circular to ovate. A looped digestive system, multiple pairs of excretory organs, many gills, and a pair of gonads are present in these animals. The monoplacophorans were believed extinct and only known via fossil records until the discovery of Neopilina galathaea in 1952. Today, scientists have identified nearly two dozen extant species.

Class Polyplacophora

Animals in the class Polyplacophora (“bearing many plates”) are commonly known as “chitons” and bear an armor-like, eight-plated dorsal shell. These animals have a broad, ventral foot that is adapted for suction to rocks and other substrates, and a mantle that extends beyond the shell in the form of a girdle. Calcareous spines may be present on the girdle to offer protection from predators. Chitons live worldwide, in cold water, warm water, and the tropics. Most chiton species inhabit intertidal or subtidal zones, and do not extend beyond the photic zone. Some species live quite high in the intertidal zone and are exposed to the air and light for long periods.



Figure $28.3F.1$: Chiton morphology: The underside of the gumboot chiton, Cryptochiton stellari, showing the foot in the center, surrounded by the gills and mantle. The mouth is visible to the left in this image.

Class Bivalvia

Bivalvia is a class of marine and freshwater molluscs with laterally compressed bodies enclosed by a shell in two hinged parts. Bivalves include clams, oysters, mussels, scallops, and numerous other families of shells. The majority are filter feeders and have no head or radula. The gills have evolved into ctenidia, specialised organs for feeding and breathing. Most bivalves bury themselves in sediment on the seabed, while others lie on the sea floor or attach themselves to rocks or other hard surfaces.

The shell of a bivalve is composed of calcium carbonate, and consists of two, usually similar, parts called valves. These are joined together along one edge by a flexible ligament that, in conjunction with interlocking “teeth” on each of the valves, forms the hinge.



Figure $28.3F.1$: Empty shell of a bivalve: The empty shell of the giant clam, Tridacna gigas. Note the pair of shells that are hinged together, a characteristic of members of the class Bivalvia.

Class Gastropoda

Animals in class Gastropoda (“stomach foot”) include well-known mollusks like snails, slugs, conchs, sea hares, and sea butterflies.

Gastropoda includes shell-bearing species as well as species with a reduced shell. These animals are asymmetrical and usually present a coiled shell. 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.

The visceral mass in the shelled species displays torsion around the perpendicular axis on the center of the foot, which is the key characteristic of this group, along with a foot that is modified for crawling. Most gastropods bear a head with tentacles, eyes, and a style. A complex radula is used by the digestive system and aids in the ingestion of food. Eyes may be absent in some gastropods species. The mantle cavity encloses the ctenidia (singluar: ctenidium) as well as a pair of nephridia (singular: nephridium).



Figure $28.3F.1$: Gastropod foot: Gastropods, such as this Roman snail, have a large foot that is modified for crawling.

Class Cephalopoda

Class Cephalopoda ("head foot" animals) includes octopuses, squids, cuttlefish, and nautilus. Cephalopods are a class of shell-bearing animals as well as mollusks with a reduced shell. They display vivid coloration, typically seen in squids and octopuses which is used for camouflage. All animals in this class are carnivorous predators and have beak-like jaws at the anterior end. All cephalopods show the presence of a very well-developed nervous system along with eyes, as well as a closed circulatory system. The foot is lobed and developed into tentacles and a funnel, which is used as the mode of locomotion. Locomotion in cephalopods is facilitated by ejecting a stream of water for propulsion ("jet" propulsion). Cephalopods, such as squids and octopuses, also produce sepia or a dark ink, which is squirted upon a predator to assist in a quick getaway. Suckers are present on the tentacles in octopuses and squid. Ctenidia are enclosed in a large mantle cavity serviced by blood vessels, each with its own associated heart. The mantle has siphonophores that facilitate exchange of water.



Figure $28.3F.1$: Cephalopods: Cephalopods (“head foot”) include this octopus, which ejects a stream of water from a funnel in its body to propel itself through the water.

A pair of nephridia is present within the mantle cavity. Sexual dimorphism is seen in this class of animals. Members of a species mate, then the female 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. Reproduction in cephalopods is different from other mollusks in that the egg hatches to produce a juvenile adult without undergoing the trochophore and veliger larval stages.

Class Scaphopoda

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. Scaphopods are usually buried in sand with the anterior opening exposed to water. These animals bear a single conical shell, which has both ends open. The head is rudimentary and protrudes out of the posterior end of the shell. These animals do not possess eyes, but they have a radula, as well as a foot modified into tentacles with a bulbous end, known as captaculae. Captaculae serve to catch and manipulate prey. Ctenidia are absent in these animals.



Figure $28.3F.1$: The Scaphopods: The Scaphopods (“boat feet”) include the Antalis vulgaris, the shell of which is depicted here.

Key Points

- Mollusks can be segregated into seven classes: Aplacophora, Monoplacophora, Polyplacophora, Bivalvia, Gastropoda, Cephalopoda, and Scaphopoda. These classes are distinguished by, among other criteria, the presence and types of shells they possess.
- Class Aplacophora includes worm-like animals with no shell and a rudimentary body structure.
- Members of class Monoplacophora have a single shell that encloses the body.
- Members of class Polyplacophora are better known as “chitons;” these molluscs have a large foot on the ventral side and a shell composed of eight hard plates on the dorsal side.
- Class Bivalvia consists of mollusks with two shells held together by a muscle; these include oysters, clams, and mussels.
- Members of class Gastropoda have an asymmetrical body plan and usually have a shell, which can be planospiral or conispiral. Their key characteristic is the torsion around the perpendicular axis on the center of the foot that is modified for crawling.
- Class Scaphopoda consists of mollusks with a single conical shell through which the head protrudes, and a foot modified into tentacles known as captaculae that are used to catch and manipulate prey.

Key Terms

- **ctenidium**: a respiratory system, in the form of a comb, in some molluscs
- **captacula**: the foot of a Scaphalopod, modified into tentacles for capturing prey
- **nephridium**: a tubular excretory organ in some invertebrates

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28.3G: Phylum Annelida

Learning Objectives

- Describe the morphological and anatomical features of annelids

Phylum Annelida

Phylum Annelida contains the class Polychaeta (the polychaetes) and the class Oligochaeta (the earthworms, leeches, and their relatives). These animals are found in marine, terrestrial, and freshwater habitats, but a presence of water or humidity is a critical factor for their survival, especially in terrestrial habitats. The name of the phylum is derived from the Latin word annellus, which means a small ring. Animals in this phylum show parasitic and commensal symbioses with other species in their habitat. Approximately 16,500 species have been described in phylum Annelida. The phylum includes earthworms, polychaete worms, and leeches. Annelids show protostomic development in embryonic stages and are often called “segmented worms” due to their key characteristic of metamerism, or true segmentation.

Morphology

Annelids display bilateral symmetry and are worm-like in overall morphology. They have a segmented body plan where the 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. This metamerism is thought to arise from identical teloblast cells in the embryonic stage, which develop into identical mesodermal structures. The overall body can be divided into head, body, and pygidium (or tail). The clitellum is a reproductive structure that generates mucus that aids in sperm transfer and gives rise to a cocoon within which fertilization occurs; it appears as a fused band in the anterior third of the animal.



Figure $28.3G.1$: Clitellum: The clitellum is the reproductive structure of an annelid. It creates mucus that aids in sperm transfer and gives rise to a cocoon within which fertilization occurs. It can be seen in this image as the enlarged band around the animal.

Anatomy

The epidermis is protected by an acellular, external cuticle, but this 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 hairlike extensions, anchored in the epidermis and projecting from the cuticle, called setae/chaetae are present in

every segment. Annelids show the presence of a true coelom, derived from embryonic mesoderm and protostomy. Hence, they are the most advanced worms. A well-developed and complete digestive system is present in earthworms (oligochaetes) with a mouth, muscular pharynx, esophagus, crop, and gizzard being present. The gizzard leads to the intestine and ends in an anal opening. Each segment is limited by a membranous septum that divides the coelomic cavity into a series of compartments.

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, these vessels are connected by transverse loops in every segment. These animals lack a well-developed respiratory system; gas exchange occurs across the moist body surface. 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 towards the ventral side. Annelids show well-developed nervous systems with a nerve ring of fused ganglia present around the pharynx. The nerve cord is ventral in position, bearing enlarged nodes or ganglia in each segment.

Annelids may be either monoecious, with permanent gonads (as in earthworms and leeches), or dioecious, with temporary or seasonal gonads that develop (as in polychaetes). However, cross-fertilization is preferred in hermaphroditic animals. These animals may also show simultaneous hermaphroditism, participating in simultaneous sperm exchange when they are aligned for copulation.

Earthworms are the most abundant members of the class Oligochaeta, distinguished by the presence of the clitellum as well as few, reduced chaetae (“oligo- = “few”; -chaetae = “hairs”). The number and size of chaetae are greatly diminished in Oligochaeta compared to the polychaetes (poly=many, chaetae = hairs). The many chetae of polychaetes are also arranged within fleshy, flat, paired appendages that protrude from each segment. These parapodia may be specialized for different functions in the polychates. A significant difference between leeches and other annelids is the development of suckers at the anterior and posterior ends and an absence of chaetae. Additionally, 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.



Figure 28.3G.1: Leeches: Unlike earthworms, leeches lack chaetae and have suckers at both ends of the body.

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Key Points

- Annelids are often called “segmented worms” because they possess true segmentation of their bodies, with both internal and external morphological features repeated in each body segment.
- The clitellum is a structure on the anterior portion of the worm that generates mucus to aid in sperm transfer from one worm to another; it also forms a cocoon within which fertilization occurs.
- Most annelids have chitinous hairlike extensions in every segment called chaetae that are anchored in the epidermis, although the number and size of chaetae can vary in the different classes.

- Annelids possess a closed circulatory system, lack a well-developed respiratory system, but have well-developed nervous systems.
- Annelids can either have distinct male and female forms or be hermaphrodites (having both male and female reproductive organs). Earthworms are hermaphrodites and can self-fertilize, but prefer to cross-fertilize if possible.

Key Terms

- **clitellum**: a glandular swelling in the epidermis of some annelid worms; it secretes a viscous fluid in which the eggs are deposited
- **chaeta**: a chitinous bristle of an annelid worm
- **metamerism**: the segmentation of the body into similar discrete units

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28.4: SUPERPHYLUM ECDYSOZOA

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- Topic hierarchy

28.4A: Superphylum Ecdysozoa
28.4B: Phylum Nematoda
28.4C: Phylum Arthropoda
28.4D: Subphyla of Arthropoda

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28.4A: Superphylum Ecdysozoa

Learning Objectives

- Discuss the phylogenetic position of Ecdysozoa

Superphylum Ecdysozoa

The superphylum Ecdysozoa contains an incredibly large number of species. This is because it includes two of the most diverse animal groups: Phylum Nematoda (the roundworms) and Phylum Arthropoda (the arthropods). The most distinguishing and prominent feature of Ecdysozoans is their cuticle: a tough, but flexible exoskeleton that protects these animals from water loss, predators, and other aspects of the external environment. All members of this superphylum periodically molt or shed their cuticle as they grow. After molting, they secrete a new cuticle that will last until their next growth phase. The process of molting and replacing the cuticle is called ecdysis, which is the derivation of the superphylum's name.



Figure 28.4A.1: Molting in arthropods: This cicada is in the middle of the molting process. The old cuticle splits and the insect climbs out. At this time, the insect's body is very soft. The cicada will then eat the old shell to replace nutrients that would otherwise be lost. This encourages the new shell to harden.

Phylogenetic Hypotheses

There are two main hypotheses about the phylogeny of the Ecdysozoans. The first is called the Articulata hypothesis. This grouping scheme is widely accepted, although some zoologists still hold to the original view that Panarthropoda should be classified with Annelida in a group called the Articulata, and that Ecdysozoa are polyphyletic. Others have suggested that a possible solution is to regard Ecdysozoa as a sister-group of Annelida, though many scientists consider them unrelated. Inclusion of the roundworms within the Ecdysozoa was initially contested, but since 2003, a broad consensus has formed supporting the Ecdysozoa, placing them in a new set of groupings that include the Ecdysozoa, the Lophotrochozoa, and the Deuterostomia.

The other idea about the phylogeny of the Ecdysozoa is called the coelomate hypothesis. Before Ecdysozoa, one of the prevailing theories for the evolution of the bilateral animals was based on the morphology of their body cavities. There were three types, or grades, of organization: the Acoelomata (no coelom), the Pseudocoelomata (partial coelom), and the Eucoelomata (true coelom). With the introduction of molecular phylogenetics, the coelomate hypothesis was abandoned, although some molecular, phylogenetic support for the Coelomata continued until 2005.

Key Points

- The Ecdysozoans are the most diverse group of animals, containing the nematode worms and the arthropods.
- These organisms have an external covering called a cuticle that protects their soft internal organs from water loss and the outside environment.
- After they molt, or shed their cuticle, they grow in size and secrete a new shell; this is called ecdysis.
- The phylogeny of the Ecdysozoans has been the cause of much scientific debate with no definitive consensus in the scientific community.

Key Terms

- **cuticle**: a noncellular protective covering outside the epidermis of many invertebrates and plants
- **coelomate**: any animal possessing a fluid-filled cavity within which the digestive system is suspended.
- **ecdysis**: the shedding of an outer layer of skin in snakes, crustaceans and insects; moulting

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28.4B: Phylum Nematoda

Learning Objectives

- Describe the features of animals classified in phylum Nematoda

Phylum Nematoda

The Nematoda, similar to most other animal phyla, are triploblastic, possessing an embryonic mesoderm that is sandwiched between the ectoderm and endoderm. They are also bilaterally symmetrical: a longitudinal section will divide them into right and left sides that are symmetrical. Furthermore, the nematodes, or roundworms, possess a pseudocoelom and have both free-living and parasitic forms.

Both the nematodes and arthropods belong to the superphylum Ecdysozoa that is believed to be a clade consisting of all evolutionary descendants from one common ancestor. The name derives from the word ecdysis, which refers to the shedding, or molting, of the exoskeleton. The phyla in this group have a hard cuticle covering their bodies, which must be periodically shed and replaced for them to increase in size.

Phylum Nematoda includes more than 28,000 species with an estimated 16,000 being parasitic in nature. Nematodes are present in all habitats.

Morphology

In contrast with cnidarians, nematodes show a tubular morphology and circular cross-section. These animals are pseudocoelomates; they have a complete digestive system with a distinct mouth and anus. This is in contrast with the cnidarians where only one opening is present (an incomplete digestive system).

The cuticle of Nematodes is rich in collagen and a carbohydrate-protein polymer called chitin. It forms an external “skeleton” outside the epidermis. The cuticle also lines many of the organs internally, including the pharynx and rectum. The epidermis can be either a single layer of cells or a syncytium, which is a multinucleated cell formed from the fusion of uninucleated cells.

The overall morphology of these worms is cylindrical, while the head is radially symmetrical. A mouth opening is present at the anterior end with three or six lips. Teeth occur in some species in the form of cuticle extensions. Some nematodes may present other external modifications such as rings, head shields, or warts. Rings, however, do not reflect true internal body segmentation. The mouth leads to a muscular pharynx and intestine, which leads to a rectum and anal opening at the posterior end. In addition, the muscles of nematodes differ from those of most animals; they have a longitudinal layer only, which accounts for the whip-like motion of their movement.



Figure $28.4B.1$: Nematode shape: Scanning electron micrograph of soybean cyst nematode and its egg. Nematodes are cylindrical in shape, often looking like thin hairs. They possess an exoskeleton that prevents them from drying out. It must be shed (a process called ecdysis) in order for them to grow.

Excretory System

In nematodes, specialized excretory systems are not well developed. Nitrogenous wastes may be lost by diffusion through the entire body or into the pseudocoelom (body cavity), where they are removed by specialized cells. Regulation of water and salt content of the body is achieved by renette glands, present under the pharynx in marine nematodes.

Nervous system

Most nematodes possess 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 or lateral cords. All nerve cords fuse at the anterior end, around the pharynx, to form head ganglia, or the “brain” of the worm (taking the form of a ring around the pharynx), as well as at the posterior end to form the tail ganglia. 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 that range from monoecious to dioecious to parthenogenic, depending upon the species under consideration. *C. elegans* is a monoecious species, having development of ova contained in a uterus as well as sperm contained in the spermatheca. The uterus has an external opening known as the vulva. The female genital pore is near the middle of the body, whereas the male’s is at the tip. Specialized structures at the tail of the male keep him in place while he deposits sperm with copulatory spicules. Fertilization is internal with embryonic development beginning 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 ecdysis between each stage (L1, L2, L3, and L4) ultimately leading to the development of a young male or female adult worm. Adverse environmental conditions such as overcrowding and lack of food can result in the formation of an intermediate larval stage known as the dauer larva.

Key Points

- Nematodes are in the same phylogenetic grouping as the arthropods because of the presence of an external cuticle that protects the animal and keeps it from drying out.
- There are an estimated 28,000 species of nematodes, with approximately 16,000 of them being parasitic.
- Nematodes are tubular in shape and are considered pseudocoelomates because of they do not possess a true coelom.

- Nematodes do not have a well-developed excretory system, but do have a complete digestive system.
- Nematodes possess the ability to shed their exoskeleton in order to grow, a process called ecdysis.

Key Terms

- **exoskeleton**: a hard outer structure that provides both structure and protection to creatures such as insects, Crustacea, and Nematoda

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28.4C: Phylum Arthropoda

Learning Objectives

- Describe the morphology of arthropoda

Phylum Arthropoda

The name “arthropoda” means “jointed legs” (in the Greek, “arthros” means “joint” and “podos” means “leg”); it aptly describes the enormous number of invertebrates included in this phylum. Arthropods dominate the animal kingdom with an estimated 85 percent of known species included in this phylum; many arthropods are as yet undocumented. The principal characteristics of all the animals in this phylum are functional segmentation of the body and presence of jointed appendages. Arthropods also show the presence of an exoskeleton made principally of chitin, which is a waterproof, tough polysaccharide. Phylum Arthropoda is the largest phylum in the animal world; insects form the single largest class within this phylum. Arthropods are eucoelomate, protostomic organisms.

Phylum Arthropoda includes animals that have been successful in colonizing terrestrial, aquatic, and aerial habitats. This phylum is further classified into five subphyla: Trilobitomorpha (trilobites, all extinct), Hexapoda (insects and relatives), Myriapoda (millipedes, centipedes, and relatives), Crustaceans (crabs, lobsters, crayfish, isopods, barnacles, and some zooplankton), and Chelicerata (horseshoe crabs, arachnids, scorpions, and daddy longlegs). Trilobites are an extinct group of arthropods found chiefly in the pre-Cambrian Era that are probably most closely related to the Chelicerata. These are identified based on fossil records.



Figure $28.4C.1$: Trilobite fossil: *Acadoparadoxides*, possibly *A. briareus*, a large trilobite from about 500 million years ago from Morocco, North Africa (Middle Cambrian)

Morphology

A unique feature of animals in the arthropod phylum is the presence of a segmented body and fusion of sets of segments that give rise to functional body regions called tagma. Tagma may be in the form of a head, thorax, and abdomen, or a cephalothorax and abdomen, or a head and trunk. A central cavity, called the hemocoel (or blood cavity), is present; the open circulatory system is regulated by a tubular, or single-chambered, heart. Respiratory systems vary depending on the group of arthropod. Insects and myriapods use a series of tubes (tracheae) that branch through the body, open to the outside through openings called spiracles, and perform gas exchange directly between the cells and air in the tracheae. Other organisms use variants of gills and lungs.

Aquatic crustaceans utilize gills, terrestrial chelicerates employ book lungs, and aquatic chelicerates use book gills. 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.



Figure $28.4C.1$: Book gills: The ventral side of a horseshoe crab showing the book gills located near the telson (tail). These gills flap back and forth bringing oxygen to the blood.

Groups of arthropods also differ in the organs used for excretion. Crustaceans possess green glands while insects use Malpighian tubules, which work in conjunction with the hindgut to reabsorb water while ridding the body of nitrogenous waste. The cuticle is the 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 chitinous procuticle, which is beneath the epicuticle. Chitin is a tough, flexible polysaccharide. In order to grow, the arthropod must shed the exoskeleton during a process called ecdysis (“to strip off”); this is a cumbersome method of growth. During this time, the animal is vulnerable to predation.

Key Points

- Arthropods include the Hexapoda (insects), the Crustacea (lobsters, crabs, and shrimp), the Chelicerata (the spiders and scorpions), and the Myriapoda (the centipedes and millipedes).
- Arthropods have a segmented body plan that contains fused segments divided into regions called tagma.
- Arthropods have an open circulatory system and can use book gills, book lungs, or tracheal tubes for respiration.

Key Terms

- **tagma**: a specialized grouping of arthropodan segments, such as the head, the thorax, and the abdomen with a common function
- **malpighian tubule**: a tubule that extends from the alimentary canal to the exterior of the organism, excreting water and wastes in the form of solid nitrogenous compounds
- **spiracle**: a pore or opening used (especially by spiders and some fish) for breathing

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28.4D: Subphyla of Arthropoda

Learning Objectives

- Differentiate among the subphylums hexapoda, myriapoda, crustacea, and chelicerata

Representatives of Phylum Arthropoda

Subphylum Hexapoda

The name Hexapoda denotes the presence of six legs (three pairs) in these animals, which differentiates them from the number of pairs present in other arthropods. Hexapods are characterized by the presence of a head, thorax, and abdomen, constituting three tagma. The thorax bears the wings as well as six legs in three pairs. Many of the common insects we encounter on a daily basis, including ants, cockroaches, butterflies, and flies, are examples of Hexapoda.

Among the hexapods, the insects are the largest class in terms of species diversity as well as biomass in terrestrial habitats). Typically, the head bears one pair of sensory antennae, mandibles as mouthparts, a pair of compound eyes, and some ocelli (simple eyes), along with numerous sensory hairs. The thorax bears three pairs of legs (one pair per segment) and two pairs of wings, with one pair each on the second and third thoracic segments. The abdomen usually has eleven segments and bears reproductive apertures. Hexapoda includes insects that are winged (like fruit flies) and wingless (like fleas).



Figure $28.4D.1$: Insect showing wings and body segments: *Protaetia fieberi* in flight posture. Hexapods are characterized by having three distinct tagma, or body segments. This beetle is just one of over one million different species of insects that inhabit the Earth.

Subphylum Myriapoda

Subphylum Myriapoda includes arthropods with numerous legs. Although the name is hyperbolic in suggesting that myriad legs are present in these invertebrates, the number of legs may vary from 10 to 750. This subphylum includes 13,000 species; the most commonly-found examples are millipedes and centipedes. All myriapods are terrestrial animals, prefering a humid environment.

Myriapods are typically found in moist soils, decaying biological material, and leaf litter. Centipedes, such as *Scutigera coleoptrata*,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 venom

to prey such as spiders and cockroaches, as centipedes are predatory. Millipedes bear two pairs of legs per diplosegment, a feature that results from embryonic fusion of adjacent pairs of body segments, are usually rounder in cross-section, and are herbivores or detritivores. Millipedes have visibly more numbers of legs as compared to centipedes, although they do not bear a thousand legs.



Figure $28.4D.1$: House centipede: The house centipede (*Scutigera coleoptrata*) is one of the 13,000 species of Myriapoda. They bear one pair of legs per segment and can inject venom. The Myriapods contain the millipedes and centipedes.

Subphylum Crustacea

Crustaceans are the most dominant aquatic arthropods since the total number of marine crustacean species stands at 67,000. However, there are also freshwater and terrestrial crustacean species. Krill, shrimp, lobsters, crabs, and crayfish are all examples of crustaceans. Terrestrial species like the wood lice (*Armadillidium* spp.) (also called pill bugs, rolly pollies, potato bugs, or isopods) are also crustaceans, although the number of non-aquatic species in this subphylum is relatively low.



Figure $28.4D.1$: Mediterranean green Crab: This crab (*Carcinus aestuarii*) is one of the 67,000 species of crustaceans inhabiting the world's oceans. Most crustaceans are decapods, having ten legs.

Crustaceans possess two pairs of antennae, mandibles as mouthparts, and biramous ("two branched") appendages: their legs are formed in two parts, as distinct from the uniramous ("one branched") myriapods and hexapods.

Unlike that of the Hexapoda, the head and thorax of most crustaceans is fused to form a cephalothorax, which is covered by a plate called the carapace, thus producing a body structure of two tagma. Crustaceans have a chitinous exoskeleton that is shed by molting whenever the animal increases in size. The exoskeletons of many species are also infused with calcium carbonate, which makes them even stronger than in other arthropods. Crustaceans have an open circulatory system where blood is pumped into the hemocoel by the dorsally-located heart. Hemocyanin and hemoglobin are the respiratory pigments present in these animals.

Subphylum Chelicerata

This subphylum includes animals such as spiders, scorpions, horseshoe crabs, and sea spiders and is predominantly terrestrial, although some marine species also exist. An estimated 77,000 species, found in almost all habitats, are included in subphylum Chelicerata.

The body of chelicerates may be divided into two parts: prosoma and opisthosoma, which are basically the equivalents of cephalothorax (usually smaller) and abdomen (usually larger). A “head” tagmum is not usually discernible. The phylum derives its name from the first pair of appendages, the chelicerae, which are specialized claw-like or fang-like mouthparts. These animals do not possess antennae. The second pair of appendages is known as pedipalps. In some species, such as sea spiders, an additional pair of appendages, called ovigers, is present between the chelicerae and pedipalps.

Chelicerae are used primarily for feeding, but in spiders, these are often modified into fangs that inject venom into their prey before feeding. Members of this subphylum have an open circulatory system with a heart that pumps blood into the hemocoel. Aquatic species have gills, whereas terrestrial species have either trachea or book lungs for gaseous exchange.



Figure $28.4D.1$: Chelicera of spiders: This photo shows the chelicera of a spider being held open with a stick. Some chelicerae, such as those found in spiders, are hollow and contain (or are connected to) venom glands which are used to inject venom into prey or a (perceived) threat.

The nervous system in chelicerates consists of a brain and two ventral nerve cords. These animals use external 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.

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Key Points

- The Hexapoda include insects; the Crustacea include lobster, crabs, and shrimp; the Myriapoda include centipedes and millipedes; and the Chelicerata include spiders, scorpions.
- The Hexapoda are the largest grouping of Arthropods, containing the more than one million species of insects, having representatives with six legs and one pair of antennae.
- The Myriapoda are terrestrial, prefering humid environments; they have between 10 and 750 legs.

- The Crustacea are primarily aquatic arthropods, but also include terrestrial forms, which have a cephalothorax covered by a carapace.
- The Chelicerata, which includes the spiders, horseshoe crabs, and scorpions, have mouth parts that are fang-like and used for capturing prey.

Key Terms

- **cephalothorax**: the fused head and thorax of spiders and crustaceans
- **forcipule**: a modified pincer-like foreleg in centipedes, capable of injecting venom

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28.5: SUPERPHYLUM DEUTEROSTOMIA

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28.5A: Phylum Echinodermata

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28.5A: Phylum Echinodermata

Learning Objectives

- Describe the characteristics of echinodermata

Phylum Echinodermata

Echinodermata are so named owing to their spiny skin (from the Greek “echinos” meaning “spiny” and “dermos” meaning “skin”). This phylum is a collection of about 7,000 described living species. Echinodermata are exclusively marine organisms. Sea stars, sea cucumbers, sea urchins, sand dollars, and brittle stars are all examples of echinoderms. To date, no freshwater or terrestrial echinoderms are known.



Figure $28.5A.1$: Sea stars: Star stars are among the most familiar of marine invertebrates. They are members of the phylum Echinodermata.

Morphology and Anatomy

Adult echinoderms exhibit pentaradial symmetry and have a calcareous endoskeleton made of ossicles, although the early larval stages of all echinoderms have bilateral symmetry. The endoskeleton is developed by epidermal cells and may possess pigment cells that give vivid colors to these animals, as well as cells laden with toxins. Echinoderms possess a simple digestive system which varies according to the animal’s diet. Starfish are mostly carnivorous and have a mouth, oesophagus, two-part pyloric stomach with a pyloric duct leading to the intestine and rectum, with the anus located in the center of the aboral body surface. In many species, the large cardiac stomach can be everted and digest food outside the body. Gonads are present in each arm. In echinoderms such as sea stars, every arm bears two rows of tube feet on the oral side which help in attachment to the substratum. These animals possess a true coelom that is modified into a unique circulatory system called a water vascular system. The more notably distinct trait, which most echinoderms have, is their remarkable powers of regeneration of tissue, organs, limbs, and, in some cases, complete regeneration from a single limb.

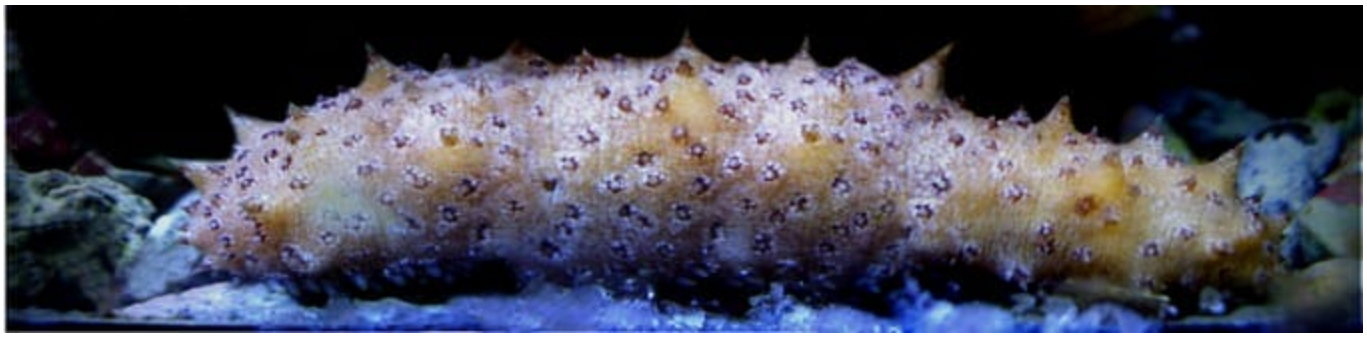


Figure 28.5A.1: Sea cucumbers: Sea cucumbers are a member of the phylum Echinodermata which are found on the sea floor worldwide. As with all echinoderms, sea cucumbers have an endoskeleton just below the skin, calcified structures that are usually reduced to isolated microscopic ossicles joined by connective tissue.

Water Vascular System

Echinoderms possess a unique ambulacral or water vascular system, consisting of a central ring canal and radial canals that extend along each arm. Water circulates through these structures and facilitates gaseous exchange as well as nutrition, predation, and locomotion. The water vascular system also projects from holes in the skeleton in the form of tube feet. These tube feet can expand or contract based on the volume of water (hydrostatic pressure) present in the system of that arm.

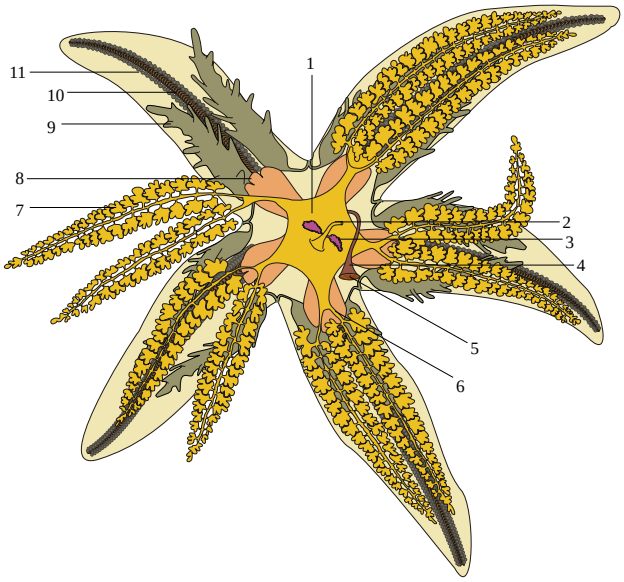


Figure 28.5A.1: The water vascular system of the sea star: 1. Pyloric stomach 2. Intestine 3. Rectal gland 4. Stone canal 5. Madreporite 6. Pyloric duct 7. Pyloric cecum 8. Cardiac stomach 9. Gonad 10. Ambulacral plates 11. Ampullae

The madreporite is a light-colored, calcerous opening used to filter water into the water vascular system of echinoderms. Acting as a pressure-equalizing valve, it is visible as a small red or yellow button-like structure (similar to a small wart) on the aboral surface of the central disk of a sea star. Close up, it is visibly structured, resembling a “madrepore” colony. From this, it derives its name. Water enters the madreporite on the aboral side of the echinoderm. From there, it passes into the stone canal, which moves water into the ring canal. The ring canal connects the radial canals (there are five in a pentaradial animal), and the radial canals move water into the ampullae, which have tube feet through which the water moves. By moving water through the unique water vascular system, the echinoderm can move and force open mollusk shells during feeding.

Other Body Systems

The nervous system in these animals is a relatively simple structure with a nerve ring at the center and five radial nerves extending outward along the arms. Structures analogous to a brain or derived from fusion of ganglia are not present in these animals.

Podocytes, cells specialized for ultrafiltration of bodily fluids, are present near the center of echinoderms. These podocytes are connected by an internal system of canals to the madreporite.

Echinoderms are sexually dimorphic and release their eggs and sperm cells into water; fertilization is external. In some species, the larvae divide asexually and multiply before they reach sexual maturity. Echinoderms may also reproduce asexually, as well as regenerate body parts lost in trauma.

Key Points

- Echinoderms live exclusively in marine systems; they are widely divergent, with over 7,000 known species in the phylum.
- Echinoderms have pentaradial symmetry and a calcareous endoskeleton that may possess pigment cells that give them a wide range of colors, as well as cells that possess toxins.
- Echinoderms have a water vascular system composed of a central ring of canals that extend along each arm, through which water circulates for gaseous exchange and nutrition.
- Echinoderms have a very simple nervous system, comprised of a nerve ring at the center and five radial nerves extending outward along the arms; there is no structure resembling a brain.
- There are two sexes in echinoderms, which each release their eggs and sperm into the water; here, the sperm will fertilize the eggs.
- Echinoderms can reproduce asexually by regeneration.

Key Terms

- **madreporite**: a lightcolored calcerous opening used to filter water into the water vascular system of echinoderms
- **podocyte**: cells that filter the bodily fluids in echinoderms
- **pentaradial symmetry**: a variant of radial symmetry that arranges roughly equal parts around a central axis at orientations of 72° apart
- **water vascular system**: a hydraulic system used by echinoderms, such as sea stars and sea urchins, for locomotion, food and waste transportation, and respiration
- **ampulla**: the dilated end of a duct

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28.5B: Classes of Echinoderms

Learning Objectives

- Differentiate among the classes of echinoderms

The phylum echinoderms 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).

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 (ambulacra; singular: ambulacrum) that extend from a central disk where organs penetrate into the arms. Sea stars use their tube feet not only for gripping surfaces, but also for grasping prey. Sea stars have two stomachs, one of which can protrude through their mouths and secrete digestive juices into or onto prey, even before ingestion. This process can essentially liquefy the prey, making digestion easier.

Brittle stars belong to the class Ophiuroidea. Unlike sea stars, which have plump arms, brittle stars have long, thin 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. Of all echinoderms, the Ophiuroidea may have the strongest tendency toward 5-segment radial (pentaradial) symmetry. Ophiuroids are generally scavengers or detritivores. Small organic particles are moved into the mouth by the tube feet. Ophiuroids may also prey on small crustaceans or worms. Some brittle stars, such as the six-armed members of the family Ophiactidae, are fissiparous (divide though fission), with the disk splitting in half. Regrowth of both the lost part of the disk and the arms occur, yielding an animal with three large arms and three small arms during the period of growth.

Sea urchins and sand dollars are examples of Echinoidea. These echinoderms do not have arms, but are hemispherical or flattened with five rows of tube feet that help them in slow movement; tube feet are extruded through pores of a continuous internal shell called a test. Like other echinoderms, sea urchins are bilaterans. Their early larvae have bilateral symmetry, but they develop fivefold symmetry as they mature. This is most apparent in the “regular” sea urchins, which have roughly spherical bodies, with five equally-sized parts radiating out from their central axes. Several sea urchins, however, including the sand dollars, are oval in shape, with distinct front and rear ends, giving them a degree of bilateral symmetry. In these urchins, the upper surface of the body is slightly domed, but the underside is flat, while the sides are devoid of tube feet. This “irregular” body form has evolved to allow the animals to burrow through sand or other soft materials.

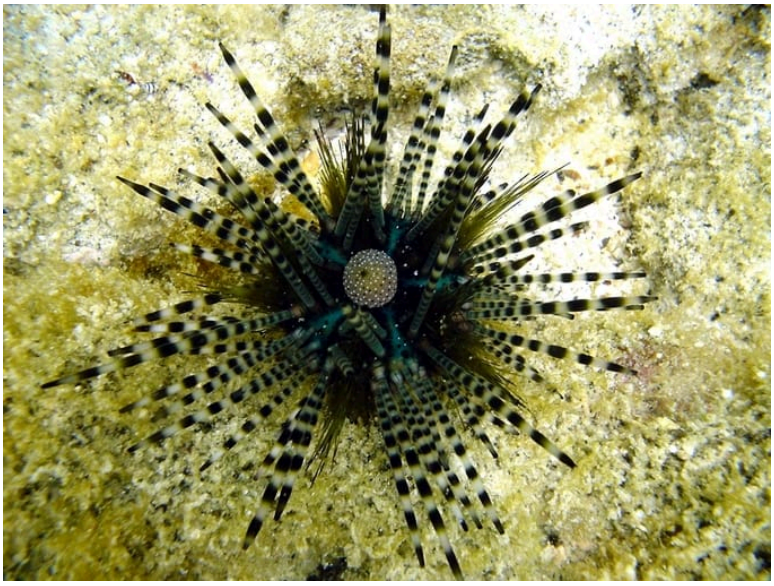


Figure $28.5B.1$: Sea urchins: Sea urchins do not have arms, but have rows of tube feet that can be extended out of pores of the internal shell.

Sea lilies and feather stars are examples of Crinoidea. Both of these species are suspension feeders. They live both in shallow

water and in depths as great as 6,000 meters. Sea lilies refer to the crinoids which, in their adult form, are attached to the sea bottom by a stalk. Feather stars or comatulids refer to the unstalked forms. Crinoids are characterized by a mouth on the top surface that is surrounded by feeding arms. They have a U-shaped gut; their anus is located next to the mouth. Although the basic echinoderm pattern of fivefold symmetry can be recognized, most crinoids have many more than five arms. Crinoids usually have a stem used to attach themselves to a substrate, but many live attached only as juveniles and become free-swimming as adults.



Figure $28.5B.1$: Sea lilies: Sea lilies, like feather stars, have a mouth on their upper surface that is surrounded by arms used for feeding.

Sea cucumbers of class Holothuroidea are extended in the oral-aboral axis and have five rows of tube feet. These are the only echinoderms that demonstrate "functional" bilateral symmetry as adults because the uniquely-extended oral-aboral axis compels the animal to lie horizontally rather than stand vertically. Like all echinoderms, sea cucumbers have an endoskeleton just below the skin: calcified structures that are usually reduced to isolated microscopic ossicles joined by connective tissue. In some species these can sometimes be enlarged to flattened plates, forming armor. In pelagic species, such as Pelagothuria natatrix, the skeleton and a calcareous ring are absent.



Figure $28.5B.1$: Sea cucumbers: Sea cucumbers are the only echinoderms that demonstrate "functional" bilateral symmetry as adults, as they lie horizontally as opposed to the vertical axis of other echinoderms.

Key Points

- Sea stars have thick arms called ambulacra that are used for gripping surfaces and grabbing hold of prey.
- Brittle stars have thin arms that wrap around prey or objects to pull themselves forward.
- Sea urchins and sand dollars embody flattened discs that do not have arms, but do have rows of tube feet they use for movement.
- Sea cucumbers demonstrate “functional” bilateral symmetry as adults because they actually lie horizontally rather than stand vertically.
- Sea lilies and feather stars are suspension feeders.

Key Terms

- **ossicle**: a small bone (or bony structure), especially one of the three of the middle ear
- **fissiparous**: of cells that reproduce through fission, splitting into two
- **ambulacrum**: a row of pores for the protrusion of appendages such as tube feet.

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28.5C: Phylum Chordata

Learning Objectives

- Name the features that distinguish the members of the phylum chordata

Phylum Chordata

Animals in the phylum Chordata share four key features that appear at some stage of their development:

- A notochord, or a longitudinal, flexible rod between the digestive tube and the nerve cord. In most vertebrates, it is replaced developmentally by the vertebral column. This is the structure for which the phylum is named.
- A dorsal nerve cord which develops from a plate of ectoderm that rolls into a tube located dorsal to the notochord. Other animal phyla have solid nerve cords ventrally located. A chordate nerve cord splits into the central nervous system: the brain and spinal cord.
- Pharyngeal slits, which allow water that enters through the mouth to exit without continuing through the entire digestive tract. In many of the invertebrate chordates, these function as suspension feeding devices; in vertebrates, they have been modified for gas exchange, jaw support, hearing, and other functions.
- A muscular, postanal tail which extends posterior to the anus. The digestive tract of most nonchordates extends the length of the body. In chordates, the tail has skeletal elements and musculature, and can provide most of the propulsion in aquatic species.

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) and Cephalochordata (lancelets). However, even though they are invertebrates, they share characteristics with other chordates that places them in this phylum. For example, tunicate larvae have both a notochord and a nerve cord which are lost in adulthood. Most tunicates live on the ocean floor and are suspension feeders. Cephalochordates, or lancelets, have a notochord and a nerve cord (but no brain or specialist sensory organs) and a very simple circulatory system. Lancelets are suspension feeders that feed on phytoplankton and other microorganisms.

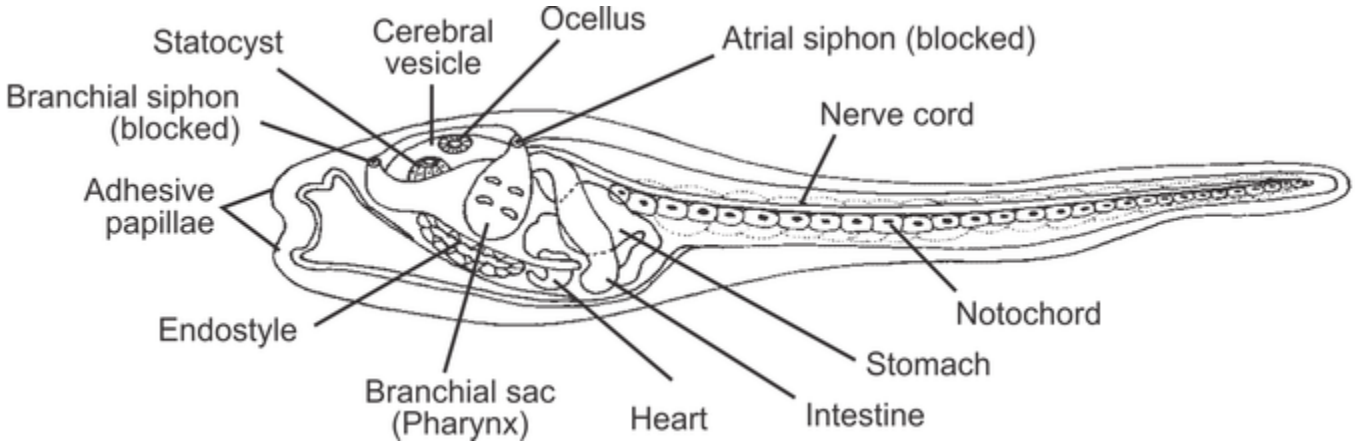


Figure $28.5C.1$: Structures present in a tunicate larva: While tunicates are invertebrates and may seem very different from the more familiar members of Chordata, the tunicate larva possesses both a notochord and a dorsal nerve cord, although both are lost in adulthood.

The phylum Chordata contains all of the animals that have a rod-like structure used to give them support. In most cases this is the spine or backbone. Within Chordata there are five classes of animals: fish, amphibians, reptiles, birds, and mammals. Three dividing factors separate these classes:

- Regulation of body temperature: animals are either homeothermic (can regulate their internal temperature so that it is kept at an optimum level) or poikilothermic (cannot regulate their internal temperature, the environment affects how hot or cold they are)

- Oxygen Absorption: the way in which oxygen is taken in from the air, which can be through gills, the skin (amphibians), or lungs
- Reproduction: this factor is particularly varied. Animals can be oviparous (lay eggs) or viviparous (birth live young). Fertilization can occur externally or internally. In mammals, the mother produces milk for the young.

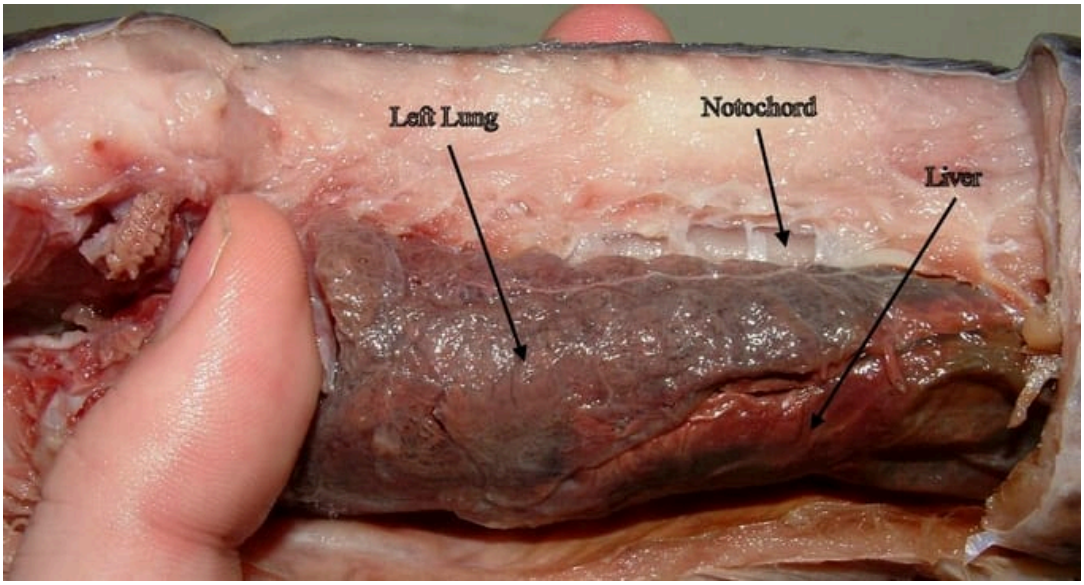


Figure $28.5C.1$: Notochord: All chordates possess a notochord, or a type of flexible support rod, at some point in their development. In this dissected lungfish, which is a member of the chordates, tissues have been dissected away to display the notochord.

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Key Points

- The phylum chordata is named for the notochord, a longitudinal, flexible rod between the digestive tube and the nerve cord; in vertebrates, this is the spinal column.
- The chordates are also characterized by a dorsal nerve cord, which splits into the brain and spinal cord.
- Chordata contains two clades of invertebrates: Urochordata (tunicates) and Cephalochordata (lancelets), both of which are

suspension feeders.
- The phylum chordata includes all animals that share four characteristics, although they might each possess some of them at different stages of their development: a notochord, a dorsal nerve cord, pharyngeal slits, and a postanal tail.
- Chordata contains five classes of animals: fish, amphibians, reptiles, birds, and mammals; these classes are separated by whether or not they can regulate their body temperature, the manner by which they consume oxygen, and their method of reproduction.

Key Terms

- **dorsal nerve cord**: a hollow cord dorsal to the notochord, formed from a part of the ectoderm that rolls, forming a hollow tube.
- **notochord**: a flexible rodlike structure that forms the main support of the body in the lowest chordates; a primitive spine
- **pharyngeal slit**: filter-feeding organs found in non-vertebrate chordates (lancelets and tunicates) and hemichordates living in aquatic environments

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29: VERTEBRATES

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29.1: CHORDATES

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29.1A: Characteristics of Chordata

Learning Objectives

- Identify the key features of the chordates

Characteristics of Chordata

Animals in the phylum Chordata share four key features that appear at some stage during their development (often, only during embryogenesis) (:

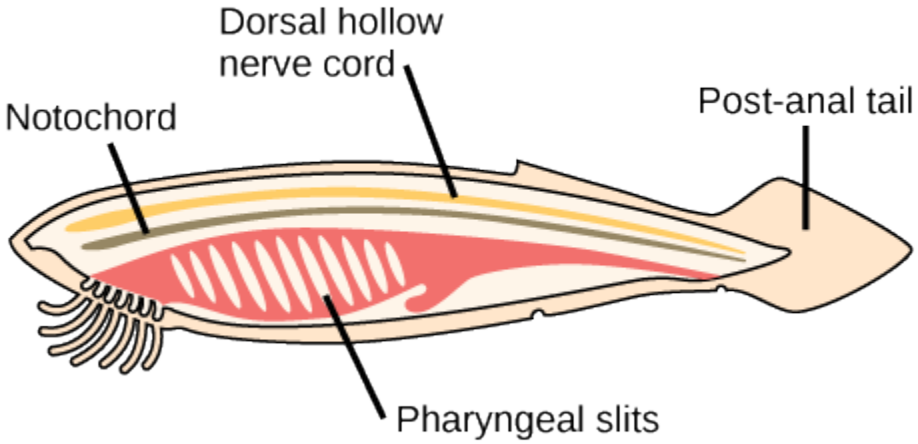


Figure 29.1A.1: Defining characteristics of chordates: In chordates, four common features appear at some point during development: a notochord, a dorsal hollow nerve cord, pharyngeal slits, and a post-anal tail.

1. a notochord
2. a dorsal hollow nerve cord
3. pharyngeal slits
4. post-anal tail

Notochord

The chordates are named for the notochord: a flexible, rod-shaped structure that is found in the embryonic stage of all chordates and also in the adult stage of some chordate species. It is located between the digestive tube and the nerve cord, providing skeletal support through the length of the body. In some chordates, the notochord acts as the primary axial support of the body throughout the animal's lifetime.

In vertebrates, the notochord is present during embryonic development, at which time it induces the development of the neural tube which serves as a support for the developing embryonic body. The notochord, however, is replaced by the vertebral column (spine) in most adult vertebrates.

Dorsal Hollow Nerve Cord

The dorsal hollow nerve cord derives from ectoderm that rolls into a hollow tube during development. In chordates, it is located dorsally (at the top of the animal) to the notochord. In contrast to the chordates, other animal phyla are characterized by solid nerve cords that are located either ventrally or laterally. The nerve cord found in most chordate embryos develops into the brain and spinal cord, which comprise the central nervous system.

Pharyngeal Slits

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. In vertebrate fishes, the pharyngeal slits develop into gill arches, the bony or cartilaginous gill supports.

In most terrestrial animals, including mammals and birds, pharyngeal slits are present only during embryonic development. In these animals, the pharyngeal slits develop into the jaw and inner ear bones.

Post-anal Tail

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. In some terrestrial vertebrates, the tail also helps with balance, courting, and signaling when danger is near. In humans and other apes, the post-anal tail is present during embryonic development, but is vestigial as an adult.

Key Points

- These characteristics are only present during embryonic development in some chordates.
- The notochord provides skeletal support, gives the phylum its name, and develops into the vertebral column in vertebrates.
- The dorsal hollow nerve cord develops into the central nervous system: the brain and spine.
- Pharyngeal slits are openings in the pharynx that develop into gill arches in bony fish and into the jaw and inner ear in terrestrial animals.
- The post-anal tail is a skeletal extension of the posterior end of the body, being absent in humans and apes, although present during embryonic development.

Key Terms

- **notochord**: a flexible rodlike structure that forms the main support of the body in the lowest chordates; a primitive spine
- **nerve cord**: a dorsal tubular cord of nervous tissue above the notochord of a chordate
- **pharyngeal slit**: filter-feeding organs found in non-vertebrate chordates (lancelets and tunicates) and hemichordates living in aquatic environments

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29.1B: Chordates and the Evolution of Vertebrates

Learning Objectives

- Describe the features and phylogenetic history of lancelets and urochordata

Chordates and the Evolution of Vertebrates

The most familiar group of chordates is the vertebrates. However, in addition to the subphylum Vertebrata, the phylum Chordata also contains two subphylums of invertebrates: Urochordata and Cephalochordata. Members of these groups also possess the four distinctive features of chordates at some point during their development: a notochord, a dorsal hollow nerve cord, pharyngeal slits, and a post-anal tail. Unlike vertebrates, urochordates and cephalochordates never develop a bony backbone.

Urochordata

Members of Urochordata are also known as tunicates. 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, only the larval form possesses all four common structures. Adults only maintain pharyngeal slits and lack a notochord, a dorsal hollow nerve cord, and a post-anal tail.

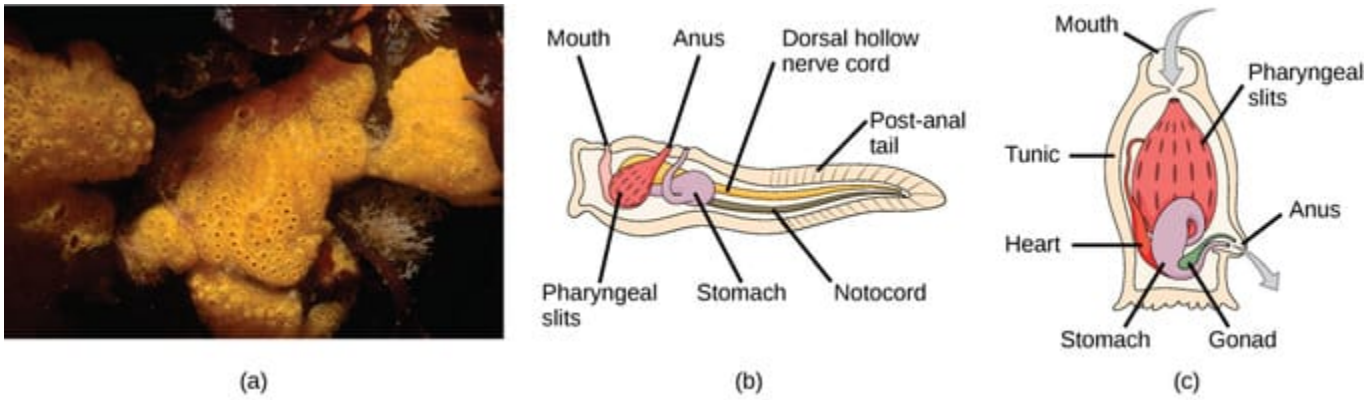


Figure $29.1B.1$: Urochordates: (a) This photograph shows a colony of the tunicate Botrylloides violaceus. (b) The larval stage of the tunicate possesses all of the features characteristic of chordates: a notochord, a dorsal hollow nerve cord, pharyngeal slits, and a post-anal tail. (c) In the adult stage, the notochord, nerve cord, and tail disappear.

Most tunicates are hermaphrodites. Tunicate larvae hatch from eggs inside the adult tunicate's body. After hatching, a tunicate larva 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.

Most tunicates live a sessile existence on the ocean floor and are suspension feeders. 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 (pharyngeal slits) 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.

Cephalochordata

Members of Cephalochordata possess a notochord, dorsal hollow nerve cord, pharyngeal slits, and a post-anal tail in the adult stage. They do not have a true brain, but the notochord extends into the head, which gives the subphylum its name ("cephalo" is Greek for head). Extinct members of this subphylum include *Pikaia*, which is the oldest known cephalochordate. *Pikaia* fossils

were recovered from the Burgess shales of Canada and dated to the middle of the Cambrian age, making them more than 500 million years old.

Extant members of Cephalochordata are the lancelets, named for their blade-like shape. Lancelets are only a few centimeters long and are usually found buried in sand at the bottom of warm temperate and tropical seas. Like tunicates, they are suspension feeders. With notochord and paired muscle blocks, the lancelet and *Pikaia* may belong to the chordate group of animals from which the vertebrates have descended.

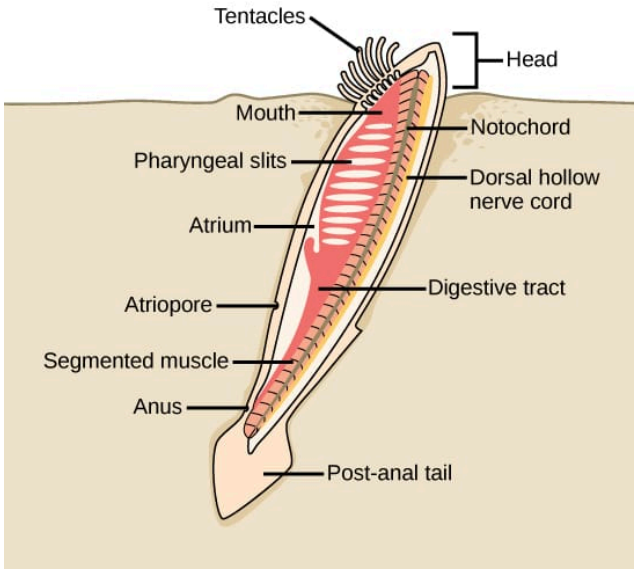


Figure 29.1B.1: Cephalochrodates: The lancelet, like all cephalochordates, has a head. Adult lancelets retain the four key features of chordates: a notochord, a dorsal hollow nerve cord, pharyngeal slits, and a post-anal tail. Water from the mouth enters the pharyngeal slits, which filter out food particles. The filtered water then collects in the atrium and exits through the atriopore.

Key Points

- Urochordata (tunicates) and Cephalochordata (lancelets) are invertebrates because they lack a backone.
- Larval tunicates (Urochordata) posses all four structures that classify chordates, but adult tunicates retain only pharyngeal slits.
- Larval tunicates swim for a few days after hatching, then attach to a marine surface and undergo metamorphosis into the sessile adult form.
- Lancelets (Cephalochordata) are marine organisms that possess all features of chordates; they are named Cephalochordata because the notochord extends into the head.
- Lancelets may be the closest-living relatives to vertebrates.

Key Terms

- **Urochordata**: a taxonomic subphylum within the phylum Chordata: the tunicates or sea squirts
- **Cephalochordata**: a taxonomic subphylum within the phylum Chordata: the lancelets
- **sessile**: permanently attached to a substrate; not free to move about; “an attached oyster”

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29.1C: The Evolution of Craniata and Vertebrata

Learning Objectives

- Explain how genomics informs scientists about chordate evolution

Craniata and Vertebrata

The clade Craniata is a subdivision of Chordata. Members of Craniata posses a cranium, which is a bony, cartilaginous, or fibrous structure surrounding the brain, jaw, and facial bones. The clade Craniata includes all vertebrates and the hagfishes (Myxini), which have a cranium but lack a backbone. Hagfish are the only known living animals that have a skull, but not a vertebral column.



Figure $29.1C.1$: Hagfish: Although it lacks a backbone, the hagfish is a member of the Craniata clade because it possesses a bony skull.

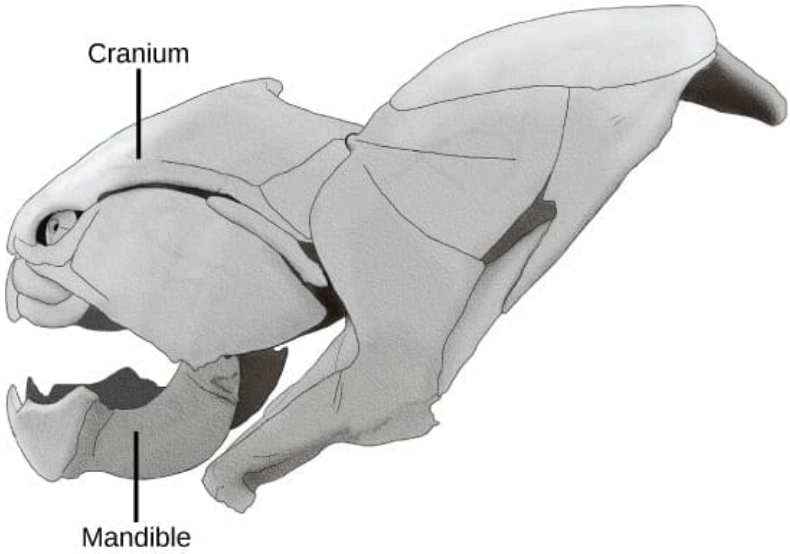


Figure $29.1C.1$: Clade Craniata: Craniata, including this fish (Dunkleosteus), are characterized by the presence of a cranium, mandible, and other facial bones.

Vertebrates are members of the subphylum Vertebrata, the clade Craniata, and the phylum Chordata. Vertebrates display the four characteristic features of chordates, but they are named for the vertebral column composed of a series of bony vertebrae joined together as a backbone. In adult vertebrates, the vertebral column replaces the embryonic notochord.

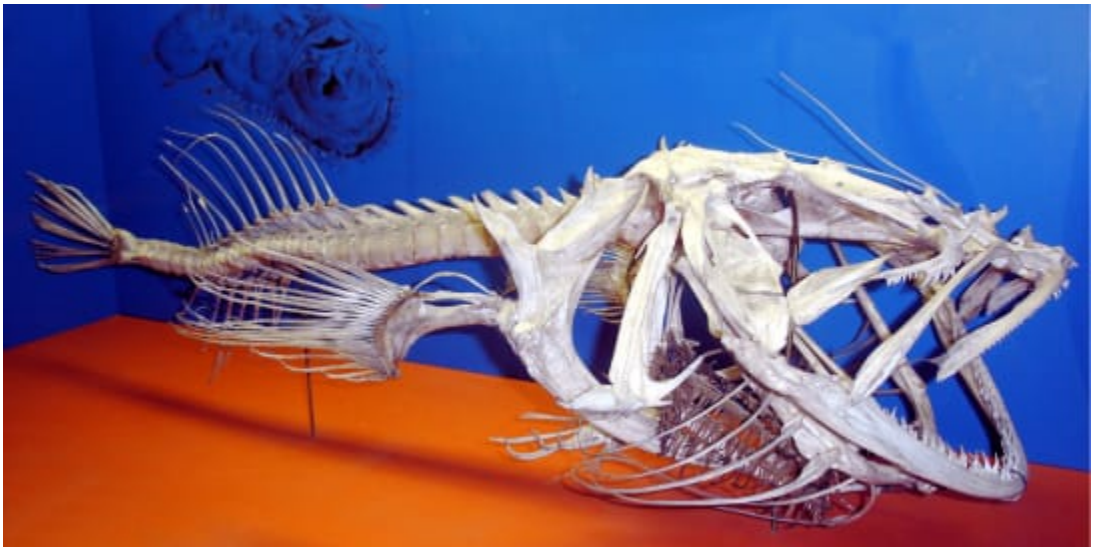


Figure 29.1C.1: Vertebrates: Vertebrata are characterized by the presence of a backbone, such as the one that runs through the middle of this fish. All vertebrates are in the Craniata clade and have a cranium.

Vertebrate Evolution

In the phylum Chordata, the closest relatives of the vertebrates are the invertebrate chordates. Based on the molecular analysis of vertebrate and invertebrate genomes (genomics), scientists can determine the evolutionary history of different phylogenetic groups.

According to these genomic analyses, vertebrates appear to be more closely related to the lancelets (cephalochordates) than to the tunicates (urochordates). This suggests that the cephalochordates first diverged from urochordates, and that vertebrates subsequently diverged from the cephalochordates. This hypothesis is further supported by the fossil of a 530 million-year-old organism with a brain and eyes like a vertebrate, but without the skull found in a craniate. A comparison of the genomes of a lancelet, tunicate, lamprey, fish, chicken, and human confirmed that two whole-genome duplications occurred in the early history of the Vertebrata subphylum.

Both fossil and genomic evidence suggests that vertebrates arose during the Cambrian explosion.The Cambrian explosion was the relatively brief span of time during the Cambrian period during which many animal groups appeared and rapidly diversified. Most modern animal phyla originated during the Cambrian explosion.

Key Points

- The clade Craniata includes animals that have a cranium: a bony, cartilaginous, or fibrous structure that surrounds the brain, jaw, and facial bones.
- Members of Craniata include the vertebrates and hagfish.
- Genomic evidence suggests that vertebrates diverged from cephalochordates (lancelets), which had previously diverged from urochordates (tunicates).
- Fossil evidence suggests that most vertebrate diversity originated in the Cambrian explosion 540 million years ago.
- Two whole- genome duplications occurred in early vertebrate history.

Key Terms

- **cranium**: the part of the skull enclosing the brain, the braincase
- **genomics**: the study of the complete genome of an organism

- **Cambrian explosion**: the relatively rapid appearance (over a period of many millions of years), around 530 million years ago, of most major animal phyla as demonstrated in the fossil record

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29.1D: Characteristics of Vertebrates

Learning Objectives

- Identify the defining characteristics of vertebrates

Characteristics of Vertebrates

Vertebrates are members of the subphylum Vertebrata, under the phylum Chordata and under the kingdom Animalia. 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 phyla: Chordata and Echinodermata. Echinoderms are invertebrate marine animals that have pentaradial symmetry and a spiny body covering; the phylum includes sea stars, sea urchins, and sea cucumbers. The phylum Chordata contains two groups of invertebrate chordates, but the most conspicuous and familiar members of Chordata are the vertebrates.

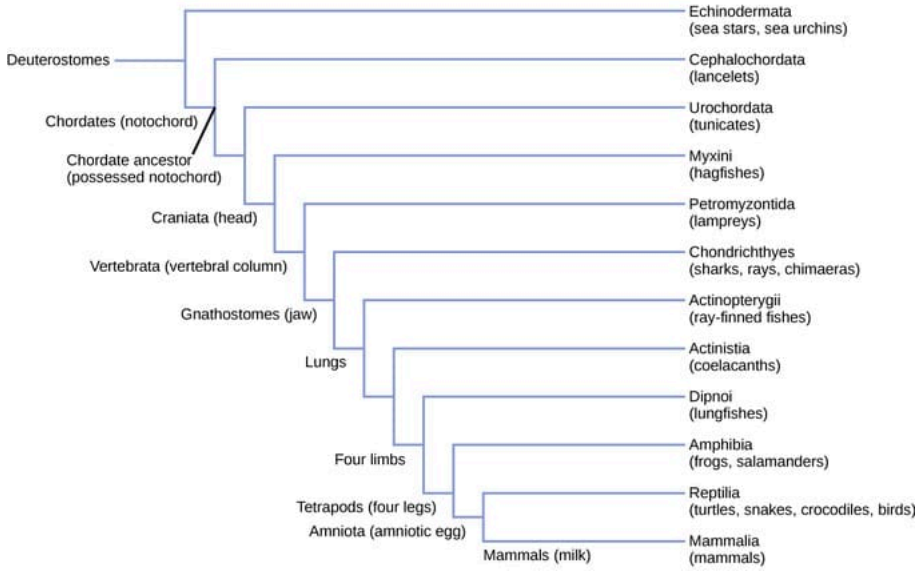


Figure $29.1D.1$: Phylum chordata: All chordates are deuterostomes, possessing a notochord. Vertebrates are differentiated by having a vertebral column.

As chordates, all vertebrates have a similar anatomy and morphology with the same qualifying characteristics: a notochord, a dorsal hollow nerve cord, pharyngeal slits, and a post-anal tail. However, the subphylum Vertebrata is distinguished from the phylum Chordata by the development of the notochord into a bony backbone. Vertebrates include the amphibians, reptiles, mammals, and birds, as well as the jawless fishes, bony fishes, sharks, and rays.

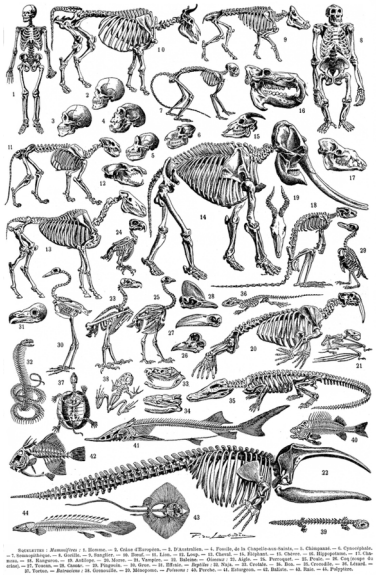


Figure 29.1D.1: Diversity of vertebrates: animals with backbones: The subphylum Vertebrata contains all animals that possess backbones, gills, and a central nervous system in at least one phase of development. Vertebrates include amphibians, reptiles, mammals, and birds, as well as the jawless fishes, bony fishes, sharks, and rays.

More than 64,000 species of vertebrates have been described, but the extant vertebrate species represent only a small portion of all the vertebrates that have existed. Vertebrates range in size from the frog species *Paedophryne amauensis* (as small as 7.7 mm (0.3 inch)) to the blue whale (as large as 33 m (110 ft)). Vertebrates comprise about 4 percent of all described animal species; the remainder are invertebrates, which lack backbones.

Anatomy and Morphology

All vertebrates are built along the basic chordate body plan: a stiff rod running through the length of the animal (vertebral column), with a hollow tube of nervous tissue (the spinal cord) above it and the gastrointestinal tract below. In all vertebrates, there is a mouth at anterior end of the animal and an anus before the posterior end of the body. There is a tail posterior to the anus during at least one phase of the animal's development.

The Vertebral Column

Vertebrates are defined by the presence of the vertebral column. In vertebrates, the notochord develops into the vertebral column or spine: a series of bony vertebrae each separated by mobile discs. These vertebrae are always found on the dorsal side of the animal. However, a few vertebrates have secondarily lost their vertebrae and, instead, retain the notochord into adulthood (e.g., the sturgeon fish).



Figure 29.1D.1: Vertebral column: A fossilized skeleton of the dinosaur Diplodocus carnegii shows an extreme example of the backbone that characterizes vertebrates.

Central Nervous System

Vertebrates are also the only members of Chordata to possess a brain. In chordates, the central nervous system is based on a hollow nerve tube that runs dorsal to the notochord along the length of the animal. In vertebrates, the anterior end of the nerve tube expands and differentiates into three brain vesicles.

Vertebrate Classification

Vertebrates are the largest group of chordates, with more than 62,000 living species. Vertebrates are grouped based on anatomical and physiological traits. The traditional groups include Agnatha, Chondrichthyes, Osteichthyes, Amphibia, Reptilia, Aves, and Mammalia.

Animals that possess jaws are known as gnathostomes, meaning “jawed mouth.” Gnathostomes include fishes and tetrapods (amphibians, reptiles, birds, and mammals). Tetrapods can be further divided into two groups: amphibians and amniotes. Amniotes are animals whose eggs are adapted for terrestrial living; this group includes mammals, reptiles, and birds. Amniotic embryos, developing in either an externally-shelled egg or an egg carried by the female, are provided with a water-retaining environment and are protected by amniotic membranes.

Key Points

- As chordates, vertebrates have the same common features: a notochord, a dorsal hollow nerve cord, pharyngeal slits, and a post-anal tail.
- Vertebrates are further differentiated from chordates by their vertebral column, which forms when their notochord develops into the column of bony vertebrae separated by discs.
- Vertebrates are the only chordates that have a brain as part of their central nervous system.

Key Terms

- **vertebral column**: the series of vertebrae that protect the spinal cord; the spinal column
- **chordate**: a member of the phylum Chordata; numerous animals having a notochord at some stage of their development; in vertebrates this develops into the spine
- **notochord**: a flexible rodlike structure that forms the main support of the body in the lowest chordates; a primitive spine

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29.2: FISHES

29.2A: Agnathans- Jawless Fishes
29.2B: Gnathostomes - Jawed Fishes

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29.2A: Agnathans- Jawless Fishes

Learning Objectives

- Differentiate between the taxa of jawless fishes

Agnathans: Jawless Fishes

Jawless fishes or agnathans are craniates that represent an ancient vertebrate lineage that arose over one half-billion years ago. “Gnathos” is Greek for “jaw” and the prefix “a” means “without,” so agnathans are “without jaws. ” Most agnathans are now extinct, but two branches still exist today: hagfishes and lampreys. Hagfishes and lampreys are recognized as separate clades, primarily because lampreys are true vertebrates, whereas hagfishes are not. A defining feature of agnathans is the lack of paired lateral appendages or fins.

Some of the earliest jawless fishes were the ostracoderms (Greek for “bone-skin”). Ostracoderms were vertebrate fishes encased in bony armor, unlike present-day jawless fishes, which lack bone in their scales.

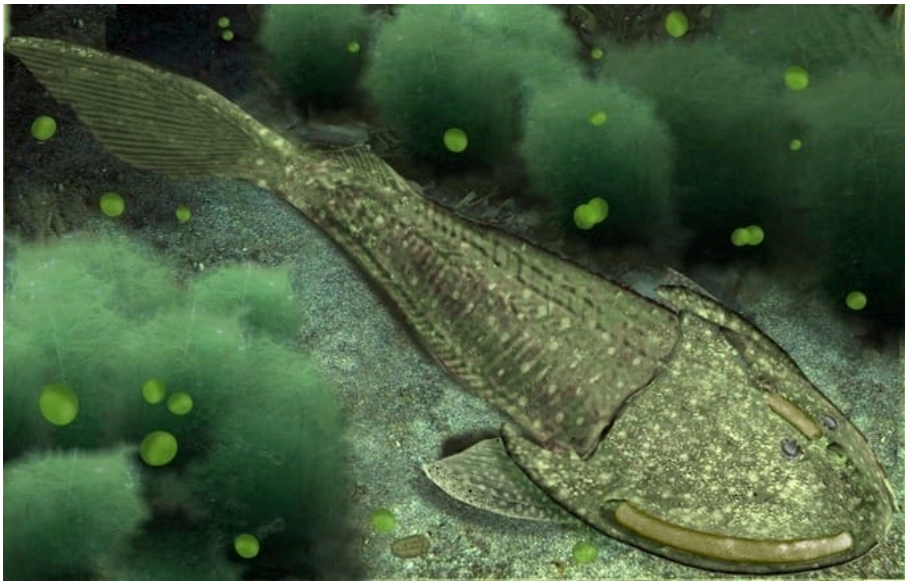


Figure $29.2A.1$: Ostracoderm: Ostracoderms were some of the earliest jawless fishes and were covered in bony armor. Present-day jawless fishes lack bone in their scales.

Myxini: Hagfishes

The clade Myxini includes at least 20 species of hagfishes. Hagfishes are eel-like scavengers that live on the ocean floor and feed on dead invertebrates, other fishes, and marine mammals. Hagfishes are entirely marine and are found in oceans around the world, except for the polar regions. Hagfish have slime glands beneath the skin that constantly release mucus, allowing them to escape from the grip of predators. Hagfish can also twist their bodies into a knot to gain a mechanical advantage while feeding and are notorious for eating carcasses from the inside out.



Figure 29.2A.1: Hagfishes: Pacific hagfish are scavengers that live on the ocean floor. These agnathans are classified as Myxini and do not have a vertebral column.

The skeleton of a hagfish is composed of cartilage, which includes a cartilaginous notochord that runs the length of the body. This notochord provides support to the hagfish's body. Unlike true vertebrates, hagfishes do not replace the notochord with a vertebral column during development. Since they have a cartilaginous skull, they are classified in the clade Craniata.

Petromyzontidae: Lampreys

The clade Petromyzontidae includes approximately 35–40 or more species of lampreys. Lampreys are morphologically similar to hagfishes and also lack paired appendages. However, lampreys develop some vertebral elements as an adult. Their notochord is surrounded by a cartilaginous structure called an arcualia, which may resemble an evolutionarily-early form of the vertebral column.

As adults, lampreys are characterized by a toothed, funnel-like sucking mouth. Many species have a parasitic stage of their life cycle during which they are ectoparasites of fishes. Lampreys live primarily in coastal and fresh waters. They are distributed worldwide, except for the tropics and polar regions. Some species are marine, but all species spawn in fresh water; eggs are fertilized externally. The larvae differ distinctly from the adult form, spending 3 to 15 years as suspension feeders. Once they reach sexual maturity, the adults die within days of reproduction.



Figure 29.2A.1: Parasitic lampreys: These parasitic sea lampreys attach to their lake trout host by suction and use their rough tongues to rasp away flesh in order to feed on the trout's blood.

Key Points

- Most agnathans are now extinct, but two branches exist today: hagfishes (not true vertebrates) and lampreys (true vertebrates).
- The earliest jawless fishes were the ostracoderms, which had bony scales as body armor.
- Hagfish are eel-like marine scavengers in the clade Myxini that produce slime and can tie themselves into knots.
- Lampreys are in the clade Petromyzontidae and appear morphologically similar to hagfish, but contain cartilaginous vertebral elements as an adult; thus, they are considered true vertebrates.

Key Terms

- **hagfish**: any of several primitive eellike creatures, of the family Myxinidae, having a sucking mouth with rasping teeth; considered edible in Japan, their skin is used to make a form of leather
- **lamprey**: any long slender primitive eel-like freshwater and saltwater fish of the Petromyzontidae family, having a sucking mouth with rasping teeth, but no jaw
- **agnathan**: a member of the superclass Agnatha of jawless vertebrates

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29.2B: Gnathostomes - Jawed Fishes

Learning Objectives

- Differentiate among the types of jawed fishes

Gnathostomes or “jaw-mouths” are vertebrates that possess jaws. One of the most significant developments in early vertebrate evolution was the development of the jaw, which is a hinged structure attached to the cranium that allows an animal to grasp and tear its food. The evolution of jaws allowed early gnathostomes to exploit food resources that were unavailable to the jawless animals. In early evolutionary history, there were gnathostomes (jawed fishes) and agnathans (jawless fishes). Gnathostomes later evolved into all tetrapods (animals with four limbs) including amphibians, birds, and mammals.

Early gnathostomes were jawed fishes that possessed two sets of paired fins, which increased their ability to maneuver accurately. These paired fins were pectoral fins, located on the anterior body, and pelvic fins, on the posterior. The evolution of the jaw combined with paired fins permitted gnathostomes to expand from the sedentary suspension feeding of jawless fishes and become mobile predators. The gnathostomes’ ability to exploit new nutrient sources led to their evolutionary success during the Devonian period. Two early groups of gnathostomes were the acanthodians and placoderms, which arose in the late Silurian period and are now extinct. Most modern gnathostomes belong to the clades Chondrichthyes and Osteichthyes.



Figure $29.2B.1$: Placoderms: Dunkleosteous was an enormous placoderm from the Devonian period, 380–360 million years ago. It measured up to 10 meters in length and weighed up to 3.6 tons. As gnathostomes, they were more mobile and could exploit more food resources than the agnathostomes.

Chondrichthyes: Cartilaginous Fishes

The clade Chondrichthyes consists of sharks, rays, and skates, together with sawfishes and a few dozen species of fishes called chimaeras, or “ghost,” sharks. 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.



Figure 29.2B.1: Hammerhead shark: Hammerhead sharks tend to school during the day and hunt prey at night. As members of Chondrichthyes, their skeletons are composed of cartilage.

Most cartilaginous fishes live in marine habitats, although a few species live in fresh water for 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. Shark teeth probably evolved from the jagged scales that cover their skin called placoid scales. Some species of sharks and rays are suspension feeders that feed on plankton.

Sharks have well-developed sense organs that aid them in locating prey, including a keen sense of smell and electroreception. Organs called ampullae of Lorenzini enable sharks to detect the electromagnetic fields that are produced by all living things, including their prey. Only aquatic or amphibious animals possess electroreception. Sharks, together with most fishes and aquatic and larval amphibians, also have a sense organ called the lateral line, which is used to detect movement and vibration in the surrounding water. It is often considered homologous to "hearing" in terrestrial vertebrates. The lateral line is visible as a darker stripe that runs along the length of a fish's body.

Rays and skates comprise more than 500 species and are closely related to sharks. They 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. Like sharks, rays and skates have a cartilaginous skeleton. Most species are marine and live on the sea floor, with nearly a worldwide distribution.

Osteichthyes: Bony Fishes

Members of the clade Osteichthyes, also called bony fish, are characterized by a bony skeleton. The vast majority of present-day fish belong to this group, which consists of approximately 30,000 species, making it the largest class of vertebrates in existence today.

Nearly all bony fish have an ossified skeleton with specialized bone cells (osteocytes) that produce and maintain a calcium phosphate matrix. A few groups of Osteichthyes, such as sturgeons and paddlefish, have primarily cartilaginous skeletons, but retain some bony elements. The skin of bony fish is often covered by overlapping scales. Skin glands secrete mucus that reduces drag when swimming and aids the fish in osmoregulation. Like sharks, bony fish have a lateral line system that detects vibrations in water. All bony fish use gills for gas exchange. Water is drawn over gills that are located in chambers covered and ventilated by a protective, muscular flap called the operculum. Many bony fish also have a swim bladder, a gas-filled organ that helps to control the buoyancy of the fish.

Bony fish are further divided into two extant clades: Actinopterygii (ray-finned fish) and Sarcopterygii (lobe-finned fish). Actinopterygii, the ray-finned fish include many familiar fish, such as tuna, bass, trout, and salmon, among others. Ray-finned fish are named for their fins that are webs of skin supported by bony spines called rays. In contrast, the fins of Sarcopterygii are fleshy and lobed, supported by bone. Although most members of this clade are extinct, living members include the less-familiar lungfishes and coelacanths. Early Sarcopterygii evolved into modern tetrapods, including reptiles, amphibians, birds, and mammals.



Figure 29.2B.1: Actinopterygii and Sarcopterygii: The (a) sockeye salmon (Actinopterygii) and (b) coelacanth (Sarcopterygii) 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.

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Key Points

- Early jawed fish (gnathostomes) were able to exploit new nutrient sources because of their jaws and paired fins.
- Chondrichthyes includes all jawed fish with cartilagenous skeletons, such as sharks, rays, skates, and chimaeras.

- Osteichthyes includes all jawed fish with ossified (bony) skeletons; this includes the majority of modern fish.
- Osteichthyes can be further separated into Actinopterygii (the ray-finned fishes) and Sarcopterygii (lobe-finned fishes).
- The majority of modern fish species are actinopterygii, from trout to clownfish.
- Early Sarcopterygii (lobe-finned fishes) evolved into modern tetrapods, including reptiles, amphibians, birds, and mammals.

Key Terms

- **ossified**: composed of bone, which is a calcium phosphate matrix created by special cells called osteoblasts
- **operculum**: a covering flap or lidlike structure in plants and animals, such as a gill cover
- **Chondrichthyes**: a taxonomic class within the subphylum Vertebrata: the cartilaginous fish
- **Osteichthyes**: a taxonomic class within the subphylum vertebrata: the bony fish

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29.3: AMPHIBIANS

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- Topic hierarchy

29.3A: Characteristics and Evolution of Amphibians

29.3B: Modern Amphibians

29.3C: Evolution of Amniotes

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29.3A: Characteristics and Evolution of Amphibians

Amphibians evolved from fish 400 million years ago and are characterized by four limbs, moist skin, and sensitive inner ear structures.

LEARNING OBJECTIVES

Describe the evolutionary characteristics that distinguish the amphibian

KEY TAKEAWAYS

Key Points

- Most amphibians are characterized by four well-developed limbs, but some species of salamanders and all caecilians are functionally limbless.
- Amphibians have a moist, permeable skin that is achieved via mucus glands that keep the skin lubricated in order to perform cutaneous respiration.
- All extant adult amphibians are carnivorous; some terrestrial amphibians have a sticky tongue that is used to capture prey.
- Additional characteristics of amphibians include pedicellate teeth, papilla amphibiorum, papilla basilaris, and auricular operculum.
- The tetrapod-like fish, *Tiktaalik roseae*, preceded Acanthostega and lived in a shallow water environment about 375 million years ago.
- All extant adult amphibians are carnivorous, and some terrestrial amphibians have a sticky tongue that is used to capture prey.

Key Terms

- **cutaneous respiration**: exchange of oxygen and carbon dioxide with the environment that takes place through the permeable skin
- **pedicellate teeth**: teeth in which the root and crown are calcified, separated by a zone of noncalcified tissue
- **auricular operculum**: an extra bone in the ear that transmits sounds to the inner ear

Characteristics of Amphibians

As tetrapods, most amphibians are characterized by four well-developed limbs. Some species of salamanders and all caecilians are functionally limbless; their limbs are vestigial. An important characteristic of extant amphibians is a moist, permeable skin that is achieved via mucus glands that keep the skin moist; thus, exchange of oxygen and carbon dioxide with the environment can take place through it (cutaneous respiration). Additional characteristics of amphibians include pedicellate teeth (teeth in which the root and crown are calcified, separated by a zone of noncalcified tissue) and a papilla amphibiorum and papilla basilaris (structures of the inner ear that are sensitive to frequencies below and above 10,00 hertz, respectively). Amphibians also have an auricular operculum, which is an extra bone in the ear that transmits sounds to the inner ear. All extant adult amphibians are carnivorous. Some terrestrial amphibians have a sticky tongue that is used to capture prey.

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 fishes 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. One of the earliest known tetrapods is from the genus Acanthostega. Acanthostega was aquatic; fossils show that it had gills similar to fishes. However, it also had four limbs, with the skeletal structure of limbs found in present-day tetrapods, including amphibians. Therefore, it is thought that Acanthostega lived in shallow waters and was an intermediate form between lobe-finned fishes and early, fully terrestrial tetrapods. What preceded Acanthostega?

In 2006, researchers published news of their discovery of a fossil of a “tetrapod-like fish,” *Tiktaalik roseae*, which seems to be an intermediate form between fishes having fins and tetrapods having limbs. *Tiktaalik* probably lived in a shallow water environment about 375 million years ago.

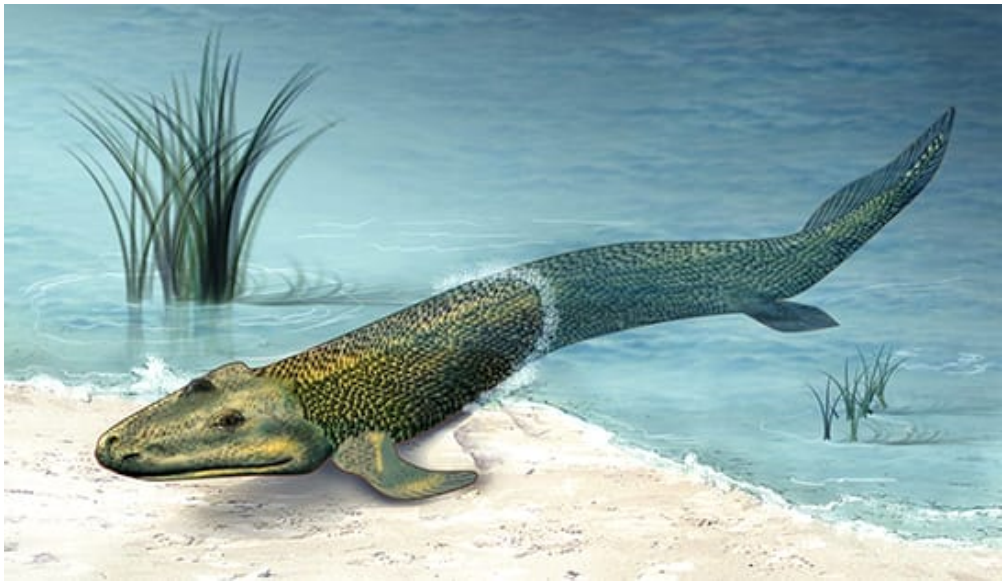


Figure 29.3A.1: Tiktaalik roseae: The recent fossil discovery of Tiktaalik roseae suggests evidence for an animal intermediate to finned fish and legged tetrapods.

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: sometimes called the “Age of the Amphibians.”

Modern

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29.3B: Modern Amphibians

Learning Objectives

- Differentiate among the orders of amphibians

Modern Amphibians

Amphibia comprises an estimated 6,770 extant species that inhabit tropical and temperate regions around the world. Amphibians can be divided into three clades: Urodela (“tailed-ones”), the salamanders; Anura (“tail-less ones”), the frogs; and Apoda (“legless ones”), the caecilians.



Figure $29.3B.1$: Salamanders: Most salamanders have legs and a tail, but respiration varies among species.

Urodela: Salamanders

Salamanders are amphibians that belong to the order Urodela. Living salamanders include approximately 620 species, some of which are aquatic, other terrestrial, and some that live on land only as adults. Adult salamanders usually have a generalized tetrapod body plan with four limbs and a tail. They move by bending their bodies from side to side, called lateral undulation, in a fish-like manner while “walking” their arms and legs back and forth. It is thought that their gait is similar to that used by early tetrapods. Respiration differs among the species. The majority of salamanders are lungless, with respiration occurring through the skin or through external gills. Some terrestrial salamanders have primitive lungs; a few species have both gills and lungs.

Unlike frogs, virtually all salamanders rely on internal fertilization of the eggs. The only male amphibians that possess copulatory structures are the caecilians, so fertilization among salamanders typically involves an elaborate and often prolonged courtship. Such a courtship allows the successful transfer of sperm from male to female via a spermatophore. Development in many of the most highly-evolved salamanders, which are fully terrestrial, occurs during a prolonged egg stage, with the eggs guarded by the mother. During this time, the gilled larval stage is found only within the egg capsule, with the gills being resorbed, and metamorphosis being completed, before hatching. Hatchlings resemble tiny adults.



Figure $29.3B.1$: Frogs: The Australian green tree frog is a nocturnal predator that lives in the canopies of trees near a water source.

Anura: Frogs

Frogs are amphibians that belong to the order Anura. Anurans are among the most diverse groups of vertebrates, with approximately 5,965 species occurring on all of the continents except Antarctica. Anurans have a body plan that is more specialized for movement. Adult frogs use their hind limbs to jump on land. 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.



Figure $29.3B.1$: Frog metamorphosis: A juvenile frog metamorphoses into a frog. Here, the frog has started to develop limbs, but its tadpole tail is still evident.

Frog eggs are fertilized externally. As with other amphibians, frogs generally lay their eggs in moist environments. This is required as eggs lack a shell and will dehydrate quickly in dry environments. Frogs demonstrate a great diversity of parental behaviors: some species lay many eggs and exhibit little parental care; other species carry eggs and tadpoles on their hind legs or backs. The life cycle of frogs, as with other amphibians, consists of two distinct stages: 1) the larval stage followed by 2) metamorphosis to an adult stage. The larval stage of a frog, the tadpole, is often a filter-feeding herbivore. Tadpoles usually have gills, a lateral line system, long-finned tails, and lack limbs. At the end of the tadpole stage, frogs undergo metamorphosis into the adult form. 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, while 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.

Apoda: Caecilians

An estimated 185 species comprise caecilians, a group of amphibians that belong to the order Apoda. Although they are vertebrates, a complete lack of limbs leads to their resemblance to earthworms in appearance. They are adapted for a soil-burrowing or aquatic lifestyle; they are nearly blind. These animals are found in the tropics of South America, Africa, and Southern Asia. They have vestigial limbs which is evidence that they evolved from a legged ancestor.

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Key Points

- Adult salamanders usually have four limbs and a tail, moving by lateral undulation in a fish-like manner while “walking” their arms and legs forward and back.
- The majority of salamanders are lungless; respiration occurs through the skin or through external gills; some terrestrial salamanders have primitive lungs; a few species have both lungs and gills.
- Salamanders utilize internal fertilization after males transfer sperm to the eggs via the spermatophore; there is a prolonged egg phase; metamorphosis occurs before hatching.
- Caecilians are blind, limbless vertebrates that resemble earthworms and are adapted for a soil-burrowing or an aquatic lifestyle.
- Adult frogs use their hind legs to jump; they fertilize externally, laying their shell-less eggs in moist environments.
- Tadpoles (the larval stage of a frog) have gills, a lateral line system, long-finned tails, and lack limbs; when tadpoles become adults, gills, tails, and the lateral line disappear, while an eardrum and lungs develop.

Key Terms

- **lateral undulation**: movement by bending the body from side to side
- **spermatophore**: a capsule or mass created by males, containing sperm and transferred in entirety to the female during fertilization
- **metamorphosis**: a change in the form and often habits of an animal after the embryonic stage during normal development

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29.3C: Evolution of Amniotes

Learning Objectives

- Outline the evolution of amniotes

Evolution of Amniotes

The first amniotes evolved from their amphibian ancestors approximately 340 million years ago during the Carboniferous period. The early amniotes diverged into two main lines soon after the first amniotes arose. The initial split was into synapsids and sauropsids. Synapsids include all mammals, including extinct mammalian species. Synapsids also include therapsids, which were mammal-like reptiles from which mammals evolved. Sauropsids include reptiles and birds and can be further divided into anapsids and diapsids. The key differences between the synapsids, anapsids, and diapsids are the structures of the skull and the number of temporal fenestrae behind each eye. Temporal fenestrae are post-orbital openings in the skull that allow muscles to expand and lengthen. Anapsids have no temporal fenestrae, synapsids have one, and diapsids have two. Anapsids include extinct organisms and may, based on anatomy, include turtles (Testudines), which have an anapsid-like skull with one opening. However, this is still controversial, and turtles are sometimes classified as diapsids based on molecular evidence. The diapsids include birds and all other living and extinct reptiles.

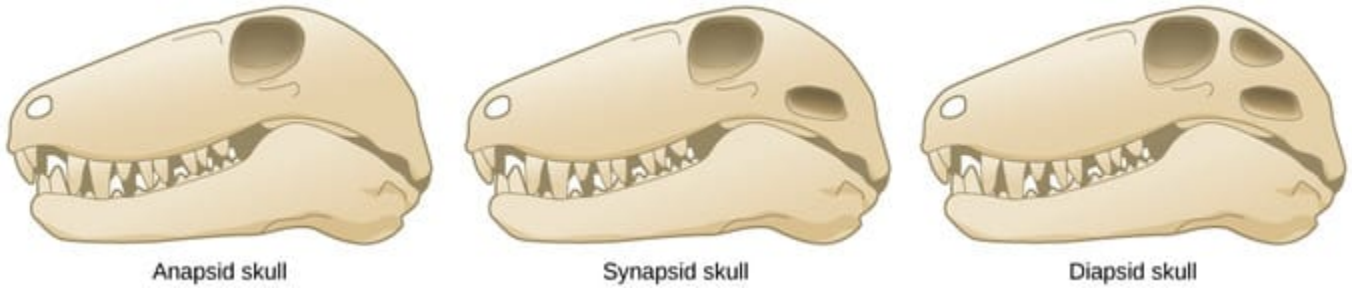


Figure $29.3C.1$: Tempral fenestrae: The image illustrates the differences in the skulls and temporal fenestrae of anapsids, synapsids, and diapsids. Anapsids have no openings, synapsids have one opening, and diapsids have two openings.

The diapsids diverged into two groups, the Archosauromorpha (“ancient lizard form”) and the Lepidosauromorpha (“scaly lizard form”) during the Mesozoic period. The lepidosaurs include modern lizards, snakes, and tuataras. The archosaurs include modern crocodiles and alligators, and the extinct pterosaurs (“winged lizard”) and dinosaurs (“terrible lizard”). Clade Dinosauria includes birds, which evolved from a branch of dinosaurs.

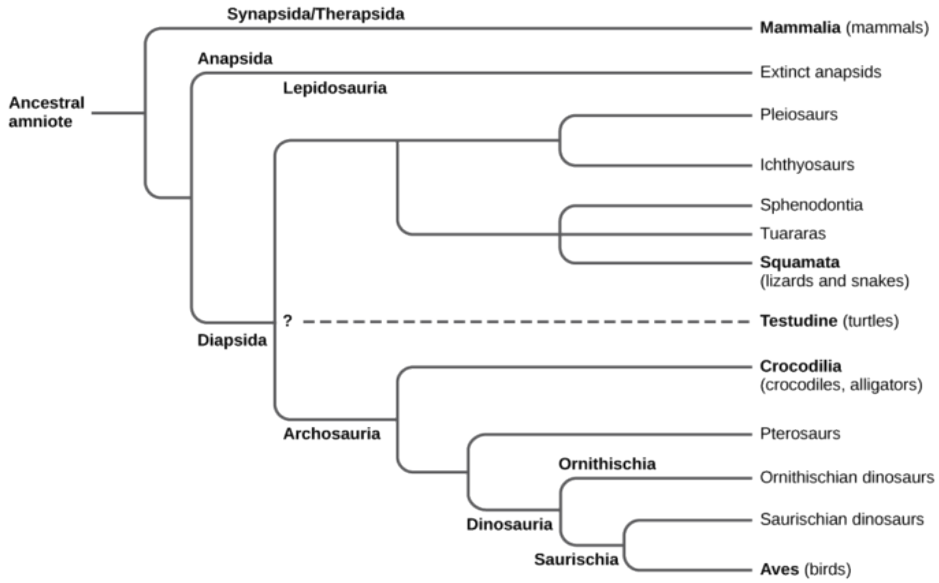


Figure $29.3C.1$: Evolution of amniotes: This chart shows the evolution of amniotes. The placement of Testudines (turtles) is currently still debated.

In the past, the most common division of amniotes has been into the classes Mammalia, Reptilia, and Aves. Birds are descended, however, from dinosaurs, so this classical scheme results in groups that are not true clades. Birds are considered as a group distinct from reptiles with the understanding that this does not completely reflect phylogenetic history and relationships.

Key Points

- Synapsids include all mammals and therapsids, mammal-like reptiles, from which mammals evolved.
- Sauropsids, which are divided into the anapsids and diapsids, include reptiles and birds.
- The diapsids are divided into lepidosaurs (modern lizards, snakes, and tuataras) and archosaurs (modern crocodiles and alligators, pterosaurs, and dinosaurs).
- Skull structure and number of temporal fenestrae are the key differences between the synapsids, anapsids, and diapsids; anapsids have no temporal fenestrae, synapsids have one, and diapsids have two.
- Turtle classification is still unclear, but based on molecular evidence, they are sometimes classified under diapsids.
- Although birds are considered distinct from reptiles, they evolved from a group of dinosaurs, so considering them separately from reptiles is not phylogenetically accurate.

Key Terms

- **synapsid**: animals that have one opening low in the skull roof behind each eye; includes all living and extinct mammals and therapsids
- **anapsid**: amniote whose skull does not have openings near the temples; includes extinct organisms
- **diapsid**: any of very many reptiles and birds that have a pair of openings in the skull behind each eye
- **temporal fenestrae**: post-orbital openings in the skull of some amniotes that allow muscles to expand and lengthen

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29.4: REPTILES

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- Topic hierarchy

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29.4B: Characteristics of Reptiles

29.4C: Evolution of Reptiles

29.4D: Modern Reptiles

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29.4A: Characteristics of Amniotes

Learning Objectives

- Discuss the evolution of amniotes

Characteristics of Amniotes

The amniotes, reptiles, birds, and mammals, are distinguished from amphibians by their terrestrially-adapted egg, which is protected by amniotic membranes. The evolution of amniotic membranes meant that the embryos of amniotes were now provided with their own aquatic environment, which led to less dependence on water for development, allowing the amniotes to branch out into drier environments. This was a significant development that distinguished them from amphibians, which were restricted to moist environments due their shell-less eggs. Although the shells of various amniotic species vary significantly, they all allow retention of water. The shells of bird eggs are composed of calcium carbonate and are hard, but fragile. The shells of reptile eggs are leathery and require a moist environment. Most mammals do not lay eggs (except for monotremes). Instead, the embryo grows within the mother's body; however, even with this internal gestation, amniotic membranes are still present.

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, provides the embryo with water and protein, whereas the fattier egg yolk is the energy supply for the embryo, as is the case with the eggs of many other animals, such as amphibians. However, the eggs of amniotes contain three additional extra-embryonic membranes: the chorion, amnion, and allantois. Extra-embryonic membranes are those present in amniotic eggs that are not a part of the body of the developing embryo. While the inner amniotic membrane surrounds the embryo itself, the chorion surrounds the embryo and yolk sac. The chorion facilitates exchange of oxygen and carbon dioxide between the embryo and the egg's external environment. The amnion protects the embryo from mechanical shock and supports hydration. The allantois stores nitrogenous wastes produced by the embryo and also facilitates respiration. In mammals, membranes that are homologous to the extra-embryonic membranes in eggs are present in the placenta. Additional derived characteristics of amniotes include waterproof skin, due to the presence of lipids, and costal (rib) ventilation of the lungs.

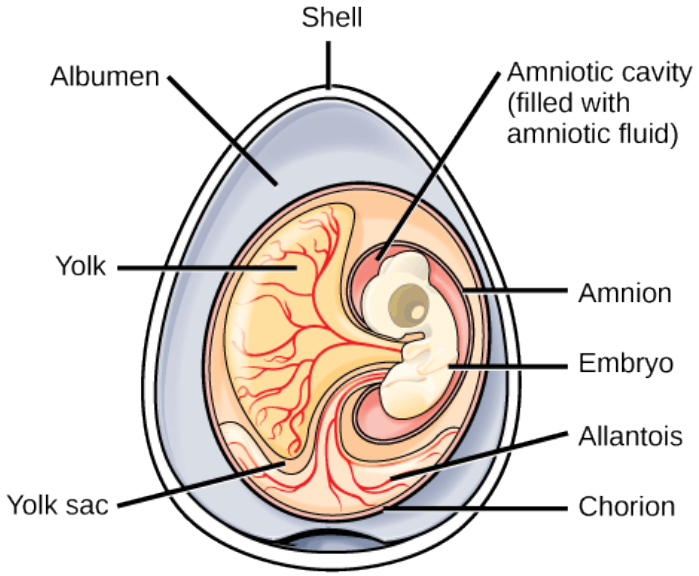


Figure 29.4A.1: Amniotic eggs: The key features of an amniotic egg are the chorion, amnion, and allantois.

Key Points

- The amniotes include reptiles, birds, and mammals; shared characteristics between this group include a shelled egg

protected by amniotic membranes, waterproof skin, and rib ventilation of the lungs.
- In amniotes, the shell of the egg provides protection for the developing embryo and allows water retention while still being permeable to gas exchange.
- Amniotic eggs contain albumin, which provides the embryo with water and protein, and an egg yolk that supplies the embryo with energy.
- The chorion, amnion, and allantois are key membranes found only in amniotic eggs.
- The chorion facilitates gas exchange between the embryo and the egg's external environment.
- The amnion protects the embryo from mechanical shock and supports hydration, while the allantois stores nitrogenous wastes and facilitates respiration.

Key Terms

- **amnion**: the innermost membrane of the fetal membranes of amniotes; the sac in which the embryo is suspended; protects the embryo from shock and carries out hydration
- **chorion**: allows exchange of oxygen and carbon dioxide between the embryo and the egg's external environment
- **allantois**: membrane in an egg that stores nitrogenous wastes produced by the embryo and facilitates respiration
- **monotreme**: a mammal that lays eggs and has a single urogenital and digestive orifice; only the echidnas and platypuses

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29.4B: Characteristics of Reptiles

Learning Objectives

- Summarize the key adaptations of reptiles

Characteristics of Reptiles

Reptiles are tetrapods. Limbless reptiles (snakes and other squamates) have vestigial limbs and, as with caecilians, are classified as tetrapods because they are descended from four-limbed ancestors. Reptiles lay on land eggs enclosed in shells. Even aquatic reptiles return to the land to lay eggs. They usually reproduce sexually with internal fertilization. Some species are ovoviviparous, with the eggs remaining in the mother's body until they are ready to hatch. Other species are viviparous, with the offspring born alive.

One of the key adaptations that permitted reptiles to live on land was the development of their scaly skin which contains the protein keratin and waxy lipids, reducing water loss from the skin. Due to this occlusive skin, reptiles cannot use their skin for respiration, as do amphibians; all breathe with lungs.

Reptiles are ectotherms: animals whose main source of body heat comes from the environment. This is in contrast to endotherms, which use heat produced by metabolism to regulate body temperature. In addition to being ectothermic, reptiles are categorized as poikilotherms: animals whose body temperatures vary rather than remain stable. Reptiles have behavioral adaptations to help regulate body temperature, such as basking in sunny places to warm up and finding shady spots or going underground to cool down. 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; the animal becomes very sluggish.



Figure $29.4B.1$: Ectotherms: Reptiles, such as these sunbathing Florida redbelly turtles, are ectotherms: they rely on their environment for body heat.

Key Points

- All reptiles, including aquatic ones, lay their eggs on land.

- Reptiles reproduce sexually through internal fertilization; some species are ovoviviparous (lay eggs) and others are viviparous (live birth).
- Because of the development of impermeable, scaly skin, reptiles were able to move onto land since their skin could not be used for respiration in water.
- Reptiles are ectotherms: they depend on their surrounding environment to control their body temperature; this leads to advantages, such as not being dependent on metabolic energy from food for body heat.
- Reptiles are also poikilotherms: animals whose body temperatures vary rather than remain stable.
- Some reptiles go into brumation: a long period during cold weather that consists of no eating and a decreased metabolism.

Key Terms

- **viviparous**: being born alive, as are most mammals, some reptiles, and a few fish (as opposed to being laid as an egg)
- **ovoviviparous**: a mode of reproduction in animals in which embryos develop inside eggs that are retained within the mother's body until they are ready to hatch
- **ectotherm**: a cold-blooded animal that regulates its body temperature by exchanging heat with its surroundings

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29.4C: Evolution of Reptiles

Learning Objectives

- Outline the evolution of reptiles

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 reptiles was *Hylonomus*. 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 archosaurs (predecessors of crocodilians and dinosaurs) and lepidosaurs (predecessors of snakes and lizards). These groups remained inconspicuous until the Triassic period when the archosaurs became the dominant terrestrial group due to the extinction of large-bodied anapsids and synapsids during the Permian-Triassic extinction. About 250 million years ago, archosaurs radiated into the dinosaurs and the pterosaurs.

Although they are sometimes mistakenly called dinosaurs, the pterosaurs were distinct from true dinosaurs. 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 $29.4C.1$: Pterosaurs: Pterosaurs, which existed from the late Triassic to the Cretaceous period (210 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.

The dinosaurs were a diverse group of terrestrial reptiles with more than 1,000 species identified to date. Paleontologists continue to discover new species of dinosaurs. Some dinosaurs were quadrupeds; others were bipeds. Some were carnivorous, whereas others were herbivorous. Dinosaurs laid eggs; a number of nests containing fossilized eggs have been found. It is not known whether dinosaurs were endotherms or ectotherms. However, given that modern birds are endothermic, the dinosaurs that served as ancestors to birds were probably endothermic as well. Some fossil evidence exists for dinosaurian parental care. Comparative biology supports this hypothesis since the archosaur birds and crocodilians display parental care.

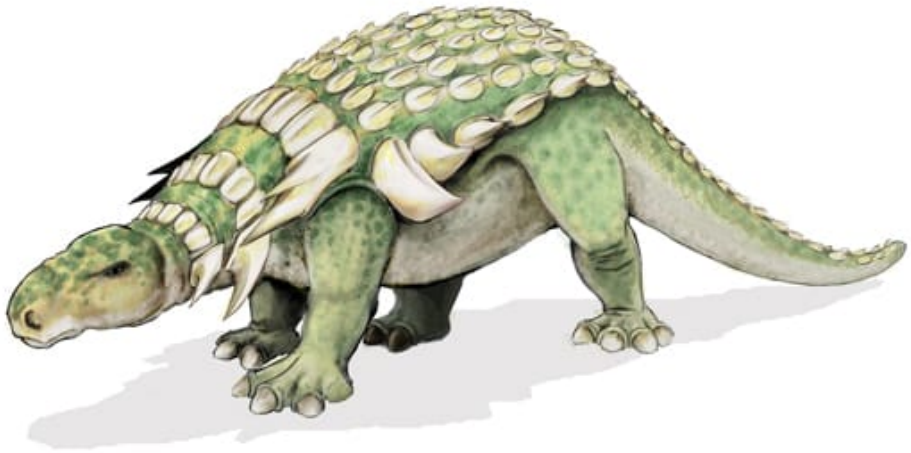


Figure $29.4C.1$: Quadruped dinosaurs: Edmontonia, an example of an extinct quadruped reptile, was an armored dinosaur that lived in the late Cretaceous period, 145.5 to 65.6 million years ago.

Dinosaurs dominated the Mesozoic Era, which was known as the “Age of Reptiles.” The dominance of dinosaurs lasted until the end of the Cretaceous period, the end 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 dinosaurs.

Key Points

- Diapsids diverged into archosaurs and lepidosaurs, but these groups did not dominate the ecosystem until the Triassic following the Permian extinction.
- Archosaurs diverged into the dinosaurs and the pterosaurs about 250 million years ago.
- Pterosaurs had the ability to fly because of their wings and hollow bones, a trait convergent to modern birds, but were not ancestral to birds.
- Dinosaurs were quadrupeds or bipeds, carnivorous or herbivorous, and laid eggs.
- It is unknown whether dinosaurs were endothermic or ectothermic, but since birds are endothermic, the dinosaur ancestors of birds were probably endothermic.
- Dinosaurs dominated the Mesozoic Era until the Cretaceous -Tertiary extinction wiped out most of these large-bodied animals.

Key Terms

- **pterosaur**: any of several extinct flying reptiles, of the order Pterosauria, including the pterodactyls
- **Cretaceous-Tertiary extinction**: mass extinction of three-quarters of plant and animal species on earth, including all non-avian dinosaurs, that occurred over a geologically-short period of time 66 million years ago

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29.4D: Modern Reptiles

Learning Objectives

- Differentiate among the types of modern reptiles

Modern Reptiles

Class Reptilia includes many diverse species that are classified into four living clades. These are the 25 species of Crocodilia, 2 species of Sphenodontia, approximately 9,200 Squamata species, and the Testudines, with about 325 species. A reptile is any amniote (a tetrapod whose egg has an additional membrane, originally to allow them to lay eggs on land) that is neither a mammal nor a bird. Unlike mammals, birds, and certain extinct reptiles, living reptiles have scales or scutes (rather than fur or feathers) and are cold-blooded. Modern reptiles inhabit every continent with the exception of Antarctica.

Crocodilia

Crocodilia ("small lizard") arose with a distinct lineage by the middle Triassic; extant species include alligators, crocodiles, and caimans. Crocodilians are large, solidly built lizard-like reptiles with long flattened snouts and laterally-compressed tails, and eyes, ears, and nostrils at the top of the head. Their skin is thick and covered in non-overlapping scales. They have conical, peg-like teeth and a powerful bite. As with birds, they have a four-chambered heart and a unidirectional system of air flow around the lungs; however, in contrast to birds, they are ectotherms, as are all other reptiles. Crocodilians 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; they spend most of their time in water. Some species are able to move on land due to their semi-erect posture.



Figure $29.4D.1$: Crocodilians: Crocodilians, such as this Siamese crocodile (Crocodylus siamensis), have large flattened snouts and thick skin.

Sphenodontia

Sphenodontia ("wedge tooth") arose in the Mesozoic era and includes only one living genus, Tuatara, which comprises two species that are found in New Zealand. Tuataras measure up to 80 centimeters and weigh about 1 kilogram. Although quite lizard-like in gross appearance, several unique features of the skull and jaws clearly define them and distinguish the group from the squamates. Their dentition, in which two rows of teeth in the upper jaw overlap one row on the lower jaw, is unique among living species.

They are also unusual in having a pronounced photoreceptive eye, dubbed the “third eye”, whose current function is a subject of ongoing research, but is thought to be involved in setting circadian and seasonal cycles.



Figure $29.4D.1$: Tuatara: Tuataras may resemble a lizard but belongs to a distinct lineage, the Sphenodontidae family.

Squamata

Squamata (“scaly”) arose in the late Permian; extant species include lizards and snakes. They are most closely-related to tuataras; both groups evolved from a lepidosaurian ancestor. Squamata is the largest extant clade of reptiles. Most lizards differ from snakes by having four limbs, although these have been variously lost or significantly reduced in at least 60 lineages. Snakes lack eyelids and external ears, which are present in lizards. Lizard species range in size from chameleons and geckos, which are a few centimeters in length, to the Komodo dragon, which is about 3 meters in length. Most lizards are carnivorous, but some large species, such as iguanas, are herbivores.



Figure $29.4D.1$: Squamata: The Squamata, which includes lizards and snakes, are the largest group of reptiles. The garter snake belongs to the genus Thamnophis, the most widely-distributed reptile genus in North America.

Snakes are thought to have descended from either burrowing lizards or aquatic lizards over 100 million years ago. Snakes comprise about 3,000 species and range in size from 10 centimeter-long thread snakes to 10 meter-long pythons and anacondas. All snakes are carnivorous, eating small animals, birds, eggs, fish, and insects. Although variations exist, 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 expansion of the gape and independent motion of the two sides; both advantages in swallowing big items.

Testudines

Turtles are members of the clade Testudines ("having a shell"). Turtles are characterized by a bony or cartilaginous shell. The shell consists of the ventral surface called the plastron and the dorsal surface called the carapace, which develops from the ribs. The plastron is made of scutes or plates; the scutes can be used to differentiate species of turtles. The two clades of turtles are most easily recognized by how they retract their necks. The dominant group, which includes all North American species, retracts its neck in a vertical S-curve. Turtles in the less speciose clade retract the neck with a horizontal curve.



Figure $29.4D.1$: Testudines: Testudines include all shelled reptiles, such as the African spurred tortoise (Geochelone sulcata) that lives at the southern edge of the Sahara Desert. It is the third-largest tortoise in the world.

Turtles arose approximately 200 million years ago, predating crocodiles, lizards, and snakes. Similar to other reptiles, turtles are ectotherms. They lay 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.

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Key Points

- Reptile are amniotes that lay their eggs on land; they have scales or scutes and are ectothermic.
- Crocodilia includes the alligators, crocodiles, and caimans; they are mostly aquatic species, but some are able to move on land because of their semi-erect posture.
- Tuataras are classified as the only group under Sphenodontia; they may be lizard-like, but skull and jaw differences set them apart from true lizards.
- Squamata, the largest group of reptiles, includes the lizards and snakes.
- Snakes, which lack the eyelids and external ears present in lizards, are believed to have evolved from burrowing or aquatic lizards.
- Turtles are grouped under the Testudines; species in this group all have bony or cartilaginous shells.

Key Terms

- **scute**: a horny, chitinous, or bony external plate or scale, as on the shell of a turtle or the skin of crocodiles
- **plastron**: the nearly flat part of the shell structure of a tortoise or other animal, similar in composition to the carapace
- **amniote**: a group of vertebrates having an amnion during the development of the embryo; mammals, birds, and reptiles

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29.5: BIRDS

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29.5A: Characteristics of Birds

29.5B: Evolution of Birds

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29.5A: Characteristics of Birds

Learning Objectives

- Summarize the derived characteristics of birds

Characteristics of Birds

Birds are endothermic and, because they fly, they require large amounts of energy, necessitating a high metabolic rate. As with mammals, which are also endothermic, birds have an insulating covering that keeps heat in the body: feathers. Specialized feathers called down feathers are especially insulating, trapping air in spaces between each feather to decrease the rate of heat loss. Certain parts of a bird's body are covered in down feathers; the base of other feathers have a downy portion, while newly-hatched birds are covered in down.

Feathers not only act as insulation, but also allow for flight, enabling the lift and thrust necessary to become airborne. The feathers on a wing are flexible, so the collective feathers move and separate as air moves through them, reducing the drag on the wing. Flight feathers are asymmetrical, which affects airflow over them and provides some of the lifting and thrusting force required for flight. Two types of flight feathers are found on the wings: primary feathers and secondary feathers. Primary feathers are located at the tip of the wing and provide thrust. Secondary feathers are located closer to the body, attach to the forearm portion of the wing, and provide lift. Contour feathers are those found on the body. They help reduce drag produced by wind resistance during flight, creating a smooth, aerodynamic surface allowing air to flow smoothly over the bird's body for efficient flight.

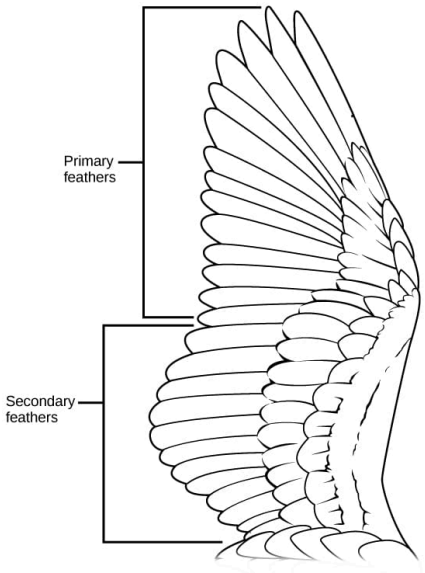


Figure $29.5A.1$: Bird feathers: Primary feathers are located at the wing tip and provide thrust; secondary feathers are located close to the body and provide lift.

Flapping of the entire wing occurs primarily through the actions of the chest muscles: the pectoralis and the supracoracoideus. These muscles, highly developed in birds and accounting for a higher percentage of body mass than in most mammals, attach to a blade-shaped keel, similar to that of a boat, located on the sternum. The sternum of birds is larger than that of other vertebrates, which accommodates the large muscles required to generate enough upward force to generate lift with the flapping of the wings. 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 of flight is a low body weight. As body weight increases, the muscle output required for flying increases. The largest living bird is the ostrich. While it is much smaller than the largest mammals, it is 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 are hollow rather than filled with tissue. They contain air spaces that are sometimes connected to air sacs and they have struts of bone to provide structural reinforcement. Pneumatic bones are not found in all birds; 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.



Figure 29.5A.1: Pneumatic bones of birds: 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: a structure that allows water to be reabsorbed from waste back into the bloodstream. Uric acid is not expelled as a liquid, but is concentrated into urate salts, which are expelled along with fecal matter. In this way, water is not held in the urinary bladder, which would increase body weight. Most bird species possess only one ovary rather than two, further reducing body mass.

The air sacs that extend into bones, making them pneumatic, also join with the lungs and function in respiration. In contrast to mammalian lungs in which air flows in two directions, as it is breathed in and out, airflow through bird lungs travels in one direction. Air sacs allow for this unidirectional airflow, which also creates a cross-current exchange system with the blood. In a cross-current or counter-current system, the air flows in one direction and the blood flows in the opposite direction, creating a very efficient means of gas exchange.

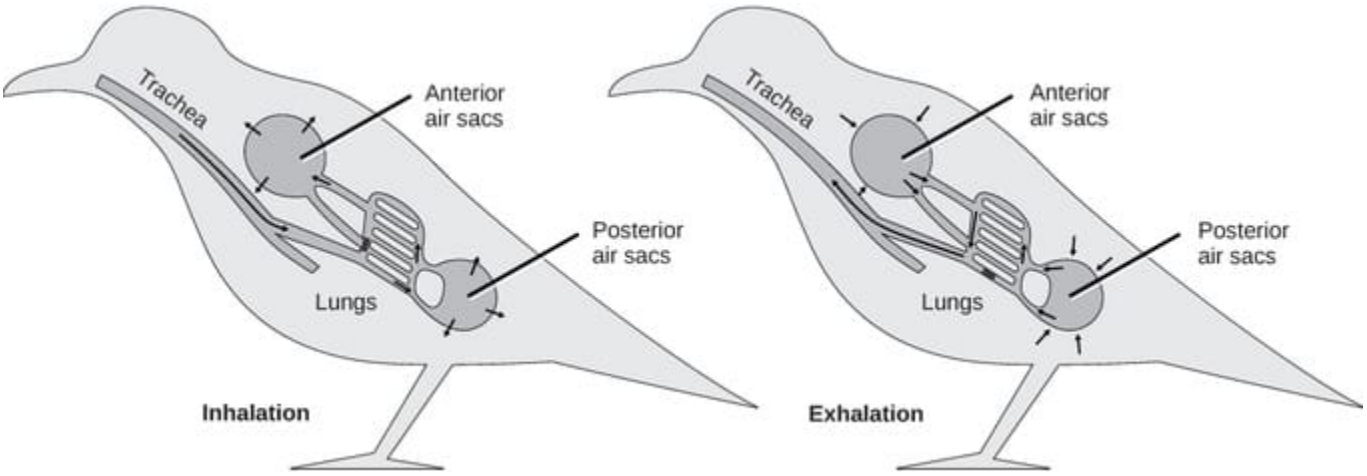


Figure 29.5A.1: Avian respiration: Avian respiration is an efficient system of gas exchange with air flowing unidirectionally. During inhalation, air passes from the trachea into posterior air sacs, then through the lungs to anterior air sacs. The air sacs are connected to the hollow interior of bones. During exhalation, air from air sacs passes into the lungs and out the trachea.

Key Points

- Birds have down feathers that provide insulation and two types of flight feathers found on the wings: thrust-producing primary feathers at the tip of the wing and lift-providing secondary feathers closer to the body.
- Contour feathers found on the body create a smooth, aerodynamic surface.
- The chest muscles of birds are highly developed as they are responsible for the flapping of the entire wing.
- The two clavicles of birds are fused, forming the furcula or wishbone, which is both flexible and strong enough to support to the shoulder girdle during flapping.

- In order to keep body weight low, birds have pneumatic bones, no urinary bladders, and usually only one ovary.
- Birds have developed an efficient respiratory system using air sacs and unidirectional airflow and a cross-current exchange system with the blood.

Key Terms

- **pneumatic**: having cavities filled with air
- **endothermic**: an animal whose body temperature is regulated by internal factors
- **furcula**: the forked bone formed by the fusion of the clavicles in birds; the wishbone
- **cloaca**: the common duct in fish, reptiles, birds, and some primitive mammals that serves as the anus as well as the genital opening

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29.5B: Evolution of Birds

Learning Objectives

- Explain the evolution of birds

Evolution of Birds

The evolutionary history of birds is still somewhat unclear. Due to the fragility of bird bones, they do not fossilize as well as other vertebrates. Birds are diapsids, meaning they have two fenestrations, or openings, in their skulls. Birds belong to a group of diapsids called the archosaurs, which also includes crocodiles and dinosaurs. It is commonly accepted that birds evolved from dinosaurs.

Dinosaurs were subdivided into two groups, the Saurischia ("lizard like") and the Ornithischia ("bird like"). Despite the names of these groups, it was not the bird-like 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, includes the ancestors of modern birds. This course of evolution is suggested by similarities between 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 fusing of the clavicles.

One important fossil of an animal intermediate to dinosaurs and birds is Archaeopteryx, which is from the Jurassic period and has characteristics of both dinosaurs and birds. Some scientists propose classifying it as a bird, but others prefer to classify it as a dinosaur. The fossilized skeleton of Archaeopteryx looks like that of a dinosaur. It had teeth and birds do not, but it also had feathers modified for flight, a trait associated only with birds among modern animals. Fossils of older, feathered dinosaurs exist, but the feathers do not have the characteristics of flight feathers.



Figure $29.5B.1$: Bird fossils: (a) Archaeopteryx lived in the late Jurassic Period around 150 million years ago. It had teeth like a dinosaur, but had (b) flight feathers like modern birds, which can be seen in this fossil.

It is still unclear exactly how flight evolved in birds. Two main theories exist: 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 was the stimulus for flight, as wings could be used to improve running and then became used for flapping flight. As with the question of how flight evolved, the question of how endothermy evolved in birds still is unanswered. Feathers provide insulation, but this is only beneficial if body heat is being produced internally. Similarly, internal heat production is only viable if

insulation is present to retain that heat. It has been suggested that one or the other (feathers or endothermy) evolved in response to some other selective pressure.

During the Cretaceous period, a group known as the Enantiornithes was the dominant bird type. Enantiornithes means “opposite birds,” which refers to the fact that certain bones of the feet are joined differently than the way the bones are joined in modern birds. These birds formed an evolutionary line separate from modern birds; they did not survive past the Cretaceous. Along with the Enantiornithes, Ornithurae birds (the evolutionary line that includes modern birds) were also present in the Cretaceous. After the extinction of Enantiornithes, modern birds became the dominant bird, with a large radiation occurring during the Cenozoic Era. Referred to as Neornithes (“new birds”), modern birds are now classified into two groups, the Paleognathae (“old jaw”) or ratites (a group of flightless birds including ostriches, emus, rheas, and kiwis) and the Neognathae (“new jaw”), all other birds.



Figure $29.5B.1$: Example of an extinct bird: *Shanweiniao cooperorum* was a species of Enantiornithes, which evolved separately from modern birds. It did not survive past the Cretaceous period.

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Key Points

- Birds have two fenestrations, or openings, in their skulls making them diapsids like crocodiles and dinosaurs.
- Birds did not descend from bird-like dinosaurs (Ornithischia), but rather from a divergent group of lizard-like dinosaurs (Saurischia) called theropods, which were bipedal predators.
- A Jurassic period fossil intermediate to dinosaurs and birds is *Archaeopteryx*, which had teeth like dinosaurs, and feathers modified for flight.
- The arboreal ("tree") hypothesis and the terrestrial ("land") hypothesis are two theories on how flight evolved; these theories propose that wings developed to aid in jumping from branch to branch or to aid in running, respectively.
- It was not until after the extinction of Enantiornithes (a separate evolutionary line of bird-like animals) during the Cretaceous period that the Ornithurae (the evolutionary line of modern birds) became dominant. and prospered.

Key Terms

- **diapsid**: any of very many reptiles and birds that have a pair of openings in the skull behind each eye
- **Archaeopteryx**: a taxonomic genus within the family Archaeopterygidae, known from fossils and widely accepted as the earliest and most primitive known bird
- **fenestration**: an opening in the surface of an organ, etc.

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29.6: MAMMALS

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29.6A: Characteristics of Mammals

29.6B: Evolution of Mammals

29.6C: Living Mammals

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29.6A: Characteristics of Mammals

Learning Objectives

- Summarize the distinguishing characteristics of mammals

Characteristics of Mammals

The presence of hair is one of the most obvious traits of a mammal. Although it is not very extensive on certain species, such as whales, hair has many important functions for mammals. Mammals are endothermic so hair provides insulation to retain heat generated by metabolic work by trapping a layer of air close to the body. Along with insulation, hair can serve as a sensory mechanism via specialized hairs called vibrissae, better known as whiskers. These attach to nerves that transmit information about 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. "



Figure $29.6A.1$: Mammalian fur as insulation: Polar bears use their fur for warmth. While their skin is black, their transparent fur appears white, providing camouflage while hunting and serving as protection by hiding cubs in the snow.

Mammalian integument, or skin, includes secretory glands with various functions. Sebaceous glands produce a lipid mixture called sebum that is secreted onto the hair and skin for water resistance and lubrication. Sebaceous glands are located over most of the body. Eccrine glands produce sweat, or perspiration, which is mainly composed of water. In most mammals, eccrine glands are limited to certain areas of the body; some mammals do not possess them at all. However, in primates, especially humans, sweat figures prominently in thermoregulation, regulating the body through evaporative cooling. Sweat glands are located over most of the body surface in primates. 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. While male monotremes and eutherians possess mammary glands, male marsupials do not. Mammary glands are probably 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. The jaws of other vertebrates are composed of more than one bone. In mammals, the dentary bone joins the skull at the squamosal bone, while in other vertebrates, the quadrate bone of the jaw joins with the articular bone of the skull. These bones are present in mammals, but they have been modified to function in hearing and form bones in the middle ear. Other vertebrates possess only one middle ear bone, the stapes. Mammals have three: the malleus, incus, and stapes. The malleus originated 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.

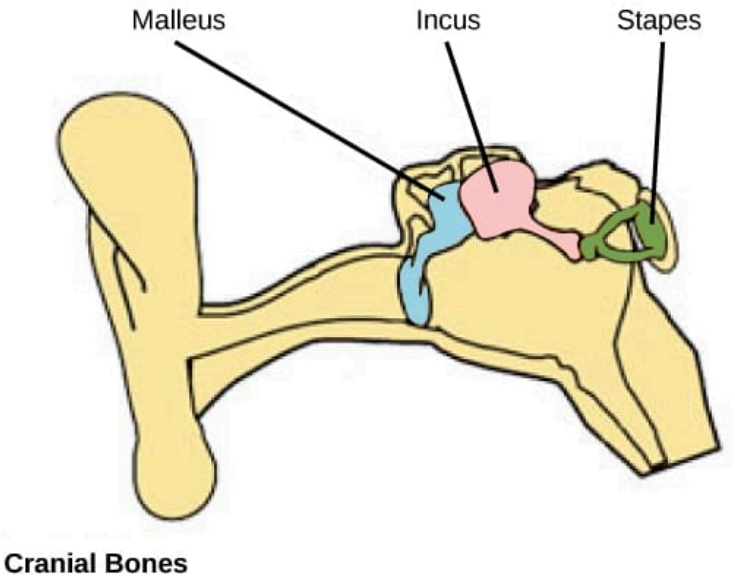


Figure 29.6A.1: Bones of the mammalian inner ear: Bones of the mammalian inner ear are modified from bones of the jaw and skull.

The adductor muscle that closes the jaw is composed of two muscles in mammals: the temporalis and the masseter. These allow side-to-side movement 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 rather than just one type and shape of tooth. Most mammals are diphyodonts, meaning that they have two sets of teeth in their lifetime: deciduous, or “baby” teeth, and permanent teeth. Other vertebrates are polyphyodonts: their teeth are replaced throughout their entire life.

Mammals, like birds, possess a four-chambered heart. Mammals also have a specialized group of cardiac fibers located in the walls of their right atrium called the sinoatrial node, or pacemaker, which determines the rate at which the heart beats. As for blood, mammalian erythrocytes (red blood cells) do not have nuclei, whereas the erythrocytes of other vertebrates are nucleated.

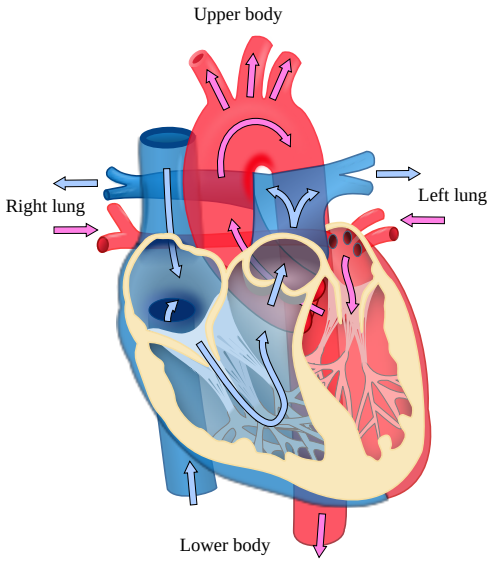


Figure 29.6A.1: Mammalian heart: Mammals possess a four-chambered heart, with two atria and two ventricles, that circulates blood through the body.

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: 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.

Mammalian brains have certain characteristics that differ from other vertebrates. In some, but not all mammals, the cerebral

cortex, the outermost part of the cerebrum, is highly 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, whereas other vertebrates possess a single, undivided lobe. Eutherian mammals also possess a specialized structure that links the two cerebral hemispheres, called the corpus callosum.

Key Points

- The various traits which are used to define mammals include: the presence of hair; the integument system which contains specialized secretory glands; the skeletal and muscular systems; the heart and brain structure.
- Mammals contain specialized glands which have various functions: secretion of chemical compounds used for communication; glands that produce milk; glands that produce perspiration used for thermoregulation; and glands that produce sebum, which is used for lubrication.
- Mammals have four-chambered hearts that are defined by the ability to regulate the heart beat with the presence of specialized pacemaker cells.
- A mammal's hair has many purposes, including insulation, sensory perception, protective coloration, and social signaling.
- Mammals possess many unique skeletal structures including a single lower jaw bone that joins the skull at the squamosal bone and three bones in the inner ear.

Key Terms

- **vibrissa**: any of the tactile whiskers on the nose of an animal
- **sebum**: a thick oily substance, secreted by the sebaceous glands of the skin, that consists of fat, keratin and cellular debris
- **diphyodont**: having two successive sets of teeth (deciduous and permanent), one succeeding the other
- **sinoatrial node**: the impulse-generating (pacemaker) tissue located in the right atrium of the heart, and thus the generator of normal sinus rhythm
- **integument**: an outer protective covering such as the feathers or skin of an animal, a rind or shell

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29.6B: Evolution of Mammals

Learning Objectives

- Outline the evolution of mammals

Evolution of Mammals

The evolution of mammals passed through many stages since the first appearance of their synapsid ancestors in the late Carboniferous period. Mammals are synapsids: they have a single 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 be the ancestors of mammals. By the mid-Triassic, there were many synapsid species that looked like mammals. The lineage leading to today's mammals split in the Jurassic. Synapsids from this period include Dryolestes (more closely related to extant placentals and marsupials than to monotremes) as well as Ambondro (more closely related to monotremes). Later, the eutherian and metatherian lineages separated. Metatherians are the animals more closely related to the marsupials, while eutherians are those more closely related to the placentals. Eutherians are distinguished from noneutherians by various features of the feet, ankles, jaws, and teeth. One of the major differences between placental and nonplacental eutherians is that placentals lack epipubic bones, which are present in all other fossil and living mammals (marsupials and monotremes).



Figure $29.6B.1$: Cynodonts: Cynodonts, which first appeared in the Late Permian period 260 million years ago, are thought to be the ancestors of modern mammals.

Since Juramaia, the earliest-known eutherian, lived 160 million years ago in the Jurassic, this divergence must have occurred in the same period. After the Cretaceous–Paleogene extinction event wiped out the non-avian dinosaurs (birds are generally regarded as the surviving dinosaurs) and several other mammalian groups, placental and marsupial mammals diversified into many new forms and ecological niches throughout the Paleogene and Neogene, by the end of which all modern orders had appeared.

The synapsid lineage became distinct from the sauropsid lineage in the late Carboniferous period, between 320 and 315 million years ago. The sauropsids are today's reptiles and birds, along with all the extinct animals more closely related to them than to mammals. This does not include the mammal-like reptiles, a group more closely related to the mammals. Throughout the Permian period, the synapsids included the dominant carnivores and several important herbivores. In the subsequent Triassic period, however, a previously-obscure group of sauropsids, the archosaurs, became the dominant vertebrates. The mammaliaforms appeared during this period; their superior sense of smell, backed up by a large brain, facilitated entry into nocturnal niches with

less exposure to archosaur predation. The nocturnal lifestyle may have contributed greatly to the development of mammalian traits such as endothermy and hair. Later in the Mesozoic, after theropod dinosaurs replaced rauisuchians as the dominant carnivores, mammals spread into other ecological niches. For example, some became aquatic, some were gliders, and some even fed on juvenile dinosaurs. Most of the evidence consists of fossils. For many years, fossils of Mesozoic mammals and their immediate ancestors were very rare and fragmentary; however, since the mid-1990s, there have been many important new finds, especially in China. The relatively new techniques of molecular phylogenetics have also shed light on some aspects of mammalian evolution by estimating the timing of important divergence points for modern species. When used carefully, these techniques often, but not always, agree with the fossil record. Although mammary glands are a signature feature of modern mammals, little is known about the evolution of lactation. This is because these soft tissues are not often preserved in the fossil record. Most study of the evolution of mammals centers, rather, around the shapes of the teeth, the hardest parts of the tetrapod body. Other much-studied aspects include the evolution of the middle ear bones, erect limb posture, a bony secondary palate, fur and hair, and warm-bloodedness.

A key characteristic of synapsids is endothermy, rather than the ectothermy seen in most other vertebrates. The increased metabolic rate required to internally-modify body temperature went hand-in-hand with changes to certain skeletal structures. The later synapsids, which had more-evolved characteristics unique to mammals, possess cheeks for holding food and heterodont teeth (specialized for chewing by mechanically breaking down food to speed digestion and releasing the energy needed to produce heat). Chewing also requires the ability to chew and breathe at the same time, which is facilitated by the presence of a secondary palate. It separates the area of the mouth where chewing occurs from the area above where respiration occurs, allowing breathing to proceed uninterrupted during 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 the masseter muscle, which closes the jaw and functions in chewing.

Key Points

- Synapsids are defined by a single opening in the skull and the fact that they are endothermic.
- Mammals are the only living synapsids, derived from a lineage in the Jurassic period.
- Two groups of mammals include the eutherians, which are closely related to placentals and the metatherians, which are more closely related to the marsupials.
- Mammalian lineages from the Jurassic include Dryolestes, related to placentals and marsupials, and Ambondro, related to monotremes.
- Later synapsids had specialized structures for chewing, including teeth, cheeks that can hold food, and a secondary palate, which gave them the ability to chew and breathe at the same time.

Key Terms

- **eutherian**: the mammals more closely related to animals like humans and rodents than to marsupials
- **metatherian**: belonging or pertaining to the infraclass Metatheria of marsupials

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29.6C: Living Mammals

Learning Objectives

- Name and describe the distinguishing features of the three main groups of mammals

Living Mammals

Living mammals can be classified into three major classes: eutherians, monotremes, and metatherians. The eutherians, or placental mammals, and the metatherians, or marsupials, together comprise the clade of therian mammals. Monotremes form their sister clade.

There are three living species of monotremes: the platypus and two 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”). The platypus and one species of echidna are found in Australia; the other species of echidna is found in New Guinea. Monotremes are unique among mammals as they lay eggs rather than giving birth to live young. The shells of their eggs are not like the hard shells of birds, but are leathery, similar to the shells of reptile eggs. All monotremes possess a cloaca which serves as the opening for the intestinal, reproductive, and urinary tracts. Additionally, monotremes have no teeth.

Marsupials are found primarily in Australia,although the opossum is found in North America. Australian marsupials include the kangaroo, koala, bandicoot,Tasmanian devil, and several other species. Most species of marsupials possess a pouch in which the very premature young reside after birth, receiving milk and continuing to develop. Marsupials differ from eutherians in that there is a less complex placental connection. The young are born at an extremely early age and latch onto the nipple within the pouch.



Figure $29.6C.1$: Tasmanian devil: The Tasmanian devil is one of several marsupials native to Australia. (credit: Wayne McLean)

Eutherians are the most widespread of the mammals, occurring throughout the world. There are 18 to 20 orders of placental mammals. Some examples are Insectivora, the insect eaters; Edentata, the toothless anteaters; Rodentia, the rodents; Cetacea, the aquatic mammals including whales; Carnivora, carnivorous mammals including dogs, cats, and bears; and Primates, which includes humans. Eutherian mammals are sometimes called placental mammals because all species possess a complex placenta that connects a fetus to the mother, allowing for gas, fluid, and nutrient exchange. While other mammals possess a less complex placenta or briefly have a placenta, all eutherians possess a complex placenta during gestation.



Figure 29.6C.1: A red fox: Red foxes are eutherian (placental) mammals because the mothers nourish their young via a placenta during fetal development. The placenta enables a mother to exchange gases, fluids, and nutrients with the growing embryos.

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Key Points

- Monotremes include the platypus which are defined by their ability to lay eggs instead of giving birth to live young.
- Metatherians are classified as the marsupials which possess a pouch where the premature young reside and nurse while continuing to develop.
- Eutherians are the most common type of mammal and are defined by the presence of a complex placenta which connects the developing fetus to the mother during gestation.

Key Terms

- **marsupial**: a mammal of which the female has a pouch in which it rears its young, which are born immature, through early infancy
- **placental**: a mammal having a placenta; most members of Mammalia

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29.7: THE EVOLUTION OF PRIMATES

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- Topic hierarchy

29.7A: Characteristics and Evolution of Primates

29.7B: Early Human Evolution

29.7C: Early Hominins

29.7D: Genus Homo

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29.7A: Characteristics and Evolution of Primates

Learning Objectives

- Identify key characteristics of primates

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 adaptations that include, but are not limited to: 1) a rotating shoulder joint; 2) a big toe that is widely separated from the other toes and thumbs, that are widely separated from fingers (except humans), which 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 (larger brain/body ratio than similar-sized non-primates), claws that have been modified into flattened nails, typically only one offspring per pregnancy, and a trend toward holding the body upright.

The Order Primates is divided into two groups: prosimians and anthropoids. Prosimians include the bush babies and pottos of Africa, the lemurs of Madagascar, and the lorises of Southeast Asia. Tarsier, also from Southeast Asia, show some prosimian-like and some anthropoid-like features. Anthropoids include monkeys, apes, and humans. In general, prosimians tend to be nocturnal (in contrast to diurnal anthropoids, excluding the nocturnal *Aotus*, owl monkey) and have a smaller brain/body ratio than anthropoids.

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 fragmentary. These proto-primates will remain largely mysterious creatures until more fossil evidence becomes available. The oldest known primate-like mammal with a relatively robust fossil record is *Plesiadapis* (although some researchers do not agree that *Plesiadapis* was a proto-primate). Fossils of this primate have been dated to approximately 55 million years ago. Plesiadapiforms had some features of the teeth and skeleton in common with true primates. They were found in North America and Europe in the Cenozoic, going extinct by the end of the Eocene.

The first true primates were found in North America, Europe, Asia, and Africa in the Eocene Epoch. 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.

Evidence shows that the anthropoid monkeys evolved from prosimians during the Oligocene Epoch. By 35 million years ago, evidence indicates that monkeys were present the Old World (Africa and Asia) and in the New World (South America) by 30 million years ago. New World monkeys are also called Platyrrhini: a reference to their broad noses. Old World monkeys (and apes) are called Catarrhini: a reference to their narrow 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 by drifting on log rafts or mangrove floating 'islands'. 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 arboreal and ground-dwelling species.



Figure 29.7A.1: Howler monkey: The howler monkey, a member of the Platyrrhini, is native to Central and South America. It makes a call that sounds like a lion roaring.

Apes evolved from the catarrhines in Africa midway through the Cenozoic during the Miocene epoch, approximately 25 million years ago. Apes are generally larger than monkeys and do not possess a tail. All apes are capable of moving through trees, although many species spend most their time on the ground. Apes are more intelligent than monkeys as they have relatively larger brains proportionate 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). The very arboreal gibbons are smaller than the great apes; they have low sexual dimorphism (that is, the genders are not markedly different in size); and they have relatively longer arms used for swinging/brachiating through trees.

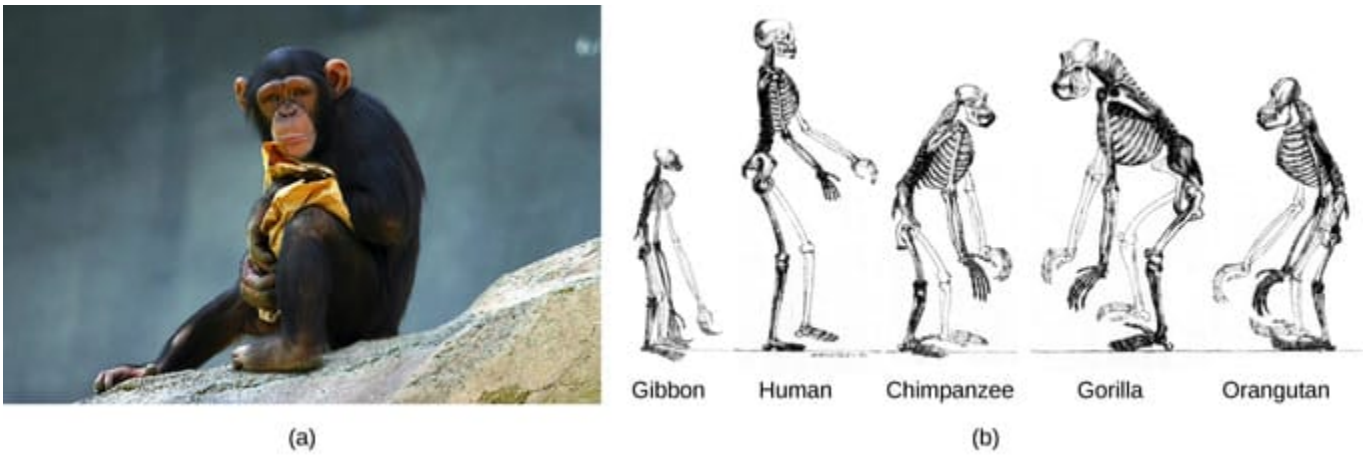


Figure 29.7A.1: Chimpanzee: The (a) chimpanzee is one of the great apes. It possesses a relatively large brain and has no tail. (b) All great apes have a similar skeletal structure.

Key Points

- All primates are descended from tree-dwellers, exhibiting adaptations which allow for tree climbing that include: a rotating shoulder joint, separated big toes and thumb for grasping, and stereoscopic vision.
- Other primate characteristics include: having one offspring per pregnancy, claws evolved into flattened nails; and larger brain/body ratio than other mammals, and tendency to hold body upright.
- True primates, ancestral to prosimians, first appear in the fossil record in the Eocene epoch around 55 million years ago; they were similar in form to lemurs.

- Anthropoids ancestral to both Old World and New World monkeys appear in the fossil record in the Oligocene epoch around 35 million years ago.
- Anthropoids ancestral to apes appear in the Miocene epoch around 25 million years ago.
- Apes are divided into two main groups of hominoids: lesser apes or hylobatids (gibbons and siamangs) and great apes (*Pongo*: orangutans, *Gorilla*: gorillas, *Pan*:chimpanzees, and *Homo*: humans).

Key Terms

- **dimorphism**: the occurrence in an animal species of two distinct types of individual
- **adaptive radiation**: the diversification of species into separate forms that each adapt to occupy a specific environmental niche

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29.7B: Early Human Evolution

Learning Objectives

- List the evolved physical traits used to differentiate hominins from other hominoids

Human Evolution

The family Hominidae of order Primates includes chimpanzees and humans. 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 6 million years ago. Several species evolved from the evolutionary branch that includes humans, although our species is the only surviving member. The term hominin (or hominid) 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. Hominins, who were bipedal in comparison to the other hominoids who were primarily quadrupedal, includes those groups that probably gave rise to our species: *Australopithecus africanus*, *Homo habilis*, and *Homo erectus*, along with non- ancestral groups such as *Australopithecus boisei*. 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. It is possible that there were 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. However, it is also possible that too many new species have been named.

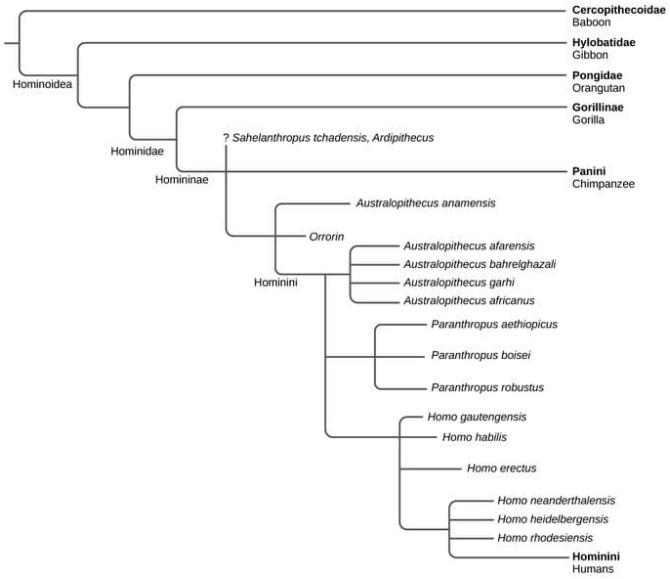


Figure $29.7B.1$: Evolution of modern humans: This chart shows the evolution of modern humans and includes the point of divergence that occurred between modern humans and the other great apes.

Very Early Hominins

There have been three species of very early hominoids which have made news in the past few years. The oldest of these, *Sahelanthropus tchadensis*, 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. To date, it is unclear how this fossil fits with the picture given by molecular data. The line leading to modern humans and modern chimpanzees apparently bifurcated (divided into branches) about six million years ago. It is not thought at this time that this species was an ancestor of modern humans. It may not have been a hominin.

A second, younger species (around 5.7 million years ago), *Orrorin tugenensis*, is also a relatively-recent discovery, found in 2000. There are several specimens of *Orrorin*. It is not known whether *Orrorin* was a human ancestor, but this possibility has not been ruled out. Some features of *Orrorin* are more similar to those of modern humans than are the australopiths, although *Orrorin* is much older.

A third genus, *Ardipithecus ramidus (*4.4 million years ago), was discovered in the 1990s. The scientists who discovered the first fossil found that some other scientists did not believe the organism to be a biped (thus, it would not be considered a hominid). In the intervening years, several more specimens of *Ardipithecus*, including a new species, *Ardipithecus kadabba* (5.6 million years ago), demonstrated that they were bipedal. Again, the status of this genus as a human ancestor is uncertain, but, given that it was bipedal, it was a hominin.

Key Points

- Modern humans are classified as hominins, which also includes extinct bipedal human relatives, such as *Australopithecus africanus*, *Homo habilis* , and *Homo erectus*.
- Few very early (prior to 4 million years ago) hominin fossils have been found so determining the lines of hominin descent is extremely difficult.
- Within the last 20 years, three new genera of hominoids were discovered: *Sahelanthropus tchadensis*, *Orrorin tugenensis,* and *Ardipithecus ramidus* and *kadabba*, but their status in regards to human ancestry is somewhat uncertain.

Key Terms

- **hominin**: the evolutionary group that includes modern humans and now-extinct bipedal relatives
- **hominoid**: any great ape (such as humans) belonging to the superfamily Hominoidea

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29.7C: Early Hominins

Learning Objectives

- Describe the physical characteristics of the Australopiths and compare them to those of modern humans

Early Hominins: Genus *Australopithecus*

Australopithecus (“southern ape”) is a genus of hominin that evolved in eastern Africa approximately 4 million years ago and became extinct about 2 million years ago. This genus is of particular interest to us as it is thought that our genus, genus *Homo*, evolved from *Australopithecus* about 2 million years ago. *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 modern humans and more similar (although larger) 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, found in Laetoli, Tanzania, are dated to 3.6 million years ago. They show that hominins at the time of *Australopithecus* were walking upright.

There were a number of *Australopithecus* species, 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* had smaller canines and molars compared to apes, but these were larger than those of modern humans. Its brain size was 380–450 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, dated to 3.24 million years ago. 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.



Figure $29.7C.1$: Adult Female *Australopithecus afarensis*: This adult female *Australopithecus afarensis* skeleton, nicknamed Lucy, was discovered in the mid 1970s.



(a) (b)

Figure 29.7C.1: Skull comparison: *Australopithecus afarensis* vs modern humans: The skull of (a) *Australopithecus afarensis*, an early hominid that lived between three and four million years ago, resembled that of (b) modern humans, but was smaller with a sloped forehead and prominent jaw.

Australopithecus africanus lived between 2 and 3 million years ago. It had a slender build and was bipedal, but had robust arm bones and, as with 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 Dead End

While most australopiths had a relatively slender, gracile build and teeth suited for soft food, there were also australopiths of a more robust build, dating to approximately 2.5 million years ago. These hominids were larger and had large grinding teeth. Their molars show heavy wear, suggesting that they had a coarse and fibrous vegetarian diet as opposed to the partially carnivorous diet of the more gracile australopiths. They include *Australopithecus robustus* of South Africa, and *Australopithecus aethiopicus* and *Australopithecus boisei* of East Africa. These hominids became extinct more than 1 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.

Key Points

- The early hominin *Australopithecus* displayed various characteristics which show more similarity to the great apes than to modern humans: great sexual dimorphism, small brain size in comparison to body mass, larger canines and molars, and a prognathic jaw.
- *Australopithecus africanus* lived between 2 and 3 million years ago and had a larger brain than *A. afarensis*, but was still less than one-third the size of the modern human brain.
- The gracile australopiths had a relatively slender build and teeth that were suited for soft food and may have had a partially carnivorous diet, while the robust australopiths probably ate tough vegetation.

Key Terms

- **dentition**: the type, number and arrangement of the normal teeth of an organism or of the actual teeth of an individual
- **sexual dimorphism**: a physical difference between male and female individuals of the same species
- **bipedalism**: the habit of standing and walking on two feet

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29.7D: Genus Homo

Learning Objectives

- Compare and contrast the evolution and characteristics associated with the various Homo species: Homo habilis, erectus, and sapiens

Early Hominins: Genus *Homo*

The human genus, *Homo*, first appeared around 2.3 million years ago. For many years, fossils of a species called *Homo habilis* were the oldest examples in the genus *Homo*, but in 2010, a new species called *Homo gautengensis* was proposed that may be older, although it is not well accepted. In comparison to *Australopithecus africanus*, *H. habilis* had a number of features more similar to modern humans. *H. habilis* had a jaw that was less prognathic (forward projection of the jaw) than the australopiths and a larger brain, at 600–750 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.

H. erectus appeared approximately 1.8 million years ago. 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, sizes similar to those of modern humans. Its degree of sexual dimorphism was less than earlier species, with males being 20 to 30 percent larger than females, which is close to the size difference seen in our species. *H. erectus* had a larger brain than earlier species at 775–1,100 cubic centimeters, which compares to the 1,130–1,260 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.



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 archaic *H. sapiens* had a brain size similar to that of modern humans, averaging 1,200–1,400 cubic centimeters. They differed from modern humans by having a thick skull, a prominent brow ridge, and a receding chin. Some of these populations survived until 30,000–10,000 years ago, overlapping with anatomically-modern humans.



Figure $29.7D.1$: Homo sapiens neanderthalensis Tools: The *Homo sapiens 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. The multiregional hypothesis holds that humans first arose near the beginning of the Pleistocene two million years ago and subsequent human evolution has been within a single, continuous human species. This species encompasses archaic human forms such as *Homo erectus* and Neanderthals as well as modern forms, which evolved worldwide to the diverse populations of modern *Homo sapiens sapiens*. The hypothesis contends that humans evolve through a combination of adaptation within various regions of the world and gene flow between those regions. Proponents of multiregional origin point to fossil and genomic data and continuity of archaeological cultures as support for their hypothesis.

The primary alternative hypothesis is the recent African origin of modern humans, which holds that modern humans arose in Africa around 100,000–200,000 years ago, moving out of Africa around 50,000–60,000 years ago to replace archaic human forms with limited interbreeding: at least once with Neanderthals and once with Denisovans.

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Key Points

- *Homo erectus*, appearing 1.8 million years ago, was the first hominin species to migrate out of East Africa, use fire, and hunt.
- Compared to *Homo habilis*, *Homo erectus* was more similar to modern humans due to its height and weight, brain size, limited sexual dimorphism, and downward-facing nostrils.
- Archaic *Homo sapiens* had a similar brain size to modern humans (*Homo sapiens sapiens*), but, unlike modern humans, they had a thick skull, prominent brow ridge, and a receding chin.
- The multiregional hypothesis of modern human origins states that there is an unbroken line of evolution involving regional adaptations and gene flow from *H. erectus* to *H. sapiens sapiens*.
- The recent out of Africa hypothesis of modern human origins states that *H. sapiens sapiens* arose in Africa between 100,000 – 200,000 years, left Africa around 60,000 years ago, and replaced all archaic humans, with very little inter-breeding.
- All men today inherited a Y chromosome from a male that lived in Africa about 140,000 years ago.

Key Terms

- **Homo habilis**: ("handy man") an extinct taxonomic species within the genus Homo that had long arms and may have used stone tools
- **Homo erectus**: ("upright man) extinct species of hominin that appeared 1.8 million years ago; the first hominin to use fire, hunt, and have a home base
- **Homo sapiens**: evolved from H. erectus starting about 500,000 years ago; humans

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30: PLANT FORM AND PHYSIOLOGY

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30.1: The Plant Body - Plant Tissues and Organ Systems

Learning Objectives

- Differentiate among the types of plant tissues and organs

Plant Tissues

Plants are multicellular eukaryotes with tissue systems made of various cell types that carry out specific functions. Plant tissue systems fall into one of two general types: meristematic tissue and permanent (or non-meristematic) tissue. Cells of the meristematic tissue are found in meristems, which are plant regions of continuous cell division and growth. Meristematic tissue cells are either undifferentiated or incompletely differentiated; they continue to divide and contribute to the growth of the plant. In contrast, permanent tissue consists of plant cells that are no longer actively dividing.

Meristematic tissues consist of three types, based on their location in the plant. Apical meristems contain meristematic tissue located at the tips of stems and roots, which enable a plant to extend in length. Lateral meristems facilitate growth in thickness or girth in a maturing plant. Intercalary meristems occur only in monocots at the bases of leaf blades and at nodes (the areas where leaves attach to a stem). This tissue enables the monocot leaf blade to increase in length from the leaf base; for example, it allows lawn grass leaves to elongate even after repeated mowing.

Meristems produce cells that quickly differentiate, or specialize, and become permanent tissue. Such cells take on specific roles and lose their ability to divide further. They differentiate into three main types: dermal, vascular, and ground tissue. Dermal tissue covers and protects the plant. Vascular tissue transports water, minerals, and sugars to different parts of the plant. Ground tissue serves as a site for photosynthesis, provides a supporting matrix for the vascular tissue, and helps to store water and sugars.

Plant tissues are either simple (composed of similar cell types) or complex (composed of different cell types). Dermal tissue, for example, is a simple tissue that covers the outer surface of the plant and controls gas exchange. Vascular tissue is an example of a complex tissue. It is made of two specialized conducting tissues: xylem and phloem. Xylem tissue transports water and nutrients from the roots to different parts of the plant. It includes three different cell types: vessel elements and tracheids (both of which conduct water) and xylem parenchyma. Phloem tissue, which transports organic compounds from the site of photosynthesis to other parts of the plant, consists of four different cell types: sieve cells (which conduct photosynthates), companion cells, phloem parenchyma, and phloem fibers. Unlike xylem-conducting cells, phloem-conducting cells are alive at maturity. The xylem and phloem always lie adjacent to each other. In stems, the xylem and the phloem form a structure called a vascular bundle; in roots, this is termed the vascular stele or vascular cylinder.

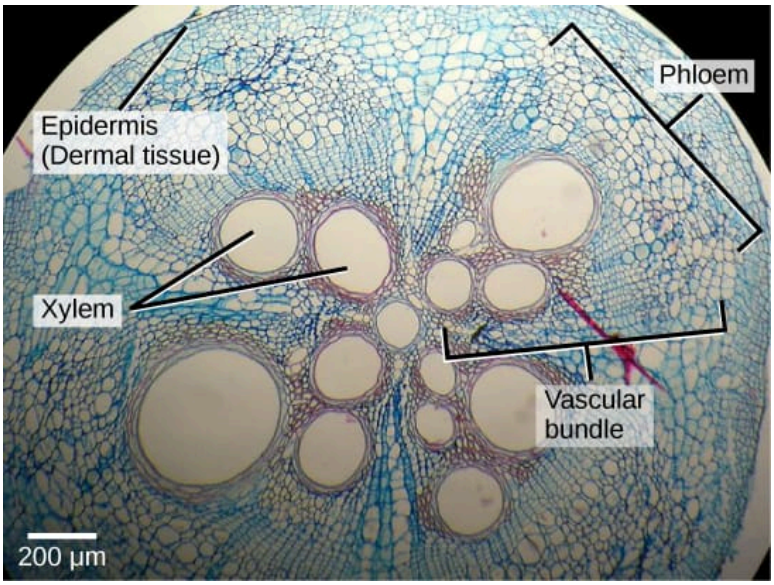


Figure 30.1.1: Cross section of a squash stem showing a vascular bundle: This light micrograph shows a cross section of a squash (Curcurbita maxima) stem. Each teardrop-shaped vascular bundle consists of large xylem vessels toward the inside and smaller phloem cells toward the outside. Xylem cells, which transport water and nutrients from the roots to the rest of the plant, are dead at functional maturity. Phloem cells, which transport sugars and other organic compounds from photosynthetic tissue to the rest of the plant, are living. The vascular bundles are encased in ground tissue and surrounded by dermal tissue.

Plant Organ Systems

In plants, just as in animals, similar cells working together form a tissue. When different types of tissues work together to perform a unique function, they form an organ; organs working together form organ systems. Vascular plants have two distinct organ systems: a shoot system and a root system. The shoot system consists of two portions: the vegetative (non-reproductive) parts of the plant, such as the leaves and the stems; and the reproductive parts of the plant, which include flowers and fruits. The shoot system generally grows above ground, where it absorbs the light needed for photosynthesis. The root system, which supports the plants and absorbs water and minerals, is usually underground.

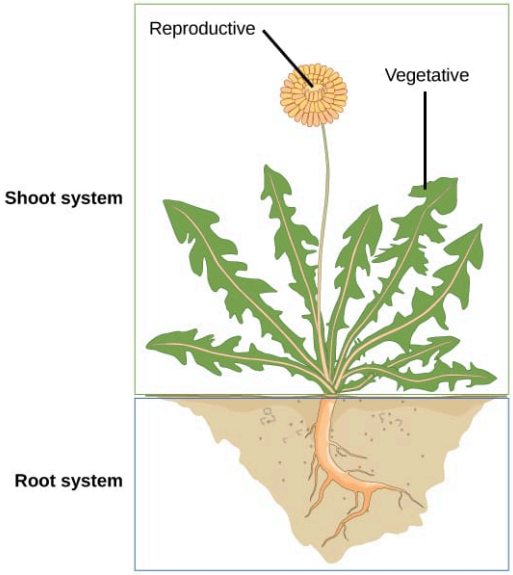


Figure 30.1.1: Example plant organ systems: The shoot system of a plant consists of leaves, stems, flowers, and fruits. The root system anchors the plant while absorbing water and minerals from the soil.

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Key Points

- There are two types of plant tissues: meristematic tissue found in plant regions of continuous cell division and growth, and permanent (or non-meristematic) tissue consisting of cells that are no longer actively dividing.
- Meristems produce cells that differentiate into three secondary tissue types: dermal tissue which covers and protects the plant, vascular tissue which transports water, minerals, and sugars and ground tissue which serves as a site for photosynthesis, supports vascular tissue, and stores nutrients.
- Vascular tissue is made of xylem tissue which transports water and nutrients from the roots to different parts of the plant and phloem tissue which transports organic compounds from the site of photosynthesis to other parts of the plant.
- The xylem and phloem always lie next to each other forming a structure called a vascular bundle in stems and a vascular stele or vascular cylinder in roots.
- Parts of the shoot system include the vegetative parts, such as the leaves and the stems, and the reproductive parts, such as the flowers and fruits.

Key Terms

- **meristem**: the plant tissue composed of totipotent cells that allows plant growth
- **parenchyma**: the ground tissue making up most of the non-woody parts of a plant
- **xylem**: a vascular tissue in land plants primarily responsible for the distribution of water and minerals taken up by the roots; also the primary component of wood
- **phloem**: a vascular tissue in land plants primarily responsible for the distribution of sugars and nutrients manufactured in the shoot
- **tracheid**: elongated cells in the xylem of vascular plants that serve in the transport of water and mineral salts

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30.2: Stems - Functions of Stems

Learning Objectives

- Summarize the main function and basic structure of stems

Stems

Stems are a part of the shoot system of a plant. They may range in length from a few millimeters to hundreds of meters. They also vary in diameter, depending on the plant type. Stems are usually above ground, although the stems of some plants, such as the potato, also grow underground. Stems may be herbaceous (soft) or woody in nature. Their main function is to provide support to the plant, holding leaves, flowers, and buds; in some cases, stems also store food for the plant. A stem may be unbranched, like that of a palm tree, or it may be highly branched, like that of a magnolia tree. The stem of the plant connects the roots to the leaves, helping to transport absorbed water and minerals to different parts of the plant. The stem also helps to transport the products of photosynthesis (i.e., sugars) from the leaves to the rest of the plant.

Plant stems, whether above or below ground, are characterized by the presence of nodes and internodes. Nodes are points of attachment for leaves, aerial roots, and flowers. The stem region between two nodes is called an internode. The stalk that extends from the stem to the base of the leaf is the petiole. An axillary bud is usually found in the axil (the area between the base of a leaf and the stem) where it can give rise to a branch or a flower. The apex (tip) of the shoot contains the apical meristem within the apical bud.

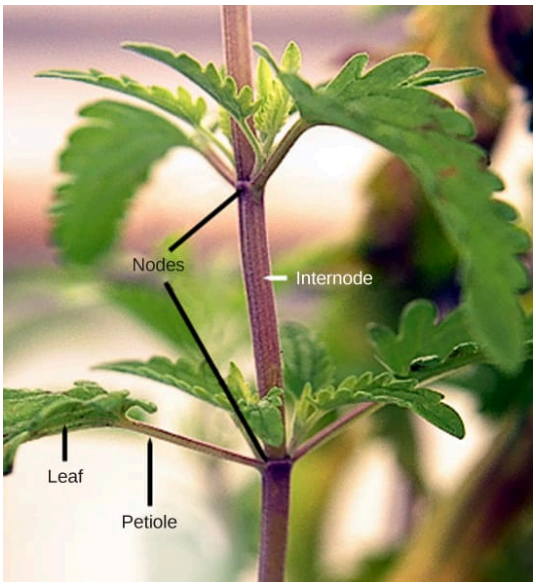


Figure 30.2.1: Parts of a stem: Leaves are attached to the plant stem at areas called nodes. An internode is the stem region between two nodes. The petiole is the stalk connecting the leaf to the stem. The leaves just above the nodes arise from axillary buds.

Key Points

- Most stems are found above ground, but some of them grow underground.
- Stems can be either unbranched or highly branched; they may be herbaceous or woody.
- Stems connect the roots to the leaves, helping to transport water, minerals, and sugars to different parts of the plant.
- Plant stems always have nodes (points of attachments for leaves, roots, and flowers) and internodes (regions between nodes).
- The petiole is the stalk that extends from the stem to the base of the leaf.
- An axillary bud gives rise to a branch or a flower; it is usually found in the axil: the junction of the stem and petiole.

Key Terms

- **node**: points of attachment for leaves, aerial roots, and flowers
- **internode**: a section of stem between two stem nodes
- **petiole**: stalk that extends from the stem to the base of the leaf
- **axillary bud**: embryonic shoot that lies at the junction of the stem and petiole that gives rise to a branch or flower

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30.3: Stems - Stem Anatomy

Learning Objectives

- Summarize the roles of dermal tissue, vascular tissue, and ground tissue

Stem Anatomy

The stem and other plant organs are primarily made from three simple cell types: parenchyma, collenchyma, and sclerenchyma cells. Parenchyma cells are the most common plant cells. They are found in the stem, the root, the inside of the leaf, and the pulp of the fruit. Parenchyma cells are responsible for metabolic functions, such as photosynthesis. They also help repair and heal wounds. In addition, some parenchyma cells store starch.



Figure 30.3.1: Parenchyma cells in plants: The stem of common St John's Wort (*Hypericum perforatum*) is shown in cross section in this light micrograph. The central pith (greenish-blue, in the center) and peripheral cortex (narrow zone 3–5 cells thick, just inside the epidermis) are composed of parenchyma cells. Vascular tissue composed of xylem (red) and phloem tissue (green, between the xylem and cortex) surrounds the pith.

Collenchyma cells are elongated cells with unevenly-thickened walls. They provide structural support, mainly to the stem and leaves. These cells are alive at maturity and are usually found below the epidermis. The "strings" of a celery stalk are an example of collenchyma cells.

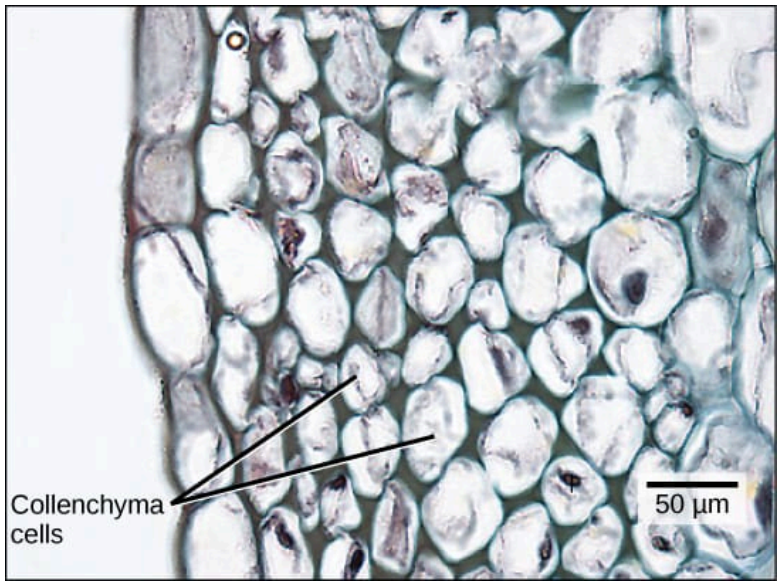


Figure 30.3.1: Collenchyma cells in plants: Collenchyma cell walls are uneven in thickness, as seen in this light micrograph. They provide support to plant structures.

Sclerenchyma cells also provide support to the plant, but unlike collenchyma cells, many of them are dead at maturity. There are two types of sclerenchyma cells: fibers and sclereids. Both types have secondary cell walls that are thickened with deposits of lignin, an organic compound that is a key component of wood. Fibers are long, slender cells; sclereids are smaller-sized. Sclereids give pears their gritty texture. Humans use sclerenchyma fibers to make linen and rope.

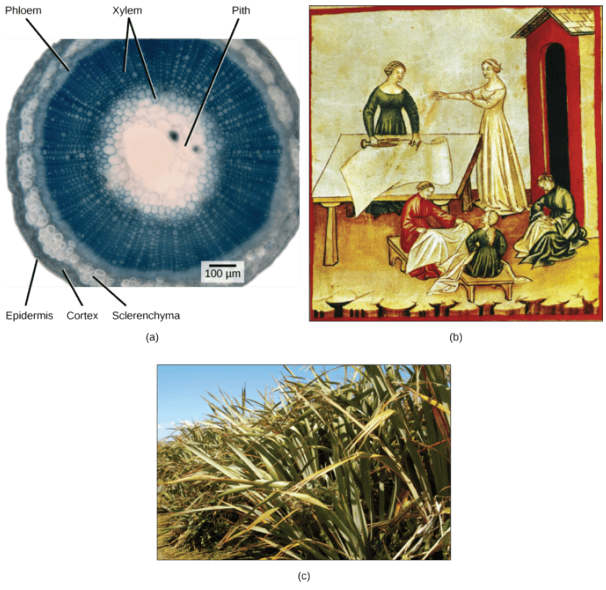


Figure 30.3.1: Sclerenchyma cells in plants: The central pith and outer cortex of the (a) flax stem are made up of parenchyma cells. Inside the cortex is a layer of sclerenchyma cells, which make up the fibers in flax rope and clothing. Humans have grown and harvested flax for thousands of years. In (b) this drawing, fourteenth-century women prepare linen. The (c) flax plant is grown and harvested for its fibers, which are used to weave linen, and for its seeds, which are the source of linseed oil.

As with the rest of the plant, the stem has three tissue systems: dermal, vascular, and ground tissue. Each is distinguished by characteristic cell types that perform specific tasks necessary for the plant's growth and survival.

Dermal Tissue

The dermal tissue of the stem consists primarily of epidermis: a single layer of cells covering and protecting the underlying tissue. Woody plants have a tough, waterproof outer layer of cork cells commonly known as bark, which further protects the plant from

damage. Epidermal cells are the most-numerous and least-differentiated of the cells in the epidermis. The epidermis of a leaf also contains openings, known as stomata, through which the exchange of gases takes place. Two cells, known as guard cells, surround each leaf stoma, controlling its opening and closing and, thus, regulating the uptake of carbon dioxide and the release of oxygen and water vapor. Trichomes are hair-like structures on the epidermal surface. They help to reduce transpiration (the loss of water by aboveground plant parts), increase solar reflectance, and store compounds that defend the leaves against predation by herbivores.

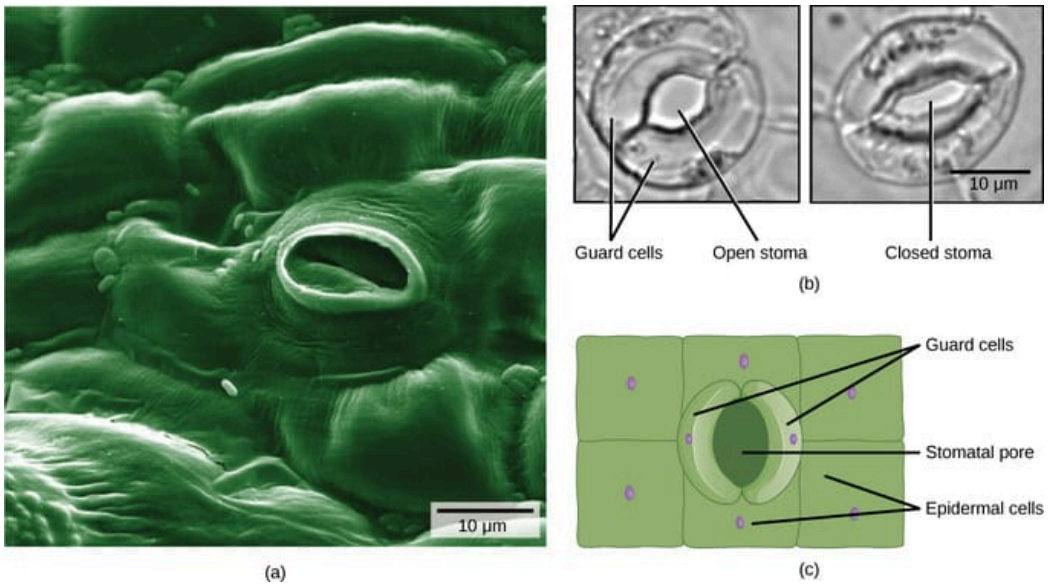


Figure 30.3.1: Stomata: Openings called stomata (singular: stoma) allow a plant to take up carbon dioxide and release oxygen and water vapor. The (a) colorized scanning-electron micrograph shows a closed stoma of a dicot. Each stoma is flanked by two guard cells that regulate its (b) opening and closing. The (c) guard cells sit within the layer of epidermal cells.

Vascular Tissue

The xylem and phloem that make up the vascular tissue of the stem are arranged in distinct strands called vascular bundles, which run up and down the length of the stem. Both are considered complex plant tissue because they are composed of more than one simple cell type that work in concert with each other. When the stem is viewed in cross section, the vascular bundles of dicot stems are arranged in a ring. In plants with stems that live for more than one year, the individual bundles grow together and produce the characteristic growth rings. In monocot stems, the vascular bundles are randomly scattered throughout the ground tissue.

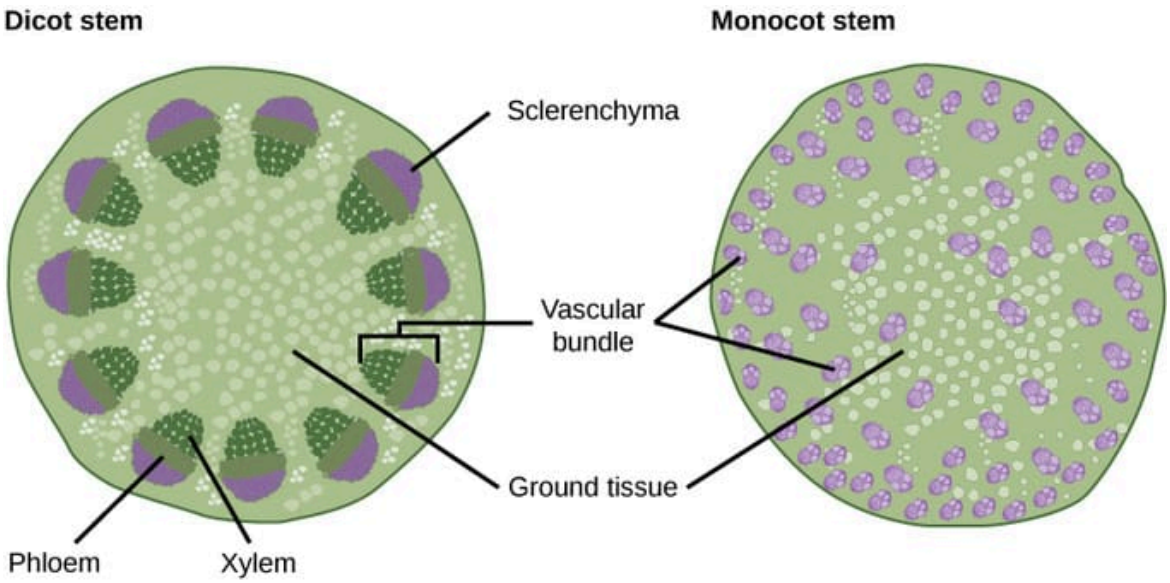


Figure 30.3.1: Vascular bundles: In (a) dicot stems, vascular bundles are arranged around the periphery of the ground tissue. The xylem tissue is located toward the interior of the vascular bundle; phloem is located toward the exterior. Sclerenchyma fibers cap the vascular bundles. In (b) monocot stems, vascular bundles composed of xylem and phloem tissues are scattered throughout the ground tissue.

Xylem tissue has three types of cells: xylem parenchyma, tracheids, and vessel elements. The latter two types conduct water and are dead at maturity. Tracheids are xylem cells with thick secondary cell walls that are lignified. Water moves from one tracheid to another through regions on the side walls known as pits where secondary walls are absent. Vessel elements are xylem cells with thinner walls; they are shorter than tracheids. Each vessel element is connected to the next by means of a perforation plate at the end walls of the element. Water moves through the perforation plates to travel up the plant.

Phloem tissue is composed of sieve-tube cells, companion cells, phloem parenchyma, and phloem fibers. A series of sieve-tube cells (also called sieve-tube elements) are arranged end-to-end to create a long sieve tube, which transports organic substances such as sugars and amino acids. The sugars flow from one sieve-tube cell to the next through perforated sieve plates, which are found at the end junctions between two cells. Although still alive at maturity, the nucleus and other cell components of the sieve-tube cells have disintegrated. Companion cells are found alongside the sieve-tube cells, providing them with metabolic support. The companion cells contain more ribosomes and mitochondria than do the sieve-tube cells, which lack some cellular organelles.

Ground Tissue

Ground tissue is mostly made up of parenchyma cells, but may also contain collenchyma and sclerenchyma cells that help support the stem. The ground tissue towards the interior of the vascular tissue in a stem or root is known as pith, while the layer of tissue between the vascular tissue and the epidermis is known as the cortex.

Key Points

- The stem has three simple cell types: the parenchyma, collenchyma, and sclerenchyma cells that are responsible for metabolic functions, repairing and healing wounds, and storing starch.
- The stem is composed of three tissue systems that include the epidermis, vascular, and ground tissues, all of which are made from the simple cell types..
- The xylem and phloem carry water and nutrients up and down the length of the stem and are arranged in distinct strands called vascular bundles.
- The epidermis is a single layer of cells that makes up the dermal tissue covering the stem and protecting the underlying tissue. Woody plants have an extra layer of protection on top of the epidermis made of cork cells known as bark.
- The vascular tissue of the stem consists of the complex tissues xylem and phloem which carry water and nutrients up and down the length of the stem and are arranged in distinct strands called vascular bundles.
- Ground tissue helps support the stem and is called pith when it is located towards the middle of the stem and called the cortex when it is between the vascular tissue and the epidermis.

Key Terms

- **collenchyma**: a supporting ground tissue just under the surface of various leaf structures formed before vascular differentiation
- **sclerenchyma**: a mechanical, supportive ground tissue in plants consisting of aggregates of cells having thick, often mineralized walls
- **sclereid**: a reduced form of sclerenchyma cells with highly-thickened, lignified walls
- **lignin**: a complex, non-carbohydrate, aromatic polymer present in all wood
- **stoma**: a pore found in the leaf and stem epidermis used for gaseous exchange
- **trichome**: a hair- or scale-like extension of the epidermis of a plant
- **xylem**: a vascular tissue in land plants primarily responsible for the distribution of water and minerals taken up by the roots; also the primary component of wood
- **phloem**: a vascular tissue in land plants primarily responsible for the distribution of sugars and nutrients manufactured in the shoot
- **tracheid**: elongated cells in the xylem of vascular plants that serve in the transport of water and mineral salts
- **pith**: the soft spongy substance in the center of the stems of many plants and trees
- **cortex**: the tissue of a stem or root that lies inward from the epidermis, but exterior to the vascular tissue
- **parenchyma**: the ground tissue making up most of the non-woody parts of a plant

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30.4: Stems - Primary and Secondary Growth in Stems

Learning Objectives

- Distinguish between primary and secondary growth in stems

Growth in plants occurs as the stems and roots lengthen. Some plants, especially those that are woody, also increase in thickness during their life span. The increase in length of the shoot and the root is referred to as primary growth. It is the result of cell division in the shoot apical meristem. Secondary growth is characterized by an increase in thickness or girth of the plant. It is caused by cell division in the lateral meristem. Herbaceous plants mostly undergo primary growth, with little secondary growth or increase in thickness. Secondary growth, or "wood", is noticeable in woody plants; it occurs in some dicots, but occurs very rarely in monocots.

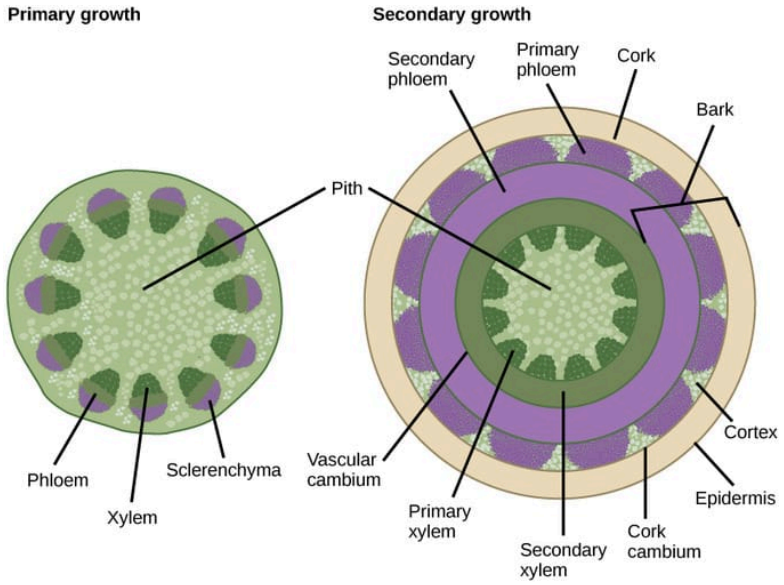


Figure 30.4.1: Primary and secondary growth: In woody plants, primary growth is followed by secondary growth, which allows the plant stem to increase in thickness or girth. Secondary vascular tissue is added as the plant grows, as well as a cork layer. The bark of a tree extends from the vascular cambium to the epidermis.

Some plant parts, such as stems and roots, continue to grow throughout a plant's life: a phenomenon called indeterminate growth. Other plant parts, such as leaves and flowers, exhibit determinate growth, which ceases when a plant part reaches a particular size.

Primary Growth

Most primary growth occurs at the apices, or tips, of stems and roots. Primary growth is a result of rapidly-dividing cells in the apical meristems at the shoot tip and root tip. Subsequent cell elongation also contributes to primary growth. The growth of shoots and roots during primary growth enables plants to continuously seek water (roots) or sunlight (shoots).

The influence of the apical bud on overall plant growth is known as apical dominance, which diminishes the growth of axillary buds that form along the sides of branches and stems. Most coniferous trees exhibit strong apical dominance, thus producing the typical conical Christmas tree shape. If the apical bud is removed, then the axillary buds will start forming lateral branches. Gardeners make use of this fact when they prune plants by cutting off the tops of branches, thus encouraging the axillary buds to grow out, giving the plant a bushy shape.

Secondary Growth

The increase in stem thickness that results from secondary growth is due to the activity of the lateral meristems, which are lacking in herbaceous plants. Lateral meristems include the vascular cambium and, in woody plants, the cork cambium. The vascular cambium is located just outside the primary xylem and to the interior of the primary phloem. The cells of the vascular cambium divide and form secondary xylem (tracheids and vessel elements) to the inside and secondary phloem (sieve elements and companion cells) to the outside. The thickening of the stem that occurs in secondary growth is due to the formation of secondary phloem and secondary xylem by the vascular cambium, plus the action of cork cambium, which forms the tough outermost layer of the stem. The cells of the secondary xylem contain lignin, which provides hardiness and strength.

In woody plants, cork cambium is the outermost lateral meristem. It produces cork cells (bark) containing a waxy substance known as suberin that can repel water. The bark protects the plant against physical damage and helps reduce water loss. The cork cambium also produces a layer of cells known as phelloderm, which grows inward from the cambium. The cork cambium, cork cells, and phelloderm are collectively termed the periderm. The periderm substitutes for the epidermis in mature plants. In some plants, the periderm has many openings, known as lenticels, which allow the interior cells to exchange gases with the outside atmosphere. This supplies oxygen to the living- and metabolically-active cells of the cortex, xylem, and phloem.



Figure 30.4.1: Example of lenticels: Lenticels on the bark of this cherry tree enable the woody stem to exchange gases with the surrounding atmosphere.

Annual Rings

The activity of the vascular cambium gives rise to annual growth rings. During the spring growing season, cells of the secondary xylem have a large internal diameter; their primary cell walls are not extensively thickened. This is known as early wood, or spring wood. During the fall season, the secondary xylem develops thickened cell walls, forming late wood, or autumn wood, which is denser than early wood. This alternation of early and late wood is due largely to a seasonal decrease in the number of vessel elements and a seasonal increase in the number of tracheids. It results in the formation of an annual ring, which can be seen as a circular ring in the cross section of the stem. An examination of the number of annual rings and their nature (such as their size and cell wall thickness) can reveal the age of the tree and the prevailing climatic conditions during each season.

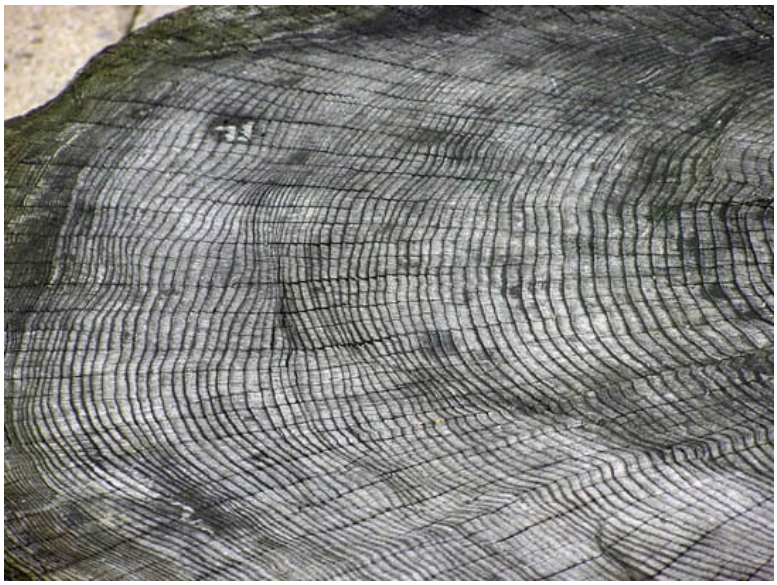


Figure 30.4.1: Annual growth rings: The rate of wood growth increases in summer and decreases in winter, producing a characteristic ring for each year of growth. Seasonal changes in weather patterns can also affect the growth rate. Note how the rings vary in thickness.

Key Points

- Indeterminate growth continues throughout a plant's life, while determinate growth stops when a plant element (such as a leaf) reaches a particular size.
- Primary growth of stems is a result of rapidly-dividing cells in the apical meristems at the shoot tips.
- Apical dominance reduces the growth along the sides of branches and stems, giving the tree a conical shape.
- The growth of the lateral meristems, which includes the vascular cambium and the cork cambium (in woody plants), increases the thickness of the stem during secondary growth.
- Cork cells (bark) protect the plant against physical damage and water loss; they contain a waxy substance known as suberin that prevents water from penetrating the tissue.
- The secondary xylem develops dense wood during the fall and thin wood during the spring, which produces a characteristic ring for each year of growth.

Key Terms

- **lenticel**: small, oval, rounded spots upon the stem or branch of a plant that allow the exchange of gases with the surrounding atmosphere
- **periderm**: the outer layer of plant tissue; the outer bark
- **suberin**: a waxy material found in bark that can repel water

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30.5: Stems - Stem Modifications

Learning Objectives

- Explain the reasons for stem modifications

Some plant species have modified stems that are especially suited to a particular habitat and environment. A rhizome is a modified stem that grows horizontally underground; it has nodes and internodes. Vertical shoots may arise from the buds on the rhizome of some plants, such as ginger and ferns. Corms are similar to rhizomes, except they are more rounded and fleshy (such as in gladiolus). Corms contain stored food that enables some plants to survive the winter. Stolons are stems that run almost parallel to the ground, or just below the surface, and can give rise to new plants at the nodes. Runners are a type of stolon that runs above the ground and produces new clone plants at nodes at varying intervals: strawberries are an example. Tubers are modified stems that may store starch, as seen in the potato. Tubers arise as swollen ends of stolons, and contain many adventitious or unusual buds (familiar to us as the “eyes” on potatoes). A bulb, which functions as an underground storage unit, is a modification of a stem that has the appearance of enlarged fleshy leaves emerging from the stem or surrounding the base of the stem, as seen in the iris.



Figure 30.5.1: Stem modifications: Stem modifications enable plants to thrive in a variety of environments. Shown are (a) ginger (Zingiber officinale) rhizomes, (b) a carrion flower (Amorphophallus titanum) corm (c) Rhodes grass (Chloris gayana) stolons, (d) strawberry (Fragaria ananassa) runners, (e) potato (Solanum tuberosum) tubers, and (f) red onion (Allium) bulbs.

Modifications to the aerial stems, vegetative buds, and floral buds of plants perform functions such as climbing, protection, and synthesis of food vegetative propagation. Aerial modifications of stems include the following:



Figure 30.5.1: Aerial modifications of stems: Found in southeastern United States, (a) buckwheat vine (Brunnichia ovata) is a weedy plant that climbs with the aid of tendrils. This one is shown climbing up a wooden stake. (b) Thorns are modified branches.

- Tendrils are slender, twining strands that enable a plant (like the buckwheat vine) to seek support by climbing on other surfaces. These may develop from either the axillary bud or the terminal bud of the stem.
- Thorns are modified branches appearing as hard, woody, sharp outgrowths that protect the plant; common examples include roses, osage orange, and devil's walking stick.
- Bulbils are axillary buds that have become fleshy and rounded due to storage of food. They become detached from the plant, fall on ground and develop into a new plant.
- Cladodes are green branches of limited growth (usually one internode long) which have taken up the functions of photosynthesis.

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Key Points

- Modified stems that grow horizontally underground are either rhizomes, from which vertical shoots grow, or fleshier, food-storing corms.
- New plants can arise from the nodes of stolons and runners (an aboveground stolon): stems that run parallel to the ground, or just below the surface.
- Potatoes are examples of tubers: the swollen ends of stolons that may store starch.
- The stem modification that has enlarged fleshy leaves emerging from the stem or surrounding the base of the stem is called a bulb; it is also used to store food.
- Aerial modifications of stems include tendrils, thorns, bulbils, and cladodes..

Key Terms

- **stolon**: a shoot that grows along the ground and produces roots at its nodes; a runner
- **tuber**: a fleshy, thickened, underground stem of a plant, usually containing stored starch, as for example a potato or arrowroot
- **cladode**: green branches of limited growth which have taken up the functions of photosynthesis
- **rhizome**: a horizontal underground stem of some plants that sends out roots and shoots from its nodes
- **corm**: a short, vertical, swollen underground stem of a plant that serves as a storage organ to enable the plant to survive winter or other adverse conditions such as drought
- **bulb**: the bulb-shaped root portion of a plant such as a tulip, from which the rest of the plant may be regrown
- **tendril**: a thin, spirally-coiling stem that attaches a plant to its support
- **thorn**: a sharp, protective spine of a plant
- **bulbil**: a bulb-shaped bud in the place of a flower or in a leaf axil

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30.6: Roots - Types of Root Systems and Zones of Growth

Learning Objectives

- Describe the three zones of the root tip and summarize the role of each zone in root growth

Types of Root Systems

There are two main types of root systems. Dicots have a tap root system, while monocots have a fibrous root system, which is also known as an adventitious root system. A tap root system has a main root that grows down vertically, from which many smaller lateral roots arise. Dandelions are a common example; their tap roots usually break off when these weeds are pulled from the ground; they can regrow another shoot from the remaining root. A tap root system penetrates deep into the soil. In contrast, a fibrous root system is located closer to the soil surface where it forms a dense network of roots that also helps prevent soil erosion (lawn grasses are a good example, as are wheat, rice, and corn). Some plants have a combination of tap roots and fibrous roots. Plants that grow in dry areas often have deep root systems, whereas plants that grow in areas with abundant water are likely to have shallower root systems.



Figure 30.6.1: Main types of root systems: (a) Tap root systems have a main root that grows down, while (b) fibrous root systems consist of many small roots.

Zones of the Root Tip

Root growth begins with seed germination. When the plant embryo emerges from the seed, the radicle of the embryo forms the root system. The tip of the root is protected by the root cap, a structure exclusive to roots and unlike any other plant structure. The root cap is continuously replaced because it is easily damaged as the root pushes through soil. The root tip can be divided into three zones: a zone of cell division, a zone of elongation, and a zone of maturation. The zone of cell division is closest to the root tip and is made up of the actively-dividing cells of the root meristem, which contains the undifferentiated cells of the germinating plant. The zone of elongation is where the newly-formed cells increase in length, thereby lengthening the root. Beginning at the first root hair is the zone of cell maturation where the root cells differentiate into specialized cell types. All three zones are in approximately the first centimeter of the root tip.

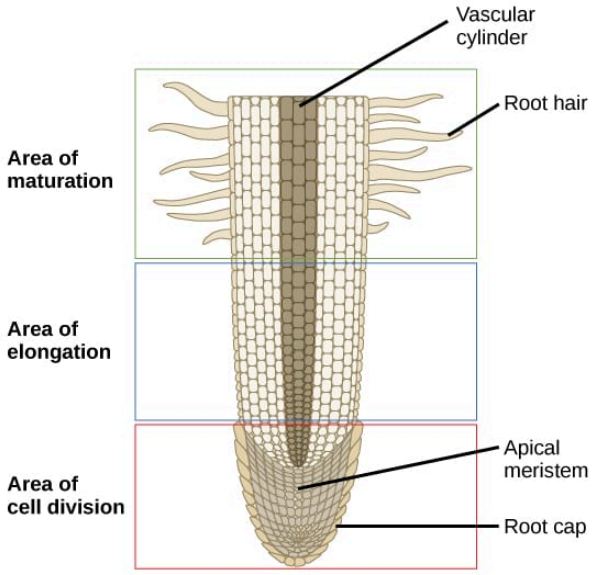


Figure 30.6.1: Zones of the root tip: A longitudinal view of the root reveals the zones of cell division, elongation, and maturation. Cell division occurs in the apical meristem.

Key Points

- Root tips ultimately develop into two main types of root systems: tap roots and fibrous roots.
- The growing root tip is protected by a root cap.
- Within the root tip, cells differentiate, actively divide, and increase in length, depending on in which zone the cells are located.
- Dividing cells make up the zone of cell division in a germinating plant.
- The newly-forming root increases in size in the zone of elongation.
- Differentiating cells make up the zone of cell maturation.

Key Terms

- **radicle**: the rudimentary shoot of a plant that supports the cotyledons in the seed and from which the root is developed downward; the root of the embryo
- **meristem**: the plant tissue composed of totipotent cells that allows plant growth
- **germination**: the beginning of vegetation or growth from a seed or spore

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30.7: Roots - Root Modifications

Learning Objectives

- Explain the reasons for root modifications

Plants have different root structures for specific purposes. There are many different types of specialized roots, but two of the more familiar types of roots include aerial roots and storage roots. Aerial roots grow above the ground, typically providing structural support. Storage roots (for example, taproots and tuberous roots) are modified for food storage.

Aerial roots are found in many different kinds of plants, offering varying functions depending on the location of the plant. Epiphytic roots are a type of aerial root that enable a plant to grow on another plant in a non-parasitic manner. The banyan tree begins as an epiphyte, germinating in the branches of a host tree. Aerial prop roots develop from the branches and eventually reach the ground, providing additional support. Over time, many roots will come together to form what appears to be a trunk. The epiphytic roots of orchids develop a spongy tissue to absorb moisture and nutrients from any organic material on their roots. In screwpine, a palm-like tree that grows in sandy tropical soils, aerial roots develop to provide additional support that help the tree remain upright in shifting sand and water conditions.



Figure 30.7.1: Aerial roots: The (a) banyan tree, also known as the strangler fig, begins life as an epiphyte in a host tree. Aerial roots extend to the ground, supporting the growing plant, which eventually strangles the host tree. The (b) screwpine develops aerial roots that help support the plant in sandy soils.

Storage roots, such as carrots, beets, and sweet potatoes, are examples of roots that are specially modified for storage of starch and water. They usually grow underground as protection from plant-eating animals. Some plants, however, such as leaf succulents and cacti, store energy in their leaves and stems, respectively, instead of in their roots.



Figure 30.7.1: Storage roots: Many vegetables, such as carrots and beets, are modified roots that store food and water.

Other examples of modified roots are aerating roots and haustorial roots. Aerating roots, which rise above the ground, especially above water, are commonly seen in mangrove forests that grow along salt water coastlines. Haustorial roots are often seen in parasitic plants such as mistletoe. Their roots allow the plants to absorb water and nutrients from other plants.

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Key Points

- Storage roots, which include a large number of edible vegetables such as potatoes and carrots, are some of the most commonly-known types of modified roots.
- Aerial roots encompass a variety of shapes, yet function similarly as structural support for the plant.
- Parasitic plants have special haustorial roots that allow the plant to absorb nutrients from a host plant.

Key Terms

- **succulent**: having fleshy leaves or other tissues that store water
- **epiphyte**: a plant that grows on another, using it as a physical support but neither obtaining nutrients from it nor causing it any damage if also offering no benefit

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30.8: Leaves - Leaf Structure and Arrangment

Learning Objectives

- Sketch the basic structure of a typical leaf

Structure of a Typical Leaf

Each leaf typically has a leaf blade called the lamina, which is also the widest part of the leaf. Some leaves are attached to the plant stem by a petiole. Leaves that do not have a petiole and are directly attached to the plant stem are called sessile leaves. Leaves also have stipules, small green appendages usually found at the base of the petiole. Most leaves have a midrib, which travels the length of the leaf and branches to each side to produce veins of vascular tissue. The edge of the leaf is called the **margin**.

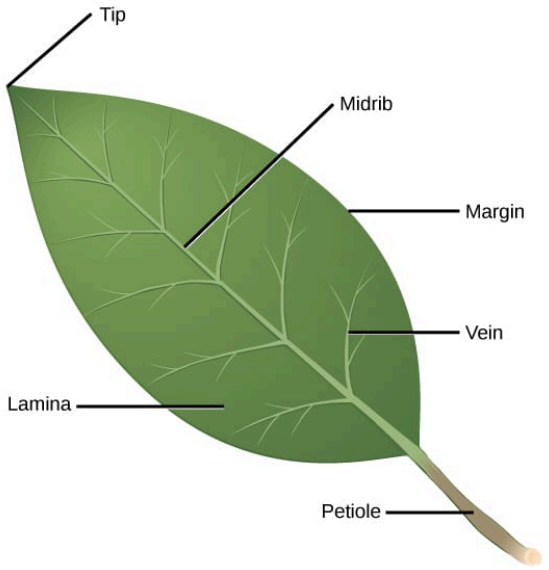


Figure 30.8.1: Parts of a leaf: A leaf may seem simple in appearance, but it is a highly-efficient structure. Petioles, stipules, veins, and a midrib are all essential structures of a leaf.

Within each leaf, the vascular tissue forms veins. The arrangement of veins in a leaf is called the **venation pattern**. Monocots and dicots differ in their patterns of venation. Monocots have parallel venation in which the veins run in straight lines across the length of the leaf without converging. In dicots, however, the veins of the leaf have a net-like appearance, forming a pattern known as reticulate venation. *Ginkgo biloba* is an example of a plant with dichotomous venation.

Leaf Arrangement

The arrangement of leaves on a stem is known as **phyllotaxy**. The number and placement of a plant's leaves will vary depending on the species, with each species exhibiting a characteristic leaf arrangement. Leaves are classified as either alternate, spiral, opposite, or whorled. Plants that have only one leaf per node have leaves that are said to be either alternate or spiral. Alternate leaves alternate on each side of the stem in a flat plane, and spiral leaves are arranged in a spiral along the stem. In an opposite leaf arrangement, two leaves arise at the same point, with the leaves connecting opposite each other along the branch. If there are three or more leaves connected at a node, the leaf arrangement is classified as whorled.

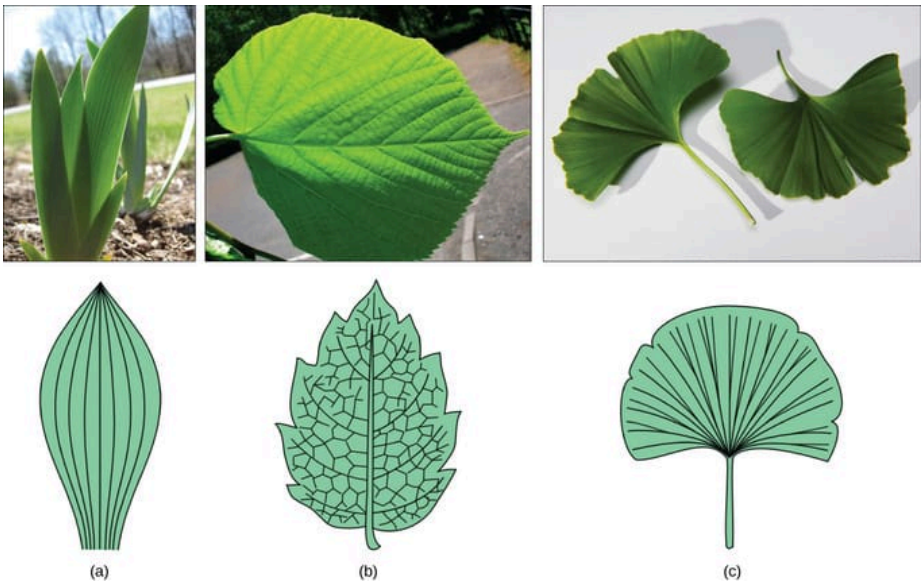


Figure 30.8.1: Venation patterns: (a) Tulip (*Tulipa*), a monocot, has leaves with parallel venation. (b) The netlike venation in this linden (*Tilia cordata*) leaf distinguishes it as a dicot. (c) The Ginkgo biloba tree has dichotomous venation.

Key Points

- Each leaf typically has a leaf blade (lamina), stipules, a midrib, and a margin.
- Some leaves have a petiole, which attaches the leaf to the stem; leaves that do not have petioles are directly attached to the plant stem and are called sessile leaves.
- The arrangement of veins in a leaf is called the venation pattern; monocots have parallel venation, while dicots have reticulate venation.
- The arrangement of leaves on a stem is known as phyllotaxy; leaves can be classified as either alternate, spiral, opposite, or whorled.
- Plants with alternate and spiral leaf arrangements have only one leaf per node.
- In an opposite leaf arrangement, two leaves connect at a node. In a whorled arrangement, three or more leaves connect at a node.

Key Terms

- **petiole**: stalk that extends from the stem to the base of the leaf
- **lamina**: the flat part of a leaf; the blade, which is the widest part of the leaf
- **stipule**: small green appendage usually found at the base of the petiole

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30.9: Leaves - Types of Leaf Forms

Learning Objectives

- Differentiate among the types of leaf forms

Leaf Form

There are two basic forms of leaves that can be described considering the way the blade (or lamina) is divided. Leaves may be simple or compound.

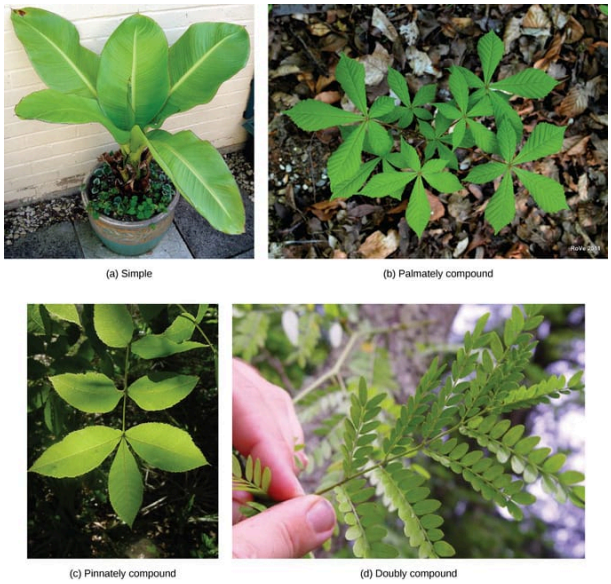


Figure 30.9.1: Simple and compound leaves: Leaves may be simple or compound. In simple leaves, the lamina is continuous. (a) The banana plant (*Musa sp.*) has simple leaves. In compound leaves, the lamina is separated into leaflets. Compound leaves may be palmate or pinnate. (b) In palmately compound leaves, such as those of the horse chestnut (*Aesculus hippocastanum*), the leaflets branch from the petiole. (c) In pinnately compound leaves, the leaflets branch from the midrib, as on a scrub hickory (*Carya floridana*). (d) The honey locust has double compound leaves, in which leaflets branch from the veins.

In a simple leaf, such as the banana leaf, the blade is completely undivided. The leaf shape may also be formed of lobes where the gaps between lobes do not reach to the main vein. An example of this type is the maple leaf.

In a compound leaf, the leaf blade is completely divided, forming leaflets, as in the locust tree. Compound leaves are a characteristic of some families of higher plants. Each leaflet is attached to the rachis (middle vein), but may have its own stalk. A palmately compound leaf has its leaflets radiating outwards from the end of the petiole, like fingers off the palm of a hand. Examples of plants with palmately compound leaves include poison ivy, the buckeye tree, or the familiar house plant *Schefflera sp.* (commonly called “umbrella plant”). Pinnately compound leaves take their name from their feather-like appearance; the leaflets are arranged along the middle vein, as in rose leaves or the leaves of hickory, pecan, ash, or walnut trees. In a pinnately compound leaf, the middle vein is called the midrib. Bipinnately compound (or double compound) leaves are twice divided; the leaflets are arranged along a secondary vein, which is one of several veins branching off the middle vein. Each leaflet is called a “pinnule”. The pinnules on one secondary vein are called “pinna”. The silk tree (*Albizia*) is an example of a plant with bipinnate leaves.

Key Points

- In a simple leaf, the blade is completely undivided; leaves may also be formed of lobes where the gaps between lobes do not reach to the main vein.

- In a compound leaf, the leaf blade is divided, forming leaflets that are attached to the middle vein, but have their own stalks.
- The leaflets of palmately-compound leaves radiate outwards from the end of the petiole.
- Pinnately-compound leaves have their leaflets arranged along the middle vein.
- Bipinnately-compound (double-compound) leaves have their leaflets arranged along a secondary vein, which is one of several veins branching off the middle vein.

Key Terms

- **simple leaf**: a leaf with an undivided blade
- **compound leaf**: a leaf where the blade is divided, forming leaflets
- **palmately compound leaf**: leaf that has its leaflets radiating outwards from the end of the petiole
- **pinnately compound leaf**: a leaf where the leaflets are arranged along the middle vein

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30.10: Leaves - Leaf Structure, Function, and Adaptation

Learning Objectives

- Describe the internal structure and function of a leaf

Leaf Structure and Function

The outermost layer of the leaf is the epidermis. It consists of the upper and lower epidermis, which are present on either side of the leaf. Botanists call the upper side the adaxial surface (or adaxis) and the lower side the abaxial surface (or abaxis). The epidermis aids in the regulation of gas exchange. It contains stomata, which are openings through which the exchange of gases takes place. Two guard cells surround each stoma, regulating its opening and closing. Guard cells are the only epidermal cells to contain chloroplasts.

The epidermis is usually one cell layer thick. However, in plants that grow in very hot or very cold conditions, the epidermis may be several layers thick to protect against excessive water loss from transpiration. A waxy layer known as the cuticle covers the leaves of all plant species. The cuticle reduces the rate of water loss from the leaf surface. Other leaves may have small hairs (trichomes) on the leaf surface. Trichomes help to avert herbivory by restricting insect movements or by storing toxic or bad-tasting compounds. They can also reduce the rate of transpiration by blocking air flow across the leaf surface.

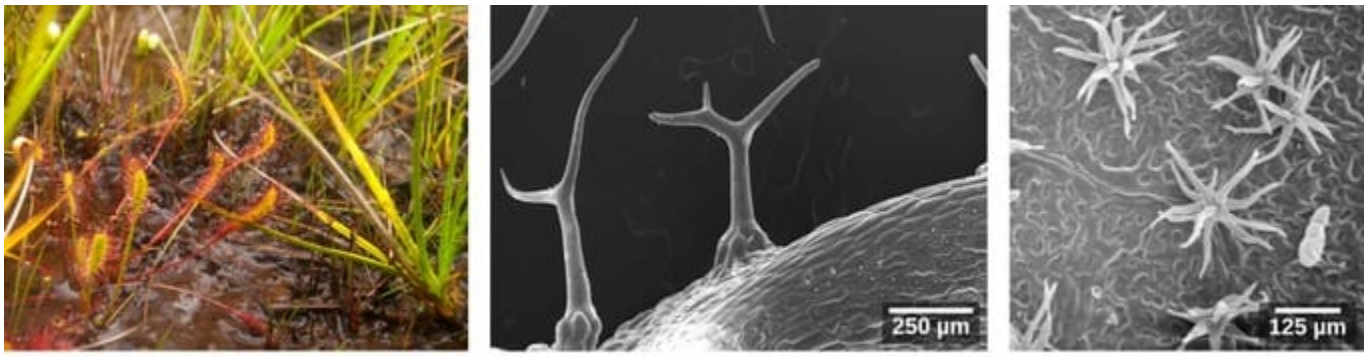


Figure 30.10.1: Trichomes: Trichomes give leaves a fuzzy appearance as in this (a) sundew *(Drosera sp.)*. Leaf trichomes include (b) branched trichomes on the leaf of *Arabidopsis lyrata* and (c) multibranched trichomes on a mature *Quercus marilandica* leaf.

Below the epidermis of dicot leaves are layers of cells known as the mesophyll, or “middle leaf.” The mesophyll of most leaves typically contains two arrangements of parenchyma cells: the palisade parenchyma and spongy parenchyma. The palisade parenchyma (also called the palisade mesophyll) aids in photosynthesis and has column-shaped, tightly-packed cells. It may be present in one, two, or three layers. Below the palisade parenchyma are loosely-arranged cells of an irregular shape. These are the cells of the spongy parenchyma (or spongy mesophyll). The air space found between the spongy parenchyma cells allows gaseous exchange between the leaf and the outside atmosphere through the stomata. In aquatic plants, the intercellular spaces in the spongy parenchyma help the leaf float. Both layers of the mesophyll contain many chloroplasts.

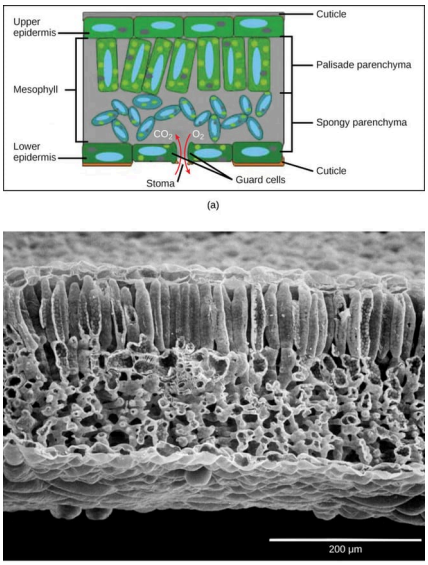


Figure 30.10.1: Mesophyll: (a) (top) The central mesophyll is sandwiched between an upper and lower epidermis. The mesophyll has two layers: an upper palisade layer and a lower spongy layer. Stomata on the leaf underside allow gas exchange. A waxy cuticle covers all aerial surfaces of land plants to minimize water loss. (b) (bottom) These leaf layers are clearly visible in the scanning electron micrograph. The numerous small bumps in the palisade parenchyma cells are chloroplasts. The bumps protruding from the lower surface of the leaf are glandular trichomes.

Similar to the stem, the leaf contains vascular bundles composed of xylem and phloem. The xylem consists of tracheids and vessels, which transport water and minerals to the leaves. The phloem transports the photosynthetic products from the leaf to the other parts of the plant. A single vascular bundle, no matter how large or small, always contains both xylem and phloem tissues.

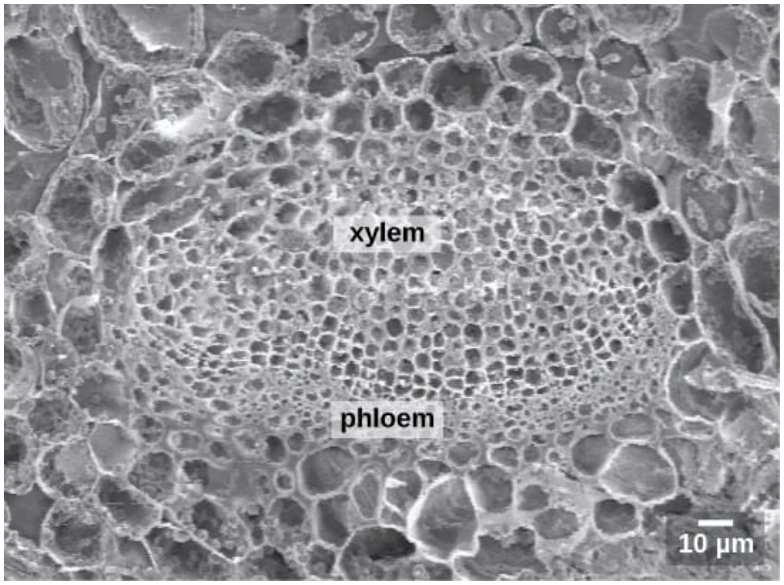


Figure 30.10.1: Xylem and phloem: This scanning electron micrograph shows xylem and phloem in the leaf vascular bundle.

Leaf Adaptations

Coniferous plant species that thrive in cold environments, such as spruce, fir, and pine, have leaves that are reduced in size and needle-like in appearance. These needle-like leaves have sunken stomata and a smaller surface area, two attributes that aid in reducing water loss. In hot climates, plants such as cacti have succulent leaves that help to conserve water. Many aquatic plants have leaves with wide lamina that can float on the surface of the water; a thick waxy cuticle on the leaf surface that repels water.

Key Points

- The epidermis consists of the upper and lower epidermis; it aids in the regulation of gas exchange via stomata.
- The epidermis is one layer thick, but may have more layers to prevent transpiration.
- The cuticle is located outside the epidermis and protects against water loss; trichomes discourage predation.
- The mesophyll is found between the upper and lower epidermis; it aids in gas exchange and photosynthesis via chloroplasts.
- The xylem transports water and minerals to the leaves; the phloem transports the photosynthetic products to the other parts of the plant.
- Plants in cold climates have needle-like leaves that are reduced in size; plants in hot climates have succulent leaves that help to conserve water.

Key Terms

- **trichome**: a hair- or scale-like extension of the epidermis of a plant
- **cuticle**: a noncellular protective covering outside the epidermis of many invertebrates and plants
- **mesophyll**: the inner tissue (parenchyma) of a leaf, containing many chloroplasts.

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30.11: Plant Development - Meristems

Learning Objectives

- Discuss the attributes of meristem tissue and its role in plant development and growth

The adult body of vascular plants is the result of meristematic activity. Plant meristems are centers of mitotic cell division, and are composed of a group of undifferentiated self-renewing stem cells from which most plant structures arise. Meristematic cells are also responsible for keeping the plant growing. The Shoot Apical Meristem (SAM) gives rise to organs like the leaves and flowers, while the Root Apical Meristem (RAM) provides the meristematic cells for the future root growth. The cells of the shoot and root apical meristems divide rapidly and are considered to be indeterminate, which means that they do not possess any defined end fate. In that sense, the meristematic cells are frequently compared to the stem cells in animals, which have an analogous behavior and function.

Meristem tissue and plant development

Meristematic tissues are cells or group of cells that have the ability to divide. These tissues in a plant consist of small, densely packed cells that can keep dividing to form new cells. Meristematic tissue is characterized by small cells, thin cell walls, large cell nuclei, absent or small vacuoles, and no intercellular spaces.

Meristematic tissues are found in many locations, including near the tips of roots and stems (apical meristems), in the buds and nodes of stems, in the cambium between the xylem and phloem in dicotyledonous trees and shrubs, under the epidermis of dicotyledonous trees and shrubs (cork cambium), and in the pericycle of roots, producing branch roots. The two types of meristems are primary meristems and secondary meristems.

Meristem Zones

The apical meristem, also known as the “growing tip,” is an undifferentiated meristematic tissue found in the buds and growing tips of roots in plants. Its main function is to trigger the growth of new cells in young seedlings at the tips of roots and shoots and forming buds. Apical meristems are organized into four zones: (1) the central zone, (2) the peripheral zone, (3) the medullary meristem and (3) the medullary tissue.

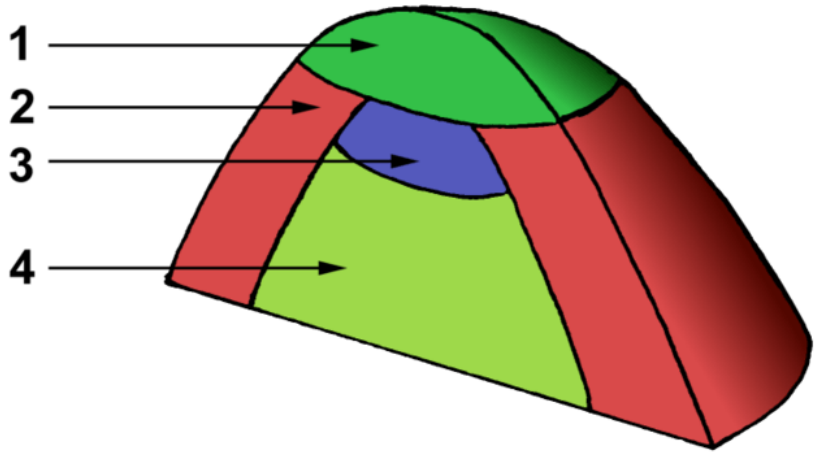


Figure 30.11.1: Meristematic zones: Each zone of the apical meristem has a particular function. Pictured here are the (1) central zone, (2) peripheral zone, (3) medullary meristem and (3) medullary tissue.



Figure 30.11.1: Apical meristem: The apical meristem, pictured in the center of the leaves of this image, is also termed the “growing tip”. Its main function is to begin growth of new cells in young seedlings at the tips of roots and shoots (forming buds, among other things).

The central zone is located at the meristem summit, where a small group of slowly dividing cells can be found. Cells of this zone have a stem cell function and are essential for meristem maintenance. The proliferation and growth rates at the meristem summit usually differ considerably from those at the periphery. Surrounding the central zone is the peripheral zone. The rate of cell division in the peripheral zone is higher than that of the central zone. Peripheral zone cells give rise to cells which contribute to the organs of the plant, including leaves, inflorescence meristems, and floral meristems.

An active apical meristem lays down a growing root or shoot behind itself, pushing itself forward. They are very small compared to the cylinder-shaped lateral meristems, and are composed of several layers, which varies according to plant type. The outermost layer is called the tunica, while the innermost layers are cumulatively called the corpus.

Key Points

- Mitotic cell division happens in plant meristems, which are composed of a group of self-renewing stem cells from which most plant structures arise.
- The cells of the shoot and root apical meristems divide rapidly and are “indeterminate”, which means that they are not designed for any specific end goal.
- The Shoot Apical Meristem (SAM) gives rise to organs like the leaves and flowers, while the Root Apical Meristem (RAM) provides cells for future root growth.
- Meristematic tissue has a number of defining features, including small cells, thin cell walls, large cell nuclei, absent or small vacuoles, and no intercellular spaces.
- The apical meristem (the growing tip) functions to trigger the growth of new cells in young seedlings at the tips of roots and shoots and forming buds.
- The apical meristem is organized into four meristematic zones: (1) central zone, (2) peripheral zone, (3) medullary meristem and (3) medullary tissue.

Key Terms

- **meristem**: the plant tissue composed of totipotent cells that allows plant growth
- **undifferentiated**: describes tissues where the individual cells have not yet developed mature or distinguishing features, or describes embryonic organisms where the organs cannot be identified
- **apical**: situated at the growing tip of the plant or its roots, in comparison with intercalary growth situated between zones of permanent tissue

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30.12: Plant Development - Genetic Control of Flowers

Learning Objectives

- Diagram the ABC model of flower development and identify the genes that control that development

Flower development is the process by which angiosperms produce a pattern of gene expression in meristems that leads to the appearance of a flower. A flower (also referred to as a bloom or blossom) is the reproductive structure found in flowering plants. There are three physiological developments that must occur in order for reproduction to take place:

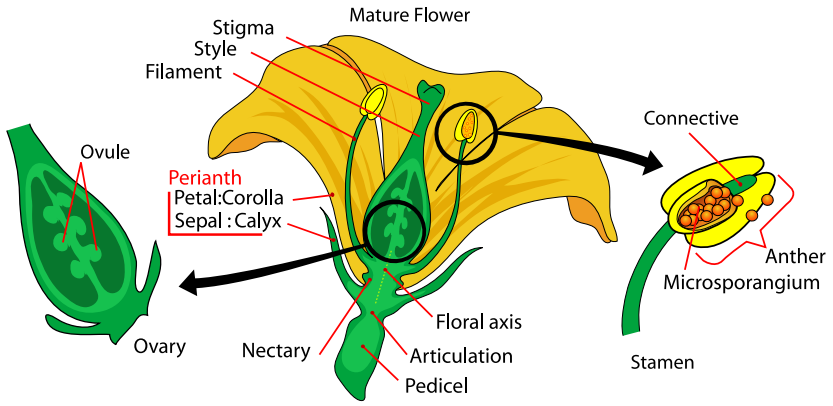


Figure 30.12.1: Anatomy of a flower: Mature flowers aid in reproduction for the plant. In order to achieve reproduction, the plant must become sexually mature, the apical meristem must become a floral meristem, and the flower must develop its individual reproductive organs.

1. the plant must pass from sexual immaturity into a sexually mature state
2. the apical meristem must transform from a vegetative meristem into a floral meristem or inflorescence
3. the flowers individual organs must grow (modeled using the ABC model)

Flower Development

A flower develops on a modified shoot or axis from a determinate apical meristem (determinate meaning the axis grows to a set size). The transition to flowering is one of the major phase changes that a plant makes during its life cycle. The transition must take place at a time that is favorable for fertilization and the formation of seeds, hence ensuring maximal reproductive success. In order to flower at an appropriate time, a plant can interpret important endogenous and environmental cues such as changes in levels of plant hormones and seasonable temperature and photoperiod changes. Many perennial and most biennial plants require vernalization to flower.

Genetic Control of Flower Development

When plants recognize an opportunity to flower, signals are transmitted through florigen, which involves a variety of genes, including CONSTANS, FLOWERING LOCUS C and FLOWERING LOCUS T. Florigen is produced in the leaves in reproductively favorable conditions and acts in buds and growing tips to induce a number of different physiological and morphological changes.

From a genetic perspective, two phenotypic changes that control vegetative and floral growth are programmed in the plant. The first genetic change involves the switch from the vegetative to the floral state. If this genetic change is not functioning properly, then flowering will not occur. The second genetic event follows the commitment of the plant to form flowers. The sequential development of plant organs suggests that a genetic mechanism exists in which a series of genes are sequentially turned on and off. This switching is necessary for each whorl to obtain its final unique identity.

ABC Model of Flower Development

In the simple ABC model of floral development, three gene activities (termed A, B, and C-functions) interact to determine the developmental identities of the organ primordia (singular: primordium) within the floral meristem. The ABC model of flower development was first developed to describe the collection of genetic mechanisms that establish floral organ identity in the Rosids and the Asterids; both species have four verticils (sepals, petals, stamens and carpels), which are defined by the differential expression of a number of homeotic genes present in each verticil.

In the first floral whorl only A-genes are expressed, leading to the formation of sepals. In the second whorl both A- and B-genes are expressed, leading to the formation of petals. In the third whorl, B and C genes interact to form stamens and in the center of the flower C-genes alone give rise to carpels. For example, when there is a loss of B-gene function, mutant flowers are produced with sepals in the first whorl as usual, but also in the second whorl instead of the normal petal formation. In the third whorl the lack of B function but presence of C-function mimics the fourth whorl, leading to the formation of carpels also in the third whorl.

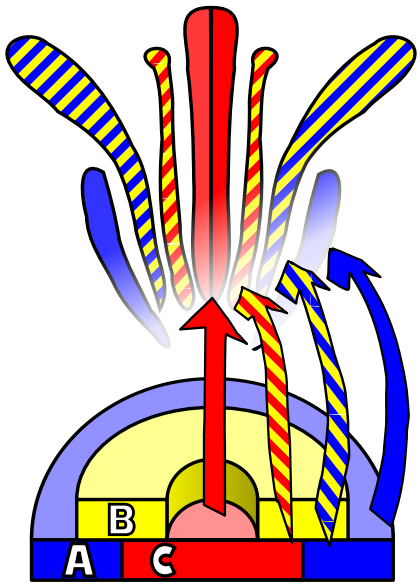


Figure 30.12.1: ABC model of flower development: Class A genes (blue) affect sepals and petals, class B genes (yellow) affect petals and stamens, class C genes (red) affect stamens and carpels.

Most genes central in this model belong to the MADS-box genes and are transcription factors that regulate the expression of the genes specific for each floral organ.

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Key Points

- Flower development describes the process by which angiosperms (flowering plants) produce a pattern of gene expression in meristems that leads to the appearance of a flower; the biological function of a flower is to aid in reproduction.
- In order for flowering to occur, three developments must take place: (1) the plant must reach sexual maturity, (2) the apical meristem must transform from a vegetative meristem to a floral meristem, and (3) the plant must grow individual flower organs.
- These developments are initiated using the transmission of a complex signal known as florigen, which involves a variety of genes, including CONSTANS, FLOWERING LOCUS C and FLOWERING LOCUS T.
- The last development (the growth of the flower's individual organs) has been modeled using the ABC model of flower development.
- Class A genes affect sepals and petals, class B genes affect petals and stamens, class C genes affect stamens and carpels.

Key Terms

- **sepal**: a part of an angiosperm, and one of the component parts of the calyx; collectively the sepals are called the calyx (plural calyces), the outermost whorl of parts that form a flower
- **stamen**: in flowering plants, the structure in a flower that produces pollen, typically consisting of an anther and a filament
- **verticil**: a whorl; a group of similar parts such as leaves radiating from a shared axis
- **biennial**: a plant that requires two years to complete its life cycle
- **whorl**: a circle of three or more leaves, flowers, or other organs, about the same part or joint of a stem
- **apical meristem**: the tissue in most plants containing undifferentiated cells (meristematic cells), found in zones of the plant where growth can take place at the tip of a root or shoot.
- **angiosperm**: a plant whose ovules are enclosed in an ovary
- **perennial**: a plant that is active throughout the year or survives for more than two growing seasons
- **primordium**: an aggregation of cells that is the first stage in the development of an organ

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30.13: Transport of Water and Solutes in Plants - Water and Solute Potential

Learning Objectives

- Describe the water and solute potential in plants

Water Potential

Plants are phenomenal hydraulic engineers. Using only the basic laws of physics and the simple manipulation of potential energy, plants can move water to the top of a 116-meter-tall tree. Plants can also use hydraulics to generate enough force to split rocks and buckle sidewalks. Water potential is critical for moving water to leaves so that photosynthesis can take place.



Figure 30.13.1: Water potential in plants: With heights nearing 116 meters, (a) coastal redwoods (Sequoia sempervirens) are the tallest trees in the world. Plant roots can easily generate enough force to (b) buckle and break concrete sidewalks.

Water potential is a measure of the potential energy in water, or the difference in potential energy between a given water sample and pure water (at atmospheric pressure and ambient temperature). Water potential is denoted by the Greek letter ψ (psi) and is expressed in units of pressure (pressure is a form of energy) called megapascals (MPa). The potential of pure water ($\Psi_w^{\text{pure H2O}}$) is designated a value of zero (even though pure water contains plenty of potential energy, that energy is ignored). Water potential values for the water in a plant root, stem, or leaf are, therefore, expressed in relation to $\Psi_w^{\text{pure H2O}}$.

The water potential in plant solutions is influenced by solute concentration, pressure, gravity, and factors called matrix effects. Water potential can be broken down into its individual components using the following equation:

$$\Psi_{system} = \Psi_{total} = \Psi_s + \Psi_p + \Psi_g + \Psi_m$$

where

- Ψ_s = solute potential
- Ψ_p, = pressure potential
- Ψ_g, = gravity potential
- Ψ_m = matric potential

"System" can refer to the water potential of the soil water (Ψ^{soil}), root water (Ψ^{root}), stem water (Ψ^{stem}), leaf water (Ψ^{leaf}), or the water in the atmosphere ($\Psi^{atmosphere}$), whichever aqueous system is under consideration. As the individual components change, they raise or lower the total water potential of a system. When this happens, water moves to equilibrate, moving from the system or compartment with a higher water potential to the system or compartment with a lower water potential. This brings the difference in water potential between the two systems (Δ) back to zero ($\Delta = 0$). Therefore, for water to move through the plant from the soil to the air (a process called transpiration), the conditions must exist as such:

$\Psi^{soil} > \Psi^{root} > \Psi^{stem} > \Psi^{leaf} > \Psi^{atmosphere}$.

Water only moves in response to Δ, not in response to the individual components. However, because the individual components influence the total Ψ_{system}, a plant can control water movement by manipulating the individual components (especially Ψ_s).

Solute Potential

Solute potential (Ψ_s), also called osmotic potential, is negative in a plant cell and zero in distilled water. Typical values for cell cytoplasm are –0.5 to –1.0 MPa. Solutes reduce water potential (resulting in a negative Ψ_w) by consuming some of the potential energy available in the water. Solute molecules can dissolve in water because water molecules can bind to them via hydrogen bonds; a hydrophobic molecule like oil, which cannot bind to water, cannot go into solution. The energy in the hydrogen bonds between solute molecules and water is no longer available to do work in the system because it is tied up in the bond. In other words, the amount of available potential energy is reduced when solutes are added to an aqueous system. Thus, Ψ_s decreases with increasing solute concentration. Because Ψ_s is one of the four components of Ψ_{system} or Ψ_{total}, a decrease in Ψ_s will cause a decrease in Ψ_{total}. The internal water potential of a plant cell is more negative than pure water because of the cytoplasm's high solute content. Because of this difference in water potential, water will move from the soil into a plant's root cells via the process of osmosis. This is why solute potential is sometimes called osmotic potential.

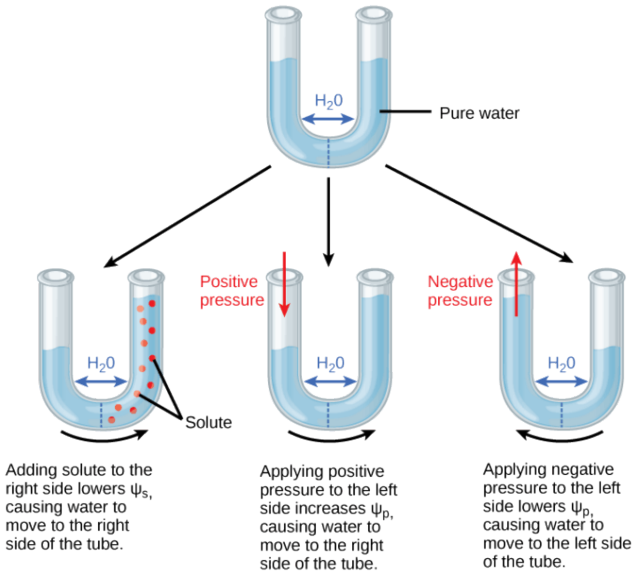


Figure 30.13.1: Solute potential: In this example with a semipermeable membrane between two aqueous systems, water will move from a region of higher to lower water potential until equilibrium is reached. Solutes (Ψ_s), pressure (Ψ_p), and gravity (Ψ_g) influence total water potential for each side of the tube ($\Psi_{total\ right\ or\ left}$) and, therefore, the difference between Ψ_{total} on each side (Δ). (Ψ_m, the potential due to interaction of water with solid substrates, is ignored in this example because glass is not especially hydrophilic). Water moves in response to the difference in water potential between two systems (the left and right sides of the tube).

Plant cells can metabolically manipulate Ψ_s (and by extension, Ψ_{total}) by adding or removing solute molecules. Therefore, plants have control over Ψ_{total} via their ability to exert metabolic control over Ψ_s.

Key Points

- Plants use water potential to transport water to the leaves so that photosynthesis can take place.

- Water potential is a measure of the potential energy in water as well as the difference between the potential in a given water sample and pure water.
- Water potential is represented by the equation $\Psi_{system} = \Psi_{total} = \Psi_s + \Psi_p + \Psi_g + \Psi_m$.
- Water always moves from the system with a higher water potential to the system with a lower water potential.
- Solute potential (Ψ_s) decreases with increasing solute concentration; a decrease in Ψs causes a decrease in the total water potential.
- The internal water potential of a plant cell is more negative than pure water; this causes water to move from the soil into plant roots via osmosis..

Key Terms

- **solute potential**: (osmotic potential) pressure which needs to be applied to a solution to prevent the inward flow of water across a semipermeable membrane
- **transpiration**: the loss of water by evaporation in terrestrial plants, especially through the stomata; accompanied by a corresponding uptake from the roots
- **water potential**: the potential energy of water per unit volume; designated by ψ

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30.14: Transport of Water and Solutes in Plants - Pressure, Gravity, and Matric Potential

Learning Objectives

- Differentiate among pressure, gravity, and matric potentials in plants

Pressure Potential

Pressure potential is also called turgor potential or turgor pressure and is represented by Ψ_p. Pressure potential may be positive or negative; the higher the pressure, the greater potential energy in a system, and vice versa. Therefore, a positive Ψ_p (compression) increases Ψ_{total}, while a negative Ψ_p (tension) decreases Ψ_{total}. Positive pressure inside cells is contained by the cell wall, producing turgor pressure in a plant. Turgor pressure ensures that a plant can maintain its shape. A plant's leaves wilt when the turgor pressure decreases and revive when the plant has been watered. Pressure potentials are typically around 0.6–0.8 MPa, but can reach as high as 1.5 MPa in a well-watered plant. As a comparison, most automobile tires are kept at a pressure of 30–34 psi or about 0.207-0.234 MPa. Water is lost from the leaves via transpiration (approaching Ψ_p = 0 MPa at the wilting point) and restored by uptake via the roots.



Figure 30.14.1: Turgor pressure: When (a) total water potential (Ψtotal) is lower outside the cells than inside, water moves out of the cells and the plant wilts. When (b) the total water potential is higher outside the plant cells than inside, water moves into the cells, resulting in turgor pressure (Ψp), keeping the plant erect.

A plant can manipulate Ψ_p via its ability to manipulate Ψ_s (solute potential) and by the process of osmosis. Plants must overcome the negative forces of gravity potential (Ψg) and matric potential (Ψm) to maintain a positive pressure potential. If a plant cell increases the cytoplasmic solute concentration:

1. Ψ_s will decline
2. Ψ_{total} will decline
3. the Δ between the cell and the surrounding tissue will decline
4. water will move into the cell by osmosis
5. Ψ_p will increase.

Plants can also regulate Ψ_p by opening and closing the stomata. Stomatal openings allow water to evaporate from the leaf,

reducing Ψ_p and Ψ_{total}. This increases water potential between the water in the the petiole (base of the leaf) and in the leaf, thereby encouraging water to flow from the petiole into the leaf.

Gravity Potential

Gravity potential (Ψ_g) is always negative or zero in a plant with no height. Without height, there is no potential energy in the system. The force of gravity pulls water downwards to the soil, which reduces the total amount of potential energy in the water in the plant (Ψ_{total}). The taller the plant, the taller the water column, and the more influential Ψ_g becomes. On a cellular scale and in short plants, this effect is negligible and easily ignored. However, over the height of a tall tree like a giant coastal redwood, the plant must overcome an extra 1MPa of resistance because of the gravitational pull of -0.1 MPa m^{-1}.

Matric Potential

Matric potential (Ψ_m) is the amount of water bound to the matrix of a plant via hydrogen bonds and is always negative to zero. In a dry system, it can be as low as –2 MPa in a dry seed or as high as zero in a water-saturated system. Every plant cell has a cellulosic cell wall, which is hydrophilic and provides a matrix for water adhesion, hence the name matric potential. The binding of water to a matrix always removes or consumes potential energy from the system. Ψ_m is similar to solute potential because the hydrogen bonds remove energy from the total system. However, in solute potential, the other components are soluble, hydrophilic solute molecules, whereas in Ψ_m, the other components are insoluble, hydrophilic molecules of the plant cell wall. $_m$ cannot be manipulated by the plant and is typically ignored in well-watered roots, stems, and leaves.

Key Points

- The higher the pressure potential (Ψ_p), the more potential energy in a system: a positive Ψ_p increases Ψ_{total}, while a negative Ψ_p decreases Ψ_{total}.
- Positive pressure inside cells is contained by the cell wall, producing turgor pressure, which is responsible for maintaining the structure of leaves; absence of turgor pressure causes wilting.
- Plants lose water (and turgor pressure) via transpiration through the stomata in the leaves and replenish it via positive pressure in the roots.
- Pressure potential is controlled by solute potential (when solute potential decreases, pressure potential increases) and the opening and closing of stomata.
- Gravity potential (Ψ_g) removes potential energy from the system because gravity pulls water downwards to the soil, reducing Ψ_{total}.
- Matric potential (Ψ_m) removes energy from the system because water molecules bind to the cellulose matrix of the plant's cell walls.

Key Terms

- **turgor pressure**: pushes the plasma membrane against the cell wall of plant; caused by the osmotic flow of water from outside of the cell into the cell's vacuole

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30.15: Transport of Water and Solutes in Plants - Movement of Water and Minerals in the Xylem

Learning Objectives

- Outline the movement of water and minerals in the xylem

Movement of Water and Minerals in the Xylem

Most plants obtain the water and minerals they need through their roots. The path taken is: soil -> roots -> stems -> leaves. The minerals (e.g., K+, Ca2+) travel dissolved in the water (often accompanied by various organic molecules supplied by root cells). Water and minerals enter the root by separate paths which eventually converge in the stele, or central vascular bundle in roots.

Transpiration is the loss of water from the plant through evaporation at the leaf surface. It is the main driver of water movement in the xylem. Transpiration is caused by the evaporation of water at the leaf, or atmosphere interface; it creates negative pressure (tension) equivalent to –2 MPa at the leaf surface. However, this value varies greatly depending on the vapor pressure deficit, which can be insignificant at high relative humidity (RH) and substantial at low RH. Water from the roots is pulled up by this tension. At night, when stomata close and transpiration stops, the water is held in the stem and leaf by the cohesion of water molecules to each other as well as the adhesion of water to the cell walls of the xylem vessels and tracheids. This is called the cohesion–tension theory of sap ascent.

The cohesion-tension theory explains how water moves up through the xylem. Inside the leaf at the cellular level, water on the surface of mesophyll cells saturates the cellulose microfibrils of the primary cell wall. The leaf contains many large intercellular air spaces for the exchange of oxygen for carbon dioxide, which is required for photosynthesis. The wet cell wall is exposed to the internal air space and the water on the surface of the cells evaporates into the air spaces. This decreases the thin film on the surface of the mesophyll cells. The decrease creates a greater tension on the water in the mesophyll cells, thereby increasing the pull on the water in the xylem vessels. The xylem vessels and tracheids are structurally adapted to cope with large changes in pressure. Small perforations between vessel elements reduce the number and size of gas bubbles that form via a process called cavitation. The formation of gas bubbles in the xylem is detrimental since it interrupts the continuous stream of water from the base to the top of the plant, causing a break (embolism) in the flow of xylem sap. The taller the tree, the greater the tension forces needed to pull water in a continuous column, increasing the number of cavitation events. In larger trees, the resulting embolisms can plug xylem vessels, making them non-functional.

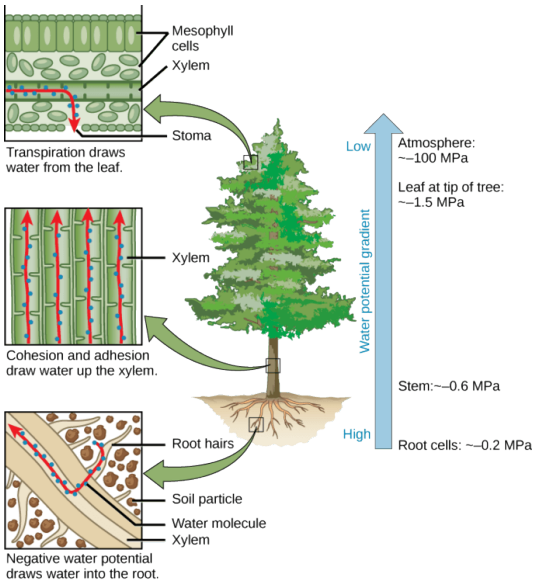


Figure 30.15.1: Cohesion–Tension Theory of Sap Ascent: The cohesion–tension theory of sap ascent is shown. Evaporation from the mesophyll cells produces a negative water potential gradient that causes water to move upwards from the roots through the xylem.

Control of Transpiration

Transpiration is a passive process: metabolic energy in the form of ATP is not required for water movement. The energy driving transpiration is the difference in energy between the water in the soil and the water in the atmosphere. However, transpiration is tightly controlled. The atmosphere to which the leaf is exposed drives transpiration, but it also causes massive water loss from the plant. Up to 90 percent of the water taken up by roots may be lost through transpiration.

Leaves are covered by a waxy cuticle on the outer surface that prevents the loss of water. Regulation of transpiration, therefore, is achieved primarily through the opening and closing of stomata on the leaf surface. Stomata are surrounded by two specialized cells called guard cells, which open and close in response to environmental cues such as light intensity and quality, leaf water status, and carbon dioxide concentrations. Stomata must open to allow air containing carbon dioxide and oxygen to diffuse into the leaf for photosynthesis and respiration. When stomata are open, however, water vapor is lost to the external environment, increasing the rate of transpiration. Therefore, plants must maintain a balance between efficient photosynthesis and water loss.

Plants have evolved over time to adapt to their local environment and reduce transpiration. Desert plant (xerophytes) and plants that grow on other plants (epiphytes) have limited access to water. Such plants usually have a much thicker waxy cuticle than those growing in more moderate, well-watered environments (mesophytes). Aquatic plants (hydrophytes) also have their own set of anatomical and morphological leaf adaptations.

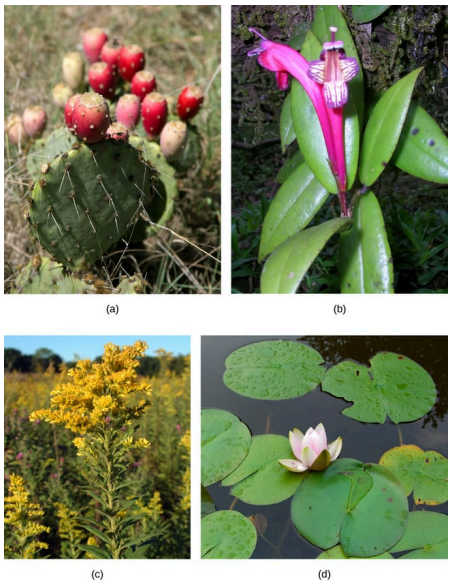


Figure 30.15.1: Reducing Transpiration: Plants are suited to their local environment. (a) Xerophytes, like this prickly pear cactus (*Opuntia* sp.) and (b) epiphytes such as this tropical *Aeschynanthus perrottetii* have adapted to very limited water resources. The leaves of a prickly pear are modified into spines, which lowers the surface-to-volume ratio and reduces water loss. Photosynthesis takes place in the stem, which also stores water. (b) *A. perrottetii* leaves have a waxy cuticle that prevents water loss. (c) Goldenrod (*Solidago* sp.) is a mesophyte, well suited for moderate environments. (d) Hydrophytes, like this fragrant water lily (*Nymphaea odorata*), are adapted to thrive in aquatic environments.

Xerophytes and epiphytes often have a thick covering of trichomes or stomata that are sunken below the leaf's surface. Trichomes are specialized hair-like epidermal cells that secrete oils and other substances. These adaptations impede air flow across the stomatal pore and reduce transpiration. Multiple epidermal layers are also commonly found in these types of plants.

Key Points

- The cohesion – tension theory of sap ascent explains how how water is pulled up from the roots to the top of the plant.
- Evaporation from mesophyll cells in the leaves produces a negative water potential gradient that causes water and minerals to move upwards from the roots through the xylem.
- Gas bubbles in the xylem can interrupt the flow of water in the plant, so they must be reduced through small perforations between vessel elements.
- Transpiration is controlled by the opening and closing of stomata in response to environmental cues.
- Stomata must open for photosynthesis and respiration, but when stomata are open, water vapor is lost to the external environment, increasing the rate of transpiration.
- Desert plants and plants with limited water access prevent transpiration and excess water loss by utilizing a thicker cuticle, trichomes, or multiple epidermal layers.

Key Terms

- **cohesion–tension theory of sap ascent**: explains the process of water flow upwards (against the force of gravity) through the xylem of plants
- **cavitation**: the formation, in a fluid, of vapor bubbles that can interrupt water flow through the plant
- **trichome**: a hair- or scale-like extension of the epidermis of a plant

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30.16: Transport of Water and Solutes in Plants - Transportation of Photosynthates in the Phloem

Learning Objectives

- Explain the transport of photosynthates in the phloem

Transportation of Photosynthates in the Phloem

Plants need an energy source to grow. In seeds and bulbs, food is stored in polymers (such as starch) that are converted by metabolic processes into sucrose for newly-developing plants. Once green shoots and leaves begin to grow, plants can produce their own food by photosynthesis. The products of photosynthesis are called photosynthates, which are usually in the form of simple sugars such as sucrose.

Sources and Sinks

Sources are the structures that produce photosynthates for the growing plant. The sugars produced in the sources, such as leaves, must be delivered to growing parts of the plant. These sugars are transported through the plant via the phloem in a process called translocation. The points of sugar delivery, such as roots, young shoots, and developing seeds, are called sinks. Seeds, tubers, and bulbs can be either a source or a sink, depending on the plant's stage of development and the season.

The products from the source are usually translocated to the nearest sink through the phloem. For example, photosynthates produced in the upper leaves will travel upward to the growing shoot tip, while photosynthates in the lower leaves will travel downward to the roots. Intermediate leaves will send products in both directions. The multidirectional flow of phloem contrasts the flow of xylem, which is always unidirectional (soil to leaf to atmosphere). However, the pattern of photosynthate flow changes as the plant grows and develops. Photosynthates are directed primarily to the roots during early development, to shoots and leaves during vegetative growth, and to seeds and fruits during reproductive development. They are also directed to tubers for storage.

Translocation: Transport from Source to Sink

Photosynthates are produced in the mesophyll cells of photosynthesizing leaves. From there, they are translocated through the phloem where they are used or stored. Mesophyll cells are connected by cytoplasmic channels called plasmodesmata. Photosynthates move through plasmodesmata to reach phloem sieve-tube elements (STEs) in the vascular bundles. From the mesophyll cells, the photosynthates are loaded into the phloem STEs. The sucrose is actively transported against its concentration gradient (a process requiring ATP) into the phloem cells using the electrochemical potential of the proton gradient. This is coupled to the uptake of sucrose with a carrier protein called the sucrose-H^+ symporter.

Phloem STEs have reduced cytoplasmic contents and are connected by sieve plates with pores that allow for pressure-driven bulk flow, or translocation, of phloem sap. Companion cells are associated with STEs. They assist with metabolic activities and produce energy for the STEs.

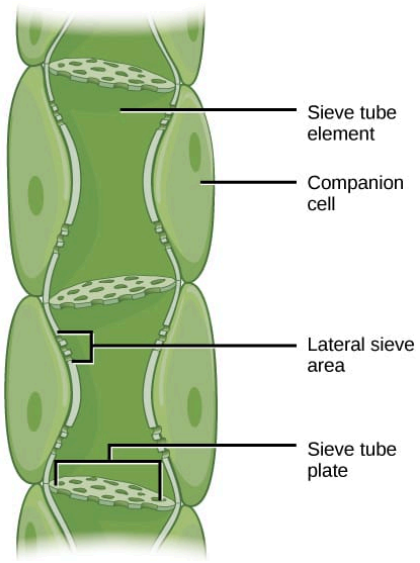


Figure 30.16.1: Translocation to the phloem: Phloem is comprised of cells called sieve-tube elements. Phloem sap travels through perforations called sieve tube plates. Neighboring companion cells carry out metabolic functions for the sieve-tube elements and provide them with energy. Lateral sieve areas connect the sieve-tube elements to the companion cells.

Once in the phloem, the photosynthates are translocated to the closest sink. Phloem sap is an aqueous solution that contains up to 30 percent sugar, minerals, amino acids, and plant growth regulators. The high percentage of sugar decreases Ψ_s, which decreases the total water potential, causing water to move by osmosis from the adjacent xylem into the phloem tubes. This flow of water increases water pressure inside the phloem, causing the bulk flow of phloem sap from source to sink. Sucrose concentration in the sink cells is lower than in the phloem STEs because the sink sucrose has been metabolized for growth or converted to starch (for storage) or other polymers (for structural integrity). Unloading at the sink end of the phloem tube occurs by either diffusion or active transport of sucrose molecules from an area of high concentration to one of low concentration. Water diffuses from the phloem by osmosis and is then transpired or recycled via the xylem back into the phloem sap.

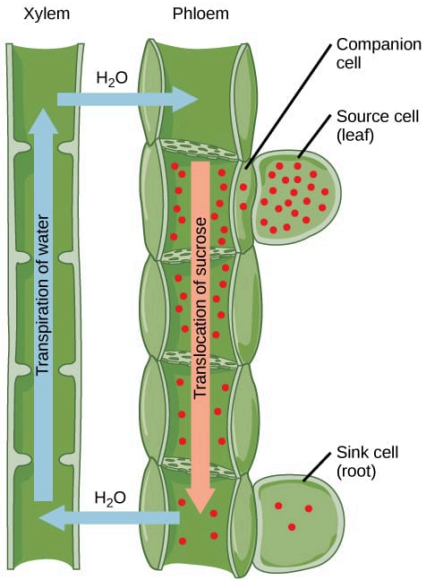


Figure 30.16.1: Translocation to the sink: Sucrose is actively transported from source cells into companion cells and then into the sieve-tube elements. This reduces the water potential, which causes water to enter the phloem from the xylem. The resulting positive pressure forces the sucrose-water mixture down toward the roots, where sucrose is unloaded. Transpiration causes water to return to the leaves through the xylem vessels.

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Key Points

- The products of photosynthesis are called photosynthates; they are usually in the form of simple sugars, such as sucrose.
- Photosynthates are produced by sources and are translocated to sinks.
- Photosynthates are directed primarily to the roots during early development, to shoots and leaves during vegetative growth, and to seeds and fruits during reproductive development.
- Photosynthates are produced in the mesophyll cells of leaves and are translocated through the phloem; they are then transported to STEs and translocated to the nearest sink.
- The high percentage of sugar in phloem sap causes water to move from the xylem into the phloem, which increases water pressure inside the phloem, causing the sap to move from source to sink.
- Sucrose concentration in the sink cells is lower than in the phloem STEs, so unloading at the sink end of the phloem tube occurs by either diffusion or active transport of sucrose molecules from an area of high concentration to one of low concentration.

Key Terms

- **source**: structure that produces photosynthates
- **photosynthate**: any compound that is a product of photosynthesis
- **sieve-tube element**: a type of plant cell located in the phloem that is involved in the movement of carbohydrates
- **sink**: where sugars are delivered in a plant, such as the roots, young shoots, and developing seeds

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30.17: Plant Sensory Systems and Responses - Plant Responses to Light

Learning Objectives

- Compare the ways plants respond to light

Plant Responses to Light

Plants have a number of sophisticated uses for light that go far beyond their ability to perform photosynthesis. Plants can differentiate and develop in response to light (known as photomorphogenesis), which allows plants to optimize their use of light and space. Plants use light to track time, which is known as photoperiodism. They can tell the time of day and time of year by sensing and using various wavelengths of sunlight. Light can also elicit a directional response in plants that allows them to grow toward, or even away from, light; this is known as phototropism.



Figure 30.17.1: Phototropism of an orchid plant: This orchid plant placed next to a window grows toward the sunlight through the window. This is an example of positive phototropism.

The sensing of light in the environment is important to plants; it can be crucial for competition and survival. The response of plants to light is mediated by different photoreceptors: a protein covalently-bonded to a light-absorbing pigment called a chromophore; together, called a chromoprotein. The chromophore of the photoreceptor absorbs light of specific wavelengths, causing structural changes in the photoreceptor protein. The structural changes then elicit a cascade of signaling throughout the plant.

The red, far-red, and violet-blue regions of the visible light spectrum trigger structural development in plants. Sensory photoreceptors absorb light in these particular regions of the visible light spectrum because of the quality of light available in the daylight spectrum. In terrestrial habitats, light absorption by chlorophylls peaks in the blue and red regions of the spectrum. As light filters through the canopy and the blue and red wavelengths are absorbed, the spectrum shifts to the far-red end, shifting the plant community to those plants better adapted to respond to far-red light. Blue-light receptors allow plants to gauge the direction and abundance of sunlight, which is rich in blue–green emissions. Water absorbs red light, which makes the detection of blue light essential for algae and aquatic plants.

Key Points

- Plants grow and differentiate to optimize their space, using light in a process known as photomorphogenesis.
- Plants grow and move toward or away from light depending on their needs; this process is known as phototropism.
- Photoperiodism is illustrated by how plants flower and grow at certain times of the day or year through the use of photoreceptors that sense the wavelengths of sunlight available during the day (versus night) and throughout the seasons.
- The various wavelengths of light, red/far-red or blue regions of the visible light spectrum, trigger structural responses in plants suited for responding to those wavelengths.

Key Terms

- **photoreceptor**: a specialized protein that is able to detect and react to light
- **photoperiodism**: the growth, development and other responses of plants and animals according to the length of day and/or night
- **photomorphogenesis**: the regulatory effect of light on the growth, development and differentiation of plant cells, tissues and organs
- **phototropism**: the movement of a plant toward or away from light

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30.18: Plant Sensory Systems and Responses - The Phytochrome System and Red Light Response

Learning Objectives

- Explain the response of the phytochrome system to red/far-red light

The phytochromes are a family of chromoproteins with a linear tetrapyrrole chromophore, similar to the ringed tetrapyrrole light-absorbing head group of chlorophyll. Phytochromes have two photo-interconvertible forms: Pr and Pfr. Pr absorbs red light (~667 nm) and is immediately converted to Pfr. Pfr absorbs far-red light (~730 nm) and is quickly converted back to Pr. Absorption of red or far-red light causes a massive change to the shape of the chromophore, altering the conformation and activity of the phytochrome protein to which it is bound. Pfr is the physiologically-active form of the protein; exposure to red light yields physiological activity in the plant. Exposure to far-red light converts the Pfr to the inactive Pr form, inhibiting phytochrome activity. Together, the two forms represent the phytochrome system.

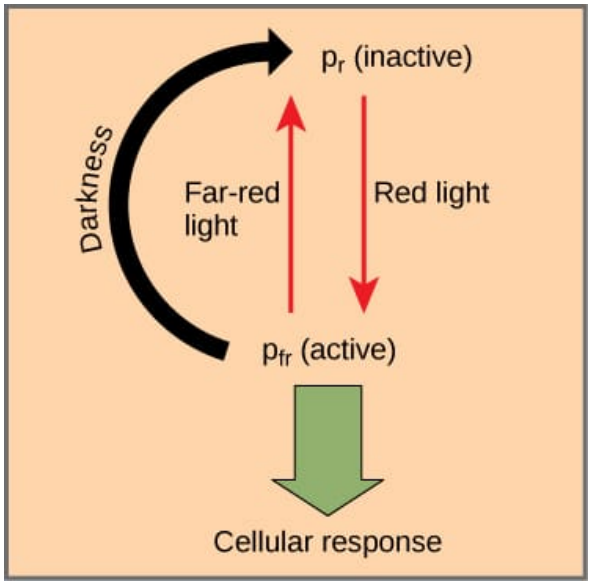


Figure 30.18.1: Phytochrome system: The biologically-inactive form of phytochrome (Pr) is converted to the biologically-active form Pfr under illumination with red light. Far-red light and darkness convert the molecule back to the inactive form.

The phytochrome system acts as a biological light switch. It monitors the level, intensity, duration, and color of environmental light. The effect of red light is reversible by immediately shining far-red light on the sample, which converts the chromoprotein to the inactive Pr form. Additionally, Pfr can slowly revert to Pr in the dark or break down over time. In all instances, the physiological response induced by red light is reversed. The active form of phytochrome (Pfr) can directly activate other molecules in the cytoplasm, or it can be trafficked to the nucleus, where it directly activates or represses specific gene expression.

The Phytochrome System and Growth

Plants use the phytochrome system to grow away from shade and toward light. Unfiltered, full sunlight contains much more red light than far-red light. Any plant in the shade of another plant will be exposed to red-depleted, far-red-enriched light because the other plant has absorbed most of the other red light. The exposure to red light converts phytochrome in the shaded leaves to the Pr (inactive) form, which slows growth. The leaves in full sunlight are exposed to red light and have activated Pfr, which induces growth toward sunlit areas. Because competition for light is so fierce in a dense plant community, those plants who could grow toward light the fastest and most efficiently became the most successful.

The Phytochrome System in Seeds

In seeds, the phytochrome system is used to determine the presence or absence of light, rather than the quality. This is especially important in species with very small seeds and, therefore, food reserves. For example, if lettuce seedlings germinated a centimeter under the soil surface, the seedling would exhaust its food resources and die before reaching the surface. A seed will only germinate if exposed to light at the surface of the soil, causing Pr to be converted to Pfr, signaling the start of germination. In the dark, phytochrome is in the inactive Pr form so the seed will not germinate.

Photoperiodism

Plants also use the phytochrome system to adjust growth according to the seasons. Photoperiodism is a biological response to the timing and duration of dark and light periods. Since unfiltered sunlight is rich in red light, but deficient in far-red light, at dawn, all the phytochrome molecules in a leaf convert to the active Pfr form and remain in that form until sunset. Since Pfr reverts to Pr during darkness, there will be no Pfr remaining at sunrise if the night is long (winter) and some Pfr remaining if the night is short (summer). The amount of Pfr present stimulates flowering, setting of winter buds, and vegetative growth according to the seasons.

In addition, the phytochrome system enables plants to compare the length of dark periods over several days. Shortening nights indicate springtime to the plant; lengthening nights indicate autumn. This information, along with sensing temperature and water availability, allows plants to determine the time of the year and adjust their physiology accordingly. Short-day (long-night) plants use this information to flower in the late summer and early fall when nights exceed a critical length (often eight or fewer hours). Long-day (short-night) plants flower during the spring when darkness is less than a critical length (often 8 to 15 hours). However, day-neutral plants do not regulate flowering by day length. Not all plants use the phyotochrome system to adjust their physiological responses to the seasons.

Key Points

- Exposure to red light converts the chromoprotein to the functional, active form (Pfr), while darkness or exposure to far-red light converts the chromophore to the inactive form (Pr).
- Plants grow toward sunlight because the red light from the sun converts the chromoprotein into the active form (Pfr), which triggers plant growth; plants in shade slow growth because the inactive form (Pr) is produced.
- If seeds sense light using the phytochrome system, they will germinate.
- Plants regulate photoperiodism by measuring the Pfr/Pr ratio at dawn, which then stimulates physiological processes such as flowering, setting winter buds, and vegetative growth.

Key Terms

- **phytochrome**: any of a class of pigments that control most photomorphogenic responses in higher plants
- **chromophore**: the group of atoms in a molecule in which the electronic transition responsible for a given spectral band is located
- **photoperiodism**: the growth, development and other responses of plants and animals according to the length of day and/or night

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30.19: Plant Sensory Systems and Responses - Blue Light Response

Learning Objectives

- Differentiate among blue light responses of plants

Phototropism is the directional bending of a plant toward or away from a light source of blue wavelengths of light. Positive phototropism is growth toward a light source, while negative phototropism (also called skototropism) is growth away from light. Several proteins use blue light to control various physiological processes in the plant.



Figure 30.19.1: Blue light response of azure bluets: Azure bluets (Houstonia caerulea) display a phototropic response by bending toward the light.

Phototropins and Physiological Responses

Phototropins are protein-based receptors responsible for mediating the phototropic response in plants. Like all plant photoreceptors, phototropins consist of a protein portion and a light-absorbing portion, called the chromophore, which senses blue wavelengths of light. Phototropins belong to a class of proteins called flavoproteins because the chromophore is a covalently-bound molecule of flavin.

Phototropins control other physiological responses including leaf opening and closing, chloroplast movement, and the opening of stomata. However, of all responses controlled by phototropins, phototropism has been studied the longest and is the best understood.

Phototropism and Auxin

In 1880, Charles Darwin and his son Francis first described phototropism as the bending of seedlings toward light. Darwin observed that light was perceived by the the apical meristem (tip of the plant), but that the plant bent in response in a different part of the plant. The Darwins concluded that the signal had to travel from the apical meristem to the base of the plant, where it bent.

In 1913, Peter Boysen-Jensen conducted an experiment that demonstrated that a chemical signal produced in the plant tip was

responsible for the plant's bending response at the base. He cut off the tip of a seedling, covered the cut section with a permeable layer of gelatin, and then replaced the tip. The seedling bent toward the light when illuminated even though the layer of gelatin was present. However, when impermeable mica flakes were inserted between the tip and the cut base, the seedling did not bend.

A refinement of Boysen-Jensen's experiment showed that the signal traveled on the shaded side of the seedling. When the mica plate was inserted on the illuminated side, the plant still bent toward the light. Therefore, the chemical signal from the sunlight, which is blue wavelengths of light, was a growth stimulant; the phototropic response involved faster cell elongation on the shaded side than on the illuminated side, causing the plant to bend. We now know that as light passes through a plant stem, it is diffracted and generates phototropin activation across the stem. Most activation occurs on the lit side, causing the plant hormones indole acetic acid (IAA) or auxin to accumulate on the shaded side. Stem cells elongate under the influence of IAA.

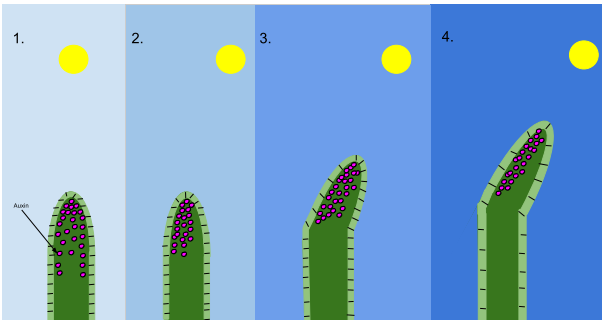


Figure 30.19.1: Phototropism and the distribution of auxin: Phototropism is the growth of plants in response to light. When the sun is positioned almost directly over the plant, the hormone auxin (pink dots) in the plant stem is evenly distributed. As the sun moves, the auxin is repositioned on the other side of the plant. This overload of auxin next to these cells causes them to start to grow or elongate, tipping the growth of the stem toward the light.

Cryptochromes

Cryptochromes are another class of blue-light absorbing photoreceptors. Their chromophores also contain a flavin-based chromophore. Cryptochromes set the plant's circadian rhythm (the 24-hour activity cycle) using blue light receptors. There is some evidence that cryptochromes work by sensing light-dependent redox reactions and that, together with phototropins, they mediate the phototropic response.

Key Points

- In addition to phototropism, phototropins sense blue light to control leaf opening and closing, chloroplast movement, and the opening of stomata.
- When phototropins are activated by blue light, the hormone auxin accumulates on the shaded side of the plant, triggering elongation of stem cells and phototropism.
- Cryptochromes sense blue light-dependent redox reactions to control the circadian rhythm of plants.

Key Terms

- **skototropism**: growth or movement away from light
- **phototropin**: any of a class of photoreceptor flavoproteins that mediate phototropism in higher plants
- **auxin**: a class of plant growth hormones that is responsible for elongation in phototropism and gravitropism and for other growth processes in the plant life cycle
- **cryptochrome**: any of several light-sensitive flavoproteins, in the protoreceptors of plants, that regulate germination, elongation, and photoperiodism

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30.20: Plant Sensory Systems and Responses - Plant Responses to Gravity

Learning Objectives

- Describe the role of amyloplasts in gravitropism

Whether or not they germinate in the light or in total darkness, shoots usually sprout up from the ground, while roots grow downward into the ground. A plant laid on its side in the dark will send shoots upward when given enough time. Gravitropism ensures that roots grow into the soil and that shoots grow toward sunlight. Growth of the shoot apical tip upward is called negative gravitropism, whereas growth of the roots downward is called positive gravitropism.

Time-lapse of pea shoot and root growth: Time-lapse of a pea plant growing from seed, showing both the shoot and root system. The roots grown downward in the direction of gravity, which is positive gravitropism, and the shoot grows upward away from gravity, which is negative gravitropism.

The reason plants know which way to grow in response to gravity is due to amyloplasts in the plants. Amyloplasts (also known as statoliths) are specialized plastids that contain starch granules and settle downward in response to gravity. Amyloplasts are found in shoots and in specialized cells of the root cap. When a plant is tilted, the statoliths drop to the new bottom cell wall. A few hours later, the shoot or root will show growth in the new vertical direction.



Figure 30.20.1: Gravitropism: This is an image of an upright tree with high curvature at the base as a result of negative gravitropism. Despite being tilted, amyloplasts will cause the shoot to grow in a vertical direction.

The mechanism that mediates gravitropism is reasonably well understood. When amyloplasts settle to the bottom of the gravity-sensing cells in the root or shoot, they physically contact the endoplasmic reticulum (ER). This causes the release of calcium ions from inside the ER. This calcium signaling in the cells causes polar transport of the plant hormone indole acetic acid (IAA) to the bottom of the cell. In roots, a high concentration of IAA inhibits cell elongation. The effect slows growth on the lower side of the root while cells develop normally on the upper side. IAA has the opposite effect in shoots, where a higher concentration at the lower side of the shoot stimulates cell expansion and causes the shoot to grow up. After the shoot or root begin to grow vertically, the amyloplasts return to their normal position. Other hypotheses, which involve the entire cell in the gravitropism effect, have been proposed to explain why some mutants that lack amyloplasts may still exhibit a weak gravitropic response.

Key Points

- Positive gravitropism occurs when roots grow into soil because they grow in the direction of gravity while negative gravitropism occurs when shoots grow up toward sunlight in the opposite direction of gravity.
- Amyloplasts settle at the bottom of the cells of the shoots and roots in response to gravity, causing calcium signaling and the release of indole acetic acid.
- Indole acetic acid inhibits cell elongation in the lower side of roots, but stimulates cell expansion in shoots, which causes shoots to grow upward.

Key Terms

- **amyloplast**: a non-pigmented organelle found in some plant cells that is responsible for the synthesis and storage of starch granules through the polymerization of glucose
- **statolith**: a specialized form of amyloplast involved in graviperception by plant roots and most invertebrates
- **gravitropism**: a plant's ability to change its growth in response to gravity

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30.21: Plant Sensory Systems and Responses - Auxins, Cytokinins, and Gibberellins

Learning Objectives

- Differentiate among the types of plant hormones and their effects on plant growth

Growth Responses

A plant's sensory response to external stimuli relies on hormones, which are simply chemical messengers. Plant hormones affect all aspects of plant life, from flowering to fruit setting and maturation, and from phototropism to leaf fall. Potentially, every cell in a plant can produce plant hormones. The hormones can act in their cell of origin or be transported to other portions of the plant body, with many plant responses involving the synergistic or antagonistic interaction of two or more hormones. In contrast, animal hormones are produced in specific glands and transported to a distant site for action, acting alone.

Plant hormones are a group of unrelated chemical substances that affect plant morphogenesis. Five major plant hormones are traditionally described: auxins, cytokinins, gibberellins, ethylene, and abscisic acid. In addition, other nutrients and environmental conditions can be characterized as growth factors. The first three plant hormones largely affect plant growth, as described below.

Auxins

The term auxin is derived from the Greek word auxein, which means "to grow. " Auxins are the main hormones responsible for cell elongation in phototropism and gravitropism. They also control the differentiation of meristem into vascular tissue and promote leaf development and arrangement. While many synthetic auxins are used as herbicides, indole acetic acid (IAA) is the only naturally-occurring auxin that shows physiological activity. Apical dominance (the inhibition of lateral bud formation) is triggered by auxins produced in the apical meristem. Flowering, fruit setting and ripening, and inhibition of abscission (leaf falling) are other plant responses under the direct or indirect control of auxins. Auxins also act as a relay for the effects of the blue light and red/far-red responses.

Commercial use of auxins is widespread in plant nurseries and for crop production. IAA is used as a rooting hormone to promote growth of adventitious roots on cuttings and detached leaves. Applying synthetic auxins to tomato plants in greenhouses promotes normal fruit development. Outdoor application of auxin promotes synchronization of fruit setting and dropping, which coordinates the harvesting season. Fruits such as seedless cucumbers can be induced to set fruit by treating unfertilized plant flowers with auxins.

Cytokinins

The effect of cytokinins was first reported when it was found that adding the liquid endosperm of coconuts to developing plant embryos in culture stimulated their growth. The stimulating growth factor was found to be cytokinin, a hormone that promotes cytokinesis (cell division). Almost 200 naturally-occurring or synthetic cytokinins are known, to date. Cytokinins are most abundant in growing tissues, such as roots, embryos, and fruits, where cell division is occurring. Cytokinins are known to delay senescence in leaf tissues, promote mitosis, and stimulate differentiation of the meristem in shoots and roots. Many effects on plant development are under the influence of cytokinins, either in conjunction with auxin or another hormone. For example, apical dominance seems to result from a balance between auxins that inhibit lateral buds and cytokinins that promote bushier growth.

Gibberellins

Gibberellins (GAs) are a group of about 125 closely-related plant hormones that stimulate shoot elongation, seed germination, and fruit and flower maturation. GAs are synthesized in the root and stem apical meristems, young leaves, and seed embryos.

In urban areas, GA antagonists are sometimes applied to trees under power lines to control growth and reduce the frequency of pruning.

GAs break dormancy (a state of inhibited growth and development) in the seeds of plants that require exposure to cold or light to germinate. Abscisic acid is a strong antagonist of GA action. Other effects of GAs include gender expression, seedless fruit development, and the delay of senescence in leaves and fruit. Seedless grapes are obtained through standard breeding methods; they contain inconspicuous seeds that fail to develop. Because GAs are produced by the seeds and because fruit development and stem elongation are under GA control, these varieties of grapes would normally produce small fruit in compact clusters. Maturing grapes are routinely treated with GA to promote larger fruit size, as well as looser bunches (longer stems), which reduces the incidence of mildew infection.



Figure 30.21.1: Effect of gibberellins on grapes: In grapes, application of gibberellic acid increases the size of fruit and loosens clustering.

Key Points

- During phototropism and gravitropism, the plant hormone auxin controls cell elongation.
- The plant hormone cytokinin promotes cell division, controling many developmental processes in plants.
- Gibberellins control many aspects of plant physiology including shoot elongation, seed germination, fruit and flower maturation, seed dormancy, gender expression, seedless fruit development, and the delay of senescence in leaves and fruit.

Key Terms

- **gibberellin**: any of a class of diterpene plant growth hormones that stimulate shoot elongation, seed germination, and fruit and flower maturation
- **auxin**: a class of plant growth hormones that is responsible for elongation in phototropism and gravitropism and for other growth processes in the plant life cycle
- **cytokinin**: any of a class of plant hormones involved in cell growth and division

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30.22: Plant Sensory Systems and Responses - Abscisic Acid, Ethylene, and Nontraditional Hormones

Learning Objectives

- Describe the roles played by ethylene and nontraditional hormones in plant development

Growth Responses

In addition to the growth hormones auxins, cytokinins, gibberellins, there are two more major types of plant hormones, abscisic acid and ethylene, as well as several other less-studied compounds that control plant physiology.

Abscisic Acid

The plant hormone abscisic acid (ABA) was first discovered as the agent that causes the abscission or dropping of cotton bolls. However, more-recent studies indicate that ABA plays only a minor role in the abscission process. ABA accumulates as a response to stressful environmental conditions, such as dehydration, cold temperatures, or shortened day lengths. Its activity counters many of the growth-promoting effects of GAs and auxins. ABA inhibits stem elongation and induces dormancy in lateral buds.

ABA induces dormancy in seeds by blocking germination and promoting the synthesis of storage proteins. Plants adapted to temperate climates require a long period of cold temperature before seeds germinate. This mechanism protects young plants from sprouting too early during unseasonably warm weather in winter. As the hormone gradually breaks down over winter, the seed is released from dormancy and germinates when conditions are favorable in spring. Another effect of ABA is to promote the development of winter buds; it mediates the conversion of the apical meristem into a dormant bud. Low soil moisture causes an increase in ABA, which causes stomata to close, reducing water loss in winter buds.

Ethylene

Ethylene is associated with fruit ripening, flower wilting, and leaf fall. Ethylene is unusual because it is a volatile gas (C_2H_4). Hundreds of years ago, when gas street lamps were installed in city streets, trees that grew close to lamp posts developed twisted, thickened trunks, shedding their leaves earlier than expected. These effects were caused by ethylene volatilizing from the lamps.

Aging tissues (especially senescing leaves) and nodes of stems produce ethylene. The best-known effect of the hormone, however, is the promotion of fruit ripening. Ethylene stimulates the conversion of starch and acids to sugars. Some people store unripe fruit, such as avocados, in a sealed paper bag to accelerate ripening; the gas released by the first fruit to mature will speed up the maturation of the remaining fruit. Ethylene also triggers leaf and fruit abscission, flower fading and dropping, and promotes germination in some cereals and sprouting of bulbs and potatoes.



Figure 30.22.1: Date ripening: The plant hormone ethylene promotes ripening, as seen in the ripening of dates.

Ethylene is widely used in agriculture. Commercial fruit growers control the timing of fruit ripening with application of the gas.

Horticulturalists inhibit leaf dropping in ornamental plants by removing ethylene from greenhouses using fans and ventilation.

Nontraditional Hormones

Recent research has discovered a number of compounds that also influence plant development. Their roles are less understood than the effects of the major hormones described so far.

Jasmonates play a major role in defense responses to herbivory. Their levels increase when a plant is wounded by a predator, resulting in an increase in toxic secondary metabolites. They contribute to the production of volatile compounds that attract natural enemies of predators. For example, chewing of tomato plants by caterpillars leads to an increase in jasmonic acid levels, which in turn triggers the release of volatile compounds that attract predators of the pest.

Oligosaccharins also play a role in plant defense against bacterial and fungal infections. They act locally at the site of injury; they can also be transported to other tissues. Strigolactones promote seed germination in some species and inhibit lateral apical development in the absence of auxins. Strigolactones also play a role in the establishment of mycorrhizae, a mutualistic association of plant roots and fungi. Brassinosteroids are important to many developmental and physiological processes. Signals between these compounds and other hormones, notably auxin and GAs, amplify their physiological effect. Apical dominance, seed germination, gravitropism, and resistance to freezing are all positively influenced by hormones. Root growth and fruit dropping are inhibited by steroids.

Key Points

- Under stress, abscisic acid accumulates in plants, inhibiting stem elongation and inducing bud dormancy.
- The plant hormone ethylene controls fruit ripening, flower wilting, and leaf fall by stimulating the conversion of starch and acids to sugars.
- Other nontraditional hormones such as jasmonates and oligosaccharins control defense responses from herbivores and bacterial/fungal infections, respectively.

Key Terms

- **abscisic acid**: a plant hormone that functions in many plant developmental processes, including bud dormancy, inhibition of seed germination, and plant stress tolerance.
- **jasmonate**: any of several esters of jasmonic acid that act as plant hormones
- **ethylene**: a plant hormone that is involved in fruit ripening, flower wilting, and leaf fall

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30.23: Plant Sensory Systems and Responses - Plant Responses to Wind and Touch

Learning Objectives

- Compare the ways plants respond to directional and non-directional stimuli

The shoot of a pea plant wraps around a trellis while a tree grows on an angle in response to strong prevailing winds. These are examples of how plants respond to touch or wind.

The movement of a plant subjected to constant directional pressure is called thigmotropism, from the Greek words thigma meaning “touch,” and tropism, implying “direction.” Tendrils are one example of this. A tendril is a specialized stem, leaf, or petiole with a threadlike shape that is used by climbing plants for support.The meristematic region of tendrils is very touch sensitive; light touch will evoke a quick coiling response. Cells in contact with a support surface contract, whereas cells on the opposite side of the support expand. Application of jasmonic acid is sufficient to trigger tendril coiling without a mechanical stimulus.



Figure 30.23.1: Thigmotropism in a redvine: Tendrils of a redvine produce auxin in response to touching a support stick and then transfer the auxin to non-touching cells. The non-touching cells elongate faster to curl around the support stick.

A thigmonastic response is a touch response independent of the direction of stimulus. In the Venus flytrap, two modified leaves are joined at a hinge and lined with thin, fork-like tines along the outer edges. Tiny hairs are located inside the trap. When an insect brushes against these trigger hairs, touching two or more of them in succession, the leaves close quickly, trapping the prey. Glands on the leaf surface secrete enzymes that slowly digest the insect. The released nutrients are absorbed by the leaves, which reopen for the next meal.

Thigmomorphogenesis is a slow developmental change in the shape of a plant subjected to continuous mechanical stress. When trees bend in the wind, for example, growth is usually stunted and the trunk thickens. Strengthening tissue, especially xylem, is produced to add stiffness to resist the wind’s force. Researchers hypothesize that mechanical strain from wind, rain, or movement by other living things induces growth and differentiation to strengthen the tissues. Ethylene and jasmonate are likely involved in thigmomorphogenesis.

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Key Points

- When subjected to constant directional pressure, such as a trellis, plants move to grow around the object providing the pressure; this process is known as thigmotropism.
- Thigmonastic responses include opening and closing leaves, petals, or other parts of the plant as a reaction to touch.
- Through thigmomorphogenesis, plants change their growth in response to repeated mechanical stress from wind, rain, or other living things.

Key Terms

- **thigmotropism**: plant growth or motion in response to touch
- **thigmomorphogenesis**: the response by plants to mechanical sensation (touch) by altering their growth patterns
- **thigmonastic response**: a touch response independent of the direction of stimulus

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30.24: Plant Defense Mechanisms - Against Herbivores

Learning Objectives

- Identify plant defense responses to herbivores

Defense Responses Against Herbivores

Herbivores, both large and small, use plants as food and actively chew them. Plants have developed a variety of strategies to discourage or kill attackers.

Mechanical Defenses

The first line of defense in plants is an intact and impenetrable barrier composed of bark and a waxy cuticle. Both protect plants against herbivores. Other adaptations against herbivores include hard shells, thorns (modified branches), and spines (modified leaves). They discourage animals by causing physical damage or by inducing rashes and allergic reactions. Some Acacia tree species have developed mutualistic relationships with ant colonies: they offer the ants shelter in their hollow thorns in exchange for the ants' defense of the tree's leaves.



Figure 30.24.1: Acacia collinsii: The large thorn-like stipules of Acacia collinsii are hollow and offer shelter for ants, which in return protect the plant against herbivores.



Figure 30.24.1: Modified leaves on a cactus: The spines on cactus plants are modified leaves that act as a mechanical defense against predators.

Chemical Defenses

A plant's exterior protection can be compromised by mechanical damage, which may provide an entry point for pathogens. If the first line of defense is breached, the plant must resort to a different set of defense mechanisms, such as toxins and enzymes. Secondary metabolites are compounds that are not directly derived from photosynthesis and are not necessary for respiration or plant growth and development.

Many metabolites are toxic and can even be lethal to animals that ingest them. Some metabolites are alkaloids, which discourage predators with noxious odors (such as the volatile oils of mint and sage) or repellent tastes (like the bitterness of quinine). Other alkaloids affect herbivores by causing either excessive stimulation (caffeine is one example) or the lethargy associated with opioids. Some compounds become toxic after ingestion; for instance, glycol cyanide in the cassava root releases cyanide only upon ingestion by the herbivore. Foxgloves produce several deadly chemicals, namely cardiac and steroidal glycosides. Ingestion can cause nausea, vomiting, hallucinations, convulsions, or death.



Figure 30.24.1: Foxgloves: Foxgloves produce several deadly chemicals, namely cardiac and steroidal glycosides. Ingestion can cause nausea, vomiting, hallucinations, convulsions, or death.

Timing

Mechanical wounding and predator attacks activate defense and protective mechanisms in the damaged tissue and elicit long-distancing signaling or activation of defense and protective mechanisms at sites farther from the injury location. Some defense reactions occur within minutes, while others may take several hours. In addition, long-distance signaling elicits a systemic response aimed at deterring predators. As tissue is damaged, jasmonates may promote the synthesis of compounds that are toxic to predators. Jasmonates also elicit the synthesis of volatile compounds that attract parasitoids: insects that spend their developing stages in or on another insect, eventually killing their host. The plant may activate abscission of injured tissue if it is damaged beyond repair.

Key Points

- Many plants have impenetrable barriers, such as bark and waxy cuticles, or adaptations, such as thorns and spines, to protect them from herbivores.
- If herbivores breach a plant's barriers, the plant can respond with secondary metabolites, which are often toxic compounds, such as glycol cyanide, that may harm the herbivore.
- When attacked by a predator, damaged plant tissue releases jasmonate hormones that promote the release of volatile compounds, attracting parasitoids, which use, and eventually kill, the predators as host insects.

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30.25: Plant Defense Mechanisms - Against Pathogens

Plants defend against pathogens with barriers, secondary metabolites, and antimicrobial compounds.

Learning Objectives

- Identify plant defense responses to pathogens

Defense Responses Against Pathogens

Pathogens are agents of disease. These infectious microorganisms, such as fungi, bacteria, and nematodes, live off of the plant and damage its tissues. Plants have developed a variety of strategies to discourage or kill attackers.

The first line of defense in plants is an intact and impenetrable barrier composed of bark and a waxy cuticle. Both protect plants against pathogens.

A plant's exterior protection can be compromised by mechanical damage, which may provide an entry point for pathogens. If the first line of defense is breached, the plant must resort to a different set of defense mechanisms, such as toxins and enzymes. Secondary metabolites are compounds that are not directly derived from photosynthesis and are not necessary for respiration or plant growth and development. Many metabolites are toxic and can even be lethal to animals that ingest them.

Additionally, plants have a variety of inducible defenses in the presence of pathogens. In addition to secondary metabolites, plants produce antimicrobial chemicals, antimicrobial proteins, and antimicrobial enzymes that are able to fight the pathogens. Plants can close stomata to prevent the pathogen from entering the plant. A hypersensitive response, in which the plant experiences rapid cell death to fight off the infection, can be initiated by the plant; or it may use endophyte assistance: the roots release chemicals that attract other beneficial bacteria to fight the infection.

Mechanical wounding and predator attacks activate defense and protective mechanisms in the damaged tissue and elicit long-distancing signaling or activation of defense and protective mechanisms at sites farther from the injury location. Some defense reactions occur within minutes, while others may take several hours.

Key Points

- Many plants have impenetrable barriers, such as bark and waxy cuticles, or adaptations, such as thorns and spines, to protect them from pathogens.
- If pathogens breach a plant's barriers, the plant can respond with secondary metabolites, which are often toxic compounds, such as glycol cyanide, that may harm the pathogen.
- Plants produce antimicrobial chemicals, antimicrobial proteins, and antimicrobial enzymes that are able to fight the pathogens.

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31: SOIL AND PLANT NUTRITION

31.1: Nutritional Requirements of Plants

31.1A: Plant Nutrition

31.1B: The Chemical Composition of Plants

31.1C: Essential Nutrients for Plants

31.2: The Soil

31.2A: Soil Composition

31.2B: Soil Formation

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31.3: Nutritional Adaptations of Plants

31.3A: Nitrogen Fixation- Root and Bacteria Interactions

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31.3C: Nutrients from Other Sources

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31.1: NUTRITIONAL REQUIREMENTS OF PLANTS



- Topic hierarchy

31.1A: Plant Nutrition

31.1B: The Chemical Composition of Plants

31.1C: Essential Nutrients for Plants

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31.1A: Plant Nutrition

Learning Objectives

- Describe how the nutritional requirements of plants are met

Introduction

Plants are unique organisms that can absorb nutrients and water through their root system, as well as carbon dioxide from the atmosphere. Soil quality and climate are the major determinants of plant distribution and growth. The combination of soil nutrients, water, and carbon dioxide, along with sunlight, allows plants to grow. In order to develop into mature, fruit -bearing plants, many requirements must be met and events must be coordinated.

Take for example the Cucurbitaceae family of plants that were the first cultivated in Mesoamerica, although several species are native to North America. The family includes many edible species, such as squash and pumpkin, as well as inedible gourds. First, seeds must germinate under the right conditions in the soil; therefore, temperature, moisture, and soil quality are important factors that play a role in germination and seedling development. Soil quality and climate are significant to plant distribution and growth. Second, the young seedling will eventually grow into a mature plant with the roots absorbing nutrients and water from the soil. At the same time, the aboveground parts of the plant will absorb carbon dioxide from the atmosphere and use energy from sunlight to produce organic compounds through photosynthesis. Finally, the fruit are grown and matured and the cycle begins all over again with the new seeds.



Figure 31.1A.1: Examples of fruit bearing plants: For this (a) squash seedling (Cucurbita maxima) to develop into a mature plant bearing its (b) fruit, numerous nutritional requirements must be met.

There is a complex dynamic between plants and soils that ultimately determines the outcome and viability of plant life. The following sections of this chapter will discuss the many aspects of the nutritional requirements of plants in greater detail.

Key Points

- Nutrients and water are absorbed through the plants root system.
- Carbon dioxide is absorbed through the leaves.
- From seedling to mature plant, there is a complex dynamic between plants and their environment (soil and atmosphere).

Key Terms

- **germinate**: to sprout or produce buds
- **photosynthesis**: the process by which plants and other photoautotrophs generate carbohydrates and oxygen from carbon dioxide, water, and light energy in chloroplasts
- **nutrient**: a source of nourishment, such as food, that can be metabolized by an organism to give energy and build tissue

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31.1B: The Chemical Composition of Plants

Learning Objectives

- Describe the chemical composition of plants

The Chemical Composition of Plants

Water

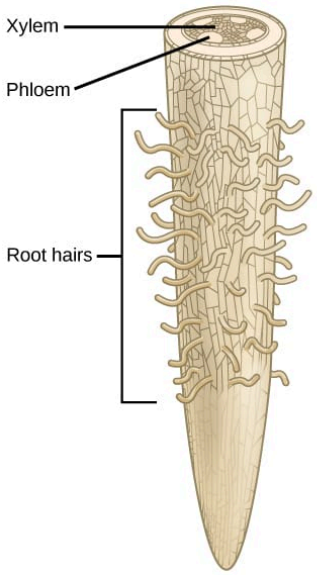


Figure $31.1B.1$: Water absorption by the roots: Water is absorbed through the root hairs and moves up the xylem to the leaves.

Since plants require nutrients in the form of elements such as carbon and potassium, it is important to understand the chemical composition of plants. The majority of volume in a plant cell is water; it typically comprises 80 to 90 percent of the plant's total weight. Soil is the water source for land plants. It can be an abundant source of water even if it appears dry. Plant roots absorb water from the soil through root hairs and transport it up to the leaves through the xylem. As water vapor is lost from the leaves, the process of transpiration and the polarity of water molecules (which enables them to form hydrogen bonds) draws more water from the roots up through the plant to the leaves. Plants need water to support cell structure, for metabolic functions, to carry nutrients, and for photosynthesis.

Nutrients

Plant cells need essential substances, collectively called nutrients, to sustain life. Plant nutrients may be composed of either organic or inorganic compounds. An organic compound is a chemical compound that contains carbon, such as carbon dioxide obtained from the atmosphere. Carbon that was obtained from atmospheric CO_2 composes the majority of the dry mass within most plants. An inorganic compound does not contain carbon and is not part of, or produced by, a living organism. Inorganic substances (which form the majority of the soil substance) are commonly called minerals: those required by plants include nitrogen (N) and potassium (K), for structure and regulation.

Key Points

- Water comprises a large percentage of a plant's total weight and is used to support cell structure, for metabolic functions, to

carry nutrients, and for photosynthesis.
- Water is absorbed from the soil through root hairs and is carried to the rest of the plant through the xylem.
- Many essential organic and inorganic nutrients are required to sustain plant life.

Key Terms

- **organic**: relating to the compounds of carbon, relating to natural products
- **inorganic**: relating to a compound that does not contain carbon
- **xylem**: a vascular tissue in land plants primarily responsible for the distribution of water and minerals taken up by the roots; also the primary component of wood
- **transpiration**: the loss of water by evaporation in terrestrial plants, especially through the stomata; accompanied by a corresponding uptake from the roots

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31.1C: Essential Nutrients for Plants

Learning Objectives

- Distinguish among the essential nutrients for plants

Essential Nutrients

Plants require only light, water, and about 20 elements to support all their biochemical needs. These 20 elements are called essential nutrients. For an element to be regarded as essential, three criteria are required:

1. a plant cannot complete its life cycle without the element
2. no other element can perform the function of the element
3. the element is directly involved in plant nutrition

Macronutrients and Micronutrients

The essential elements can be divided into macronutrients and micronutrients. Nutrients that plants require in larger amounts are called macronutrients. About half of the essential elements are considered macronutrients: carbon, hydrogen, oxygen, nitrogen, phosphorus, potassium, calcium, magnesium, and sulfur. The first of these macronutrients, carbon (C), is required to form carbohydrates, proteins, nucleic acids, and many other compounds; it is, therefore, present in all macromolecules. On average, the dry weight (excluding water) of a cell is 50 percent carbon, making it a key part of plant biomolecules.

Essential Elements for Plant Growth	
Macronutrients	**Micronutrients**
Carbon (C)	Iron (Fe)
Hydrogen (H)	Manganese (Mn)
Oxygen (O)	Boron (B)
Nitrogen (N)	Molybdenum (Mo)
Phosphorus (P)	Copper (Cu)
Potassium (K)	Zinc (Zn)
Calcium (Ca)	Chlorine (Cl)
Magnesium (Mg)	Nickel (Ni)
Sulfur (S)	Cobalt (Co)
	Sodium (S)
	Silicon (Si)

Figure $31.1C.1$: Essential elements required by plants: For an element to be regarded as essential a plant cannot complete its life cycle without the element, no other element can perform the function of the element, and the element is directly involved in plant nutrition.

The next-most-abundant element in plant cells is nitrogen (N); it is part of proteins and nucleic acids. Nitrogen is also used in the synthesis of some vitamins. Hydrogen and oxygen are macronutrients that are part of many organic compounds and also form water. Oxygen is necessary for cellular respiration; plants use oxygen to store energy in the form of ATP. Phosphorus (P), another macromolecule, is necessary to synthesize nucleic acids and phospholipids. As part of ATP, phosphorus enables food energy to be converted into chemical energy through oxidative phosphorylation. Light energy is converted into chemical energy during photophosphorylation in photosynthesis; and into chemical energy to be extracted during respiration. Sulfur is part of certain amino acids, such as cysteine and methionine, and is present in several coenzymes. Sulfur also plays a role in photosynthesis as part of the electron transport chain where hydrogen gradients are key in the conversion of light energy into ATP. Potassium

(K) is important because of its role in regulating stomatal opening and closing. As the openings for gas exchange, stomata help maintain a healthy water balance; a potassium ion pump supports this process.

Magnesium (Mg) and calcium (Ca) are also important macronutrients. The role of calcium is twofold: to regulate nutrient transport and to support many enzyme functions. Magnesium is important to the photosynthetic process. These minerals, along with the micronutrients, also contribute to the plant's ionic balance.

In addition to macronutrients, organisms require various elements in small amounts. These micronutrients, or trace elements, are present in very small quantities. The seven main micronutrients include boron, chlorine, manganese, iron, zinc, copper, and molybdenum. Boron (B) is believed to be involved in carbohydrate transport in plants; it also assists in metabolic regulation. Boron deficiency will often result in bud dieback. Chlorine (Cl) is necessary for osmosis and ionic balance; it also plays a role in photosynthesis. Copper (Cu) is a component of some enzymes. Symptoms of copper deficiency include browning of leaf tips and chlorosis (yellowing of the leaves). Iron (Fe) is essential for chlorophyll synthesis, which is why an iron deficiency results in chlorosis. Manganese (Mn) activates some important enzymes involved in chlorophyll formation. Manganese-deficient plants will develop chlorosis between the veins of its leaves. The availability of manganese is partially dependent on soil pH. Molybdenum (Mo) is essential to plant health as it is used by plants to reduce nitrates into usable forms. Some plants use it for nitrogen fixation; thus, it may need to be added to some soils before seeding legumes. Zinc (Zn) participates in chlorophyll formation and also activates many enzymes. Symptoms of zinc deficiency include chlorosis and stunted growth.

Deficiencies in any of these nutrients, particularly the macronutrients, can adversely affect plant growth. Depending on the specific nutrient, a lack can cause stunted growth, slow growth, or chlorosis. Extreme deficiencies may result in leaves showing signs of cell death.

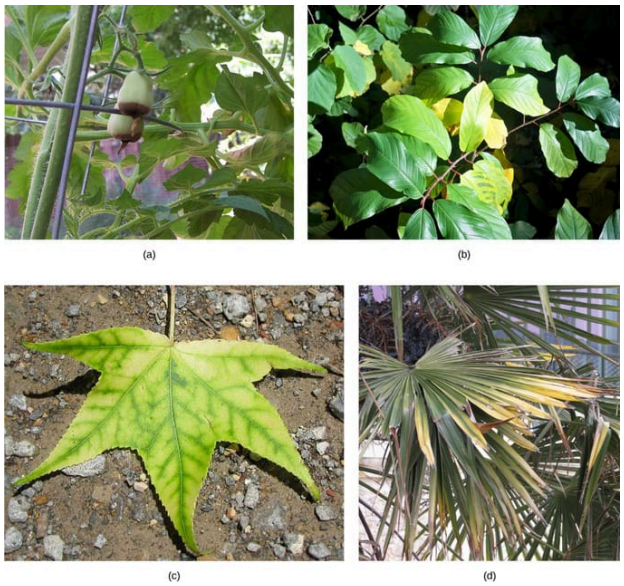


Figure $31.1C.1$: Nutrient deficiency in plants: Nutrient deficiency is evident in the symptoms these plants show. This (a) grape tomato suffers from blossom end rot caused by calcium deficiency. The yellowing in this (b) Frangula alnus results from magnesium deficiency. Inadequate magnesium also leads to (c) intervenal chlorosis, seen here in a sweetgum leaf. This (d) palm is affected by potassium deficiency.

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Key Points

- An element is essential if a plant cannot complete its life cycle without it, if no other element can perform the same function, and if it is directly involved in nutrition.
- An essential nutrient required by the plant in large amounts is called a macronutrient, while one required in very small amounts is termed a micronutrient.
- Missing or inadequate supplies of nutrients adversely affect plant growth, leading to stunted growth, slow growth, chlorosis, or cell death.
- About half the essential nutrients are micronutrients such as boron, chlorine, manganese, iron, zinc, copper, molybdenum, nickel, silicon, and sodium.

Key Terms

- **micronutrient**: a mineral, vitamin, or other substance that is essential, even in very small quantities, for growth or metabolism
- **chlorosis**: a yellowing of plant tissue due to loss or absence of chlorophyll
- **macronutrient**: any of the elements required in large amounts by all living things

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31.2: THE SOIL

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- Topic hierarchy

31.2A: Soil Composition

31.2B: Soil Formation

31.2C: Physical Properties of Soil

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31.2A: Soil Composition

Learning Objectives

- Explain soil composition

Soil Composition

Plants obtain inorganic elements from the soil, which serves as a natural medium for land plants. Soil is the outer, loose layer that covers the surface of Earth. Soil quality, a major determinant, along with climate, of plant distribution and growth, depends not only on the chemical composition of the soil, but also the topography (regional surface features) and the presence of living organisms.

Soil consists of these major components:

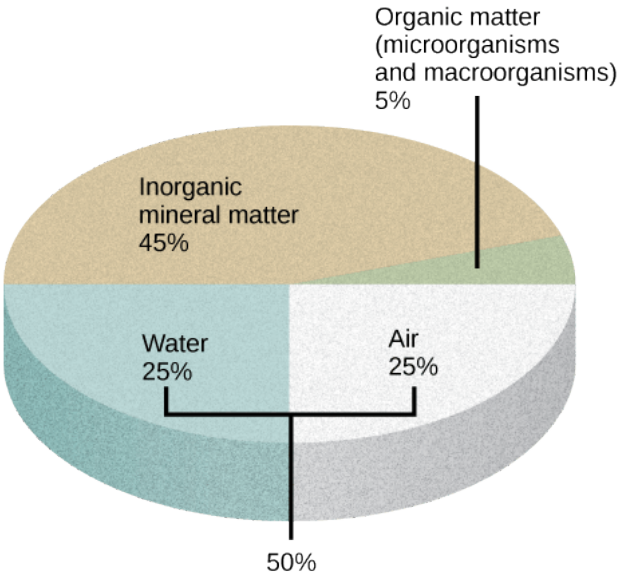


Figure 31.2A.1: Components of soil: The four major components of soil are shown: inorganic minerals, organic matter, water, and air.

- inorganic mineral matter, about 40 to 45 percent of the soil volume
- organic matter, about 5 percent of the soil volume
- water, about 25 percent of the soil volume
- air, about 25 percent of the soil volume

The amount of each of the four major components of soil depends on the quantity of vegetation, soil compaction, and water present in the soil. A good, healthy soil has sufficient air, water, minerals, and organic material to promote and sustain plant life.

The organic material of soil, called humus, is made up of microorganisms (dead and alive), and dead animals and plants in varying stages of decay. Humus improves soil structure, providing plants with water and minerals. The inorganic material of soil is composed of rock, slowly broken down into smaller particles that vary in size. Soil particles that are 0.1 to 2 mm in diameter are sand. Soil particles between 0.002 and 0.1 mm are called silt, and even smaller particles, less than 0.002 mm in diameter, are called clay. Some soils have no dominant particle size, containing a mixture of sand, silt, and humus; these soils are called loams.

Key Points

- The chemical composition of the soil, the topography, and the presence of living organisms determines the quality of soil.

- In general, soil contains 40-45% inorganic matter, 5% organic matter, 25% water, and 25% air.
- In order to sustain plant life, the proper mix of air, water, minerals, and organic material is required.
- Humus, the organic material in soil, is composed of microorganisms (dead and alive) and decaying plants.
- The inorganic material of soil is composed of rock, which is broken down into small particles of sand (0.1 to 2 mm), silt (0.002 to 0.1 mm), and clay (less than 0.002 mm).
- Loam is a soil that is a mix sand, silt, and humus.

Key Terms

- **loam**: soil with no dominant particle size that contains a mixture of sand, silt, and humus
- **humus**: a large group of natural organic compounds found in the soil composed of decaying plants and dead and living microorganisms

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31.2B: Soil Formation

Learning Objectives

- Describe the five factors that account for soil formation

Soil Formation

Soil formation is the consequence of a combination of biological, physical, and chemical processes. Soil should ideally contain 50 percent solid material and 50 percent pore space. About one-half of the pore space should contain water, while the other half should contain air. The organic component of soil serves as a cementing agent, returns nutrients to the plant, allows soil to store moisture, makes soil tillable for farming, and provides energy for soil microorganisms. Most soil microorganisms, bacteria, algae, or fungi, are dormant in dry soil, but become active once moisture is available.

Soil distribution is not homogenous because its formation results in the production of layers; the vertical section of the layers of soil is called the soil profile. Within the soil profile, soil scientists define zones called horizons: a soil layer with distinct physical and chemical properties that differ from those of other layers. Five factors account for soil formation: parent material, climate, topography, biological factors, and time.

Parent Material

The organic and inorganic material in which soils form is the parent material. Mineral soils form directly from the weathering of bedrock, the solid rock that lies beneath the soil; therefore, they have a similar composition to the original rock. Other soils form in materials that came from elsewhere, such as sand and glacial drift. Materials located in the depth of the soil are relatively unchanged compared with the deposited material. Sediments in rivers may have different characteristics, depending on whether the stream moves quickly or slowly. A fast-moving river could have sediments of rocks and sand, whereas a slow-moving river could have fine-textured material, such as clay.

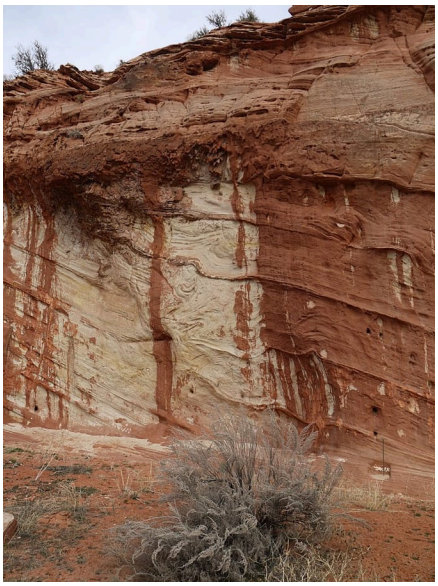


Figure $31.2B.1$: Soft sediment deformation: Soil distribution is not the same at all depths. The vertical section of soil layers is called the soil profile. The soil profile contains defined zones called horizons whicht have distinct physical and chemical properties that differ from those of other layers. An example is shown here in the soft sediment deformation in the Navajo Sandstone.

Climate

Temperature, moisture, and wind cause different patterns of weathering, which affect soil characteristics. The presence of moisture and nutrients from weathering will also promote biological activity: a key component of a quality soil.

Topography

Regional surface features (familiarly called “the lay of the land”) can have a major influence on the characteristics and fertility of a soil. Topography affects water runoff, which strips away parent material and affects plant growth. Steep soils are more prone to erosion and may be thinner than soils that are relatively flat or level.

Biological factors

The presence of living organisms greatly affects soil formation and structure. Animals and microorganisms can produce pores and crevices. Plant roots can penetrate into crevices to produce more fragmentation. Plant secretions promote the development of microorganisms around the root in an area known as the rhizosphere. Additionally, leaves and other material that fall from plants decompose and contribute to soil composition.

Time

Time is an important factor in soil formation because soils develop over long periods. Soil formation is a dynamic process. Materials are deposited over time, decompose, and transform into other materials that can be used by living organisms or deposited onto the surface of the soil.

Key Points

- Parent material is the organic and inorganic material from which soil is formed.
- Climate factors, such as temperature and wind, affect soil formation and its characteristics; the presence of moisture and nutrients is also needed to form a quality soil.
- Topography, or regional surface features, affects water runoff, which strips away parent material and affects plant growth (the steeper the soil, the more erosion takes place).
- The presence of microorganisms in soil creates pores and crevices; plants promote the presence of microorganisms and contribute to soil formation.
- Soil formation takes place over long periods of time.

Key Terms

- **rhizosphere**: the soil region subject to the influence of plant roots and their associated microorganisms
- **bedrock**: the solid rock that exists at some depth below the ground surface
- **horizon**: a soil layer with distinct physical and chemical properties that differ from those of other layers

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31.2C: Physical Properties of Soil

Learning Objectives

- Describe the physical properties or profile of soil

Physical Properties of the Soil

Soils are named and classified based on their horizons. The soil profile has four distinct layers:

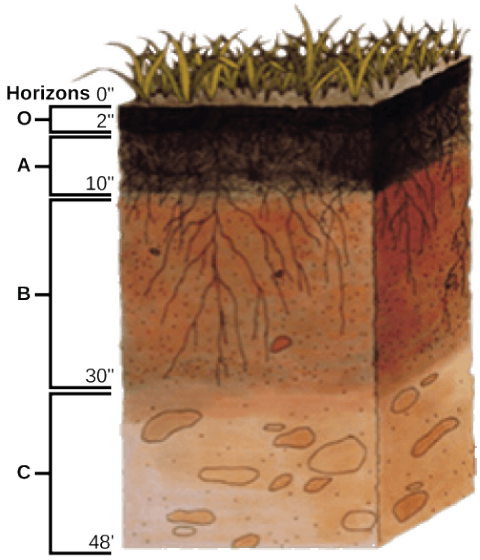


Figure $31.2C.1$: Soil profile: This soil profile shows the different soil layers (O horizon, A horizon, B horizon, and C horizon) found in typical soils.

1. The O horizon has freshly-decomposing organic matter, humus, at its surface, with decomposed vegetation at its base. Humus enriches the soil with nutrients, enhancing soil moisture retention. Topsoil, the top layer of soil, is usually two to three inches deep, but this depth can vary considerably. For instance, river deltas, such as the Mississippi River delta, have deep layers of topsoil. Topsoil is rich in organic material. Microbial processes occur there; it is responsible for plant production.
2. The A horizon consists of a mixture of organic material with inorganic products of weathering; it is the beginning of true mineral soil. This horizon is typically darkly colored because of the presence of organic matter. In this area, rainwater percolates through the soil and carries materials from the surface.
3. The B horizon, or subsoil, is an accumulation of mostly fine material that has moved downward, resulting in a dense layer in the soil. In some soils, the B horizon contains nodules or a layer of calcium carbonate.
4. The C horizon, or soil base, includes the parent material, plus the organic and inorganic material that is broken down to form soil. The parent material may be either created in its natural place or transported from elsewhere to its present location. Beneath the C horizon lies bedrock.

Some soils may have additional layers, or lack one of these layers. The thickness of the layers is also variable, depending on the factors that influence soil formation. In general, immature soils may have O, A, and C horizons, whereas mature soils may display all of these, plus additional layers.

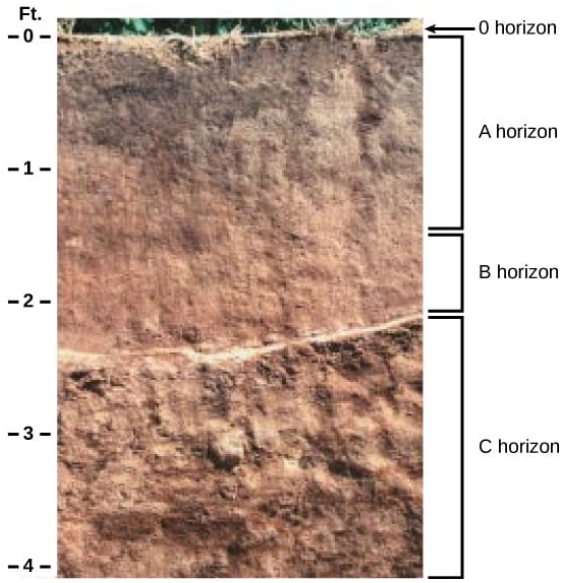


Figure 31.2C.1: Mature soil: The San Joaquin soil is a mature soil that has an O horizon, A horizon, B horizon, and C horizon.

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Key Points

- The O horizon, or topsoil, is made of decaying organisms and plant life; it is responsible for plant production.
- The A horizon is of a mixture of organic material and inorganic products of weathering; it is the beginning of true mineral soil.
- The B horizon, or subsoil, is a dense layer of mostly fine material that has been pushed down from the topsoil.
- The C horizon, or soil base, is located just above bedrock and is made of parent, organic, and inorganic material.

Key Terms

- **topsoil**: top layer of soil containing humus at its surface and decomposing vegetation at its base; the most fertile soil
- **subsoil**: dense layer of soil containing fine material that has moved downward; the layer of earth that is below the topsoil

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31.3: NUTRITIONAL ADAPTATIONS OF PLANTS

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- Topic hierarchy

31.3A: Nitrogen Fixation- Root and Bacteria Interactions
31.3B: Mycorrhizae- The Symbiotic Relationship between Fungi and Roots
31.3C: Nutrients from Other Sources

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31.3A: Nitrogen Fixation- Root and Bacteria Interactions

Learning Objectives

- Explain the process and importance of nitrogen fixation

Nitrogen is an important macronutrient because it is part of nucleic acids and proteins. Atmospheric nitrogen, which is the diatomic molecule N_2, or dinitrogen, is the largest pool of nitrogen in terrestrial ecosystems. However, plants cannot take advantage of this nitrogen because they do not have the necessary enzymes to convert it into biologically useful forms. However, nitrogen can be "fixed." It can be converted to ammonia (NH_3) through biological, physical, or chemical processes. Biological nitrogen fixation (BNF), the conversion of atmospheric nitrogen (N_2) into ammonia (NH_3), is exclusively carried out by prokaryotes, such as soil bacteria or cyanobacteria. Biological processes contribute 65 percent of the nitrogen used in agriculture.

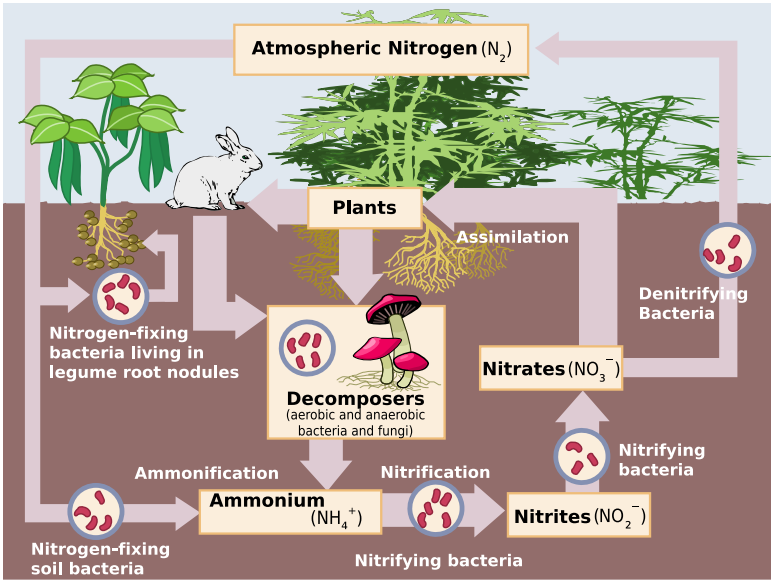


Figure 31.3A.1: Diagram of the Nitrogen Cycle: Schematic representation of the nitrogen cycle. Abiotic nitrogen fixation has been omitted.

The most important source of BNF is the symbiotic interaction between soil bacteria and legume plants, including many crops important to humans. The NH_3 resulting from fixation can be transported into plant tissue and incorporated into amino acids, which are then made into plant proteins. Some legume seeds, such as soybeans and peanuts, contain high levels of protein and are among the most important agricultural sources of protein in the world.



(a) (b) (c)

Figure 31.3A.1: Nitrogen fixation in crops: Some common edible legumes, such as (a) peanuts, (b) beans, and (c) chickpeas, are able to interact symbiotically with soil bacteria that fix nitrogen.

Soil bacteria, collectively called rhizobia, symbiotically interact with legume roots to form specialized structures called nodules in which nitrogen fixation takes place. This process entails the reduction of atmospheric nitrogen to ammonia by means of the enzyme nitrogenase. Therefore, using rhizobia is a natural and environmentally-friendly way to fertilize plants as opposed to chemical fertilization that uses a non-renewable resource, such as natural gas. Through symbiotic nitrogen fixation, the plant benefits from using an endless source of nitrogen from the atmosphere. The process simultaneously contributes to soil fertility because the plant root system leaves behind some of the biologically-available nitrogen. As in any symbiosis, both organisms benefit from the interaction: the plant obtains ammonia and bacteria obtain carbon compounds generated through photosynthesis, as well as a protected niche in which to grow.

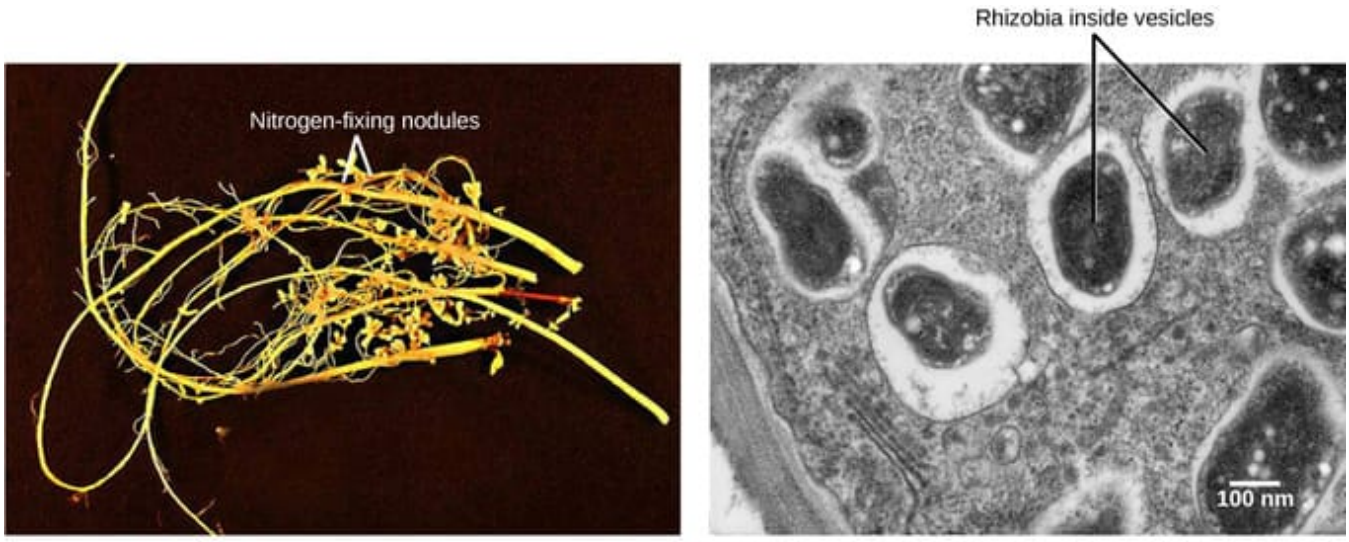


Figure 31.3A.1: Rhizobia: Soybean roots contain (a) nitrogen-fixing nodules. Cells within the nodules are infected with Bradyrhyzobium japonicum, a rhizobia or "root-loving" bacterium. The bacteria are encased in (b) vesicles inside the cell, as can be seen in this transmission electron micrograph.

Key Points

- Diatomic nitrogen is abundant in the atmosphere and soil, but plants are unable to use it because they do not have the necessary enzyme, nitrogenase, to convert it into a form that they can use to make proteins.
- Soil bacteria, or rhizobia, are able to perform biological nitrogen fixation in which atmospheric nitrogen gas (N_2) is converted into the ammonia (NH_3) that plants are able to use to synthesize proteins.
- Both the plants and the bacteria benefit from the process of nitrogen fixation; the plant obtains the nitrogen it needs to synthesize proteins, while the bacteria obtain carbon from the plant and a secure environment to inhabit within the plant roots.

Key Terms

- **rhizobia**: any of various bacteria, of the genus Rhizobium, that form nodules on the roots of legumes and fix nitrogen
- **nitrogen fixation**: the conversion of atmospheric nitrogen into ammonia and organic derivatives, by natural means, especially by microorganisms in the soil, into a form that can be assimilated by plants
- **nodule**: structures that occur on the roots of plants that associate with symbiotic nitrogen-fixing bacteria

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31.3B: Mycorrhizae- The Symbiotic Relationship between Fungi and Roots

Learning Objectives

- Describe the symbiotic relationship of mycorrhizae and plant roots

Mycorrhizae: The Symbiotic Relationship between Fungi and Roots

A nutrient depletion zone can develop when there is rapid soil solution uptake, low nutrient concentration, low diffusion rate, or low soil moisture. These conditions are very common; therefore, most plants rely on fungi to facilitate the uptake of minerals from the soil. Mycorrhizae, known as root fungi, form symbiotic associations with plant roots. In these associations, the fungi are actually integrated into the physical structure of the root. The fungi colonize the living root tissue during active plant growth.

Through mycorrhization, the plant obtains phosphate and other minerals, such as zinc and copper, from the soil. The fungus obtains nutrients, such as sugars, from the plant root. Mycorrhizae help increase the surface area of the plant root system because hyphae, which are narrow, can spread beyond the nutrient depletion zone. Hyphae are long extensions of the fungus, which can grow into small soil pores that allow access to phosphorus otherwise unavailable to the plant. The beneficial effect on the plant is best observed in poor soils. The benefit to fungi is that they can obtain up to 20 percent of the total carbon accessed by plants. Mycorrhizae function as a physical barrier to pathogens. They also provides an induction of generalized host defense mechanisms, which sometimes involves the production of antibiotic compounds by the fungi. Fungi have also been found to have a protective role for plants rooted in soils with high metal concentrations, such as acidic and contaminated soils.



Figure $31.3B.1$: Mycorrhizae: Hyphae proliferate within the mycorrhizae, which appears as off-white fuzz in this image. These hyphae greatly increase the surface area of the plant root, allowing it to reach areas that are not depleted of nutrients.

There are two types of mycorrhizae: ectomycorrhizae and endomycorrhizae. Ectomycorrhizae form an extensive dense sheath around the roots, called a mantle. Hyphae from the fungi extend from the mantle into the soil, which increases the surface area for water and mineral absorption. This type of mycorrhizae is found in forest trees, especially conifers, birches, and oaks. Endomycorrhizae, also called arbuscular mycorrhizae, do not form a dense sheath over the root. Instead, the fungal mycelium is embedded within the root tissue. Endomycorrhizae are found in the roots of more than 80 percent of terrestrial plants.



Figure $31.3B.1$: Ectomycorrhizae: Ectomycorrhizae form sheaths, called a mantle, around the roots of plants, as shown in this image.

Key Points

- Because nutrients are often depleted in the soil, most plants form symbiotic relationships called mycorrhizae with fungi that integrate into the plant's root.
- The relationship between plants and fungi is symbiotic because the plant obtains phosphate and other minerals through the fungus, while the fungus obtains sugars from the plant root.
- The long extensions of the fungus, called hyphae, help increase the surface area of the plant root system so that it can extend beyond the area of nutrient depletion.
- Ectomycorrhizae are a type of mycorrhizae that form a dense sheath around the plant roots, called a mantle, from which the hyphae grow; in endomycorrhizae, mycelium is embedded within the root tissue, as opposed to forming a sheath around it.
- In endomycorrhizae, mycelium is embedded within the root tissue, as opposed to forming a sheath around it; these are found in the roots of most terrestrial plants.

Key Terms

- **mycorrhiza**: a symbiotic association between a fungus and the roots of a vascular plant
- **hypha**: a long, branching, filamentous structure of a fungus that is the main mode of vegetative growth
- **mycelium**: the vegetative part of any fungus, consisting of a mass of branching, threadlike hyphae, often underground

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31.3C: Nutrients from Other Sources

Learning Objectives

- Differentiate among the sources of plant nutrition

Nutrients from Other Sources

Some plants cannot produce their own food and must obtain their nutrition from outside sources. This may occur with plants that are parasitic or saprophytic: ingesting and utilizing dead matter as a food source. In other cases, plants may be mutualistic symbionts, epiphytes, or insectivorous.

Plant Parasites

A parasitic plant depends on its host for survival. Some parasitic plants have no leaves. An example of this is the dodder, which has a weak, cylindrical stem that coils around the host and forms suckers. From these suckers, cells invade the host stem and grow to connect with the vascular bundles of the host. The parasitic plant obtains water and nutrients through these connections. The plant is a total parasite (a holoparasite) because it is completely dependent on its host. Other parasitic plants, called hemiparasites, are fully photosynthetic and only use the host for water and minerals. There are about 4,100 species of parasitic plants.



Figure $31.3C.1$: Parasitic plants: The dodder is a holoparasite that penetrates the host's vascular tissue and diverts nutrients for its own growth. Note that the vines of the dodder, which has white flowers, are beige. The dodder has no chlorophyll and cannot produce its own food.

Saprophytes

A saprophyte is a plant that does not have chlorophyll, obtaining its food from dead matter, similar to bacteria and fungi. (Note that fungi are often called saprophytes, which is incorrect, because fungi are not plants). Plants such as these use enzymes to convert organic food materials into simpler forms from which they can absorb nutrients. Most saprophytes do not directly digest dead matter. Instead, they parasitize mycorrhizae or other fungi that digest dead matter, ultimately obtaining photosynthate from a fungus that derived photosynthate from its host. Saprophytic plants are uncommon with only a few, described species.



Figure $31.3C.1$: Saprophytes: Saprophytes, like this Dutchmen's pipe (Monotropa hypopitys), obtain their food from dead matter and do not have chlorophyll.

Symbionts

A symbiont is a plant in a symbiotic relationship with other organisms, such as mycorrhizae (with fungi) or nodule formation. Root nodules occur on plant roots (primarily *Fabaceae*) that associate with symbiotic, nitrogen-fixing bacteria. Under nitrogen-limiting conditions, capable plants form a symbiotic relationship with a host-specific strain of bacteria known as rhizobia. Within legume nodules, nitrogen gas from the atmosphere is converted into ammonia, which is then assimilated into amino acids (the building blocks of proteins), nucleotides (the building blocks of DNA and RNA, as well as the important energy molecule ATP), and other cellular constituents such as vitamins, flavones, and hormones.

Fungi also form symbiotic associations with cyanobacteria and green algae; the resulting symbiotic organism is called a lichen. Lichens can sometimes be seen as colorful growths on the surface of rocks and trees. The algal partner (phyco- or photobiont) makes food autotrophically, some of which it shares with the fungus; the fungal partner (mycobiont) absorbs water and minerals from the environment, which are made available to the green alga. If one partner was separated from the other, they would both die.

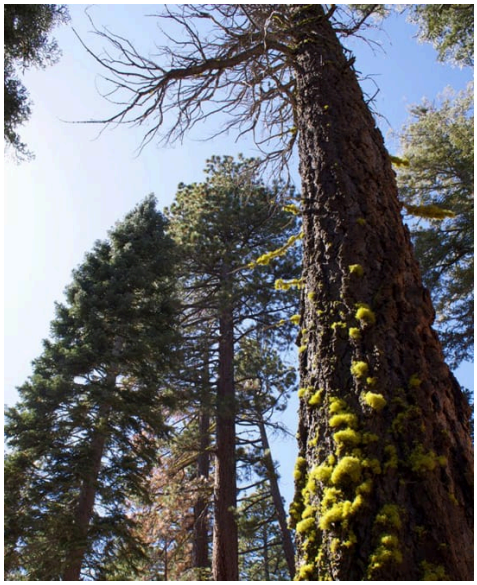


Figure $31.3C.1$: Symbionts: Lichens, which result from the symbiotic relationship between fungi and green algae, are often seen growing on trees.

Epiphytes

An epiphyte is a plant that grows on other plants, but is not dependent upon the other plant for nutrition; it is non-parasitic. The epiphyte derives its moisture and nutrients from the air, rain, and sometimes from debris accumulating around it instead of from the structure to which it is fastened. Epiphytes have two types of roots: clinging aerial roots (which absorb nutrients from humus that accumulates in the crevices of trees) and aerial roots (which absorb moisture from the atmosphere).

Insectivorous Plants

An insectivorous plant has specialized leaves to attract and digest insects. The Venus flytrap is popularly known for its insectivorous mode of nutrition and has leaves that work as traps. The minerals it obtains from prey compensate for those lacking in the boggy (low pH) soil of its native North Carolina coastal plains. There are three sensitive hairs in the center of each half of each leaf. The edges of each leaf are covered with long spines. Nectar secreted by the plant attracts flies to the leaf. When a fly touches the sensory hairs, the leaf immediately closes. Fluids and enzymes then break down the prey and minerals are absorbed by the leaf. Since this plant is popular in the horticultural trade, it is threatened in its original habitat.



Figure $31.3C.1$: Insectivorous plants: A Venus flytrap has specialized leaves to trap insects, which it uses to supplement the low level of nutrients in the soil in which it lives.

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Key Points

- Some plants are parasites, which acquire all of some of their nutrients from another host plant and are, therefore, entirely

dependent upon it for their survival.
- Saprophytes acquire nutrients from dead matter, using enzymes to convert complex organic compounds into simpler forms from which the plant can absorb nutrients.
- A symbiont experiences a mutually-beneficial arrangement with a plant; both partners contribute necessary nutrients to the other.
- An epiphyte is a plant that grows on other plants, but is not dependent upon the other plant for nutrition; instead, it uses the other plant for physical support.
- Insectivorous plants have special adapatations for attracting and trapping insects, which they use to supplement their own nutrients, depleted in the surrounding soil.

Key Terms

- **photosynthate**: any compound that is a product of photosynthesis
- **photobiont**: a photosynthetic symbiont
- **mycobiont**: the fungus that is a component of a lichen
- **saprophyte**: any organism that lives on dead organic matter, as certain fungi and bacteria
- **epiphyte**: a plant that grows on another, using it as a physical support but neither obtaining nutrients from it nor causing it any damage if also offering no benefit
- **insectivorous**: capable of trapping and absorbing insects; such as the sundew, pitcher plant and Venus flytrap

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32: PLANT REPRODUCTIVE DEVELOPMENT AND STRUCTURE

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32.1: Plant Reproductive Development and Structure - Plant Reproductive Development and Structure

Learning Objectives

- Differentiate among the ways in which plants reproduce

Introduction

Plants have evolved different reproductive strategies for the continuation of their species. Some plants reproduce sexually while others reproduce asexually, in contrast to animal species, which rely almost exclusively on sexual reproduction. Plant sexual reproduction usually depends on pollinating agents, while asexual reproduction is independent of these agents. Flowers are often the showiest or most strongly-scented part of plants. With their bright colors, fragrances, and interesting shapes and sizes, flowers attract insects, birds, and animals to serve their pollination needs. Other plants pollinate via wind or water; still others self-pollinate.

Asexual Reproduction

Vegetative reproduction is a type of asexual reproduction. Other terms that apply are vegetative propagation, clonal growth, or vegetative multiplication. Vegetative growth is enlargement of the individual plant, while vegetative reproduction is any process that results in new plant "individuals" without production of seeds or spores. It is both a natural process in many, many species as well as a process utilized or encouraged by horticulturists and farmers to obtain quantities of economically-valuable plants. In this respect, it is a form of cloning that has been carried out by humanity for thousands of years and by plants for hundreds of millions of years.

Sexual Reproduction and The Flower

The flower is the reproductive organ of plants classified as angiosperms. All plants have the means and corresponding structures for reproducing sexually. The basic function of a flower is to produce seeds through sexual reproduction. Seeds are the next generation, serving as the primary method in most plants by which individuals of the species are dispersed across the landscape. Actual dispersal is, in most species, a function of the fruit (a structural part that typically surrounds the seed).



Figure 32.1.1: Plants and sexual reproduction: Plants that reproduce sexually often achieve fertilization with the help of pollinators such as (a) bees, (b) birds, and (c) butterflies.

Key Points

- Vegetative reproduction is a type of asexual reproduction that results in new plant individuals without seed or spore production.
- Vegetative reproduction is also utilized by horticulturists to ensure production of large quantities of valuable plants.
- Plants have flowers that produce seeds through sexual reproduction; seeds are dispersed to increase propagation of the next generation.
- Seeds are often dispersed by animals via ingestion of the fruits, which surround the seeds, promoting seed dispersal.

Key Terms

- **vegetative reproduction**: a form of asexual reproduction in plants

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32.2: Plant Reproductive Development and Structure - Sexual Reproduction in Gymnosperms

Learning Objectives

- Describe the process of sexual reproduction in gymnosperms

Sexual Reproduction in Gymnosperms

As with angiosperms, the life cycle of gymnosperms is also characterized by alternation of generations. In conifers such as pines, the green leafy part of the plant is the sporophyte; the cones contain the male and female gametophytes. The female cones are larger than the male cones and are positioned towards the top of the tree; the small, male cones are located in the lower region of the tree. Because the pollen is shed and blown by the wind, this arrangement makes it difficult for a gymnosperm to self-pollinate.

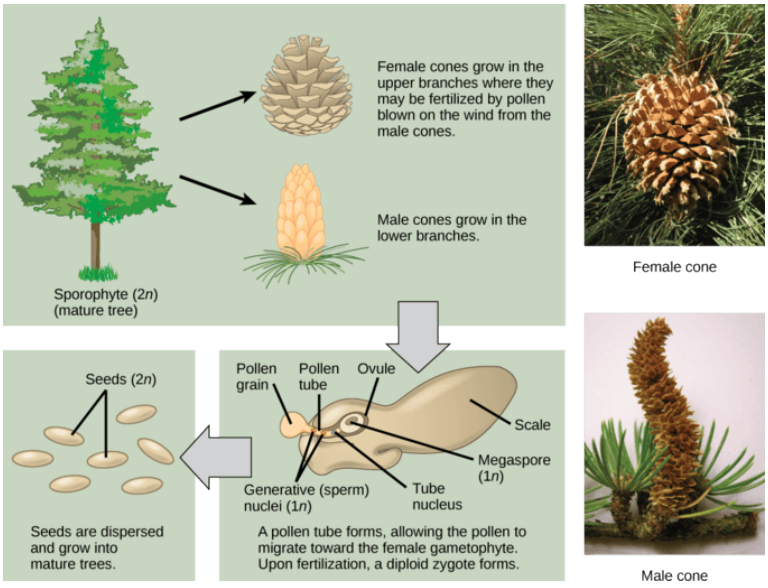


Figure 32.2.1: Conifer life cycle: This image shows the life cycle of a conifer. Pollen from male cones blows up into upper branches, where it fertilizes female cones. Examples are shown for female and male cones.

Male Gametophyte

A male cone has a central axis on which bracts, a type of modified leaf, are attached. The bracts, known as microsporophylls, are the sites where microspores will develop. The microspores develop inside the microsporangium. Within the microsporangium, cells known as microsporocytes divide by meiosis to produce four haploid microspores. Further mitosis of the microspore produces two nuclei: the generative nucleus and the tube nucleus. Upon maturity, the male gametophyte (pollen) is released from the male cones and is carried by the wind to land on female cones.

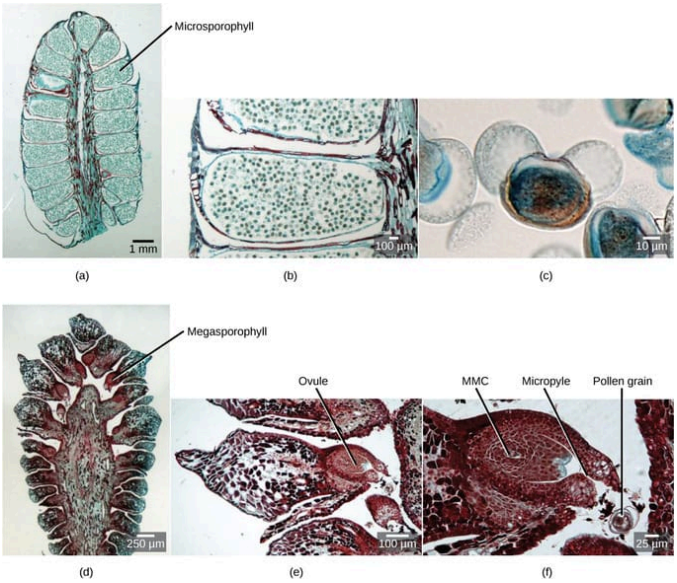


Figure 32.2.1: Male and female gametophytes: These series of micrographs shows male and female gymnosperm gametophytes. (a) This male cone, shown in cross section, has approximately 20 microsporophylls, each of which produces hundreds of male gametophytes (pollen grains). (b) Pollen grains are visible in this single microsporophyll. (c) This micrograph shows an individual pollen grain. (d) This cross section of a female cone shows portions of about 15 megasporophylls. (e) The ovule can be seen in this single megasporophyll. (f) Within this single ovule are the megaspore mother cell (MMC), micropyle, and a pollen grain.

Female Gametophyte

The female cone also has a central axis on which bracts known as megasporophylls are present. In the female cone, megaspore mother cells are present in the megasporangium. The megaspore mother cell divides by meiosis to produce four haploid megaspores. One of the megaspores divides to form the multicellular female gametophyte, while the others divide to form the rest of the structure. The female gametophyte is contained within a structure called the archegonium.

Reproductive Process

Upon landing on the female cone, the tube cell of the pollen forms the pollen tube, through which the generative cell migrates towards the female gametophyte through the micropyle. It takes approximately one year for the pollen tube to grow and migrate towards the female gametophyte. The male gametophyte containing the generative cell splits into two sperm nuclei, one of which fuses with the egg, while the other degenerates. After fertilization of the egg, the diploid zygote is formed, which divides by mitosis to form the embryo. The scales of the cones are closed during development of the seed. The seed is covered by a seed coat, which is derived from the female sporophyte. Seed development takes another one to two years. Once the seed is ready to be dispersed, the bracts of the female cones open to allow the dispersal of seed; no fruit formation takes place because gymnosperm seeds have no covering.

Angiosperms Versus Gymnosperms

Gymnosperm reproduction differs from that of angiosperms in several ways. In angiosperms, the female gametophyte in the ovule exists in an enclosed structure, the ovary; in gymnosperms, the female gametophyte is present on exposed bracts of the female cone and is not enclosed in an ovary. Double fertilization is a key event in the life cycle of angiosperms, but is completely absent in gymnosperms. The male and female gametophyte structures are present on separate male and female cones in gymnosperms, whereas in angiosperms, they are a part of the flower. Finally, wind plays an important role in pollination in gymnosperms because pollen is blown by the wind to land on the female cones. Although many angiosperms are also wind-pollinated, animal pollination is more common.

Key Points

- In gymnosperms, a leafy green sporophyte generates cones containing male and female gametophytes; female cones are bigger than male cones and are located higher up in the tree.
- A male cone contains microsporophylls where male gametophytes (pollen) are produced and are later carried by wind to female gametophytes.
- The megaspore mother cell in the female cone divides by meiosis to produce four haploid megaspores; one of the megaspores divides to form the female gametophyte.
- The male gametophyte lands on the female cone, forming a pollen tube through which the generative cell travels to meet the female gametophyte.
- One of the two sperm cells released by the generative cell fuses with the egg, forming a diploid zygote that divides to form the embryo.
- Unlike angiosperms, ovaries are absent in gymnosperms, double fertilization does not take place, male and female gametophytes are present on cones rather than flowers, and wind (not animals) drives pollination.

Key Terms

- **megasporophyll**: bears megasporangium, which produces megaspores that divide into the female gametophyte
- **microsporophyll**: a leaflike organ that bears microsporangium, which produces microspores that divide into the male gametophyte (pollen)

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32.3: Plant Reproductive Development and Structure - Sexual Reproduction in Angiosperms

Learning Objectives

- Outline the components of a flower and their function

The lifecycle of angiosperms follows the alternation of generations. In the angiosperm, the haploid gametophyte alternates with the diploid sporophyte during the sexual reproduction process of angiosperms. Flowers contain the plant's reproductive structures.

Flower Structure

A typical flower has four main parts, or whorls: the calyx, corolla, androecium, and gynoecium. The outermost whorl of the flower has green, leafy structures known as sepals, which are collectively called the calyx, and help to protect the unopened bud. The second whorl is comprised of petals, usually brightly colored, collectively called the corolla. The number of sepals and petals varies depending on whether the plant is a monocot or dicot. Together, the calyx and corolla are known as the perianth. The third whorl contains the male reproductive structures and is known as the androecium. The androecium has stamens with anthers that contain the microsporangia. The innermost group of structures in the flower is the gynoecium, or the female reproductive component(s). The carpel is the individual unit of the gynoecium and has a stigma, style, and ovary. A flower may have one or multiple carpels.

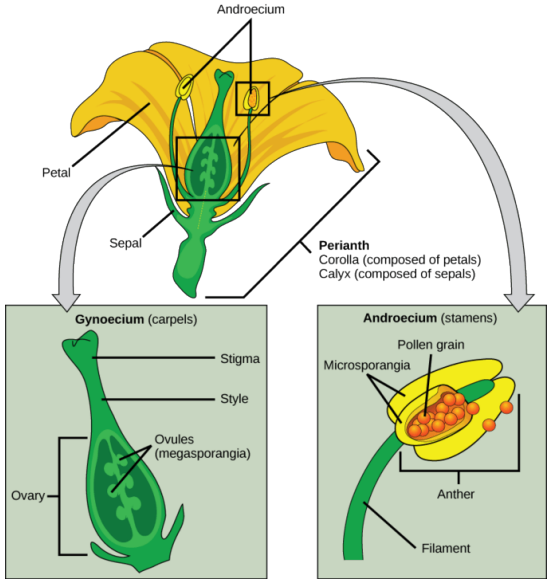


Figure 32.3.1: Structures of the flower: The four main parts of the flower are the calyx, corolla, androecium, and gynoecium. The androecium is the sum of all the male reproductive organs, and the gynoecium is the sum of the female reproductive organs.

If all four whorls are present, the flower is described as complete. If any of the four parts is missing, the flower is known as incomplete. Flowers that contain both an androecium and a gynoecium are called perfect, androgynous, or hermaphrodites. There are two types of incomplete flowers: staminate flowers contain only an androecium; and carpellate flowers have only a gynoecium.



Figure 32.3.1: Staminate and carpellate flowers: The corn plant has both staminate (male) and carpellate (female) flowers. Staminate flowers, which are clustered in the tassel at the tip of the stem, produce pollen grains. Carpellate flower are clustered in the immature ears. Each strand of silk is a stigma. The corn kernels are seeds that develop on the ear after fertilization. Also shown is the lower stem and root.

If both male and female flowers are borne on the same plant (e.g., corn or peas), the species is called monoecious (meaning “one home”). Species with male and female flowers borne on separate plants (e.g., *C. papaya* or *Cannabis*)are termed dioecious, or “two homes.” The ovary, which may contain one or multiple ovules, may be placed above other flower parts (referred to as superior); or it may be placed below the other flower parts (referred to as inferior).

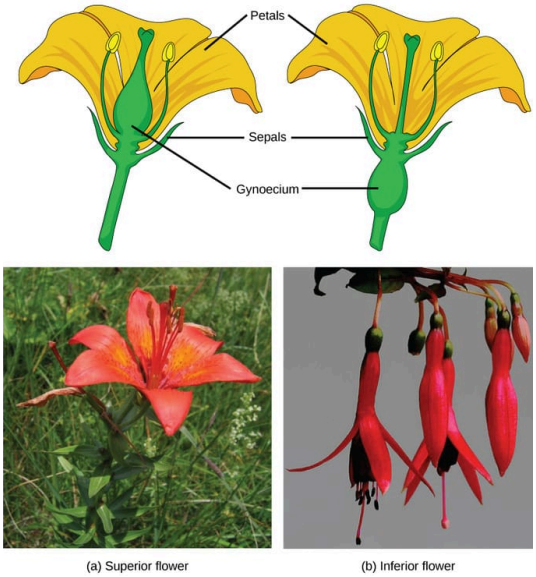


Figure 32.3.1: Superior and inferior flowers: The (a) lily is a superior flower, which has the ovary above the other flower parts. (b) Fuchsia is an inferior flower, which has the ovary beneath other flower parts.

Male Gametophyte

The male gametophyte develops and reaches maturity in an immature anther. In a plant’s male reproductive organs, development of pollen takes place in a structure known as the microsporangium. The microsporangia, usually bi-lobed, are pollen sacs in which the microspores develop into pollen grains.

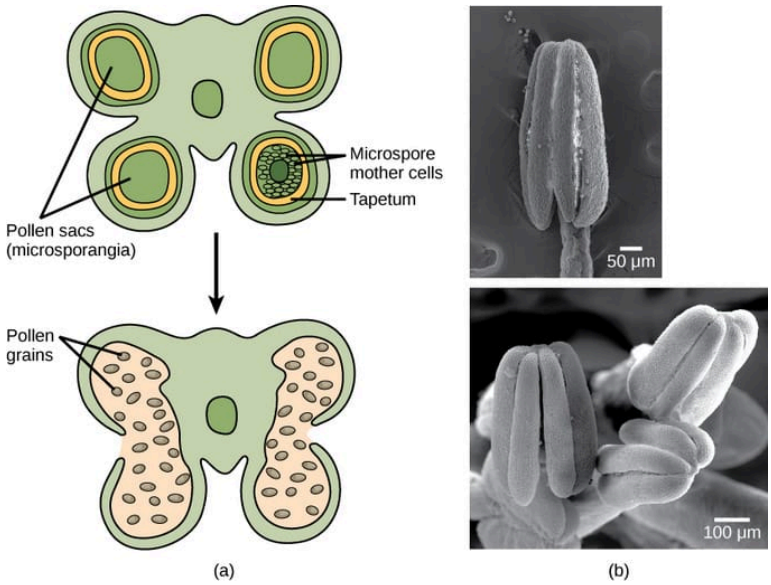


Figure 32.3.1: Microsporangium: Shown is (a) a cross section of an anther at two developmental stages. The immature anther (top) contains four microsporangia, or pollen sacs. Each microsporangium contains hundreds of microspore mother cells that will each give rise to four pollen grains. The tapetum supports the development and maturation of the pollen grains. Upon maturation of the pollen (bottom), the pollen sac walls split open and the pollen grains (male gametophytes) are released. (b) In these scanning electron micrographs, pollen sacs are ready to burst, releasing their grains.

Within the microsporangium, the microspore mother cell divides by meiosis to give rise to four microspores, each of which will ultimately form a pollen grain. An inner layer of cells, known as the tapetum, provides nutrition to the developing microspores, contributing key components to the pollen wall. Mature pollen grains contain two cells: a generative cell and a pollen tube cell. The generative cell is contained within the larger pollen tube cell. Upon germination, the tube cell forms the pollen tube through which the generative cell migrates to enter the ovary. During its transit inside the pollen tube, the generative cell divides to form two male gametes. Upon maturity, the microsporangia burst, releasing the pollen grains from the anther.

Each pollen grain has two coverings: the exine (thicker, outer layer) and the intine. The exine contains sporopollenin, a complex waterproofing substance supplied by the tapetal cells. Sporopollenin allows the pollen to survive under unfavorable conditions and to be carried by wind, water, or biological agents without undergoing damage.

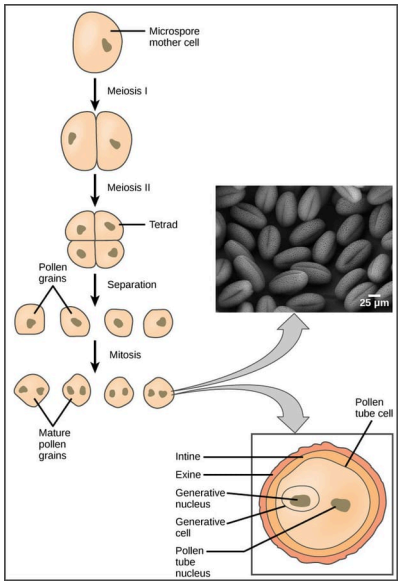


Figure 32.3.1: Pollen grain structure: Pollen develops from the microspore mother cells. The mature pollen grain is composed of two cells: the pollen tube cell and the generative cell, which is inside the tube cell. The pollen grain has two coverings: an inner layer (intine) and an outer layer (exine). The inset scanning electron micrograph shows *Arabidopsis lyrata* pollen grains.

Female Gametophyte (Embryo Sac)

The overall development of the female gametophyte has two distinct phases. First, in the process of megasporogenesis, a single cell in the diploid megasporangium undergoes meiosis to produce four megaspores, only one of which survives. During the second phase, megagametogenesis, the surviving haploid megaspore undergoes mitosis to produce an eight-nucleate, seven-cell female gametophyte, also known as the megagametophyte, or embryo sac. The polar nuclei move to the equator and fuse, forming a single, diploid central cell. This central cell later fuses with a sperm to form the triploid endosperm. Three nuclei position themselves on the end of the embryo sac opposite the micropyle and develop into the antipodal cells, which later degenerate. The nucleus closest to the micropyle becomes the female gamete, or egg cell, and the two adjacent nuclei develop into synergid cells. The synergids help guide the pollen tube for successful fertilization, after which they disintegrate. Once fertilization is complete, the resulting diploid zygote develops into the embryo; the fertilized ovule forms the other tissues of the seed.

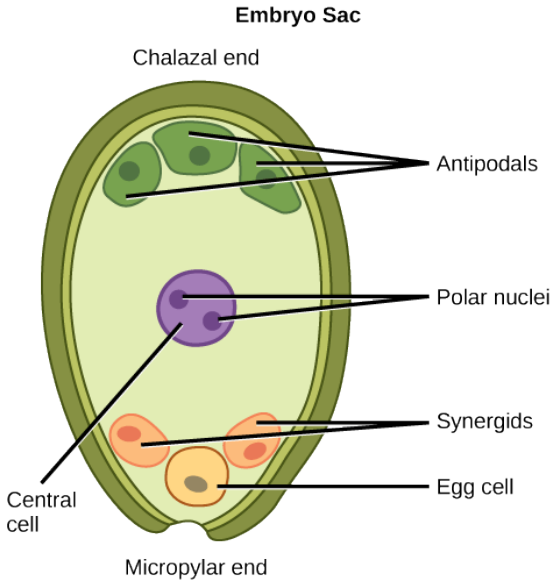


Figure 32.3.1: Embryo sac: As shown in this diagram of the embryo sac in angiosperms, the ovule is covered by integuments and has an opening called a micropyle. Inside the embryo sac are three antipodal cells, two synergids, a central cell, and the egg cell.

A double-layered integument protects the megasporangium and, later, the embryo sac. The integument will develop into the seed coat after fertilization, protecting the entire seed. The ovule wall will become part of the fruit. The integuments, while protecting the megasporangium, do not enclose it completely, but leave an opening called the micropyle. The micropyle allows the pollen tube to enter the female gametophyte for fertilization.

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Key Points

- A typical flower has four main parts, or whorls: the calyx (sepals), corolla (petals), androecium (male reproductive structure), and gynoecium (female reproductive structure).
- Angiosperms that contain both male and female gametophytes within the same flower are called complete and are considered to be androgynous or hermaphroditic.
- Angiosperms that contain only male or only female gametophytes are considered to be incomplete and are either staminate (contain only male structures) or carpellate (contain only female structures) flowers.
- Microspores develop in the microsporangium and form mature pollen grains (male gametophytes), which are then used to fertilize female gametophytes.
- During megasporogenesis, four megaspores are produced with one surviving; during megagametogenesism, the surviving megaspore undergoes mitosis to form an embryo sac (female gametophyte).
- The sperm, guided by the synergid cells, migrates to the ovary to complete fertilization; the diploid zygote develops into the embryo, while the fertilized ovule forms the other tissues of the seed.

Key Terms

- **perianth**: the calyx (sepals) and the corolla (petals)
- **androecium**: the set of a flower's stamens (male reproductive organs)
- **gynoecium**: the set of a flower's pistils (female reproductive organs)

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32.4: Pollination and Fertilization - Introduction

Learning Objectives

- Determine the differences between self-pollination and cross-pollination, and describe how plants have developed ways to avoid self-pollination

Pollination: An Introduction

In angiosperms, pollination is defined as the placement or transfer of pollen from the anther to the stigma of the same or a different flower. In gymnosperms, pollination involves pollen transfer from the male cone to the female cone. Upon transfer, the pollen germinates to form the pollen tube and the sperm that fertilize the egg.

Self-Pollination and Cross-Pollination

Pollination takes two forms: self-pollination and cross-pollination. Self-pollination occurs when the pollen from the anther is deposited on the stigma of the same flower or another flower on the same plant. Cross-pollination is the transfer of pollen from the anther of one flower to the stigma of another flower on a different individual of the same species. Self-pollination occurs in flowers where the stamen and carpel mature at the same time and are positioned so that the pollen can land on the flower's stigma. This method of pollination does not require an investment from the plant to provide nectar and pollen as food for pollinators. These types of pollination have been studied since the time of Gregor Mendel. Mendel successfully carried out self-pollination and cross-pollination in garden peas while studying how characteristics were passed on from one generation to the next. Today's crops are a result of plant breeding, which employs artificial selection to produce the present-day cultivars. An example is modern corn, which is a result of thousands of years of breeding that began with its ancestor, teosinte. The teosinte that the ancient Mesoamericans originally began cultivating had tiny seeds, vastly different from today's relatively giant ears of corn. Interestingly, though these two plants appear to be entirely different, the genetic difference between them is minuscule.



Figure 32.4.1: Teosinte: Teosinte (left) is the ancestor of modern corn (far-right). Although they are morphologically dissimilar, genetically they are not so different.

Genetic Diversity

Living species are designed to ensure survival of their progeny; those that fail become extinct. Genetic diversity is, therefore,

required so that in changing environmental or stress conditions, some of the progeny can survive. Self-pollination leads to the production of plants with less genetic diversity since genetic material from the same plant is used to form gametes and, eventually, the zygote. In contrast, cross-pollination leads to greater genetic diversity because the male and female gametophytes are derived from different plants. Because cross-pollination allows for more genetic diversity, plants have developed many ways to avoid self-pollination. In some species, the pollen and the ovary mature at different times. These flowers make self-pollination nearly impossible. By the time pollen matures and has been shed, the stigma of this flower is mature and can only be pollinated by pollen from another flower. Some flowers have developed physical features that prevent self-pollination. The primrose employs this technique. Primroses have evolved two flower types with differences in anther and stigma length: the pin-eyed flower and the thrum-eyed flower. In the pin-eyed flower, anthers are positioned at the pollen tube's halfway point, and in the thrum-eyed flower, the stigma is found at this same location. This allows insects to easily cross-pollinate while seeking nectar at the pollen tube. This phenomenon is also known as heterostyly. Many plants, such as cucumbers, have male and female flowers located on different parts of the plant, thus making self-pollination difficult. In other species, the male and female flowers are borne on different plants, making them dioecious. All of these are barriers to self-pollination; therefore, the plants depend on pollinators to transfer pollen. The majority of pollinators are biotic agents such as insects (bees, flies, and butterflies), bats, birds, and other animals. Other plant species are pollinated by abiotic agents, such as wind and water.



Figure 32.4.1: Pollinators: To maximize their avoidance of self-pollination, plants have evolved relationships with animals, such as bees, to ensure cross-pollination between members of the same species.

Key Points

- Pollination, the transfer of pollen from flower-to-flower in angiosperms or cone -to-cone in gymnosperms, takes place through self-pollination or cross-pollination.
- Cross-pollination is the most advantageous of the two types of pollination since it provides species with greater genetic diversity.
- Maturation of pollen and ovaries at different times and heterostyly are methods plants have developed to avoid self-pollination.
- The placement of male and female flowers on separate plants or different parts of the plant are also barriers to self-pollination.

Key Terms

- **pollination**: the transfer of pollen from an anther to a stigma that is carried out by insects, birds, bats, and the wind
- **heterostyly**: the condition of having unequal male (anther) and female (stigma) reproductive organs
- **cross-pollination**: fertilization by the transfer of pollen from an anther of one plant to a stigma of another
- **self-pollination**: pollination of a flower by its own pollen in a flower that has both stamens and a pistil

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32.5: Pollination and Fertilization - Pollination by Insects

Learning Objectives

- Explain how pollination by insects aids plant reproduction

Bees

Bees are perhaps the most important pollinator of many garden plants and most commercial fruit trees. The most common species of bees are bumblebees and honeybees. Since bees cannot see the color red, bee-pollinated flowers usually have shades of blue, yellow, or other colors. Bees collect energy -rich pollen or nectar for their survival and energy needs. They visit flowers that are open during the day, are brightly colored, have a strong aroma or scent, and have a tubular shape, typically with the presence of a nectar guide. A nectar guide includes regions on the flower petals that are visible only to bees, which help guide bees to the center of the flower, thus making the pollination process more efficient. The pollen sticks to the bees' fuzzy hair; when the bee visits another flower, some of the pollen is transferred to the second flower. Recently, there have been many reports about the declining population of honeybees. Many flowers will remain unpollinated, failing to bear seeds if honeybees disappear. The impact on commercial fruit growers could be devastating.



Figure 32.5.1: Pollination by insects: Insects, such as bees, are important agents of pollination. Bees are probably the most important species of pollinators for commercial and garden plant species.

Flies

Many flies are attracted to flowers that have a decaying smell or an odor of rotting flesh. These flowers, which produce nectar, usually have dull colors, such as brown or purple. They are found on the corpse flower or voodoo lily (*Amorphophallus*), dragon arum (*Dracunculus*), and carrion flower *(Stapleia, Rafflesia*). The nectar provides energy while the pollen provides protein. Wasps are also important insect pollinators, pollinating many species of figs.

Butterflies and Moths

Butterflies, such as the monarch, pollinate many garden flowers and wildflowers, which are usually found in clusters. These flowers are brightly colored, have a strong fragrance, are open during the day, and have nectar guides. The pollen is picked up and carried on the butterfly's limbs. Moths, on the other hand, pollinate flowers during the late afternoon and night. The flowers pollinated

by moths are pale or white and are flat, enabling the moths to land. One well-studied example of a moth-pollinated plant is the yucca plant, which is pollinated by the yucca moth. The shape of the flower and moth have adapted in a way to allow successful pollination. The moth deposits pollen on the sticky stigma for fertilization to occur later. The female moth also deposits eggs into the ovary. As the eggs develop into larvae, they obtain food from the flower and developing seeds. Thus, both the insect and flower benefit from each other in this symbiotic relationship. The corn earworm moth and *Gaura* plant have a similar relationship.



Figure 32.5.1: Moths as pollinators: A corn earworm (a moth) sips nectar from a night-blooming Gaura plant. Both the moth and plant benefit from each other as they have formed a symbiotic relationship; the plant is pollinated while the moth is able to obtain food.

Key Points

- Adaptations such as bright colors, strong fragrances, special shapes, and nectar guides are used to attract suitable pollinators.
- Important insect pollinators include bees, flies, wasps, butterflies, and moths.
- Bees and butterflies are attracted to brightly-colored flowers that have a strong scent and are open during the day, whereas moths are attracted to white flowers that are open at night.
- Flies are attracted to dull brown and purple flowers that have an odor of decaying meat.
- Nectar guides, which are only visible to certain insects, facilitate pollination by guiding bees to the pollen at the center of flowers.
- Insects and flowers both benefit from their specialized symbiotic relationships; plants are pollinated while insects obtain valuable sources of food.

Key Terms

- **nectar guide**: markings or patterns seen in flowers of some angiosperm species that guide pollinators to nectar or pollen

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32.6: Pollination and Fertilization - Pollination by Bats, Birds, Wind, and Water

Learning Objectives

- Differentiate among the non-insect methods of pollination

Non-Insect Methods of Pollination

Plants have developed specialized adaptations to take advantage of non-insect forms of pollination. These methods include pollination by bats, birds, wind, and water.

Pollination by Bats

In the tropics and deserts, bats are often the pollinators of nocturnal flowers such as agave, guava, and morning glory. The flowers are usually large and white or pale-colored so that they can be distinguished from their dark surroundings at night. The flowers have a strong, fruity, or musky fragrance and produce large amounts of nectar. They are naturally-large and wide-mouthed to accommodate the head of the bat. As the bats seek the nectar, their faces and heads become covered with pollen, which is then transferred to the next flower.

Pollination by Birds

Many species of small birds, such as hummingbirds and sun birds, are pollinators for plants such as orchids and other wildflowers. Flowers visited by birds are usually sturdy and are oriented in a way to allow the birds to stay near the flower without getting their wings entangled in the nearby flowers. The flower typically has a curved, tubular shape, which allows access for the bird's beak. Brightly-colored, odorless flowers that are open during the day are pollinated by birds. As a bird seeks energy-rich nectar, pollen is deposited on the bird's head and neck and is then transferred to the next flower it visits. Botanists determine the range of extinct plants by collecting and identifying pollen from 200-year-old bird specimens from the same site.



Figure 32.6.1: Pollination by birds: Hummingbirds have adaptations that allow them to reach the nectar of certain tubular flowers, thereby, aiding them in the process of pollination.

Pollination by Wind

Most species of conifers and many angiosperms, such as grasses, maples, and oaks, are pollinated by wind. Pine cones are brown and unscented, while the flowers of wind-pollinated angiosperm species are usually green, small, may have small or no petals, and produce large amounts of pollen. Unlike the typical insect-pollinated flowers, flowers adapted to pollination by wind do not produce nectar or scent. In wind-pollinated species, the microsporangia hang out of the flower, and, as the wind blows, the lightweight pollen is carried with it. The flowers usually emerge early in the spring before the leaves so that the leaves do not block the movement of the wind. The pollen is deposited on the exposed feathery stigma of the flower.



Figure 32.6.1: Wind pollination: These male (a) and female (b) catkins from the goat willow tree (*Salix caprea*) have structures that are light and feathery to better disperse and catch the wind-blown pollen.

Pollination by Water

Some weeds, such as Australian sea grass and pond weeds, are pollinated by water. The pollen floats on water. When it comes into contact with the flower, it is deposited inside the flower.

Pollination by Deception

Orchids are highly-valued flowers, with many rare varieties. They grow in a range of specific habitats, mainly in the tropics of Asia, South America, and Central America. At least 25,000 species of orchids have been identified.

Flowers often attract pollinators with food rewards, in the form of nectar. However, some species of orchid are an exception to this standard; they have evolved different ways to attract the desired pollinators. They use a method known as food deception, in which bright colors and perfumes are offered, but no food. *Anacamptis morio*, commonly known as the green-winged orchid, bears bright purple flowers and emits a strong scent. The bumblebee, its main pollinator, is attracted to the flower because of the strong scent, which usually indicates food for a bee. In the process, the bee picks up the pollen to be transported to another flower.

Other orchids use sexual deception. *Chiloglottis trapeziformis* emits a compound that smells the same as the pheromone emitted by a female wasp to attract male wasps. The male wasp is attracted to the scent, lands on the orchid flower, and, in the process, transfers pollen. Some orchids, like the Australian hammer orchid, use scent as well as visual trickery in yet another sexual deception strategy to attract wasps. The flower of this orchid mimics the appearance of a female wasp and emits a pheromone. The male wasp tries to mate with what appears to be a female wasp, but instead picks up pollen, which it then transfers to the next counterfeit mate.



Figure 32.6.1: Pollination by deception in orchids: Certain orchids use food deception or sexual deception to attract pollinators. Shown here is a bee orchid (*Ophrys apifera*).

Key Points

- Flowers that are pollinated by bats bloom at night, tending to be large, wide-mouthed, and pale-colored; they may also give off strong scents.
- Flowers that are pollinated by small birds usually have curved, tubular shapes; birds carry the pollen off on their heads and neck to the next flower they visit.
- Wind-pollinated flowers do not produce scents or nectar; instead, they tend to have small or no petals and to produce large amounts of lightweight pollen.
- Some species of flowers release pollen that can float on water; pollination occurs when the pollen reaches another plant of the same species.
- Some flowers deceive pollinators through food or sexual deception; the pollinators become attracted to the flowers with false promises of food and mating opportunities.

Key Terms

- **food deception**: a trickery method employed by some species of orchids in which only bright colors and perfume are offered to their pollinators with no food reward

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32.7: Pollination and Fertilization - Double Fertilization in Plants

Learning Objectives

- Describe the process of double fertilization in plants

Double Fertilization

After pollen is deposited on the stigma, it must germinate and grow through the style to reach the ovule. The microspores, or the pollen, contain two cells: the pollen tube cell and the generative cell. The pollen tube cell grows into a pollen tube through which the generative cell travels. The germination of the pollen tube requires water, oxygen, and certain chemical signals. As it travels through the style to reach the embryo sac, the pollen tube's growth is supported by the tissues of the style. During this process, if the generative cell has not already split into two cells, it now divides to form two sperm cells. The pollen tube is guided by the chemicals secreted by the synergids present in the embryo sac; it enters the ovule sac through the micropyle. Of the two sperm cells, one sperm fertilizes the egg cell, forming a diploid zygote; the other sperm fuses with the two polar nuclei, forming a triploid cell that develops into the endosperm. Together, these two fertilization events in angiosperms are known as double fertilization. After fertilization is complete, no other sperm can enter. The fertilized ovule forms the seed, whereas the tissues of the ovary become the fruit, usually enveloping the seed.

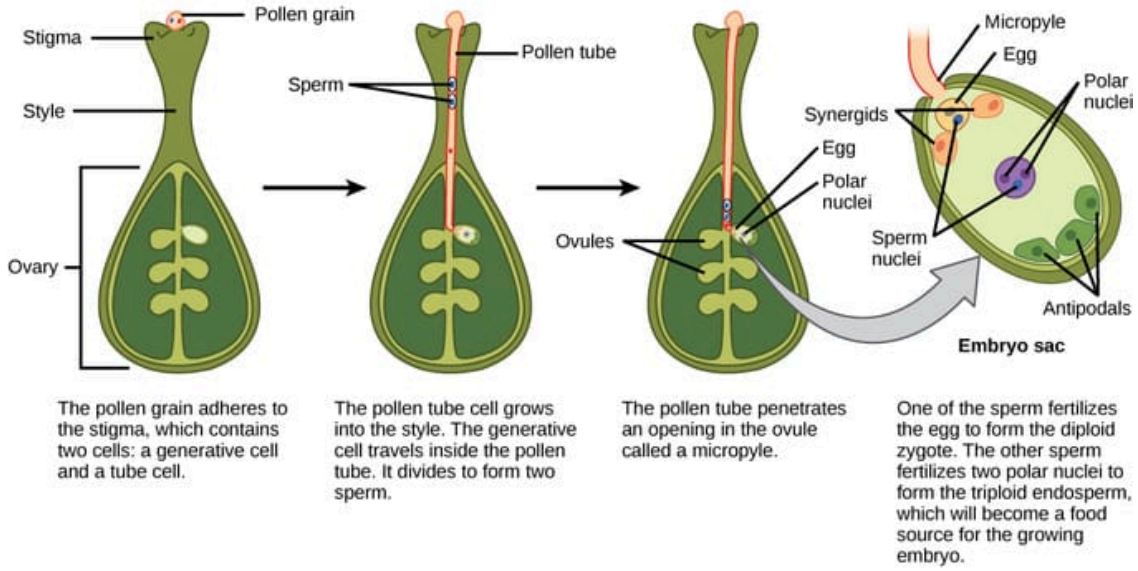


Figure 32.7.1: Double fertilization: In angiosperms, one sperm fertilizes the egg to form the 2n zygote, while the other sperm fuses with two polar nuclei to form the 3n endosperm. This is called a double fertilization.

After fertilization, embryonic development begins. The zygote divides to form two cells: the upper cell (terminal cell) and the lower cell (basal cell). The division of the basal cell gives rise to the suspensor, which eventually makes connection with the maternal tissue. The suspensor provides a route for nutrition to be transported from the mother plant to the growing embryo. The terminal cell also divides, giving rise to a globular-shaped proembryo. In dicots (eudicots), the developing embryo has a heart shape due to the presence of the two rudimentary cotyledons. In non-endospermic dicots, such as *Capsella bursa*, the endosperm develops initially, but is then digested. In this case, the food reserves are moved into the two cotyledons. As the embryo and cotyledons enlarge, they become crowded inside the developing seed and are forced to bend. Ultimately, the embryo and cotyledons fill the seed, at which point, the seed is ready for dispersal. Embryonic development is suspended after some time; growth resumes only when the seed germinates. The developing seedling will rely on the food reserves stored in the cotyledons until the first set of leaves begin photosynthesis.

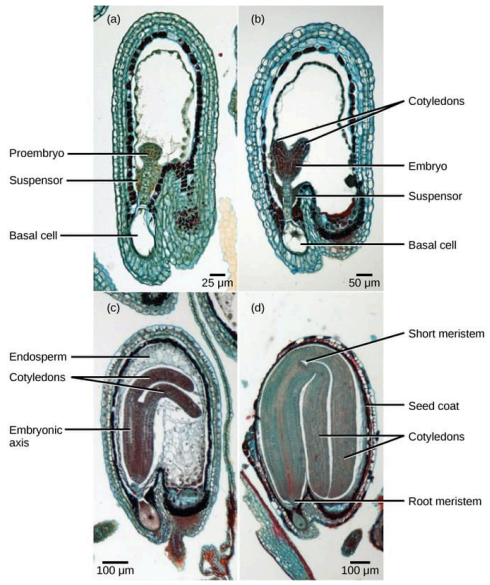


Figure 32.7.1: Embryo development: Shown are the stages of embryo development in the ovule of a shepherd's purse (*Capsella bursa*). After fertilization, the zygote divides to form an upper terminal cell and a lower basal cell. (a) In the first stage of development, the terminal cell divides, forming a globular pro-embryo. The basal cell also divides, giving rise to the suspensor. (b) In the second stage, the developing embryo has a heart shape due to the presence of cotyledons. (c) In the third stage, the growing embryo is crowded and begins to bend. (d) Eventually, it completely fills the seed.

Key Points

- Double fertilization involves two sperm cells; one fertilizes the egg cell to form the zygote, while the other fuses with the two polar nuclei that form the endosperm.
- After fertilization, the fertilized ovule forms the seed while the tissues of the ovary become the fruit.
- In the first stage of embryonic development, the zygote divides to form two cells; one will develop into a suspensor, while the other gives rise to a proembryo.
- In the second stage of embryonic development (in eudicots), the developing embryo has a heart shape due to the presence of cotyledons.
- As the embryo grows, it begins to bend as it fills the seed; at this point, the seed is ready for dispersal.

Key Terms

- **double fertilization**: a complex fertilization mechanism that has evolved in flowering plants; involves the joining of a female gametophyte with two male gametes (sperm)
- **suspensor**: found in plant zygotes in angiosperms; connects the endosperm to the embryo and provides a route for nutrition from the mother plant to the growing embryo
- **proembryo**: a cluster of cells in the ovule of a fertilized flowering plant that has not yet formed into an embryo

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32.8: Pollination and Fertilization - Development of the Seed

Learning Objectives

- Name the three parts of a seed and describe their functions and development

Parts of a Seed

The seed, along with the ovule, is protected by a seed coat that is formed from the integuments of the ovule sac. In dicots, the seed coat is further divided into an outer coat, known as the testa, and inner coat, known as the tegmen. The embryonic axis consists of three parts: the plumule, the radicle, and the hypocotyl. The portion of the embryo between the cotyledon attachment point and the radicle is known as the hypocotyl. The embryonic axis terminates in a radicle, which is the region from which the root will develop.

Seed Growth

In angiosperms, the process of seed development begins with double fertilization and involves the fusion of the egg and sperm nuclei into a zygote. The second part of this process is the fusion of the polar nuclei with a second sperm cell nucleus, thus forming a primary endosperm. Right after fertilization, the zygote is mostly inactive, but the primary endosperm divides rapidly to form the endosperm tissue. This tissue becomes the food the young plant will consume until the roots have developed after germination. The seed coat forms from the two integuments or outer layers of cells of the ovule, which derive from tissue from the mother plant: the inner integument forms the tegmen and the outer forms the testa. When the seed coat forms from only one layer, it is also called the testa, though not all such testae are homologous from one species to the next.

In gymnosperms, the two sperm cells transferred from the pollen do not develop seed by double fertilization, but one sperm nucleus unites with the egg nucleus and the other sperm is not used. Sometimes each sperm fertilizes an egg cell and one zygote is then aborted or absorbed during early development. The seed is composed of the embryo and tissue from the mother plant, which also form a cone around the seed in coniferous plants such as pine and spruce. The ovules after fertilization develop into the seeds.

Food Storage in the Seed

The storage of food reserves in angiosperm seeds differs between monocots and dicots. In monocots, the single cotyledon is called a scutellum; it is connected directly to the embryo via vascular tissue. Food reserves are stored in the large endosperm. Upon germination, enzymes are secreted by the aleurone, a single layer of cells just inside the seed coat that surrounds the endosperm and embryo. The enzymes degrade the stored carbohydrates, proteins, and lipids. These products are absorbed by the scutellum and transported via a vasculature strand to the developing embryo.

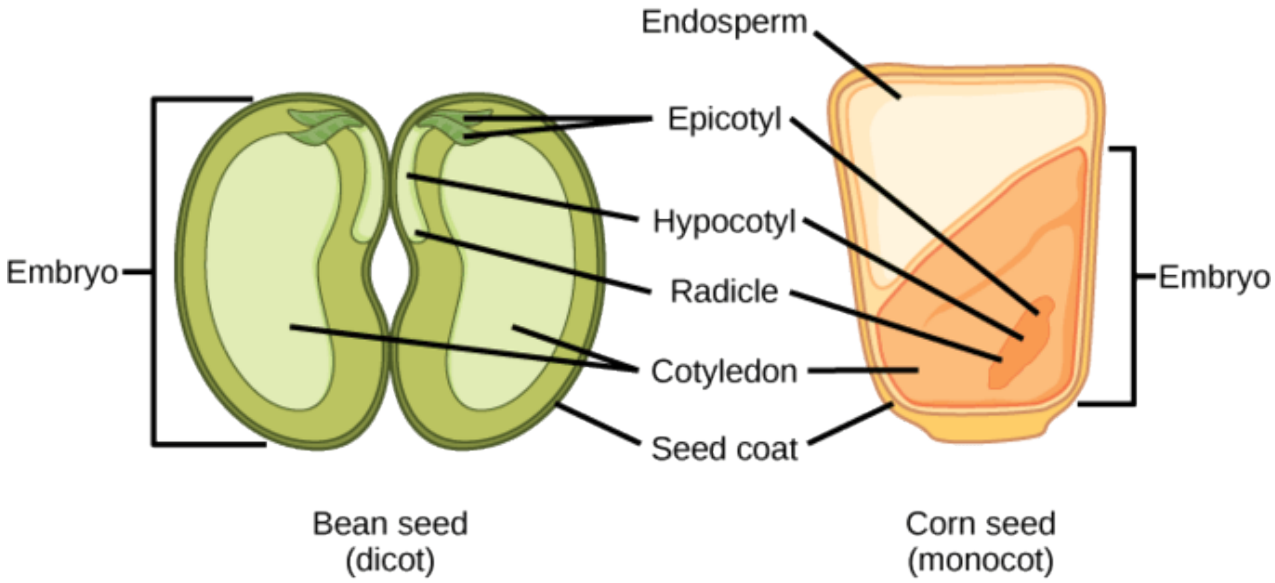


Figure 32.8.1: Monocots and dicots: The structures of dicot and monocot seeds are shown. Dicots (left) have two cotyledons. Monocots, such as corn (right), have one cotyledon, called the scutellum, which channels nutrition to the growing embryo. Both monocot and dicot embryos have a plumule that forms the leaves, a hypocotyl that forms the stem, and a radicle that forms the root. The embryonic axis comprises everything between the plumule and the radicle, not including the cotyledon(s).

In endospermic dicots, the food reserves are stored in the endosperm. During germination, the two cotyledons act as absorptive organs to take up the enzymatically-released food reserves, similar to the process in monocots. In non-endospermic dicots, the triploid endosperm develops normally following double fertilization, but the endosperm food reserves are quickly remobilized, moving into the developing cotyledon for storage.

Seed Germination

Upon germination in dicot seeds, the epicotyl is shaped like a hook with the plumule pointing downwards; this plumule hook persists as long as germination proceeds in the dark. Therefore, as the epicotyl pushes through the tough and abrasive soil, the plumule is protected from damage. Upon exposure to light, the hypocotyl hook straightens out, the young foliage leaves face the sun and expand, and the epicotyl continues to elongate. During this time, the radicle is also growing and producing the primary root. As it grows downward to form the tap root, lateral roots branch off to all sides, producing the typical dicot tap root system.

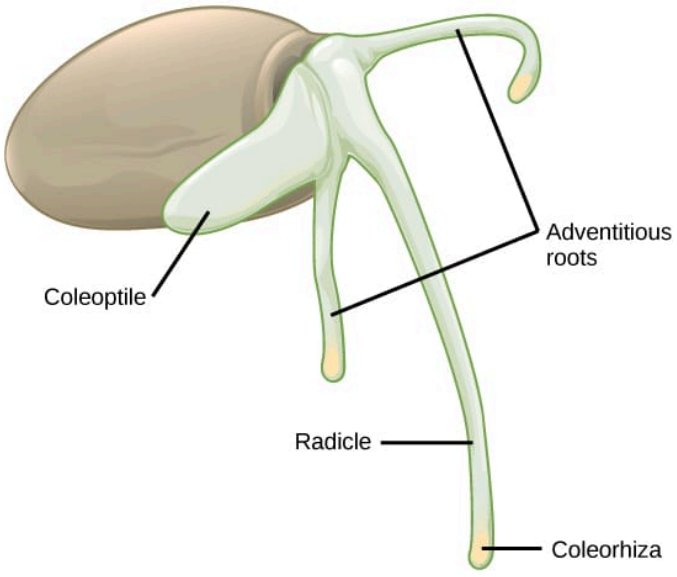


Figure 32.8.1: Monocot seeds: As this monocot grass seed germinates, the primary root, or radicle, emerges first, followed by the primary shoot, or coleoptile, and the adventitious roots.

In monocot seeds, the testa and tegmen of the seed coat are fused. As the seed germinates, the primary root emerges, protected by the root-tip covering: the coleorhiza. Next, the primary shoot emerges, protected by the coleoptile: the covering of the shoot tip. Upon exposure to light, elongation of the coleoptile ceases and the leaves expand and unfold. At the other end of the embryonic axis, the primary root soon dies, while other, adventitious roots emerge from the base of the stem. This produces the fibrous root system of the monocot.

Depending on seed size, the time it takes a seedling to emerge may vary. However, many mature seeds enter a period of dormancy marked by inactivity or extremely-low metabolic activity. This period may last for months, years, or even centuries. Dormancy helps keep seeds viable during unfavorable conditions. Upon a return to optimal conditions, seed germination takes place. These conditions may be as diverse as moisture, light, cold, fire, or chemical treatments. Scarification, the softening of the seed coat, presoaking in hot water, or passing through an acid environment, such as an animal's digestive tract, may also be needed.

Key Points

- In angiosperms, the process of seed production begins with double fertilization while in gymnosperms it does not.
- In both monocots and dicots, food reserves are stored in the endosperm; however, in non-endospermic dicots, the cotyledons act as the storage.
- In a seed, the embryo consists of three main parts: the plumule, the radicle, and the hypocotyl.
- In dicots, the hypocotyls extend above ground, giving rise to the stem of the plant, while in monocots, they remain below ground.
- In dicot seeds, the radicle grows downwards to form the tap root while lateral roots branch off to all sides, producing a dicot tap root system; in contrast, the end of germination in monocot seeds is marked by the production of a fibrous root system where adventitious roots emerge from the stem.
- Seed germination is dependent on seed size and whether or not favorable conditions are present.

Key Terms

- **testa**: the seed coat
- **radicle**: the rudimentary shoot of a plant that supports the cotyledons in the seed and from which the root is developed downward; the root of the embryo
- **hypocotyl**: in plants with seeds, the portion of the embryo or seedling between the root and cotyledons
- **plumule**: consisting of the apical meristem and the first true leaves of the young plant
- **coleoptile**: a pointed sheath that protects the emerging shoot in monocotyledons such as oats and grasses

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32.9: Pollination and Fertilization - Development of Fruit and Fruit Types

Learning Objectives

- Describe the development of a fruit in a flowering plant

After fertilization, the ovary of the flower usually develops into the fruit. Fruits are generally associated with having a sweet taste; however, not all fruits are sweet. The term “fruit” is used for a ripened ovary. In most cases, flowers in which fertilization has taken place will develop into fruits, while unfertilized flowers will not. The fruit encloses the seeds and the developing embryo, thereby providing it with protection. Fruits are diverse in their origin and texture. The sweet tissue of the blackberry, the red flesh of the tomato, the shell of the peanut, and the hull of corn (the tough, thin part that gets stuck in your teeth when you eat popcorn) are all fruits. As the fruit matures, the seeds also mature.

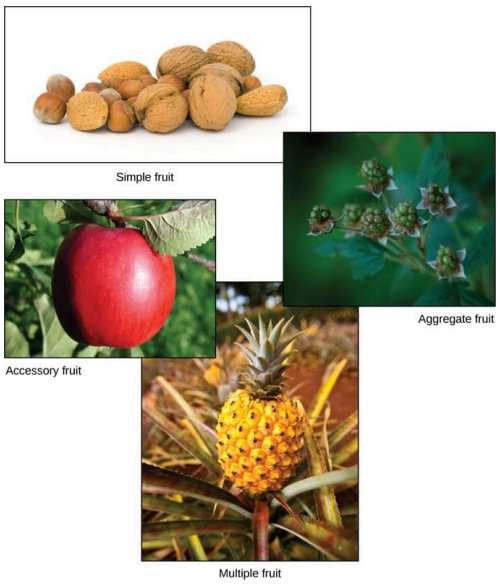


Figure 32.9.1: Types of fruit: There are four main types of fruits. Simple fruits, such as these nuts, are derived from a single ovary. Aggregate fruits, like raspberries, form from many carpels that fuse together. Multiple fruits, such as pineapple, form from a cluster of flowers called an inflorescence. Accessory fruits, like apples, are formed from a part of the plant other than the ovary.

Fruits may be classified as simple, aggregate, multiple, or accessory, depending on their origin. If the fruit develops from a single carpel or fused carpels of a single ovary, it is known as a simple fruit, as seen in nuts and beans. An aggregate fruit is one that develops from numerous carpels that are all in the same flower; the mature carpels fuse together to form the entire fruit, as seen in the raspberry. A multiple fruit develops from an inflorescence or a cluster of flowers. An example is the pineapple where the flowers fuse together to form the fruit. Accessory fruits (sometimes called false fruits) are not derived from the ovary, but from another part of the flower, such as the receptacle (strawberry) or the hypanthium (apples and pears).

Fruits generally have three parts: the exocarp (the outermost skin or covering), the mesocarp (middle part of the fruit), and the endocarp (the inner part of the fruit). Together, all three are known as the pericarp. The mesocarp is usually the fleshy, edible part of the fruit; however, in some fruits, such as the almond, the seed is the edible part (the pit in this case is the endocarp). In many fruits, two, or all three of the layers are fused, and are indistinguishable at maturity. Fruits can be dry or fleshy. Furthermore, fruits can be divided into dehiscent or indehiscent types. Dehiscent fruits, such as peas, readily release their seeds, while indehiscent fruits, like peaches, rely on decay to release their seeds.

Key Points

- Fruits can be classified as simple, aggregate, multiple, or accessory.
- Simple fruits develop from a single carpel or fused carpels of a single ovary, while aggregate fruits develop from more than one carpel found on the same flower.
- Multiple fruits develop from a cluster of flowers, while accessory fruits do not develop from an ovary, but from other parts of a plant.
- The main parts of a fruit include the exocarp (skin), the mesocarp (middle part), and the endocarp (inner part); these three parts make up the pericarp.
- Dehiscent fruits promptly release their seeds, while indehiscent fruits rely on decay to release their seeds.

Key Terms

- **exocarp**: the outermost covering of the pericarp of fruits; the skin
- **simple fruit**: fruit that develops from a single carpel or fused carpels of a single ovary
- **endocarp**: the inner part of the fruit
- **mesocarp**: middle part of the fruit
- **accessory fruit**: a fruit not derived from the ovary but from another part of the flower

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32.10: Pollination and Fertilization - Fruit and Seed Dispersal

Learning Objectives

- Summarize the ways in which fruits and seeds may be dispersed

Fruit and Seed Dispersal

In addition to protecting the embryo, the fruit plays an important role in seed dispersal. Seeds contained within fruits need to be dispersed far from the mother plant so that they may find favorable and less-competitive conditions in which to germinate and grow.

Some fruits have built-in mechanisms that allow them to disperse by themselves, whereas others require the help of agents such as wind, water, and animals. Modifications in seed structure, composition, and size aid in dispersal. Wind-dispersed fruit are lightweight and may have wing-like appendages that allow them to be carried by the wind. Some have a parachute-like structure to keep them afloat. Some fruits, such as the dandelion, have hairy, weightless structures that are suited to dispersal by wind.



Figure 32.10.1: Wind dispersal: Wind is used as a form of dispersal by lightweight seeds, such as those found on dandelions.

Seeds dispersed by water are contained in light and buoyant fruit, giving them the ability to float. Coconuts are well known for their ability to float on water to reach land where they can germinate. Similarly, willow and silver birches produce lightweight fruit that can float on water.

Animals and birds eat fruits; seeds that are not digested are excreted in their droppings some distance away. Some animals, such as squirrels, bury seed-containing fruits for later use; if the squirrel does not find its stash of fruit, and if conditions are favorable, the seeds germinate. Some fruits have hooks or sticky structures that stick to an animal's coat and are then transported to another place. Humans also play a major role in dispersing seeds when they carry fruits to new places, throwing away the inedible part that contains the seeds.

All of the above mechanisms allow for seeds to be dispersed through space, much as an animal's offspring can move to a new location. Seed dormancy allows plants to disperse their progeny through time: something animals cannot do. Dormant seeds can wait months, years, or even decades for the proper conditions for germination and propagation of the species.

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Key Points

- The means by which seeds are dispersed depend on a seed's structure, composition, and size.
- Seeds dispersed by water are found in light and buoyant fruits, while those dispersed by wind may have specialized wing-like appendages.
- Animals can disperse seeds by excreting or burying them; other fruits have structures, such as hooks, that attach themselves to animals' fur.
- Humans also play a role as dispersers by moving fruit to new places and discarding the inedible portions containing the seeds.
- Some seeds have the ability to remain dormant and germinate when favorable conditions arise.

Key Terms

- **seed dormancy**: a seed with the ability to delay germination and propagation of the species until suitable conditions are found
- **dispersal**: the movement of a few members of a species to a new geographical area, resulting in differentiation of the original group into new varieties or species

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32.11: Asexual Reproduction - Asexual Reproduction in Plants

Learning Objectives

- Summarize methods of asexual reproduction in plants

Asexual Reproduction

Many plants are able to propagate themselves using asexual reproduction. This method does not require the investment required to produce a flower, attract pollinators, or find a means of seed dispersal. Asexual reproduction produces plants that are genetically identical to the parent plant because no mixing of male and female gametes takes place. Traditionally, these plants survive well under stable environmental conditions when compared with plants produced from sexual reproduction because they carry genes identical to those of their parents.

Plants have two main types of asexual reproduction: vegetative reproduction and apomixis. Vegetative reproduction results in new plant individuals without the production of seeds or spores. Many different types of roots exhibit vegetative reproduction. The corm is used by gladiolus and garlic. Bulbs, such as a scaly bulb in lilies and a tunicate bulb in daffodils, are other common examples of this type of reproduction. A potato is a stem tuber, while parsnip propagates from a taproot. Ginger and iris produce rhizomes, while ivy uses an adventitious root (a root arising from a plant part other than the main or primary root), and the strawberry plant has a stolon, which is also called a runner.

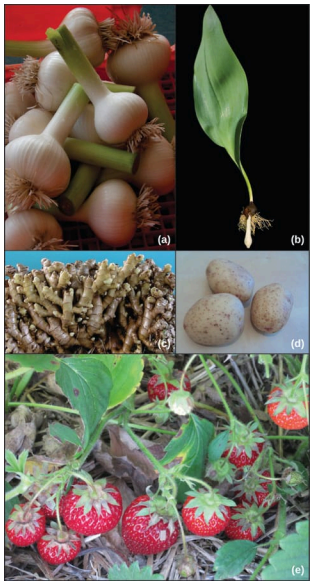


Figure 32.11.1: Roots: Different types of stems allow for asexual reproduction. (a) The corm of a garlic plant looks similar to (b) a tulip bulb, but the corm is solid tissue, while the bulb consists of layers of modified leaves that surround an underground stem. Both corms and bulbs can self-propagate, giving rise to new plants. (c) Ginger forms masses of stems called rhizomes that can give rise to multiple plants. (d) Potato plants form fleshy stem tubers. Each eye in the stem tuber can give rise to a new plant. (e) Strawberry plants form stolons: stems that grow at the soil surface or just below ground and can give rise to new plants

Some plants can produce seeds without fertilization. Either the ovule or part of the ovary, which is diploid in nature, gives rise to a new seed. This method of reproduction is known as apomixis.

An advantage of asexual reproduction is that the resulting plant will reach maturity faster. Since the new plant is arising from an adult plant or plant parts, it will also be sturdier than a seedling. Asexual reproduction can take place by natural or artificial (assisted by humans) means.

Key Points

- Asexual reproduction produces individuals that are genetically identical to the parent plant.
- Roots such as corms, stem tubers, rhizomes, and stolon undergo vegetative reproduction.
- Some plants can produce seeds without fertilization via apomixis where the ovule or ovary gives rise to new seeds.
- Advantages of asexual reproduction include an increased rate of maturity and a sturdier adult plant.
- Asexual reproduction can take place by natural or artificial means.

Key Terms

- **stolon**: a shoot that grows along the ground and produces roots at its nodes; a runner
- **apomixis**: process of reproduction in which plants produce seeds without fertilization

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32.12: Asexual Reproduction - Natural and Artificial Methods of Asexual Reproduction in Plants

Learning Objectives

- Distinguish between natural and artificial methods of asexual reproduction in plants

Natural Methods of Asexual Reproduction

Natural methods of asexual reproduction include strategies that plants have developed to self-propagate. Many plants, such as ginger, onion, gladioli, and dahlia, continue to grow from buds that are present on the surface of the stem. In some plants, such as the sweet potato, adventitious roots or runners (stolons) can give rise to new plants. In *Bryophyllum* and kalanchoe, the leaves have small buds on their margins. When these are detached from the plant, they grow into independent plants; they may also start growing into independent plants if the leaf touches the soil. Some plants can be propagated through cuttings alone.

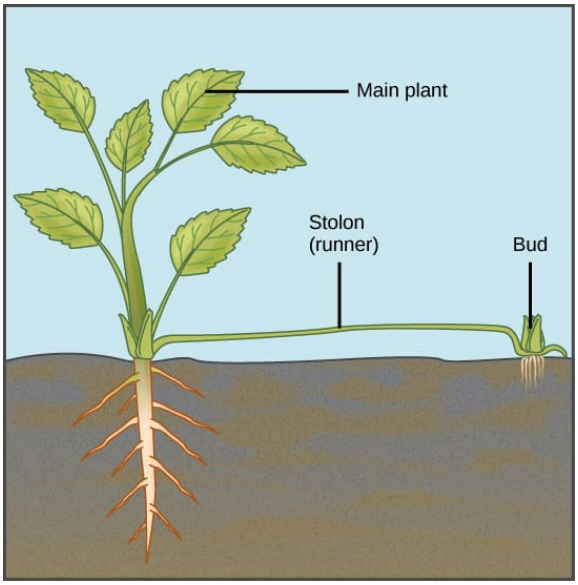


Figure 32.12.1: Runners: asexual reproduction: A stolon, or runner, is a stem that runs along the ground. At the nodes, it forms adventitious roots and buds that grow into a new plant.

Artificial Methods of Asexual Reproduction

Artificial methods of asexual reproduction are frequently employed to give rise to new, and sometimes novel, plants. They include grafting, cutting, layering, and micropropagation.

Grafting

Grafting has long been used to produce novel varieties of roses, citrus species, and other plants. In grafting, two plant species are used: part of the stem of the desirable plant is grafted onto a rooted plant called the stock. The part that is grafted or attached is called the scion. Both are cut at an oblique angle (any angle other than a right angle), placed in close contact with each other, and are then held together. Matching up these two surfaces as closely as possible is extremely important because these will be holding the plant together. The vascular systems of the two plants grow and fuse, forming a graft. After a period of time, the scion starts producing shoots, eventually bearing flowers and fruits. Grafting is widely used in viticulture (grape growing) and the citrus industry. Scions capable of producing a particular fruit variety are grafted onto root stock with specific resistance to disease.

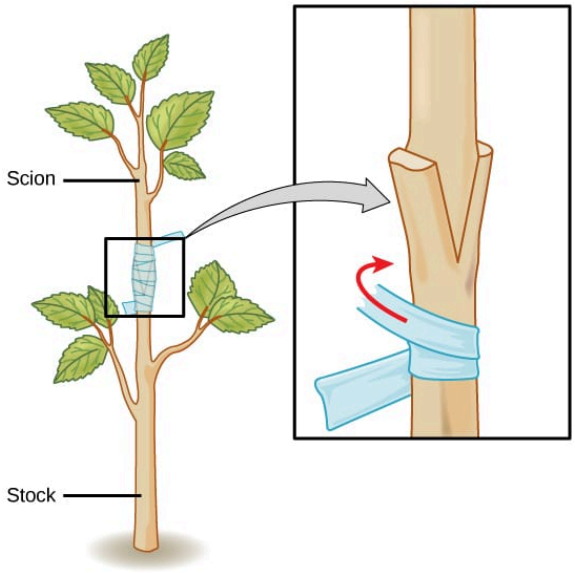


Figure 32.12.1: Grafting: Grafting is an artificial method of asexual reproduction used to produce plants combining favorable stem characteristics with favorable root characteristics. The stem of the plant to be grafted is known as the scion, and the root is called the stock.

Cutting

Plants such as coleus and money plant are propagated through stem cuttings where a portion of the stem containing nodes and internodes is placed in moist soil and allowed to root. In some species, stems can start producing a root even when placed only in water. For example, leaves of the African violet will root if kept undisturbed in water for several weeks.

Layering

Layering is a method in which a stem attached to the plant is bent and covered with soil. Young stems that can be bent easily without any injury are the preferred plant for this method. Jasmine and bougainvillea (paper flower) can be propagated this way. In some plants, a modified form of layering known as air layering is employed. A portion of the bark or outermost covering of the stem is removed and covered with moss, which is then taped. Some gardeners also apply rooting hormone. After some time, roots will appear; this portion of the plant can be removed and transplanted into a separate pot.

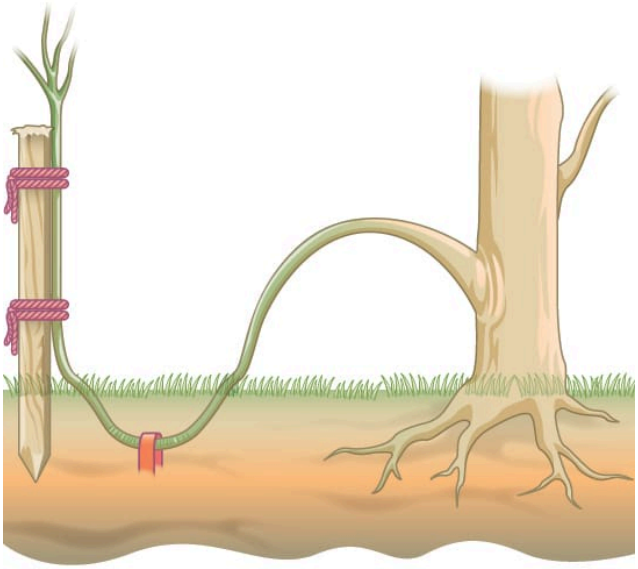


Figure 32.12.1: Layering: In layering, a part of the stem is buried so that it forms a new plant.

Micropropagation

Micropropagation (also called plant tissue culture) is a method of propagating a large number of plants from a single plant in a short time under laboratory conditions. This method allows propagation of rare, endangered species that may be difficult to grow under natural conditions, are economically important, or are in demand as disease-free plants.

To start plant tissue culture, a part of the plant such as a stem, leaf, embryo, anther, or seed can be used. The plant material is thoroughly sterilized using a combination of chemical treatments standardized for that species. Under sterile conditions, the plant material is placed on a plant tissue culture medium that contains all the minerals, vitamins, and hormones required by the plant. The plant part often gives rise to an undifferentiated mass, known as a callus, from which, after a period of time, individual plantlets begin to grow. These can be separated; they are first grown under greenhouse conditions before they are moved to field conditions.

Key Points

- In natural asexual reproduction, roots can give rise to new plants, or plants can propagate using budding or cutting.
- In grafting, part of a plant is attached to the root system of another plant; the two unite to form a new plant containing the roots of one and the stem and leaf structure of the other.
- Cutting is the process in which the stem of a plant is placed in moist soil or water to generate a new root system.
- In layering, part of the plant's stem is bent down and covered with soil; this stem can generate a new root system and, therefore, an entirely new plant.
- Micropropagation is the process in which part of a plant is placed in plant culture medium and provided with all the hormones and nutrients it needs in order to generate new plants.
- When part of a plant is placed in plant culture medium and provided with all the hormones and nutrients it needs, it can generate new plants; this is known as micropropagation.

Key Terms

- **layering**: a method of plant propagation in which a bent stem is covered with soil in order to generate new roots
- **grafting**: process of attaching part of a stem from one plant onto the root of another plant
- **micropropagation**: practice of rapidly multiplying plant material to produce a large number of progeny plants using plant tissue culture methods
- **cutting**: placing part of a stem containing nodes or internodes in water or moist soil in order to produce new plants

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32.13: Asexual Reproduction - Plant Life Spans

Learning Objectives

- Explain the process of aging in plants

Plant Life Spans

The length of time from the beginning of development to the death of a plant is called its life span. The life cycle, on the other hand, is the sequence of stages a plant goes through from seed germination to seed production of the mature plant. Some plants, such as annuals, only need a few weeks to grow, produce seeds, and die. Other plants, such as the bristlecone pine, live for thousands of years. Some bristlecone pines have a documented age of 4,500 years. Even as some parts of a plant, such as regions containing meristematic tissue (the area of active plant growth consisting of undifferentiated cells capable of cell division) continue to grow, some parts undergo programmed cell death (apoptosis). The cork found on stems and the water-conducting tissue of the xylem, for example, are composed of dead cells.



Figure 32.13.1: Plant life spans: The bristlecone pine, shown here in the Ancient Bristlecone Pine Forest in the White Mountains of eastern California, has been known to live for 4,500 years.

Annuals, Biennial, and Perennials

Plant species that complete their life cycle in one season are known as annuals, an example of which is *Arabidopsis*, or mouse-ear cress. Biennials, such as carrots, complete their life cycle in two seasons. In a biennial's first season, the plant has a vegetative phase, whereas in the next season, it completes its reproductive phase. Commercial growers harvest the carrot roots after the first year of growth and do not allow the plants to flower. Perennials, such as the magnolia, complete their life cycle in two years or more.

Monocarpic and Polycarpic Plants

In another classification based on flowering frequency, monocarpic plants flower only once in their lifetime; examples of monocarpic plants include bamboo and yucca. During the vegetative period of their life cycle (which may be as long as 120 years in some bamboo species), these plants may reproduce asexually, accumulating a great deal of food material that will be required during their once-in-a-lifetime flowering and setting of seed after fertilization. Soon after flowering, these plants die. Polycarpic

plants form flowers many times during their lifetime. Fruit trees, such as apple and orange trees, are polycarpic; they flower every year. Other polycarpic species, such as perennials, flower several times during their life span, but not each year. By this method, the plant does not require all its nutrients to be channeled towards flowering each year.

Genetics and Environmental Conditions

As is the case with all living organisms, genetics and environmental conditions have a role to play in determining how long a plant will live. Susceptibility to disease, changing environmental conditions, drought, cold, and competition for nutrients are some of the factors that determine the survival of a plant. Plants continue to grow, despite the presence of dead tissue, such as cork. Individual parts of plants, such as flowers and leaves, have different rates of survival. In many trees, the older leaves turn yellow and eventually fall from the tree. Leaf fall is triggered by factors such as a decrease in photosynthetic efficiency due to shading by upper leaves or oxidative damage incurred as a result of photosynthetic reactions. The components of the part to be shed are recycled by the plant for use in other processes, such as development of seed and storage. This process is known as nutrient recycling. However, the complex pathways of nutrient recycling within a plant are not well understood

The aging of a plant and all the associated processes is known as senescence, which is marked by several complex biochemical changes. One of the characteristics of senescence is the breakdown of chloroplasts, which is characterized by the yellowing of leaves. The chloroplasts contain components of photosynthetic machinery, such as membranes and proteins. Chloroplasts also contain DNA. The proteins, lipids, and nucleic acids are broken down by specific enzymes into smaller molecules and salvaged by the plant to support the growth of other plant tissues. Hormones are known to play a role in senescence. Applications of cytokinins and ethylene delay or prevent senescence; in contrast, abscissic acid causes premature onset of senescence.



Figure 32.13.1: Plant senescence: The autumn color of these Oregon Grape leaves is an example of programmed plant senescence.

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Key Points

- The life span of a plant is the length of time it takes from the beginning of development until death, while the life cycle is the series of stages between the germination of the seed until the plant produces its own seeds.
- Annuals complete their life cycle in one season; biennials complete their life cycle in two seasons; and perennials complete their life cycle in more than two seasons.
- Monocarpic plants flower only once in their lifetime, while polycarpic plants flower more than once.
- Plant survival depends on changing environmental conditions, drought, cold, and competition.
- Senescence refers to aging of the plant, during which components of the plant cells are broken down and used to support the growth of other plant tissues.

Key Terms

- **annual**: a plant which naturally germinates, flowers, and dies in one year
- **biennial**: a plant that requires two years to complete its life cycle
- **perennial**: a plant that is active throughout the year or survives for more than two growing seasons
- **monocarpic**: a plant that flowers and bears fruit only once before dying
- **polycarpic**: bearing fruit repeatedly, or year after year
- **senescence**: aging of a plant; accumulated damage to macromolecules, cells, tissues, and organs with the passage of time

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33: THE ANIMAL BODY- BASIC FORM AND FUNCTION

33.1: Animal Form and Function - Characteristics of the Animal Body

33.2: Animal Form and Function - Body Plans

33.3: Animal Form and Function - Limits on Animal Size and Shape

33.4: Animal Form and Function - Limiting Effects of Diffusion on Size and Development

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33.1: Animal Form and Function - Characteristics of the Animal Body

Learning Objectives

- Describe how form and function are related in an organism

Animal Form and Function

Animals vary in form and function. From a sponge to a worm to a goat, an organism has a distinct body plan that limits its size and shape. The term body plan is the “blueprint” encompassing aspects such as symmetry, segmentation, and limb disposition. Body plans have been considered to have evolved in a geologically-sudden flash during the Cambrian Explosion (roughly 542 million years ago). However, there is also evidence of a more gradual development of body plans. With a few exceptions, most notably the sponges and Placozoa, animals have bodies differentiated into separate tissues, which in turn make up more complex organs and organ systems. These include tissues such as muscles, which are able to contract and control locomotion, and nerves, which send and process signals. Typically, there is also an internal digestive chamber with one or two openings. Animals’ bodies are also designed to interact with their environments, whether in the deep sea, a rainforest canopy, or the desert. In addition, animal body plans have evolved in response to environmental pressures, as observed in fossil records, in order to enhance survival and reproductive success. Therefore, a large amount of information about the structure of an organism’s body (anatomy) and the function of its cells, tissues, and organs (physiology) can be learned by studying that organism’s environment. The arctic fox is an example of a complex animal that has adapted to its environment and illustrates the relationships between an animal’s form and function.



Figure 33.1.1: Arctic fox: An arctic fox is a complex animal, well adapted to its environment. It changes coat color with the seasons and has longer fur in winter to trap heat.

Key Points

- A body plan encompasses symmetry, segmentation, and limb disposition.
- Almost all animals have bodies made of differentiated tissues, which in turn form organs and organ systems.
- Animal bodies have evolved to interact with their environments in ways that enhance survival and reproduction.

Key Terms

- **physiology**: a branch of biology that deals with the functions and activities of life or of living matter (as organs, tissues, or cells) and of the physical and chemical phenomena involved
- **body plan**: an assemblage of morphological features shared among many members of a phylum-level group
- **anatomy**: the art of studying the different parts of any organized body, to discover their situation, structure, and economy; dissection

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33.2: Animal Form and Function - Body Plans

Learning Objectives

- Describe the body plan of an animal

Body Plans

Animal body plans follow set patterns related to symmetry. They can be asymmetrical, radial, or bilateral in form. Asymmetrical animals are those with no pattern or symmetry, such as a sponge. Radial symmetry describes an animal with an up-and-down orientation: any plane cut along its longitudinal axis through the organism produces equal halves, but not a definite right or left side. This plan is found mostly in aquatic animals, especially organisms that attach themselves to a base, such as a rock or a boat, and extract their food from the surrounding water as it flows around the organism. Bilateral symmetry is found in both land-based and aquatic animals; it enables a high level of mobility. Bilateral symmetry is illustrated in a goat. The goat also has an upper and lower component to it, but a plane cut from front to back separates the animal into definite right and left sides.

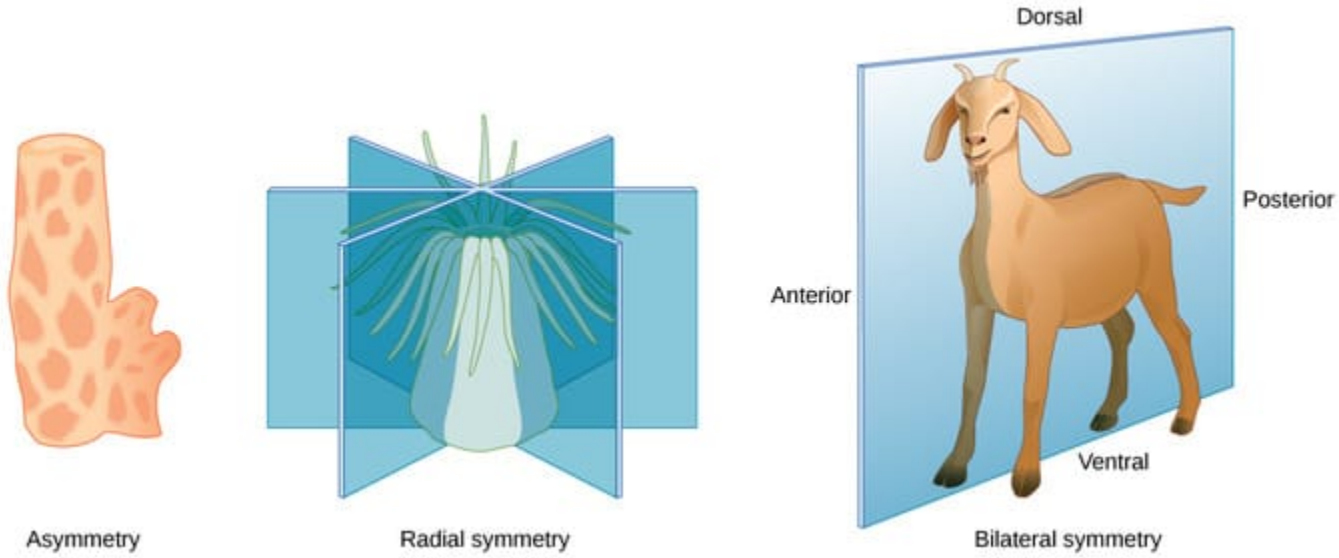


Figure 33.2.1: Body symmetry: Animals exhibit different types of body symmetry. The sponge is asymmetrical, the sea anemone has radial symmetry, and the goat has bilateral symmetry.

In order to describe structures in the body of an animal it is necessary to have a system for describing the position of parts of the body in relation to other parts. For example, it may be necessary to describe the position of the liver in relation to the diaphragm or the heart in relation to the lungs. The most common terms used when describing positions in the body are anterior (front), posterior (rear), dorsal (toward the back), and ventral (toward the stomach). Note that the terms superior and inferior are usually not used to describe animals. They are only used to describe the position of structures in the human body (and possibly apes) where the upright posture means some structures are above or superior to others.

Term	Definition	Example
Dorsal	Nearer the back of the animal than	The backbone is dorsal to the belly
Ventral	Nearer the belly of the animal than	The breastbone is ventral to the heart
Cranial (or anterior)	Nearer to the skull than	The diaphragm is cranial to the stomach
Caudal (or posterior)	Nearer to the tail than	The ribs are caudal to the neck
Proximal	Closer to the body than (only used for structures on limbs)	The shoulder is proximal to the elbow
Distal	Further from the body than (only used for structures on limbs)	The ankle is distal to the knee
Medial	Nearer to the midline than	The bladder is medial to the hips
Lateral	Further from the midline than	The ribs are lateral to the lungs
Rostral	Towards the muzzle	There are more grey hairs in the rostral part of the head
Palmar	The "walking" surface of the front paw	There is a small cut on the left palmar surface
Plantar	The "walking" surface of the hind paw	The pads are on the plantar side of the foot

Figure 33.2.1: Directional terms: The table illustrates common directional terms that are used to describe the position of body parts in relation to other body parts.

Key Points

- Some animals have a body with no pattern or symmetry, making them asymmetrical.
- Animals (mostly aquatic) with an up-and-down orientation have a radial symmetry in which there is no definite right or left side, but any longitudinal plane cut produces equal halves.
- Animals, either aquatic or terrestrial, that have a high level of mobility usually have a body plan that is bilaterally symmetric.
- Terms such as anterior (front), posterior (rear), dorsal (toward the back), and ventral (toward the stomach) are used to describe the position of parts of the body in relation to other parts.

Key Terms

- **asymmetrical**: having disproportionate arrangement of parts; exhibiting no pattern
- **bilateral symmetry**: having equal arrangement of parts (symmetry) about a vertical plane running from head to tail
- **radial symmetry**: a form of symmetry wherein identical parts are arranged in a circular fashion around a central axis

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33.3: Animal Form and Function - Limits on Animal Size and Shape

Learning Objectives

- Explain how the environment and skeletal structure can put limits on the size and shape of animals

Limits on Animal Size and Shape

Animals with bilateral symmetry that live in water tend to have a fusiform shape: a tubular shaped body that is tapered at both ends. This shape decreases the drag on the body as it moves through water and allows the animal to swim at high speeds. Certain types of sharks can swim at fifty kilometers an hour, while some dolphins can swim at 32-40 kilometers per hour. Land animals frequently travel faster (although the tortoise and snail are significantly slower than sharks or dolphins). Another difference in the adaptations of aquatic and land-dwelling organisms is that aquatic organisms are constrained in shape by the forces of drag in the water since water has higher viscosity than air. However, land-dwelling organisms are constrained mainly by gravity; drag is relatively unimportant. For example, most adaptations in birds are for gravity, not for drag.

Maximum Speed of Assorted Land Marine Animals		
Animal	**Speed (kmh)**	**Speed (mph)**
Cheetah	113	70
Quarter horse	77	48
Fox	68	42
Shortfin mako shark	50	31
Domestic house cat	48	30
Human	45	28
Dolphin	32–40	20–25
Mouse	13	8
Snail	0.05	0.03

Figure 33.3.1: Animal speeds: Land and marine animals travel at varying speeds. Land animals usually travel at higher speeds, but marine animals such as dolphins and sharks travel relatively fast.

Most animals have an exoskeleton, including insects, spiders, scorpions, horseshoe crabs, centipedes, and crustaceans. Scientists estimate that, of insects alone, there are over 30 million species on our planet. The exoskeleton is a hard covering or shell that provides benefits to the animal, such as protection against damage from predators and from water loss (for land animals); it also provides for the attachments of muscles. As the tough and resistant outer cover of an arthropod, the exoskeleton may be constructed of a tough polymer, such as chitin, and is often biomineralized with materials, such as calcium carbonate. This is fused to the animal's epidermis. Ingrowths of the exoskeleton called apodemes function as attachment sites for muscles, similar to tendons in more advanced animals. In order to grow, the animal must first synthesize a new exoskeleton underneath the old one and then shed or molt the original covering. This limits the animal's ability to grow continually. It may limit the individual's ability to mature if molting does not occur at the proper time. The thickness of the exoskeleton must be increased significantly to accommodate any increase in weight. It is estimated that a doubling of body size increases body weight by a factor of eight. The increasing thickness of the chitin necessary to support this weight limits most animals with an exoskeleton to a relatively-small size.

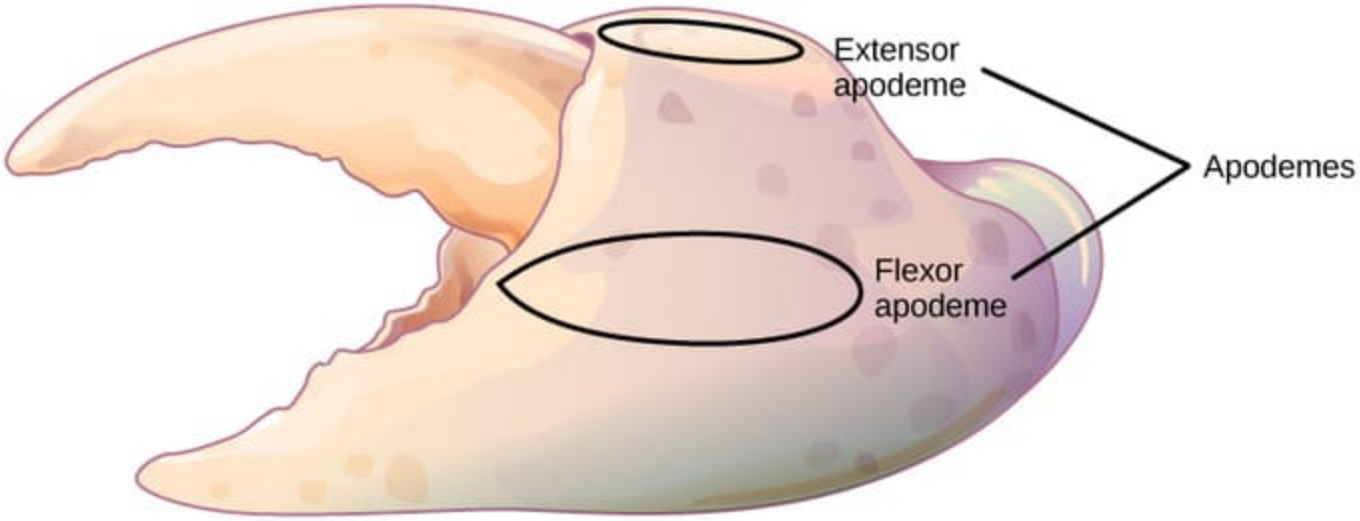


Figure 33.3.1: Apodemes: Apodemes are ingrowths on arthropod exoskeletons to which muscles attach. The apodemes on this crab leg are located above and below the fulcrum of the claw. Contraction of muscles attached to the apodemes pulls the claw closed.

The same principles apply to endoskeletons, but they are more efficient because muscles are attached on the outside, making it easier to compensate for increased mass. An animal with an endoskeleton has its size determined by the amount of skeletal system it needs in order to support the other tissues and the amount of muscle it needs for movement. As the body size increases, both bone and muscle mass increase. The speed achievable by the animal is a balance between its overall size and the bone and muscle that provide support and movement.

Key Points

- Aquatic animals tend to have tubular shaped bodies (fusiform shape) that decrease drag, enabling them to swim at high speeds.
- Terrestrial animals tend to have body shapes that are adapted to deal with gravity.
- Exoskeletons are hard protective coverings or shells that also provide attachments for muscles.
- Before shedding or molting the existing exoskeleton, an animal must first produce a new one.
- The exoskeleton must increase thickness as the animal becomes larger, which limits body size.
- The size of an animal with an endoskeleton is determined by the amount of skeletal system required to support the body and the muscles it needs to move.

Key Terms

- **fusiform**: shaped like a spindle; tapering at each end
- **exoskeleton**: a hard outer structure that provides both structure and protection to creatures such as insects, Crustacea, and Nematoda
- **apodeme**: an ingrowth of the arthropod exoskeleton, serving as an attachment site for muscles
- **endoskeleton**: the internal skeleton of an animal, which in vertebrates is comprised of bone and cartilage

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33.4: Animal Form and Function - Limiting Effects of Diffusion on Size and Development

Learning Objectives

- Describe how diffusion limits cell size and development

Limiting Effects of Diffusion on Size and Development

The exchange of nutrients and wastes between a cell and its watery environment occurs through the process of diffusion. All living cells are bathed in liquid, whether they are in a single-celled organism or a multicellular one. Diffusion is effective over a specific distance and limits the size that an individual cell can attain. If a cell is a single-celled microorganism, such as an amoeba, it can satisfy all of its nutrient and waste needs through diffusion. If the cell is too large, then diffusion is ineffective at completing all of these tasks. The center of the cell does not receive adequate nutrients nor is it able to effectively dispel its waste.

An important concept in understanding the efficiency of diffusion as a transportation mechanism is the surface-to-volume ratio. Recall that any three-dimensional object has a surface area and volume; the ratio of these two quantities is the surface-to-volume ratio. Consider a cell shaped like a perfect sphere: it has a surface area of $4\pi r^2$, and a volume of $(4/3)\pi r^3$. The surface-to-volume ratio of a sphere is 3/r; as the cell gets bigger, its surface-to-volume ratio decreases, making diffusion less efficient. The larger the size of the sphere, or animal, the less surface area for diffusion it possesses.

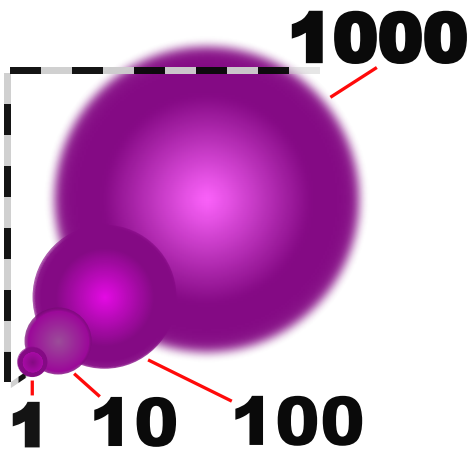


Figure 33.4.1: Surface-to-volume ratio: The image illustrates the comparison of spheres of one to one thousand volume units. The surface-to-volume ratio of a sphere decreases as the sphere gets bigger. The surface area of a sphere is 4πr2 and it has a volume of (4/3)πr3 which makes the surface-to-volume ratio 3/r. This has an effect on diffusion because it relies on the surface area of a cell: as a cell gets bigger, diffusion becomes less efficient.

The solution to producing larger organisms is for them to become multicellular. Specialization occurs in complex organisms, allowing cells to become less efficient at completing all tasks since they are now more efficient at doing fewer tasks. For example, circulatory systems bring nutrients and remove waste, while respiratory systems provide oxygen for the cells and remove carbon dioxide from them. Other organ systems have developed further specialization of cells and tissues and efficiently control body functions. Surface-to-volume ratio also applies to other areas of animal development, such as the relationship between muscle mass and cross-sectional surface area in supporting skeletons or in the relationship between muscle mass and the generation of dissipation of heat.

Key Points

- Diffusion is effective over a specific distance, so it's more efficient in small, single-celled microorganisms.

- Diffusion becomes less efficient as the surface-to-volume ratio decreases, so diffusion is less effective in larger animals.
- To overcome the limitations of diffusion, multicellular organisms have developed specialized tissues and systems that are responsible for completing a limited number of nutrient and waste tasks.

Key Terms

- **surface-to-volume ratio**: the amount of surface area per unit volume of an object or collection of objects; decreases as volume increases

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33.5: Animal Form and Function - Animal Bioenergetics

Learning Objectives

- Differentiate among the ways in which an animal's energy requirements are affected by their environment and level of activity

Animal Bioenergetics

All animals must obtain their energy from food they ingest or absorb. These nutrients are converted to adenosine triphosphate (ATP) for short-term storage and use by all cells. Some animals store energy for slightly longer times as glycogen, while others store energy for much longer times in the form of triglycerides housed in specialized adipose tissues. No energy system is one hundred percent efficient as an animal's metabolism produces waste energy in the form of heat. If an animal can conserve that heat and maintain a relatively-constant body temperature, it is classified as a warm-blooded animal: an endotherm. The insulation used to conserve the body heat comes in the forms of fur, fat, or feathers. The absence of insulation in ectothermic animals increases their dependence on the environment for body heat.

The amount of energy expended by an animal over a specific time is called its metabolic rate. The rate is measured in joules, calories, or kilocalories (1000 calories). Carbohydrates and proteins contain about 4.5-5 kcal/g, while fat contains about 9 kcal/g. Metabolic rate is estimated as the basal metabolic rate (BMR) in endothermic animals at rest and as the standard metabolic rate (SMR) in ectotherms. Human males have a BMR of 1600-1800 kcal/day, and human females have a BMR of 1300 to 1500 kcal/day. Even with insulation, endothermal animals require extensive amounts of energy to maintain a constant body temperature. An ectotherm such as an alligator has an SMR of 60 kcal/day.

Energy Requirements Related to Body Size

Smaller endothermic animals have a greater surface area for their mass than larger ones. Therefore, smaller animals lose heat at a faster rate than larger animals and require more energy to maintain a constant internal temperature. This results in a smaller endothermic animal having a higher BMR, per body weight, than a larger endothermic animal.

Species		
Mass	35 g	4,500,000 g
Metabolic rate	890 mm^3 0_2/g body mass/hr	75 mm^3 0_2/g body mass/hr

Figure 33.5.1: Body size and metabolic rate: The mouse has a much higher metabolic rate than the elephant since it has greater surface area relative to mass.

Energy Requirements Related to Levels of Activity

The more active an animal is, the more energy is needed to maintain that activity and the higher its BMR or SMR. The average

daily rate of energy consumption is about two to four times an animal's BMR or SMR. Humans are more sedentary than most animals and have an average daily rate of only 1.5 times the BMR. The diet of an endothermic animal is determined by its BMR.

Energy Requirements Related to Environment

Animals adapt to extremes of temperature or food availability through torpor. Torpor is a process that leads to a decrease in activity and metabolism, which allows animals to survive adverse conditions. Torpor can be used by animals for long periods. For example, animals can enter a state of hibernation during the winter months, which enables them to maintain a reduced body temperature. During hibernation, ground squirrels can achieve an abdominal temperature of 0° C (32° F), while a bear's internal temperature is maintained higher at about 37° C (99° F).

If torpor occurs during the summer months with high temperatures and little water, it is called estivation. Some desert animals estivate to survive the harshest months of the year. Torpor can occur on a daily basis; this is seen in bats and hummingbirds. While endothermy is limited in smaller animals by surface-to-volume ratio, some organisms can be smaller and still be endotherms because they employ daily torpor during the part of the day that is coldest. This allows them to conserve energy during the colder parts of the day when they consume more energy to maintain their body temperature.

Key Points

- An animal is endothermic (warm-blooded) if it maintains a relatively-constant body temperature by conserving heat with the help of insulation.
- An animal is ectothermic if it does not have insulation to conserve heat and must rely on its environment for body heat.
- Metabolic rate is the amount of energy expended by an animal over a specific time; in endotherms, it is described as the basal metabolic rate (BMR), while in ectotherms, as the standard metabolic rate (SMR).
- Smaller endothermic animals have a higher BMR than larger endothermic animals because they lose heat at a faster rate and require more energy to maintain a constant internal temperature.
- More active animals have higher BMRs or SMRs and require more energy to maintain their activity.
- A long period of inactivity and decreased metabolism (torpor) that occurs in the winter months is hibernation; estivation is torpor that occurs in the summer months.

Key Terms

- **endotherm**: a warm-blooded animal that maintains a constant body temperature
- **ectotherm**: a cold-blooded animal that regulates its body temperature by exchanging heat with its surroundings
- **hibernation**: a state of inactivity and metabolic depression in animals during winter
- **estivation**: to go into a state of inactivity during the summer months

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33.6: Animal Form and Function - Animal Body Planes and Cavities

Learning Objectives

- Describe the major body planes and cavities of animals

Animal Body Planes and Cavities

A standing vertebrate animal can be divided by several planes that can be used to as references to describe locations of body parts or organs. A sagittal plane divides the body into right and left portions. A midsagittal plane divides the body exactly in the middle, making two equal right and left halves. A frontal plane (also called a coronal plane) separates the front (ventral) from the back (dorsal). A transverse plane (or, horizontal plane) divides the animal into upper and lower portions. This is sometimes called a cross section; if the transverse cut is at an angle, it is called an oblique plane.

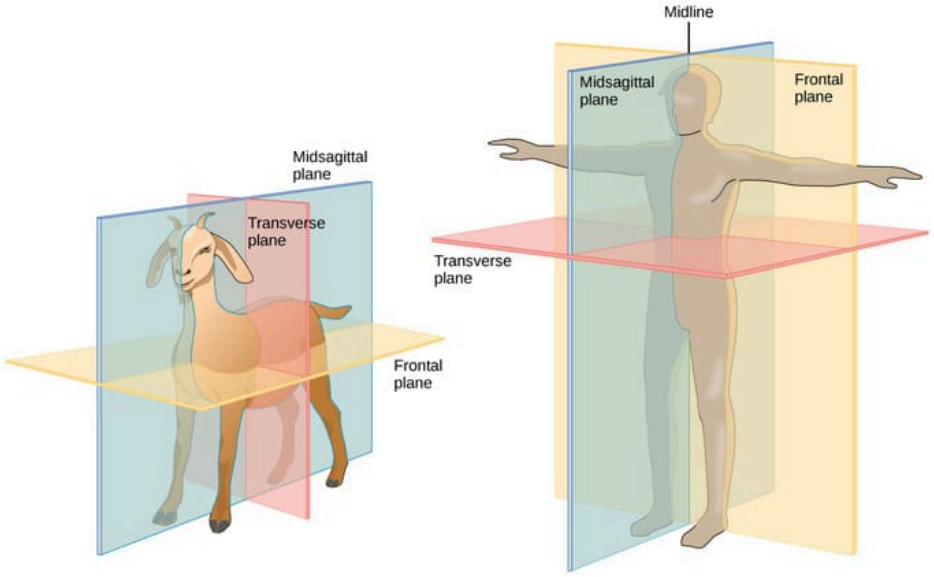


Figure 33.6.1: Body planes: Shown are the planes of a quadruped goat and a bipedal human. The midsagittal plane divides the body exactly in half into right and left portions. The frontal plane divides the front and back, while the transverse plane divides the body into upper and lower portions.

Vertebrate animals have a number of defined body cavities. The posterior (dorsal) and anterior (ventral) cavities are each subdivided into smaller cavities. In the posterior cavity, the cranial cavity houses the brain and the spinal cavity (or vertebral cavity) encloses the spinal cord. Just as the brain and spinal cord make up a continuous, uninterrupted structure, the cranial and spinal cavities that house them are also continuous. The brain and spinal cord are protected by the bones of the skull and vertebral column and by cerebrospinal fluid, a colorless fluid produced by the brain, which cushions the brain and spinal cord within the posterior (dorsal) cavity.

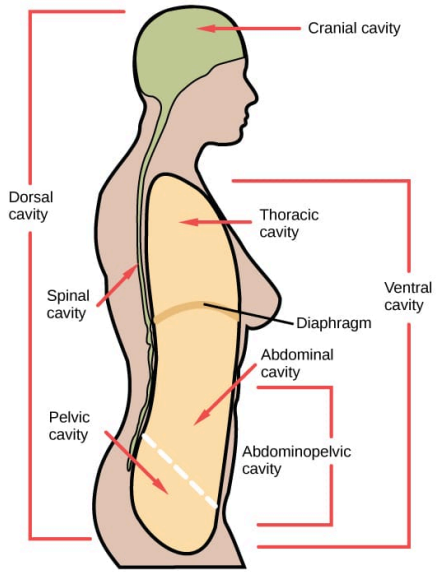


Figure 33.6.1: Body cavities: Vertebrate animals have two major body cavities. The dorsal cavity, indicated in green, contains the cranial and the spinal cavity. The ventral cavity, indicated in yellow, contains the thoracic cavity and the abdominopelvic cavity. The thoracic cavity is separated from the abdominopelvic cavity by the diaphragm. The abdominopelvic cavity is separated into the abdominal cavity and the pelvic cavity by an imaginary line parallel to the pelvis bones.

The anterior cavity has two main subdivisions: the thoracic cavity and the abdominopelvic cavity. The thoracic cavity is the more superior subdivision of the anterior cavity and is enclosed by the rib cage. The thoracic cavity contains the pleural cavity around the lungs and the pericardial cavity, which surrounds the heart. The diaphragm forms the floor of the thoracic cavity, separating it from the more inferior abdominopelvic cavity. The abdominopelvic cavity is the largest cavity in the body. Although no membrane physically divides the abdominopelvic cavity, it can be useful to distinguish between the abdominal cavity, the division that houses the digestive organs from the pelvic cavity, the division that houses the organs of reproduction.

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Key Points

- A sagittal plane divides the body into right and left portions; a midsagittal plane divides the body exactly in the middle.
- A frontal or coronal plane separates the front from the back.
- A transverse or horizontal plane divides the animal into upper and lower portions; it is called an oblique plane if it is cut at an angle.
- The posterior (dorsal) cavity is a continuous cavity that includes the cranial cavity (brain) and the spinal cavity (spinal cord).
- The anterior (ventral) cavity includes the thoracic cavity and the abdominopelvic cavity.
- The thoracic cavity is divided into the pleural cavity (lungs) and pericardial cavity (heart); the abdominopelvic cavity includes the abdominal cavity (digestive organs) and the pelvic cavity (reproductive organs).

Key Terms

- **transverse plane**: divides a body into upper and lower portions
- **frontal plane**: divides a body into dorsal (back) and ventral (front) parts
- **sagittal plane**: divides the body into right and left halves

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33.7: Animal Primary Tissues - Epithelial Tissues

Learning Objectives

- Differentiate among the types of epithelial tissues

Epithelial tissues cover the outside of organs and structures in the body. They also line the lumens of organs in a single layer or multiple layers of cells. The types of epithelia are classified by the shapes of cells present and the number of layers of cells. Epithelia composed of a single layer of cells is called simple epithelia; epithelial tissue composed of multiple layers is called stratified epithelia.

Types and Shapes of Epithelial Tissues

Squamous Epithelia

Squamous epithelial cells are generally round, flat, and have a small, centrally-located nucleus. The cell outline is slightly irregular; cells fit together to form a covering or lining. When the cells are arranged in a single layer (simple squamous epithelia), they facilitate diffusion in tissues, such as the areas of gas exchange in the lungs or the exchange of nutrients and waste at blood capillaries.

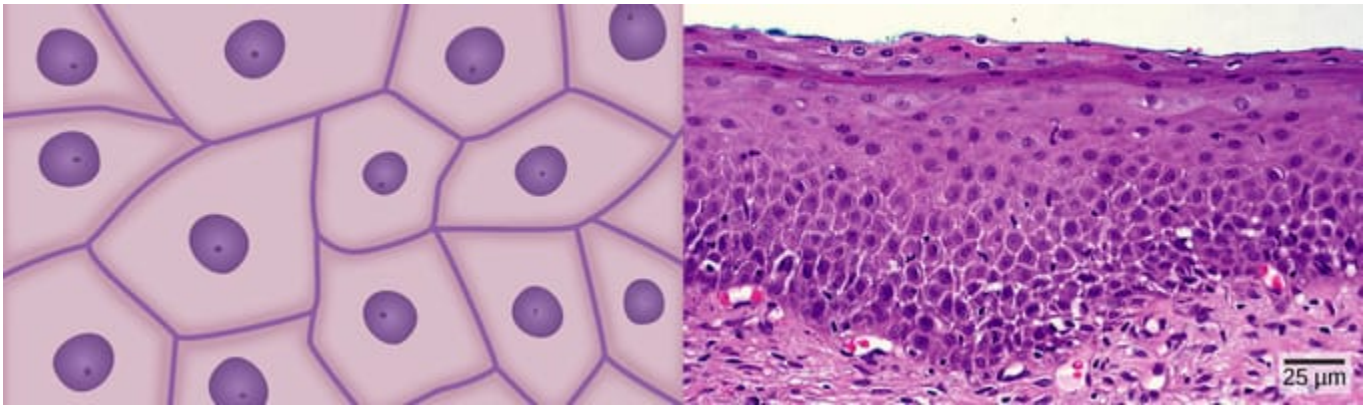


Figure 33.7.1: Squamous epithelia: Squamous epithelia cells (a) have a slightly-irregular shape and a small, centrally-located nucleus. These cells can be stratified into layers, as in (b) this human cervix specimen.

Cuboidal Epithelia

Cuboidal epithelial cells are cube-shaped with a single, central nucleus. They are most-commonly found in a single layer, such as a simple epithelia in glandular tissues throughout the body where they prepare and secrete glandular material. They are also found in the walls of tubules and in the ducts of the kidney and liver.

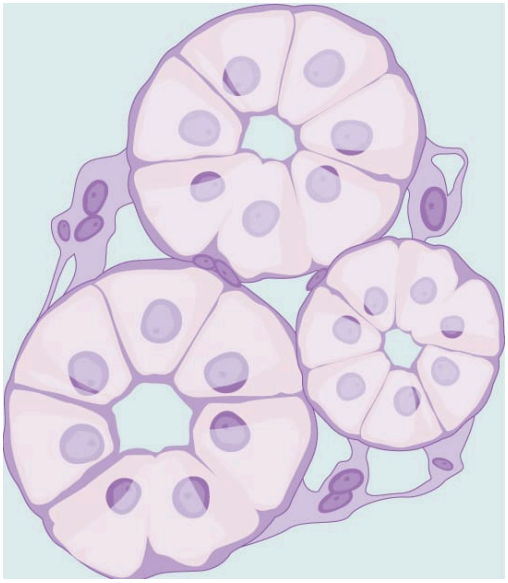


Figure 33.7.1: Cuboidal epithelia: Simple cuboidal epithelial cells line tubules in the mammalian kidney where they are involved in filtering the blood.

Columnar Epithelia

Columnar epithelial cells are taller than they are wide: they resemble a stack of columns in an epithelial layer. They are most-commonly found in a single-layer arrangement. The nuclei of columnar epithelial cells in the digestive tract appear to be lined up at the base of the cells. These cells absorb material from the lumen of the digestive tract and prepare it for entry into the body through the circulatory and lymphatic systems.

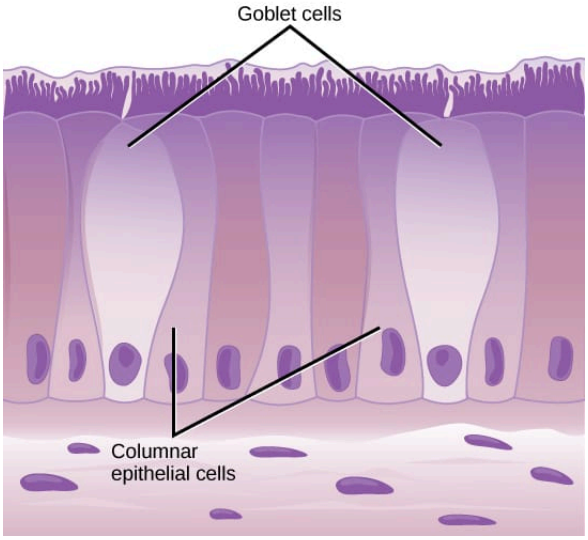


Figure 33.7.1: Columnar epithelia: Simple columnar epithelial cells absorb material from the digestive tract. The nuclei line up at the base of the cells. Goblet cells secret mucous into the digestive tract lumen.

Columnar epithelial cells lining the respiratory tract appear to be stratified. However, each cell is attached to the base membrane of the tissue and, therefore, they are simple tissues. The nuclei are arranged at different levels in the layer of cells, making it appear as though there is more than one layer. This is called pseudostratified, columnar epithelia. This cellular covering has cilia at the apical, or free, surface of the cells. The cilia enhance the movement of mucous and trapped particles out of the respiratory tract, helping to protect the system from invasive microorganisms and harmful material that has been breathed into the body. Goblet cells are interspersed in some tissues (such as the lining of the trachea). The goblet cells contain mucous that traps irritants, which, in the case of the trachea, keep these irritants from getting into the lungs.

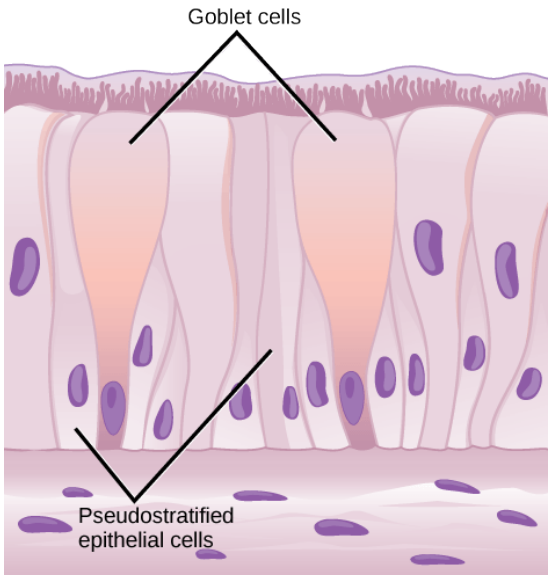


Figure 33.7.1: Pseudostratified columnar epithelia: Pseudostratified columnar epithelia line the respiratory tract. They exist in one layer, but the arrangement of nuclei at different levels makes it appear that there is more than one layer.

Transitional Epithelia

Transitional (or uroepithelial) cells appear only in the urinary system, primarily in the bladder and ureter. These cells are arranged in a stratified layer, but they have the capability of appearing to pile up on top of each other in a relaxed, empty bladder. As the urinary bladder fills, the epithelial layer unfolds and expands to hold the volume of urine introduced into it; the lining becomes thinner. In other words, the tissue transitions from thick to thin.

Key Points

- Epithelium composed of only a single layer of cells is called simple epithelium, while epithelium composed of more than one layer of cells is called stratified.
- Squamous epithelial cells are round, flat, and have an irregular border; their function is usually to diffuse or filter substances across tissues.
- Cuboidal epithelial cells, as wide as they are tall, are cube shaped; they are usually found lining glands where they secrete substances.
- Columnar epithelial cells are taller than they are wide and function mostly in absorption, such as in the digestive tract.
- Pseudostratified columnar epithelia appear to be stratified because there seems to be more than one row of nuclei, but, in fact, it is a single layer of cells with the nuclei at different levels.
- Transitional epithelium has the ability to stretch; it usually lines the interior of organs such as the bladder.

Key Terms

- **goblet cell**: glandular simple columnar epithelial cells whose function is to secrete mucin, which dissolves in water to form mucus
- **lumen**: The cavity or channel within a tube or tubular organ.

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33.8: Animal Primary Tissues - Loose, Fibrous, and Cartilage Connective Tissues

Learning Objectives

- Distinguish between the different types of connective tissue

Connective Tissues

Connective tissues are composed of a matrix consisting of living cells and a non-living substance, called the ground substance. The ground substance is composed of an organic substance (usually a protein) and an inorganic substance (usually a mineral or water). The principal cell of connective tissues is the fibroblast, an immature connective tissue cell that has not yet differentiated. This cell makes the fibers found in nearly all of the connective tissues. Fibroblasts are motile, able to carry out mitosis, and can synthesize whichever connective tissue is needed. Macrophages, lymphocytes, and, occasionally, leukocytes can be found in some of the tissues, while others may have specialized cells. The matrix in connective tissues gives the tissue its density. When a connective tissue has a high concentration of cells or fibers, it has a proportionally-less-dense matrix.

The organic portion, or protein fibers, found in connective tissues are either collagen, elastic, or reticular fibers. Collagen fibers provide strength to the tissue, preventing it from being torn or separated from the surrounding tissues. Elastic fibers are made of the protein elastin; this fiber can stretch to one and one half of its length, returning to its original size and shape. Elastic fibers provide flexibility to the tissues. Reticular fibers, the third type of protein fiber found in connective tissues, consist of thin strands of collagen that form a network of fibers to support the tissue and other organs to which it is connected.

Loose (Areolar) Connective Tissue

Loose connective tissue, also called areolar connective tissue, has a sampling of all of the components of a connective tissue. Loose connective tissue has some fibroblasts, although macrophages are present as well. Collagen fibers are relatively wide and stain a light pink, while elastic fibers are thin and stain dark blue to black. The space between the formed elements of the tissue is filled with the matrix. The material in the connective tissue gives it a loose consistency similar to a cotton ball that has been pulled apart. Loose connective tissue is found around every blood vessel, helping to keep the vessel in place. The tissue is also found around and between most body organs. In summary, areolar tissue is tough, yet flexible, and comprises membranes.

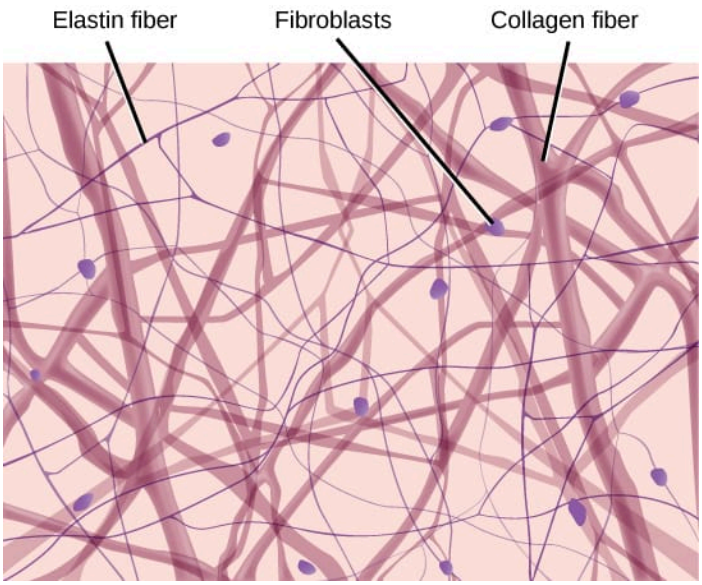


Figure 33.8.1: Loose connective tissue: Loose connective tissue is composed of loosely-woven collagen and elastic fibers. The fibers and other components of the connective tissue matrix are secreted by fibroblasts.

Fibrous Connective Tissue

Fibrous connective tissues contain large amounts of collagen fibers and few cells or matrix material. The fibers can be arranged irregularly or regularly with the strands lined up in parallel. Irregularly-arranged fibrous connective tissues are found in areas of the body where stress occurs from all directions, such as the dermis of the skin. Regular fibrous connective tissue is found in tendons (which connect muscles to bones) and ligaments (which connect bones to bones).

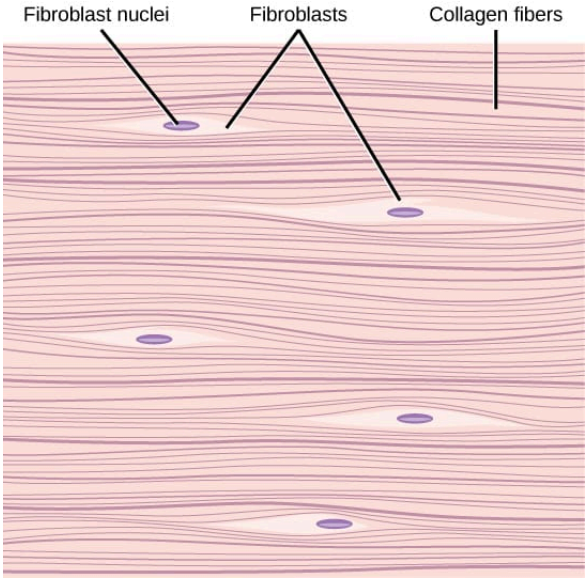


Figure 33.8.1: Fibrous connective tissue: Fibrous connective tissue from the tendon has strands of collagen fibers lined up in parallel. This arrangement helps the tissue resist tension that occurs from all directions.

Cartilage

Cartilage is a connective tissue. The cells, called chondrocytes (mature cartilage cells), make the matrix and fibers of the tissue. Chondrocytes are found in spaces within the tissue called “lacunae. ”

A cartilage with few collagen and elastic fibers is hyaline cartilage. The lacunae are randomly scattered throughout the tissue and

the matrix takes on a milky or scrubbed appearance with routine stains. Sharks have cartilaginous skeletons, as does nearly the entire human skeleton during some pre-birth developmental stages. A remnant of this cartilage persists in the outer portion of the human nose. Hyaline cartilage is also found at the ends of long bones, reducing friction and cushioning the articulations of these bones.



Figure 33.8.1: Hyaline cartilage: Hyaline cartilage consists of a matrix with cells called chondrocytes (shown here) embedded in it. The chondrocytes exist in cavities in the matrix called lacunae.

Elastic cartilage has a large amount of elastic fibers, giving it tremendous flexibility. The ears of most vertebrate animals contain this cartilage, as do portions of the larynx, or voice box. In contrast, fibrocartilage contains a large amount of collagen fibers, giving the tissue tremendous strength. Fibrocartilage comprises the intervertebral discs in vertebrate animals, which must withstand a tremendous amount of stress. Cartilage can also transform from one type to another. For example, hyaline cartilage found in movable joints, such as the knee and shoulder, often becomes damaged as a result of age or trauma. Damaged hyaline cartilage is replaced by fibrocartilage, resulting in “stiff” joints.

Key Points

- Fibroblasts are cells that generate any connective tissue that the body needs, as they can move throughout the body and can undergo mitosis to create new tissues.
- Protein fibers run throughout connective tissue, providing stability and support; they can be either collagen, elastic, or reticular fibers.
- Loose connective tissue is not particularly tough, but surrounds blood vessels and provides support to internal organs.
- Fibrous connective tissue, which is composed of parallel bundles of collagen fibers, is found in the dermis, tendons, and ligaments.
- Hyaline cartilage forms the skeleton of the embryo before it is transformed into bone; it is found in the adult body at the tip of the nose and around the ends of the long bones, where it prevents friction at the joints.
- Fibrocartilage is the strongest of the connective tissues; it is found in regions of the body that experience large amounts of stress and require a high degree of shock absorption, such as between the vertebrae.

Key Terms

- **chondrocyte**: a cell that makes up the tissue of cartilage
- **motile**: having the power to move spontaneously
- **fibroblast**: a cell found in connective tissue that produces fibers, such as collagen

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33.9: Animal Primary Tissues - Bone, Adipose, and Blood Connective Tissues

Learning Objectives

- Describe the structure and function of connective tissues made of bone, fat, and blood

Bone

Bone, or osseous tissue, is a connective tissue that has a large amount of two different types of matrix material. The organic matrix is materially similar to other connective tissues, including some amount of collagen and elastic fibers. This gives strength and flexibility to the tissue. The inorganic matrix consists of mineral salts, mostly calcium, that give the tissue hardness. Without adequate organic material in the matrix, the tissue breaks; without adequate inorganic material in the matrix, the tissue bends.

There are three types of cells in bone: osteoblasts, osteocytes, and osteoclasts. Osteoblasts are active in making bone for growth and remodeling. They deposit bone material into the matrix and, after the matrix surrounds them, they continue to live, but in a reduced metabolic state as osteocytes. Osteocytes are found in lacunae of the bone and assist in maintenance of the bone. Osteoclasts are active in breaking down bone for bone remodeling, providing access to calcium stored in tissues in order to release it into the blood. Osteoclasts are usually found on the surface of the tissue.

Bone can be divided into two types: compact and spongy. Compact bone is found in the shaft (or diaphysis) of a long bone and the surface of the flat bones, while spongy bone is found in the end (or epiphysis) of a long bone. Compact bone is organized into subunits called osteons. A blood vessel and a nerve are found in the center of the osteon within a long opening called the Haversian canal, with radiating circles of compact bone around it known as lamellae. Small spaces between these circles are called lacunae. Between the lacunae are microchannels called canaliculi; they connect the lacunae to aid diffusion between the cells. Spongy bone is made of tiny plates called trabeculae, which serve as struts, giving the spongy bone strength.

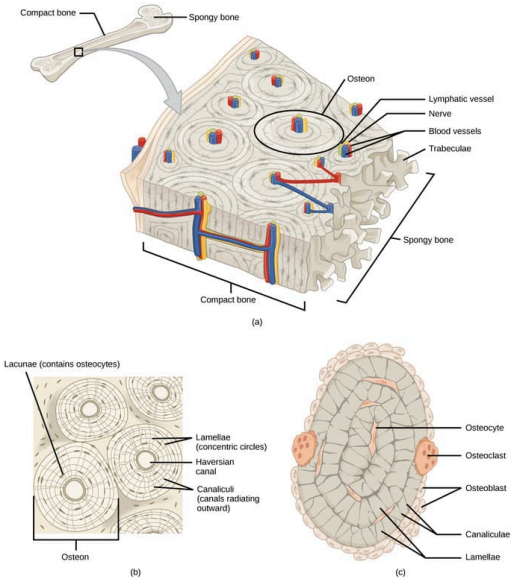


Figure 33.9.1: Bone structure: (a) Compact bone is a dense matrix on the outer surface of bone. Spongy bone, inside the compact bone, is porous with web-like trabeculae. (b) Compact bone is organized into rings called osteons. Blood vessels, nerves, and lymphatic vessels are found in the central Haversian canal. Rings of lamellae surround the Haversian canal. Between the lamellae are cavities called lacunae. Canaliculi are microchannels connecting the lacunae together. (c) Osteoblasts surround the exterior of the bone. Osteoclasts bore tunnels into the bone and osteocytes are found in the lacunae.

Adipose (Fat) Tissue

Adipose tissue, or fat tissue, is considered a connective tissue even though it does not have fibroblasts or a real matrix, and has only a few fibers. Adipose tissue is composed of cells called adipocytes that collect and store fat in the form of triglycerides for energy metabolism. Adipose tissues additionally serve as insulation to help maintain body temperatures, allowing animals to be endothermic. They also function as cushioning against damage to body organs. Under a microscope, adipose tissue cells appear empty due to the extraction of fat during the processing of the material for viewing. The thin lines in the image are the cell membranes; the nuclei are the small, black dots at the edges of the cells.

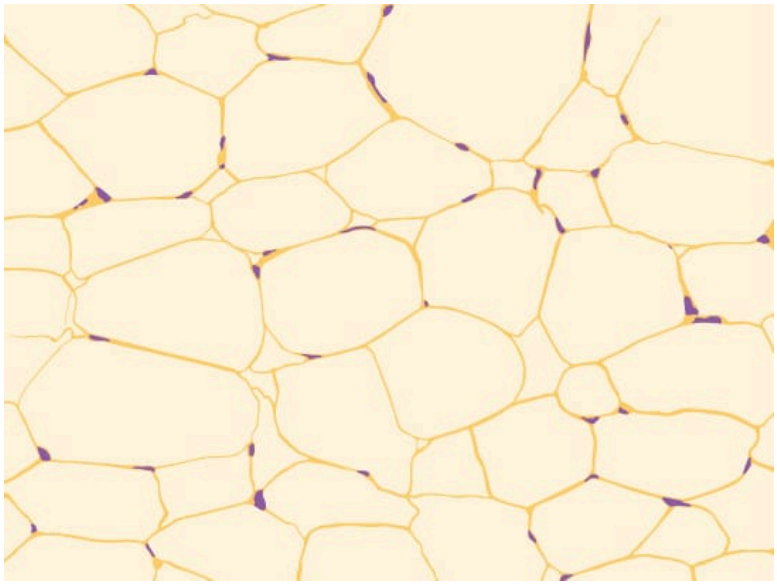


Figure 33.9.1: Adipose tissue: Adipose (fat) is a connective tissue composed of cells called adipocytes. Adipocytes have small nuclei localized at the cell edge and store fat for energy usage.

Blood

Blood is considered a connective tissue because it has a matrix. The living cell types are red blood cells, also called erythrocytes, and white blood cells, also called leukocytes. The fluid portion of whole blood, its matrix, is commonly called plasma.

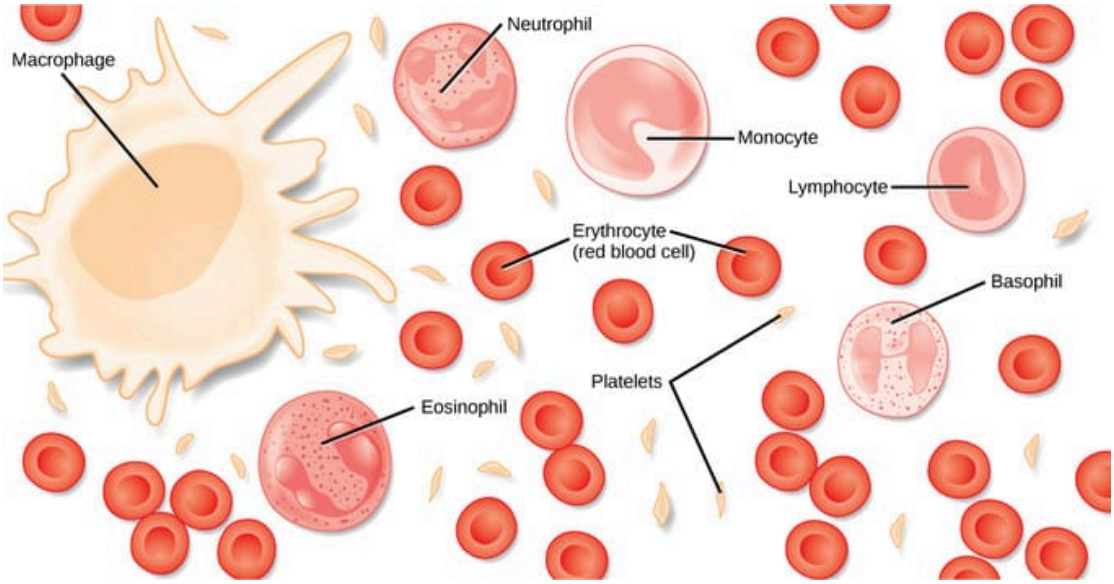


Figure 33.9.1: Blood Tissue: Blood is a connective tissue that has a fluid matrix, called plasma, and no fibers. Erythrocytes (red blood cells), the predominant cell type, are involved in the transport of oxygen and carbon dioxide. Also present are various leukocytes (white blood cells) involved in immune response.

The cell found in greatest abundance in blood is the erythrocyte, responsible for transporting oxygen to body tissues. Erythrocytes are consistently the same size in a species, but vary in size between species. Mammalian erythrocytes lose their nuclei and mitochondria when they are released from the bone marrow where they are made. Fish, amphibian, and avian red blood cells maintain their nuclei and mitochondria throughout the cell's life. The principal job of an erythrocyte is to carry and deliver oxygen to the tissues.

Leukocytes are white blood cells of the immune system involved in defending the body against both infectious disease and foreign materials. Five different and diverse types of leukocytes exist, but they are all produced and derived from a multipotent cell in the bone marrow known as a hematopoietic stem cell. Leukocytes are found throughout the body, including the blood and lymphatic system.

Different types of lymphocytes make antibodies tailored to the foreign antigens and control the production of those antibodies. Neutrophils are phagocytic cells that participate in one of the early lines of defense against microbial invaders, aiding in the removal of bacteria that has entered the body. Another leukocyte that is found in the peripheral blood is the monocyte, which give rise to phagocytic macrophages that clean up dead and damaged cells in the body, whether they are foreign or from the host animal. Two additional leukocytes in the blood are eosinophils and basophils, both of which help to facilitate the inflammatory response.

The slightly-granular material among the cells is a cytoplasmic fragment of a cell in the bone marrow. This is called a platelet or thrombocyte. Platelets participate in the stages leading up to coagulation of the blood to stop bleeding through damaged blood vessels. Blood has a number of functions, but primarily it transports material through the body to bring nutrients to cells and remove waste material from them.

Key Points

- Bone contains three types of cells: osteoblasts, which deposit bone; osteocytes, which maintain the bone; and osteoclasts, which resorb bone.
- The functional unit of compact bone is the osteon, which is made up of concentric rings of bone called lamellae surrounding a central opening called a Haversian canal, through which nerves and blood vessels travel.
- Compact bone, made of inorganic material that gives it strength and stability, is located on the shaft of long bones, while spongy bone, made of organic material, is found inside the ends of the long bones.
- Adipose (fat) tissue contains cells called adipocytes that store fat in the form of triglyerides; these can be broken down for energy by the organism.
- Blood is composed of erythrocytes (red blood cells), which distribute oxygen throughout the body; leukocytes (white blood cells), which mount immune responses; and platelets, which are involved in blood clotting.

Key Terms

- **osteon**: any of the central canals and surrounding bony layers found in compact bone
- **canaliculi**: plural form of canaliculus; any of many small canals or ducts in bone or in some plants
- **trabecula**: a small mineralized spicule that forms a network in spongy bone
- **osteoblast**: a mononucleate cell from which bone develops
- **osteoclast**: a large multinuclear cell associated with the resorption of bone

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33.10: Animal Primary Tissues - Muscle Tissues and Nervous Tissues

The function of muscle tissue (smooth, skeletal, and cardiac) is to contract, while nervous tissue is responsible for communication.

Learning Objectives

- Describe the structure and function of nervous tissue; differentiate among the types of muscle tissue

Muscle Tissues

There are three types of muscle in animal bodies: smooth, skeletal, and cardiac. They differ by the presence or absence of striations or bands, the number and location of nuclei, whether they are voluntarily or involuntarily controlled, and their location within the body.

Smooth Muscle

Smooth muscle cells have a single, centrally-located nucleus and are spindle shaped. Constriction of smooth muscle occurs under involuntary, autonomic nervous control in response to local conditions in the tissues. Smooth muscle tissue is also called non-striated as it lacks the banded appearance of skeletal and cardiac muscle. The walls of blood vessels, the tubes of the digestive system, and the tubes of the reproductive systems are composed primarily of smooth muscle. Contractions of smooth muscle move food through the digestive tracts and push blood through the blood vessels.

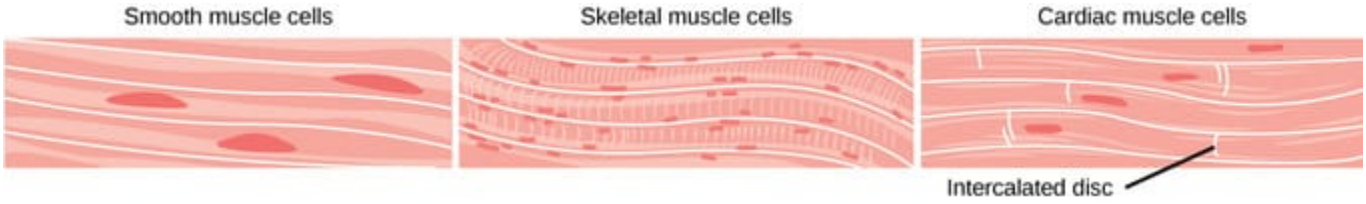


Figure 33.10.1: Types of muscle fibers: Smooth muscle cells do not have striations, while skeletal muscle cells do. Cardiac muscle cells have striations, but, unlike the multinucleate skeletal cells, they have only one nucleus. Cardiac muscle tissue also has intercalated discs, specialized regions running along the plasma membrane that join adjacent cardiac muscle cells and assist in passing an electrical impulse from cell to cell.

Skeletal Muscle

Skeletal muscle has striations across its cells caused by the arrangement of the contractile proteins, actin and myosin, that run throughout the muscle fiber. Skeletal muscle cells can contract by the attachment of myosin to actin filaments in the muscle, which then ratchets the actin filaments toward the center of the cells. These muscle cells are relatively long and have multiple nuclei along the edge of the cell. Skeletal muscle is under voluntary, somatic nervous system control and is found in the muscles that move bones. Stimulation of these cells by somatic motor neurons signals the cells to contract.

Cardiac Muscle

Cardiac muscle is found only in the heart. Similar to skeletal muscle, it has cross striations in its cells, but cardiac muscle has a single, centrally-located nucleus; the muscle branches in many directions. Cardiac muscle is not under voluntary control, but is influenced by the autonomic nervous system to speed up or slow down the heart beat. An added feature to cardiac muscle cells is a line that extends along the end of the cell as it abuts the next cardiac cell in the row. This line, an intercalated disc, assists in passing electrical impulses efficiently from one cell to the next while maintaining the strong connection between neighboring cardiac cells, allowing the cardiac muscle cells to synchronize the beating of the heart.

Nervous Tissues

Nervous tissues are made of cells specialized to receive and transmit electrical impulses from specific areas of the body and to send them to specific locations in the body organized into structures called nerves. A nerve consists of a neuron and glial cells. The main cell of the nervous system is the neuron. There is a large structure with a central nucleus: the cell body (or soma) of the neuron. Projections from the cell body are either dendrites, specialized in receiving input, or a single axon, specialized in transmitting impulses. Glial cells support the neurons. Astrocytes regulate the chemical environment of the nerve cell, while oligodendrocytes insulate the axon so the electrical nerve impulse is transferred more efficiently. Other glial cells support the nutritional and waste requirements of the neuron. Some of the glial cells are phagocytic, removing debris or damaged cells from the tissue.

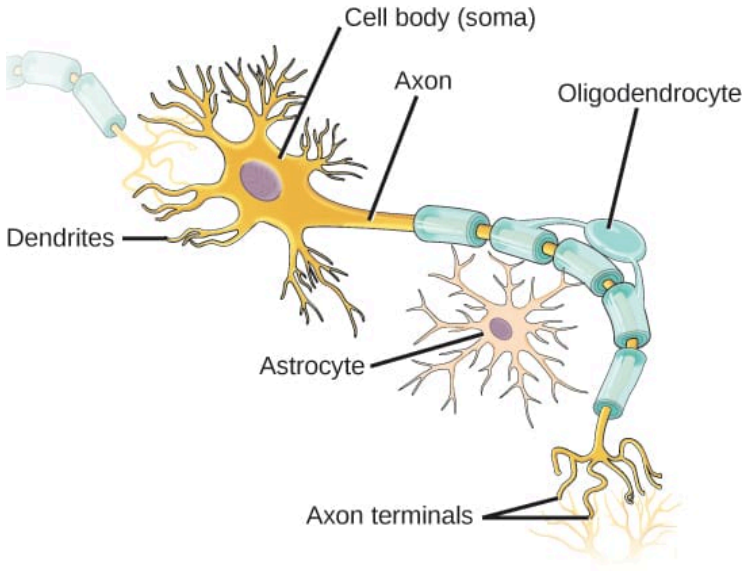


Figure 33.10.1: Neuron: The neuron has projections called dendrites that receive signals and projections called axons that send signals. Also shown are two types of glial cells: astrocytes to regulate the chemical environment of the nerve cell, and oligodendrocytes to insulate the axon so the electrical nerve impulse is transferred more efficiently.

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Key Points

- Smooth muscle cells, spindle shaped with only one nucleus, contract involuntarily to push food through the digestive tract and blood through blood vessels.
- Skeletal muscle cells, long, striated, multinucleate cells under voluntary control, are responsible for the movement of skeletal muscles.
- Cardiac muscle cells, found only in the heart, are striated and branching (with one nucleus); they are joined by intercalacted discs which allow the cells to synchronize the beating of the heart.
- Nervous tissue is comprised of nerves, which are comprised of neurons, that send and receive signals, and glial cells, which support the neurons.

Key Terms

- **intercalated disc**: identifying features of cardiac muscle; these connect individual heart muscle cells to work as a single functional organ
- **myosin**: a large family of motor proteins found in eukaryotic tissues, allowing mobility in muscles
- **oligodendrocyte**: a cell that provides support and insulation to axons in the central nervous system of some vertebrates
- **astrocyte**: a neuroglial cell, in the shape of a star, in the brain
- **actin**: A globular structural protein that polymerizes in a helical fashion to form an actin filament (or microfilament).

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33.11: Homeostasis - Homeostatic Process

Learning Objectives

- Give an example and describe a homeostatic process.

Homeostatic Process

The human organism consists of trillions of cells working together for the maintenance of the entire organism. While cells may perform very different functions, the cells are quite similar in their metabolic requirements. Maintaining a constant internal environment with everything that the cells need to survive (oxygen, glucose, mineral ions, waste removal, etc.) is necessary for the well-being of individual cells and the well-being of the entire body. The varied processes by which the body regulates its internal environment are collectively referred to as homeostasis.

Homeostasis

Homeostasis, in a general sense, refers to stability, balance, or equilibrium. Physiologically, it is the body's attempt to maintain a constant and balanced internal environment, which requires persistent monitoring and adjustments as conditions change. Adjustment of physiological systems within the body is called homeostatic regulation, which involves three parts or mechanisms: (1) the receptor, (2) the control center, and (3) the effector.

The receptor receives information that something in the environment is changing. The control center or integration center receives and processes information from the receptor. The effector responds to the commands of the control center by either opposing or enhancing the stimulus. This ongoing process continually works to restore and maintain homeostasis. For example, during body temperature regulation, temperature receptors in the skin communicate information to the brain (the control center) which signals the effectors: blood vessels and sweat glands in the skin. As the internal and external environment of the body are constantly changing, adjustments must be made continuously to stay at or near a specific value: the set point.

Purpose of Homeostasis

The ultimate goal of homeostasis is the maintenance of equilibrium around the set point. While there are normal fluctuations from the set point, the body's systems will usually attempt to revert to it. A change in the internal or external environment (a stimulus) is detected by a receptor; the response of the system is to adjust the deviation parameter toward the set point. For instance, if the body becomes too warm, adjustments are made to cool the animal. If the blood's glucose rises after a meal, adjustments are made to lower the blood glucose level by moving the nutrient into tissues in the command center that require it, or to store it for later use.

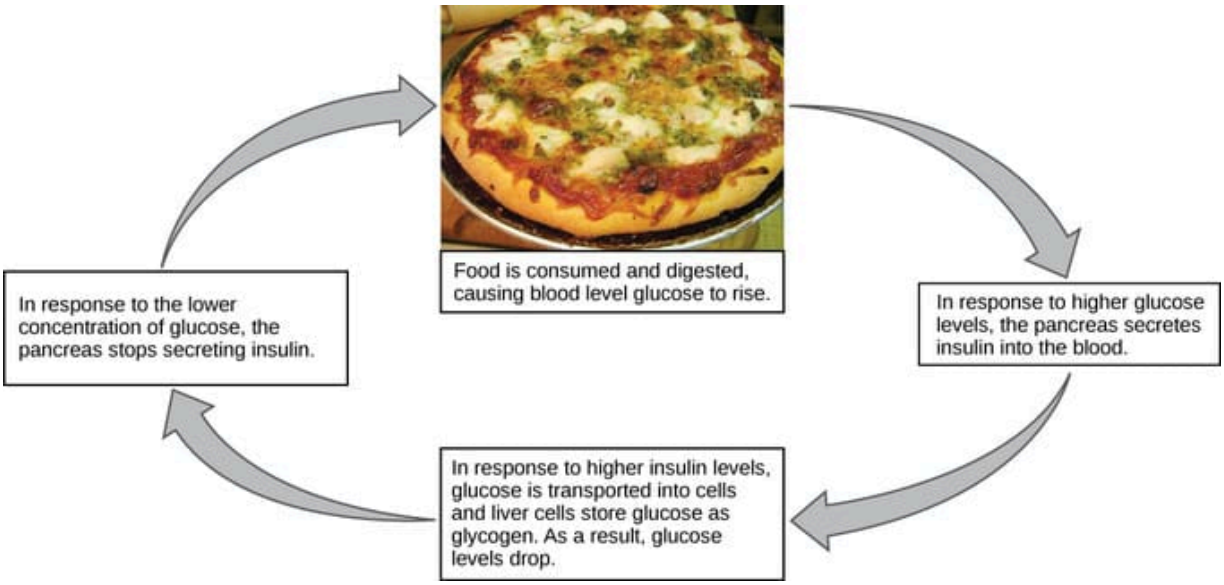


Figure 33.11.1: Blood glucose homeostasis: An example of how homeostasis is achieved by controlling blood sugar levels after a meal.

Key Points

- Homeostasis is the body's attempt to maintain a constant and balanced internal environment, which requires persistent monitoring and adjustments as conditions change.
- Homeostatic regulation is monitored and adjusted by the receptor, the command center, and the effector.
- The receptor receives information based on the internal environment; the command center, receives and processes the information; and the effector responds to the command center, opposing or enhancing the stimulus.

Key Terms

- **homeostasis**: the ability of a system or living organism to adjust its internal environment to maintain a stable equilibrium
- **effector**: any muscle, organ etc. that can respond to a stimulus from a nerve

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33.12: Homeostasis - Control of Homeostasis

Learning Objectives

- Discuss the ways in which the body maintains homeostasis and provide examples of each mechanism

Control of Homeostasis

When a change occurs in an animal's environment, an adjustment must be made. The receptors sense changes in the environment, sending a signal to the control center (in most cases, the brain), which, in turn, generates a response that is signaled to an effector. The effector is a muscle or a gland that will carry out the required response. Homeostasis is maintained by negative feedback loops within the organism. In contrast, positive feedback loops push the organism further out of homeostasis, but may be necessary for life to occur. Homeostasis is controlled by the nervous and endocrine systems in mammals.

Negative Feedback Mechanisms

Any homeostatic process that changes the direction of the stimulus is a negative feedback loop. It may either increase or decrease the stimulus, but the stimulus is not allowed to continue as it did before the receptor sensed it. In other words, if a level is too high, the body does something to bring it down; conversely, if a level is too low, the body does something to raise it; hence, the term: negative feedback. An example of negative feedback is the maintenance of blood glucose levels. When an animal has eaten, blood glucose levels rise, which is sensed by the nervous system. Specialized cells in the pancreas (part of the endocrine system) sense the increase, releasing the hormone insulin. Insulin causes blood glucose levels to decrease, as would be expected in a negative feedback system. However, if an animal has not eaten and blood glucose levels decrease, this is sensed in a different group of cells in the pancreas: the hormone glucagon is released, causing glucose levels to increase. This is still a negative feedback loop, but not in the direction expected by the use of the term "negative." Another example of an increase as a result of a feedback loop is the control of blood calcium. If calcium levels decrease, specialized cells in the parathyroid gland sense this and release parathyroid hormone (PTH), causing an increased absorption of calcium through the intestines and kidneys. The effects of PTH are to raise blood levels of calcium. Negative feedback loops are the predominant mechanism used in homeostasis.

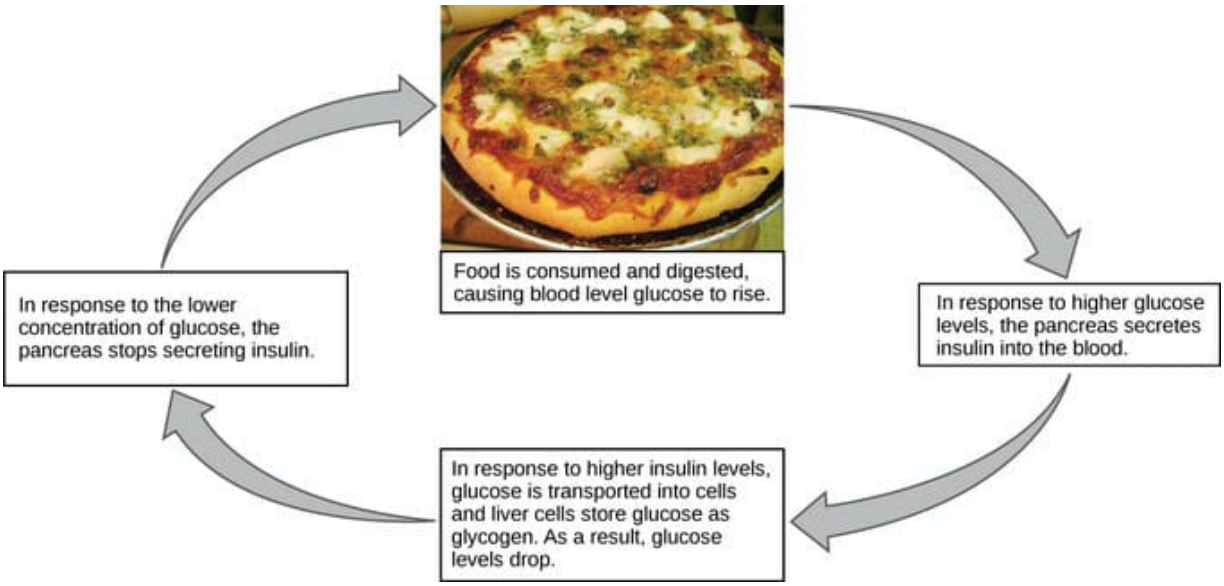


Figure 33.12.1: Negatie feedback loop: Blood sugar levels are controlled by a negative feedback loop.

Positive Feedback Loop

A positive feedback loop maintains the direction of the stimulus and possibly accelerates it. There are few examples of positive feedback loops that exist in animal bodies, but one is found in the cascade of chemical reactions that result in blood clotting, or coagulation. As one clotting factor is activated, it activates the next factor in sequence until a fibrin clot is achieved. The direction is maintained, not changed, so this is positive feedback. Another example of positive feedback is uterine contractions during childbirth. The hormone oxytocin, made by the endocrine system, stimulates the contraction of the uterus. This produces pain sensed by the nervous system. Instead of lowering the oxytocin and causing the pain to subside, more oxytocin is produced until the contractions are powerful enough to produce childbirth.

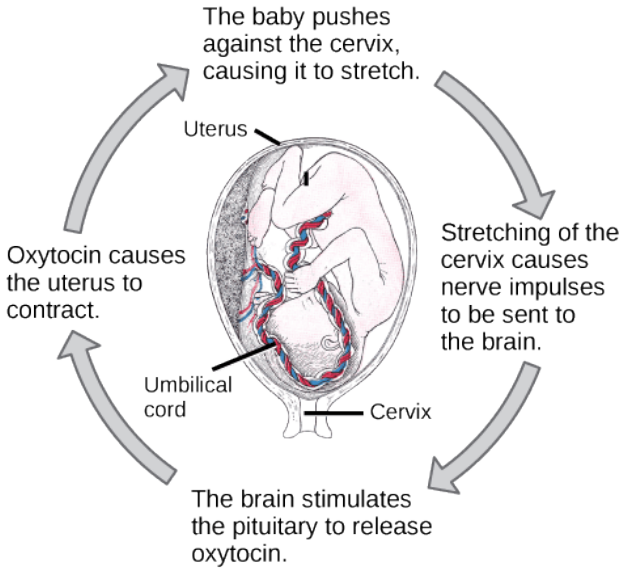


Figure 33.12.1: Positive feedback loop: The birth of a human infant is the result of positive feedback.

Set Point

Homeostasis is performed so the body can maintain its internal set point. However, there are times when the set point must be adjusted. When this happens, the feedback loop works to maintain the new setting. An example of changes in a set point can been seen in blood pressure. Over time, the normal or set point for blood pressure can increase as a result of continued increases in blood pressure. The body no longer recognizes the elevation as abnormal; there is no attempt made to return to the lower set point. The result is the maintenance of an elevated blood pressure which can have harmful effects on the body. Medication can lower blood pressure and lower the set point in the system to a more healthy level through a process of alteration of the set point in a feedback loop.

Changes can be made in a group of body organ systems in order to maintain a set point in another system. This is called acclimatization. This occurs, for instance, when an animal migrates to a higher altitude than one to which it is accustomed. In order to adjust to the lower oxygen levels at the new altitude, the body increases the number of red blood cells circulating in the blood to ensure adequate oxygen delivery to the tissues. Another example of acclimatization is animals that have seasonal changes in their coats: a heavier coat in the winter ensures adequate heat retention, while a light coat in summer assists in keeping body temperature from rising to harmful levels.

Key Points

- Negative feedback loops are used to maintain homeostasis and achieve the set point within a system.
- Negative feedback loops are characterized by their ability to either increase or decrease a stimulus, inhibiting the ability of the stimulus to continue as it did prior to sensing of the receptor.
- Positive feedback loops are characterized by their ability to maintain the direction of a stimulus and can even accelerate its effect.
- Acclimatization is characterized by the ability to change systems within an organism to maintain a set point in a different

environment.

Key Terms

- **acclimatization**: the climatic adaptation of an organism that has been moved to a new environment
- **endocrine**: Producing internal secretions that are transported around the body by the bloodstream.

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33.13: Homeostasis - Thermoregulation

Learning Objectives

- Outline the various types of processes utilized by animals to ensure thermoregulation.

Internal thermoregulation contributes to animal's ability to maintain homeostasis within a certain range of temperatures. As internal body temperature rises, physiological processes are affected, such as enzyme activity. Although enzyme activity initially increases with temperature, enzymes begin to denature and lose their function at higher temperatures (around 40-50 C for mammals). As internal body temperature decreases below normal levels, hypothermia occurs and other physiological process are affected. There are various thermoregulation mechanisms that animals use to regulate their internal body temperature.

Types of Thermoregulation (Ectothermy vs. Endothermy)

Thermoregulation in organisms runs along a spectrum from endothermy to ectothermy. Endotherms create most of their heat via metabolic processes, and are colloquially referred to as "warm-blooded." Ectotherms use external sources of temperature to regulate their body temperatures. Ectotherms are colloquially referred to as "cold-blooded" even though their body temperatures often stay within the same temperature ranges as warm-blooded animals.

Ectotherm

An ectotherm, from the Greek (ektós) "outside" and (thermós) "hot," is an organism in which internal physiological sources of heat are of relatively small or quite negligible importance in controlling body temperature. Since ectotherms rely on environmental heat sources, they can operate at economical metabolic rates. Ectotherms usually live in environments in which temperatures are constant, such as the tropics or ocean. Ectotherms have developed several behavioral thermoregulation mechanisms, such as basking in the sun to increase body temperature or seeking shade to decrease body temperature.



Figure 33.13.1: Ectotherm: The Common frog is an ecotherm and regulates its body based on the temperature of the external environment.

Endotherms

In contrast to ectotherms, endotherms regulate their own body temperature through internal metabolic processes and usually maintain a narrow range of internal temperatures. Heat is usually generated from the animal's normal metabolism, but under

conditions of excessive cold or low activity, an endotherm generate additional heat by shivering. Many endotherms have a larger number of mitochondria per cell than ectotherms. These mitochondria enables them to generate heat by increasing the rate at which they metabolize fats and sugars. However, endothermic animals must sustain their higher metabolism by eating more food more often. For example, a mouse (endotherm) must consume food every day to sustain high its metabolism, while a snake (ectotherm) may only eat once a month because its metabolism is much lower.

Homeothermy vs. Poikilothermy

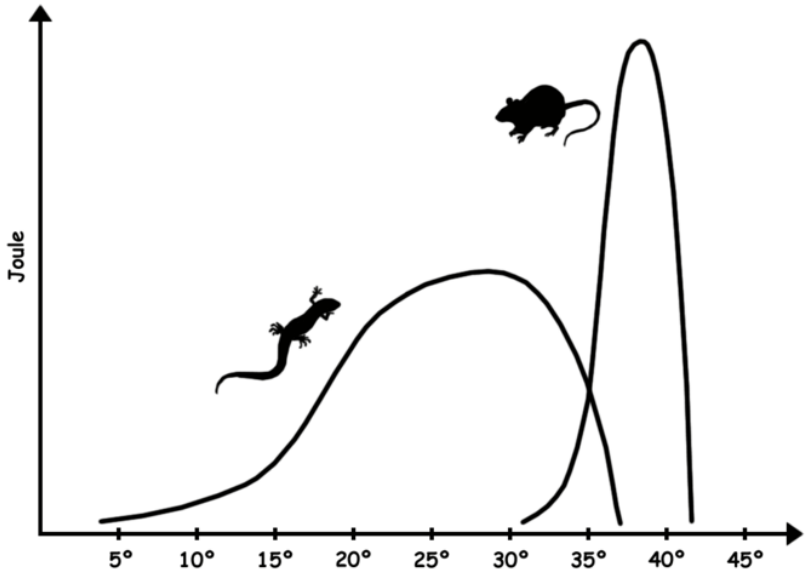


Figure 33.13.1: Homeotherm vs. Poikilotherm: Sustained energy output of an endothermic animal (mammal) and an ectothermic animal (reptile) as a function of core temperature. In this scenario, the mammal is also a homeotherm because it maintains its internal body temperature in a very narrow range. The reptile is also a poikilotherm because it can withstand a large range of temperatures.

A poikilotherm is an organism whose internal temperature varies considerably. It is the opposite of a homeotherm, an organism which maintains thermal homeostasis. Poikilotherm's internal temperature usually varies with the ambient environmental temperature, and many terrestrial ectotherms are poikilothermic. Poikilothermic animals include many species of fish, amphibians, and reptiles, as well as birds and mammals that lower their metabolism and body temperature as part of hibernation or torpor. Some ectotherms can also be homeotherms. For example, some species of tropical fish inhabit coral reefs that have such stable ambient temperatures that their internal temperature remains constant.

Means of Heat Transfer

Heat can be exchanged between an animal and its environment through four mechanisms: radiation, evaporation, convection, and conduction. Radiation is the emission of electromagnetic "heat" waves. Heat radiates from the sun and from dry skin the same manner. When a mammal sweats, evaporation removes heat from a surface with a liquid. Convection currents of air remove heat from the surface of dry skin as the air passes over it. Heat can be conducted from one surface to another during direct contact with the surfaces, such as an animal resting on a warm rock.

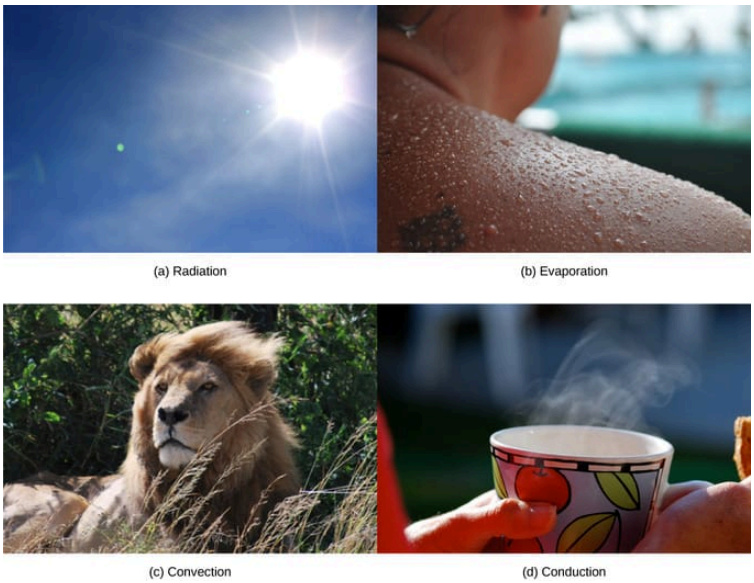


Figure 33.13.1: Mechanisms for heat exchange: Heat can be exchanged by four mechanisms: (a) radiation, (b) evaporation, (c) convection, or (d) conduction.

Key Points

- In response to varying body temperatures, processes such as enzyme production can be modified to acclimate to changes in the temperature.
- Endotherms regulate their own internal body temperature, regardless of fluctuating external temperatures, while ectotherms rely on the external environment to regulate their internal body temperature.
- Homeotherms maintain their body temperature within a narrow range, while poikilotherms can tolerate a wide variation in internal body temperature, usually because of environmental variation.
- Heat can be exchanged between environment and animals via radiation, evaporation, convection, or conduction processes.

Key Terms

- **ectotherm**: An animal that relies on external environment to regulate its internal body temperature.
- **endotherm**: An animal that regulates its own internal body temperature through metabolic processes.
- **homeotherm**: An animal that maintains a constant internal body temperature, usually within a narrow range of temperatures.
- **poikilotherm**: An animal that varies its internal body temperature within a wide range of temperatures, usually as a result of variation in the environmental temperature.

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33.14: Homeostasis - Heat Conservation and Dissipation

Learning Objectives

- Describe some of the changes animals use in order to maintain body temperature

Heat Conservation and Dissipation

Animals conserve or dissipate heat in a variety of ways. In certain climates, endothermic animals have some form of insulation, such as fur, fat, feathers, or some combination thereof. 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, yet they maintain a constant, warm, body temperature. The arctic fox uses its fluffy tail as extra insulation when it curls up to sleep in cold weather. Mammals have a residual effect from shivering and increased muscle activity: arrector pili muscles create “goose bumps,” causing small hairs to stand up when the individual is cold; this has the intended effect of increasing body temperature. Mammals use layers of fat to achieve the same end; the loss of significant amounts of body fat will compromise an individual’s ability to conserve heat.

Endotherms use their circulatory systems to help maintain body temperature. For example, vasodilation brings more blood and heat to the body surface, facilitating radiation and evaporative heat loss, which helps to cool the body. However, vasoconstriction reduces blood flow in peripheral blood vessels, forcing blood toward the core and the vital organs found there, conserving heat. Some animals have adaptions to their circulatory system that enable them to transfer heat from arteries to veins, thus, warming blood that returns to the heart. This is called a countercurrent heat exchange; it prevents the cold venous blood from cooling the heart and other internal organs. This adaption, which can be shut down in some animals to prevent overheating the internal organs, is found in many animals, including dolphins, sharks, bony fish, bees, and hummingbirds. In contrast, similar adaptations (as in dolphin flukes and elephant ears) can help cool endotherms when needed.

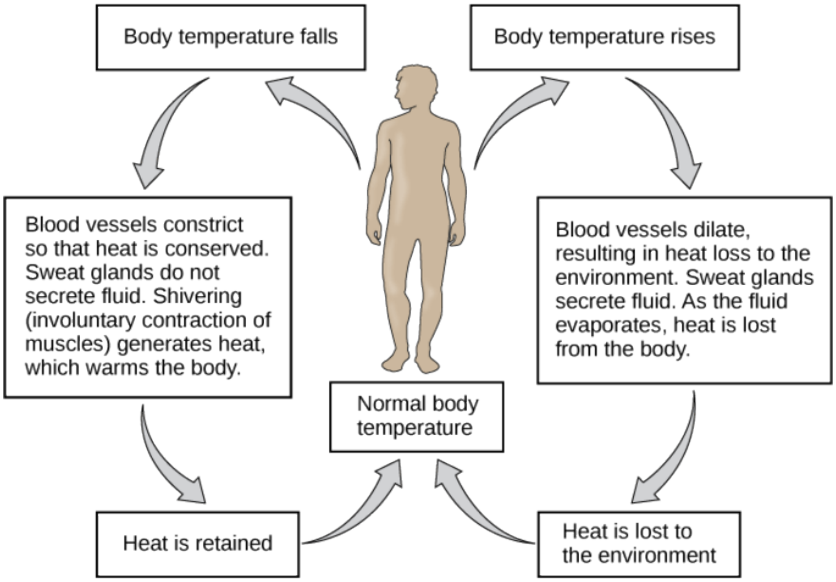


Figure 33.14.1: Control of body temperature: In endotherms, the circulatory system is used to help maintain body temperature, either by vasodilation or vasoconstriction.

Many animals, especially mammals, use metabolic waste heat as a heat source. When muscles are contracted, most of the energy from the ATP used in muscle actions is wasted energy that translates into heat. In cases of severe cold, a shivering reflex is activated that generates heat for the body. Many species also have a type of adipose tissue called brown fat that specializes in generating heat.

Ecothermic animals use changes in their behavior to help regulate body temperature. For example, a desert ectothermic animal may simply seek cooler areas during the hottest part of the day in the desert to keep from becoming too warm. The same animals

may climb onto rocks to capture heat during a cold desert night. Some animals seek water to aid evaporation in cooling them, as seen with reptiles. Other ectotherms use group activity, such as the activity of bees to warm a hive to survive winter.

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Key Points

- Heat conservation is characterized by the ability to ensure blood remains in the core by undergoing vasoconstriction, reducing blood flow to the periphery (also known as peripheral vasoconstriction).
- Heat dissipation is characterized by the ability to undergo vasodilation which increases blood flow to the periphery, resulting in evaporative heat loss.
- Endothermic animals are defined by their ability to utilize both vasoconstriction and vasodilation to maintain internal body temperature.
- Ectothermic animals are defined by their change in behavior (lying in sunlight to warm up, hiding in shade to cool down) to regulate body temperature.

Key Terms

- **endotherm**: a warm-blooded animal that maintains a constant body temperature
- **ectotherm**: a cold-blooded animal that regulates its body temperature by exchanging heat with its surroundings

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34: ANIMAL NUTRITION AND THE DIGESTIVE SYSTEM

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34.1: Digestive Systems - Introduction

Learning Objectives

- Summarize animal nutrition and the digestive system

Introduction to Animal Nutrition

All living organisms need nutrients to survive. While plants can obtain the molecules required for cellular function through the process of photosynthesis, most animals obtain their nutrients by the consumption of other organisms. At the cellular level, the biological molecules necessary for animal function are amino acids, lipid molecules, nucleotides, and simple sugars. The food consumed consists of protein, fat, and complex carbohydrates, but the requirements of each are different for each animal.



Figure 34.1.1: Balanced human diet: For humans, fruits and vegetables are important in maintaining a balanced diet. Both of these are an important source of vitamins and minerals, as well as carbohydrates, which are broken down through digestion for energy.

Animals must convert these macromolecules into the simple molecules required for maintaining cellular functions, such as assembling new molecules, cells, and tissues. The conversion of the food consumed to the nutrients required is a multi-step process involving digestion and absorption. During digestion, food particles are broken down to smaller components which will later be absorbed by the body.

Digestive System

The digestive system is one of the largest organ systems in the human body. It is responsible for processing ingested food and liquids. The cells of the human body all require a wide array of chemicals to support their metabolic activities, from organic nutrients used as fuel to the water that sustains life at the cellular level. The digestive system not only effectively chemically reduces the compounds in food into their fundamental building blocks, but also acts to retain water and excrete undigested materials. The functions of the digestive system can be summarized as follows: ingestion (eat food), digestion (breakdown of food), absorption (extraction of nutrients from the food), and defecation (removal of waste products).

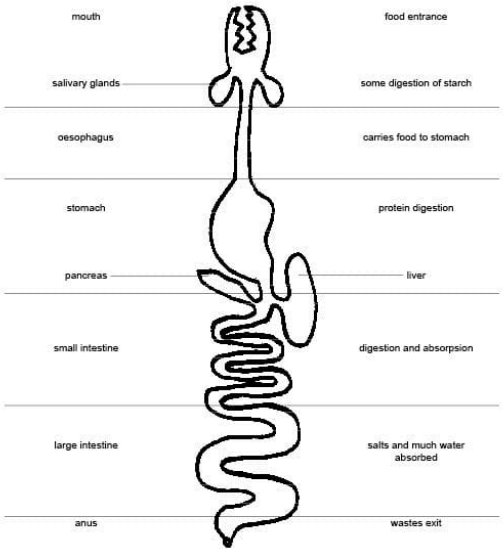


Figure 34.1.1: Generalized animal digestive system: This diagram shows a generalized animal digestive system, detailing the different organs and their functions.

The digestive system consists of a group of organs that form a closed tube-like structure called the gastrointestinal tract (GI tract) or the alimentary canal. For convenience, the GI tract is divided into upper GI tract and lower GI tract. The organs that make up the GI tract include the mouth, the esophagus, the stomach, the small intestine, and the large intestine. There are also several accessory organs that secrete various enzymes into the GI tract. These include the salivary glands, the liver, and the pancreas.

Challenges to Human Nutrition

One of the challenges in human nutrition is maintaining a balance between food intake, storage, and energy expenditure. Imbalances can have serious health consequences. For example, eating too much food while not expending much energy leads to obesity, which in turn will increase the risk of developing illnesses such as type-2 diabetes and cardiovascular disease. The recent rise in obesity and related diseases means that understanding the role of diet and nutrition in maintaining good health is more important than ever.

Key Points

- Animals obtain lipids, proteins, carbohydrates, essential vitamins, and minerals from the food they consume.
- The digestive system is composed of a series of organs, each with a specific, yet related function, that work to extract nutrients from food.
- Organs of the digestive system include the mouth, esophagus, stomach, small intestine, and the large intestine.
- Accessory organs, such as the liver and pancreas, secrete digestive juices into the gastrointestinal tract to assist with food breakdown.

Key Terms

- **digestion**: the process, in the gastrointestinal tract, by which food is converted into substances that can be utilized by the body
- **macromolecule**: a very large molecule, especially used in reference to large biological polymers (e.g. nucleic acids and proteins)
- **alimentary canal**: the organs of a human or an animal through which food passes; the digestive tract

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34.2: Digestive Systems - Herbivores, Omnivores, and Carnivores

Learning Objectives

- Differentiate among herbivores, omnivores, and carnivores

Herbivores, Omnivores, and Carnivores

Herbivores are animals whose primary food source is plant-based. Examples of herbivores include vertebrates like deer, koalas, and some bird species, as well as invertebrates such as crickets and caterpillars. These animals have evolved digestive systems capable of digesting large amounts of plant material. The plants are high in fiber and starch, which provide the main energy source in their diet. Since some parts of plant materials, such as cellulose, are hard to digest, the digestive tract of herbivores is adapted so that food may be digested properly. Many large herbivores have symbiotic bacteria within their guts to assist with the breakdown of cellulose. They have long and complex digestive tracts to allow enough space and time for microbial fermentation to occur. Herbivores can be further classified into frugivores (fruit-eaters), granivores (seed eaters), nectivores (nectar feeders), and folivores (leaf eaters).



Figure 34.2.1: Examples of herbivores: Herbivores, such as this (a) mule deer and (b) monarch caterpillar, eat primarily plant material. Some herbivores contain symbiotic bacteria within their intestines to aid with the digestion of the cellulose found in plant cell walls.

Omnivores are animals that eat both plant- and animal- derived food. Although the Latin term omnivore literally means “eater of everything”, omnivores cannot really eat everything that other animals eat. They can only eat things that are moderately easy to acquire while being moderately nutritious. For example, most omnivores cannot live by grazing, nor are they able to eat some hard-shelled animals or successfully hunt large or fast prey. Humans, bears, and chickens are examples of vertebrate omnivores; invertebrate omnivores include cockroaches and crayfish.



(a) (b)

Figure 34.2.1: Examples of omnivores: Omnivores such as the (a) bear and (b) crayfish eat both plant- and animal-based food. While their food options are greater than those of herbivores or carnivores, they are still limited by what they can find to eat, or what they can catch.

Carnivores are animals that eat other animals. The word carnivore is derived from Latin and means “meat eater.” Wild cats, such as lions and tigers, are examples of vertebrate carnivores, as are snakes and sharks, while invertebrate carnivores include sea stars, spiders, and ladybugs. Obligate carnivores are those that rely entirely on animal flesh to obtain their nutrients; examples of obligate carnivores are members of the cat family. Facultative carnivores are those that also eat non-animal food in addition to animal food. Note that there is no clear line that differentiates facultative carnivores from omnivores; dogs would be considered facultative carnivores.



(a) (b)

Figure 34.2.1: Examples of carnivores: Carnivores such as the (a) lion eat primarily meat. The (b) ladybug is also a carnivore that consumes small insects called aphids.

Key Points

- Herbivores are those animals, such as deer and koalas, that only eat plant material.
- Omnivores are those animals, such as bears and humans, that can eat a variety of food sources, but tend to prefer one type to another.
- While most carnivores, such as cats, eat only meat, facultative carnivores, such as dogs, behave more like omnivores as they can eat plant matter along with meat.
- Facultative carnivores can eat meat as well as plant material while obligate carnivores eat meat all the time.

Key Terms

- **omnivore**: an animal which is able to consume both plants (like a herbivore) and meat (like a carnivore)
- **obligate carnivore**: an animal that necessarily subsists on a diet consisting mainly of meat because it does not possess the physiology to digest vegetable matter
- **herbivore**: any animal that eats only vegetation (i.e. that eats no meat)
- **carnivore**: any animal that eats meat as the main part of its diet

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34.3: Digestive Systems - Invertebrate Digestive Systems

Learning Objectives

- Explain the digestive process in invertebrates

Invertebrate Digestive Systems

Animals have evolved different types of digestive systems break down the different types of food they consume. Invertebrates can be classified as those that use intracellular digestion and those with extracellular digestion.

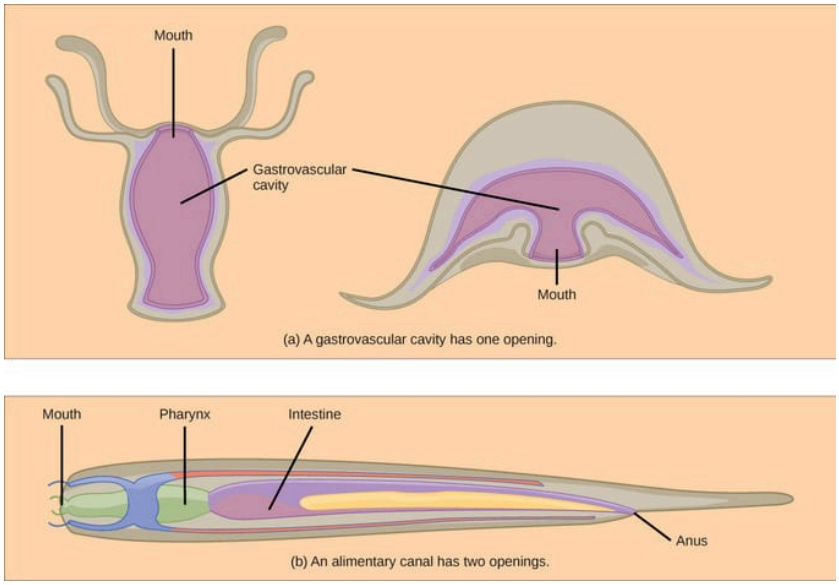


Figure 34.3.1: Invertebrate digestive systems: (a) A gastrovascular cavity has a single opening through which food is ingested and waste is excreted, as shown in this hydra and in this jellyfish medusa. (b) An alimentary canal has two openings: a mouth for ingesting food and an anus for eliminating waste, as shown in this nematode.

Intracellular Digestion

The simplest example of digestion intracellular digestion, which takes place in a gastrovascular cavity with only one opening. Most animals with soft bodies use this type of digestion, including Platyhelminthes (flatworms), Ctenophora (comb jellies), and Cnidaria (coral, jelly fish, and sea anemones). The gastrovascular cavities of these organisms contain one open which serves as both a “mouth” and an “anus”.



Figure 34.3.1: Invertebrates with Extracellular Digestion: Invertebrates like grasshoppers have alimentary canals with specialized compartments for digestion. Their food is broken down in their digestive tract (extracellular digestion), rather than inside their individual cells (intracellular digestion).

Ingested material enters the mouth and passes through a hollow, tubular cavity. The food particles are engulfed by the cells lining the gastrovascular cavity and the molecular are broken down within the cytoplasm of the cells (intracellular).

Extracellular Digestion

The alimentary canal is a more advanced digestive system than a gastrovascular cavity and carries out extracellular digestion. Most other invertebrates like segmented worms (earthworms), arthropods (grasshoppers), and arachnids (spiders) have alimentary canals. The alimentary canal is compartmentalized for different digestive functions and consists of one tube with a mouth at one end and an anus at the other.

Once the food is ingested through the mouth, it passes through the esophagus and is stored in an organ called the crop; then it passes into the gizzard where it is churned and digested. From the gizzard, the food passes through the intestine and nutrients are absorbed. Because the food has been broken down exterior to the cells, this type of digestion is called extracellular digestion. The material that the organism cannot digest is eliminated as feces, called castings, through the anus.

Most invertebrates use some form of extracellular digestion to break down their food. Flatworms and cnidarians, however, can use both types of digestion to break down their food.

Key Points

- The simplest invertebrate digestive system in a gastrovascular cavity consists of only one opening that serves as both the mouth for taking in food and the anus for excretion.
- The gastrovascular cavity has cells lining it that secrete digestive enzymes to break down the food particles through a process called intracellular digestion.
- An alimentary canal is a long tube that begins with a mouth, then goes to the esophagus, then to the crop, gizzard, intestine, and finally, to an anus; this is used in the process of extracellular digestion.
- Most invertebrates use extracellular digestion; however, there are a few phyla that can use both intracellular and extracellular digestion.

Key Terms

- **alimentary canal**: the organs of a human or an animal through which food passes; the digestive tract
- **intracellular digestion**: Intracellular digestion is a form of digestion which takes place within the cytoplasm of the organism.

Intracellular digestion takes place in animals without a digestive tract, in which food items are brought into the cell for digestion.

- **extracellular digestion**: Extracellular digestion is a process in which animals feed by secreting enzymes through the cell membrane onto the food. The enzymes break the food into molecules small enough to be taken pass through the cell membrane into the cell. These nutrients are transferred into the blood or other body fluids and distributed to the rest of the body.
- **extracellular**: occurring or found outside of a cell
- **casting**: the excreta of an earthworm or similar creature
- **intracellular**: Intracellular digestion is a form of digestion which takes place within the cytoplasm of the organism. Intracellular digestion takes place in animals without a digestive tract, in which food items are brought into the cell for digestion.

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34.4: Digestive Systems - Vertebrate Digestive Systems

Learning Objectives

- Differentiate among the types of vertebrate digestive systems

Vertebrate Digestive Systems

Vertebrates have evolved more complex digestive systems to adapt to their dietary needs. Some animals have a single stomach, while others have multi-chambered stomachs. Birds have developed a digestive system adapted to eating un-masticated (un-chewed) food.

Monogastric: Single-chambered Stomach

As the word monogastric suggests, this type of digestive system consists of one (“mono”) stomach chamber (“gastric”). Humans and many animals have a monogastric digestive system. The process of digestion begins with the mouth and the intake of food. The teeth play an important role in masticating (chewing) or physically breaking down food into smaller particles. The enzymes present in saliva also begin to chemically break down food. The esophagus is a long tube that connects the mouth to the stomach. Using peristalsis, the muscles of the esophagus push the food towards the stomach. In order to speed up the actions of enzymes in the stomach, the stomach has an extremely acidic environment, with a pH between 1.5 and 2.5. The gastric juices, which include enzymes in the stomach, act on the food particles and continue the process of digestion. In the small intestine, enzymes produced by the liver, the small intestine, and the pancreas continue the process of digestion. The nutrients are absorbed into the blood stream across the epithelial cells lining the walls of the small intestines. The waste material travels to the large intestine where water is absorbed and the drier waste material is compacted into feces that are stored until excreted through the rectum.

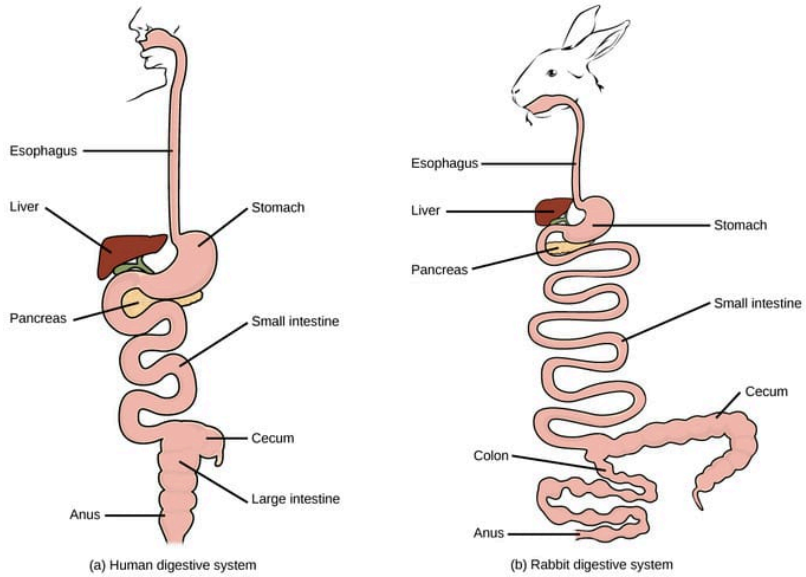


Figure 34.4.1: Mammalian digestive system (non-ruminant): (a) Humans and herbivores, such as the (b) rabbit, have a monogastric digestive system. However, in the rabbit, the small intestine and cecum are enlarged to allow more time to digest plant material. The enlarged organ provides more surface area for absorption of nutrients.

Avian

Birds face special challenges when it comes to obtaining nutrition from food. They do not have teeth, so their digestive system must be able to process un-masticated food. Birds have evolved a variety of beak types that reflect the vast variety in their diet,

ranging from seeds and insects to fruits and nuts. Because most birds fly, their metabolic rates are high in order to efficiently process food while keeping their body weight low. The stomach of birds has two chambers: the proventriculus, where gastric juices are produced to digest the food before it enters the stomach, and the gizzard, where the food is stored, soaked, and mechanically ground. The undigested material forms food pellets that are sometimes regurgitated. Most of the chemical digestion and absorption happens in the intestine, while the waste is excreted through the cloaca.

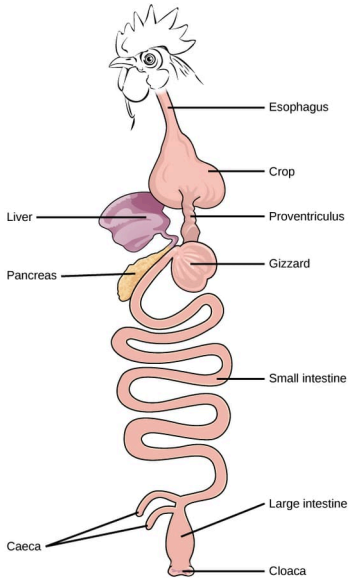


Figure 34.4.1: Bird digestive system: The avian esophagus has a pouch, called a crop, which stores food. Food passes from the crop to the first of two stomachs, called the proventriculus, which contains digestive juices that break down food. From the proventriculus, the food enters the second stomach, called the gizzard, which grinds food. Some birds swallow stones or grit, which are stored in the gizzard, to aid the grinding process. Birds do not have separate openings to excrete urine and feces. Instead, uric acid from the kidneys is secreted into the large intestine and combined with waste from the digestive process. This waste is excreted through an opening called the cloaca.

Ruminants

Ruminants are mainly herbivores, such as cows, sheep, and goats, whose entire diet consists of eating large amounts of roughage or fiber. They have evolved digestive systems that help them process vast amounts of cellulose. An interesting feature of the ruminants' mouth is that they do not have upper incisor teeth. They use their lower teeth, tongue, and lips to tear and chew their food. From the mouth, the food travels through the esophagus and into the stomach.

To help digest the large amount of plant material, the stomach of the ruminants is a multi-chambered organ. The four compartments of the stomach are called the rumen, reticulum, omasum, and abomasum. These chambers contain many microbes that break down cellulose and ferment ingested food. The abomasum, the "true" stomach, is the equivalent of the monogastric stomach chamber. This is where gastric juices are secreted. The four-compartment gastric chamber provides larger space and the microbial support necessary to digest plant material in ruminants. The fermentation process produces large amounts of gas in the stomach chamber, which must be eliminated. As in other animals, the small intestine plays an important role in nutrient absorption, while the large intestine aids in the elimination of waste.

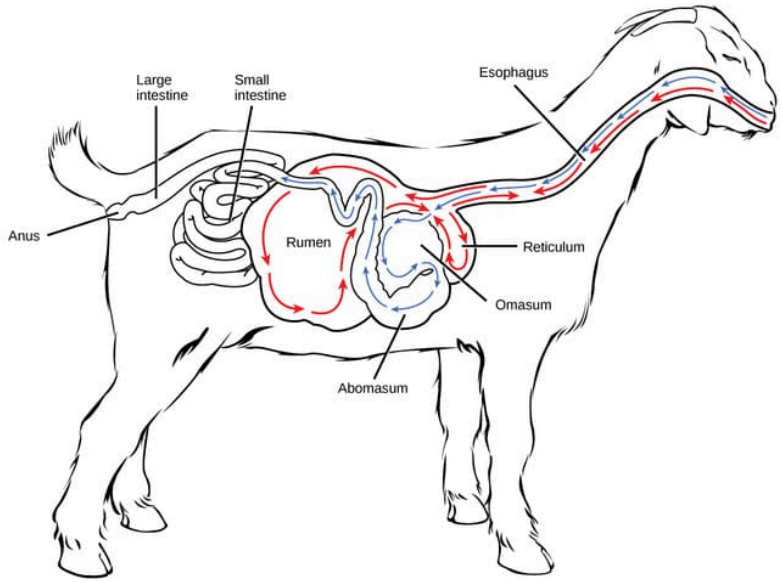


Figure 34.4.1: Ruminant mammal digestive system: Ruminant animals, such as goats and cows, have four stomachs. The first two stomachs, the rumen and the reticulum, contain prokaryotes and protists that are able to digest cellulose fiber. The ruminant regurgitates cud from the reticulum, chews it, and swallows it into a third stomach, the omasum, which removes water. The cud then passes onto the fourth stomach, the abomasum, where it is digested by enzymes produced by the ruminant.

Pseudo-ruminants

Some animals, such as camels and alpacas, are pseudo-ruminants. They eat a lot of plant material and roughage. Digesting plant material is not easy because plant cell walls contain the polymeric sugar molecule cellulose. The digestive enzymes of these animals cannot break down cellulose, but microorganisms present in the digestive system can. Since the digestive system must be able to handle large amounts of roughage and break down the cellulose, pseudo-ruminants have a three-chamber stomach. In contrast to ruminants, their cecum (a pouched organ at the beginning of the large intestine containing many microorganisms that are necessary for the digestion of plant materials) is large. This is the site where the roughage is fermented and digested. These animals do not have a rumen, but do have an omasum, abomasum, and reticulum.

Key Points

- Monogastric animals have a single stomach that secretes enzymes to break down food into smaller particles; additional gastric juices are produced by the liver, salivary glands, and pancreas to assist with the digestion of food.
- The avian digestive system has a mouth (beak), crop (for food storage), and gizzard (for breakdown), as well as a two-chambered stomach consisting of the proventriculus, which releases enzymes, and the true stomach, which finishes the breakdown.
- Ruminants, such as cows and sheep, are those animals that have four stomachs; they eat plant matter and have symbiotic bacteria living within their stomachs to help digest cellulose.
- Pseudo-ruminants (such as camels and alpacas) are similar to ruminants, but have a three-chambered stomach; the symbiotic bacteria that help them to break down cellulose is found in the cecum, a chamber close to the large intestine.

Key Terms

- **peristalsis**: the rhythmic, wave-like contraction and relaxation of muscles which propagates in a wave down a muscular tube
- **proventriculus**: the part of the avian stomach, between the crop and the gizzard, that secretes digestive enzymes
- **cellulose**: a complex carbohydrate that forms the main constituent of the cell wall in most plants

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34.5: Digestive Systems - Digestive System- Mouth and Stomach

Learning Objectives

- Describe the parts of the digestive system from the oral cavity through the stomach

Parts of the Digestive System

The vertebrate digestive system is designed to facilitate the transformation of food matter into the nutrient components that sustain organisms. The upper gastrointestinal tract includes the oral cavity, esophagus, and stomach.

Oral Cavity

The oral cavity, or mouth, is the point of entry of food into the digestive system. The food is broken into smaller particles by mastication, the chewing action of the teeth. All mammals have teeth and can chew their food.

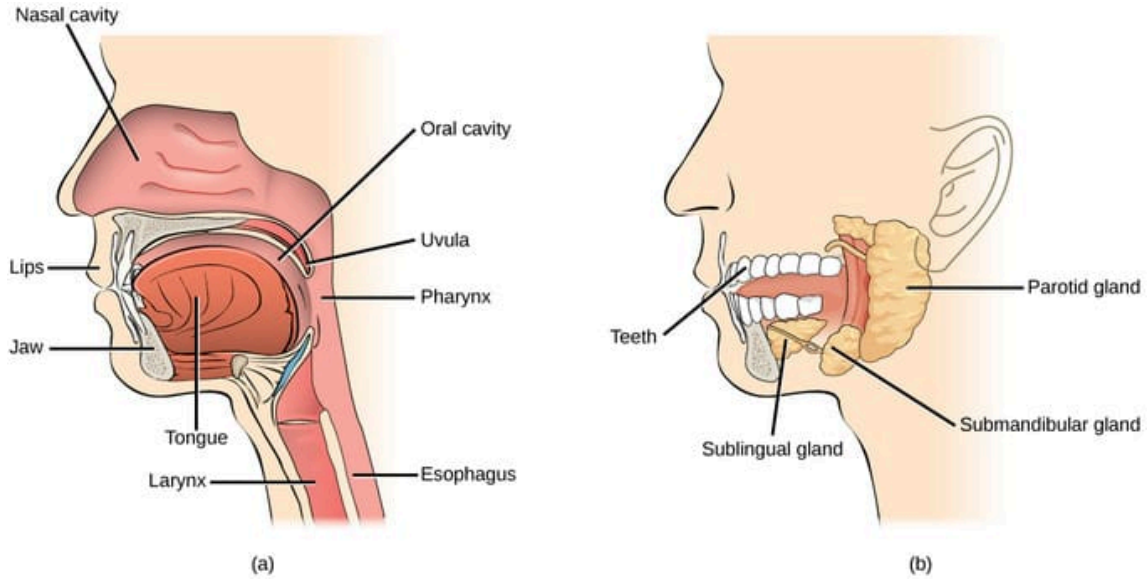


Figure 34.5.1: Digestion begins in the oral cavity: Digestion of food begins in the (a) oral cavity. Food is masticated by teeth and moistened by saliva secreted from the (b) salivary glands. Enzymes in the saliva begin to digest starches and fats. With the help of the tongue, the resulting bolus is moved into the esophagus by swallowing.

The extensive chemical process of digestion begins in the mouth. As food is chewed, saliva, produced by the salivary glands, mixes with the food. Saliva is a watery substance produced in the mouths of many animals. There are three major glands that secrete saliva: the parotid, the submandibular, and the sublingual. Saliva contains mucus that moistens food and buffers the pH of the food. Saliva also contains immunoglobulins and lysozymes, which have antibacterial action to reduce tooth decay by inhibiting growth of some bacteria. In addition, saliva contains an enzyme called salivary amylase that begins the process of converting starches in the food into a disaccharide called maltose. Another enzyme, lipase, is produced by the cells in the tongue. It is a member of a class of enzymes that can break down triglycerides. Lingual lipase begins the breakdown of fat components in the food. The chewing and wetting action provided by the teeth and saliva shape the food into a mass called the bolus for swallowing. The tongue aids in swallowing by moving the bolus from the mouth into the pharynx. The pharynx opens to two passageways: the trachea, which leads to the lungs, and the esophagus, which leads to the stomach. The tracheal opening, the glottis, is covered by a cartilaginous flap, the epiglottis. When swallowing, the epiglottis closes the glottis, allowing food to pass into the esophagus, not into the trachea, preventing food from reaching the lungs.

Esophagus

The esophagus is a tubular organ connecting the mouth to the stomach. The chewed and softened food passes through the esophagus after being swallowed. The smooth muscles of the esophagus undergo a series of wave like movements called peristalsis that push the food toward the stomach. The peristalsis wave is unidirectional: it moves food from the mouth to the stomach; reverse movement is not possible. The peristaltic movement of the esophagus is an involuntary reflex, taking place in response to the act of swallowing.

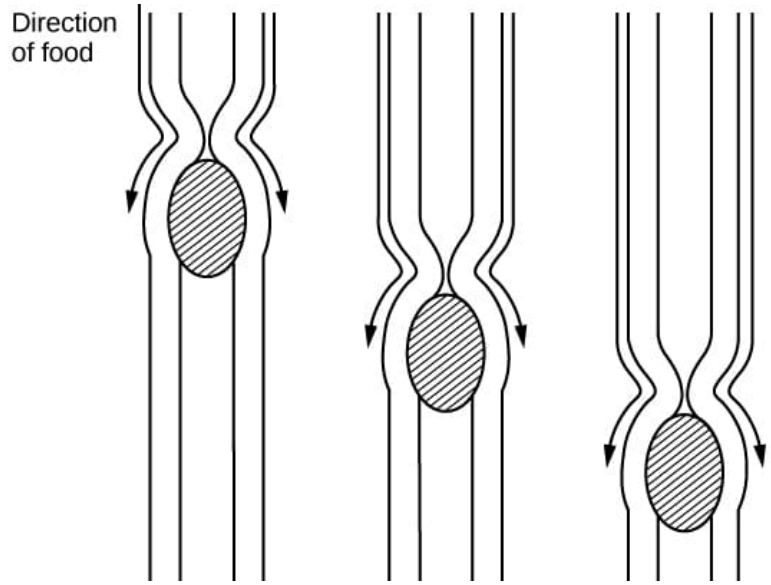


Figure 34.5.1: Esophagus: The esophagus transfers food from the mouth to the stomach through peristaltic movements.

Stomach

A large part of digestion occurs in the stomach. The stomach, a saclike organ, secretes gastric digestive juices. The pH in the stomach is between 1.5 and 2.5. This highly- acidic environment is required for the chemical breakdown of food and the extraction of nutrients. When empty, the stomach is a rather small organ; however, it can expand to up to 20 times its resting size when filled with food. This characteristic is particularly useful for animals that need to eat when food is available.

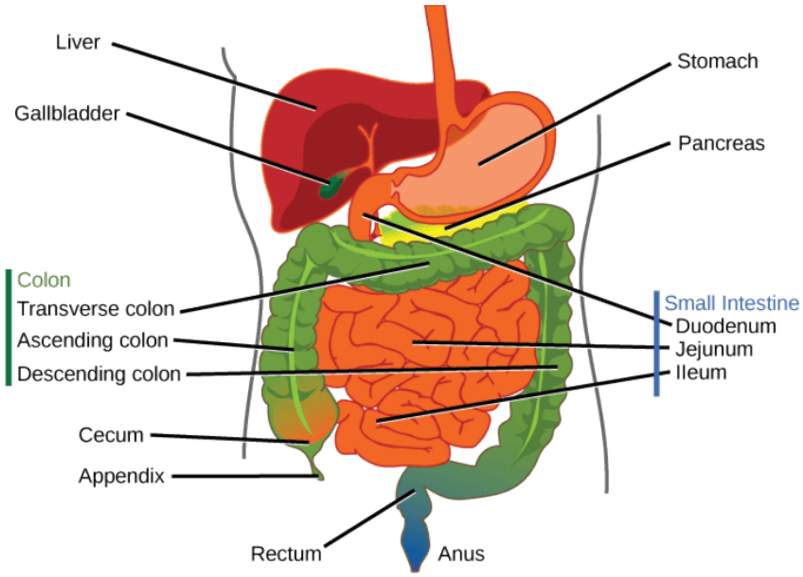


Figure 34.5.1: Stomach digestion: The human stomach has an extremely acidic environment where most of the protein gets digested.

The stomach is also the major site for protein digestion in animals other than ruminants. Protein digestion is mediated in the stomach chamber by an enzyme called pepsin, which is secreted by the chief cells in the stomach in an inactive form called pepsinogen. Another cell type, parietal cells, secrete hydrogen and chloride ions, which combine in the lumen to form hydrochloric acid, the primary acidic component of the stomach juices. Hydrochloric acid helps to convert the inactive pepsinogen to pepsin. The highly-acidic environment also kills many microorganisms in the food and, combined with the action of the enzyme pepsin, results in the hydrolysis of protein in the food. Chemical digestion is facilitated by the churning action of the stomach. Contraction and relaxation of smooth muscles mixes the stomach contents about every 20 minutes. The partially-digested food and gastric juice mixture is called chyme. Chyme passes from the stomach to the small intestine. Further protein digestion takes place in the small intestine. Gastric emptying occurs within two to six hours after a meal. Only a small amount of chyme is released into the small intestine at a time. The movement of chyme from the stomach into the small intestine is regulated by the pyloric sphincter.

Key Points

- Mechanical and chemical digestion begin in the mouth with the chewing of food and the release of saliva, which starts carbohydrate digestion.
- The epiglottis covers the trachea so the bolus (ball of chewed food) does not go down into the trachea or lungs, but rather into the esophagus.
- The tongue positions the bolus for swallowing and then peristalsis pushes the bolus down the esophagus into the stomach.
- In the stomach, acids and enzymes are secreted to break down food into its nutrient components.
- The churning of the stomach helps to mix the digestive juices with the food, turning it into a substance called chyme.

Key Terms

- **bolus**: a round mass of something, especially of chewed food in the mouth or alimentary canal
- **peristalsis**: the rhythmic, wave-like contraction and relaxation of muscles which propagates in a wave down a muscular tube
- **pepsin**: a digestive enzyme that chemically digests, or breaks down, proteins into shorter chains of amino acids
- **chyme**: the thick semifluid mass of partly digested food that is passed from the stomach to the duodenum

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34.6: Digestive Systems - Digestive System- Small and Large Intestines

Learning Objectives

- Describe the parts of the digestive system from the small intestine through the accessory organs

Parts of the Digestive System

The vertebrate digestive system is designed to facilitate the transformation of food matter into the nutrient components that sustain organisms. The lower gastrointestinal tract includes the small and large intestines, rectum, anus, and accessory organs.

Small Intestine

Chyme moves from the stomach to the small intestine: the organ where the digestion of protein, fats, and carbohydrates is completed. The small intestine is a long tube-like organ with a highly-folded surface containing finger-like projections: the villi. The apical surface of each villus has many microscopic projections: the microvilli. These structures are lined with epithelial cells on the luminal side to allow the nutrients from the digested food to be absorbed into the blood stream on the other side. The villi and microvilli, with their many folds, increase the surface area of the intestine and increase absorption efficiency of the nutrients.

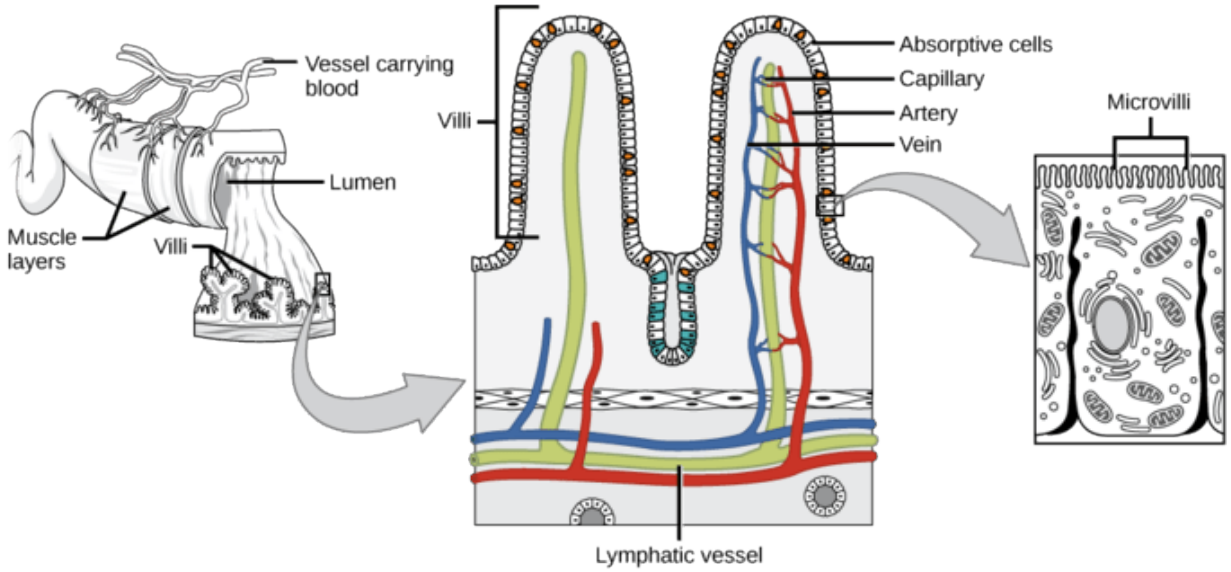


Figure 34.6.1: Villi of the small intestine: Villi are folds on the small intestine lining that increase the surface area to facilitate the absorption of nutrients.

The human small intestine, over 6 m long, is divided into three parts: the duodenum, the jejunum, and the ileum. The “C-shaped,” fixed part of the small intestine, the duodenum, is separated from the stomach by the pyloric sphincter which opens to allow chyme to move from the stomach to the duodenum where it mixes with pancreatic juices. The alkaline solution is rich in bicarbonate that neutralizes the acidity of chyme and acts as a buffer. Digestive juices from the pancreas, liver, and gallbladder, as well as from gland cells of the intestinal wall itself, enter the duodenum. Absorption of fatty acids also takes place in there.

The second part of the small intestine is called the jejunum. Here, hydrolysis of nutrients is continued while most of the carbohydrates and amino acids are absorbed through the intestinal lining. The bulk of chemical digestion and nutrient absorption occurs in the jejunum.

The ileum is the last part of the small intestine. It is here that bile salts and vitamins are absorbed into blood stream. The undigested food is sent from the ileum to the colon through the ileocecal valve via peristaltic movements of the muscle. The vermiform, "worm-like," appendix is located at the ileocecal valve. The appendix of humans secretes no enzymes and has an insignificant role in immunity.

Large Intestine

The large intestine reabsorbs water from undigested food material and processes waste material; although it is also capable of absorbing vitamins that are synthesized by the normal microflora housed herein. The human large intestine is much smaller in length than the small intestine, but larger in diameter. It has three parts: the cecum, the colon, and the rectum. The cecum joins the ileum to the colon. It is the receiving pouch for the waste matter. The colon, home to many bacteria or "intestinal flora" that aid in the digestive processes, can be divided into four regions: the ascending colon, the transverse colon, the descending colon, and the sigmoid colon. The main functions of the colon are to extract the water and mineral salts from undigested food and to store waste material. Due to their diet, carnivorous mammals have a shorter large intestine compared to herbivorous mammals.

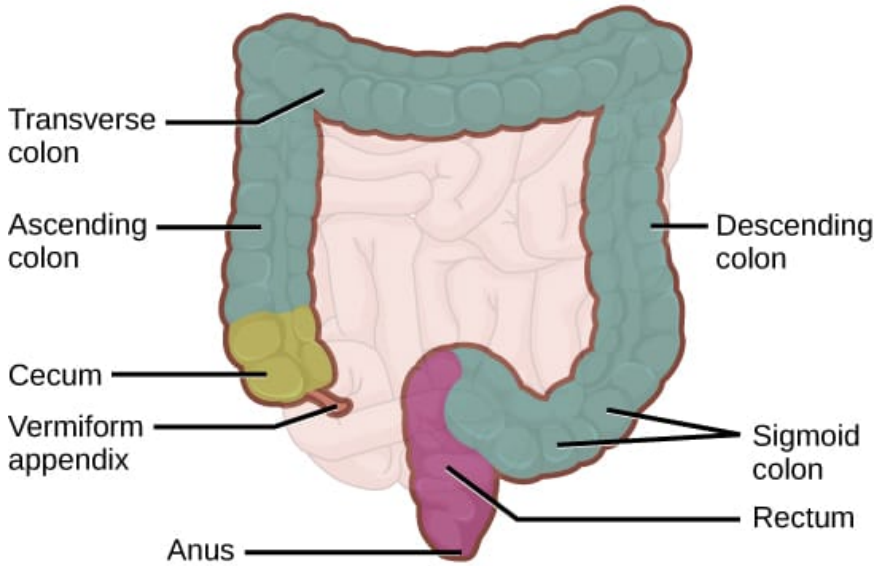


Figure 34.6.1: Large intestine: The large intestine reabsorbs water from undigested food and stores waste material until it is eliminated.

Rectum and Anus

The rectum is the terminal end of the large intestine. Its primary role is to store the feces until defecation. The feces are propelled using peristaltic movements during elimination. The anus, an opening at the far-end of the digestive tract, is the exit point for the waste material. Two sphincters between the rectum and anus control elimination: the inner sphincter is involuntary, while the outer sphincter is voluntary.

Accessory Organs

The organs discussed above are those of the digestive tract through which food passes. Accessory organs are those that add secretions (enzymes) that catabolize food into nutrients. Accessory organs include salivary glands, the liver, the pancreas, and the gallbladder. The liver, pancreas, and gallbladder are regulated by hormones in response to the food consumed.

The liver, the largest internal organ in humans, plays a very important role in digestion of fats and detoxifying blood. It produces bile: a digestive juice that is required for the breakdown of fatty components of the food in the duodenum. The liver also processes the vitamins and fats along with synthesizing many plasma proteins.

The pancreas is another important gland that secretes digestive juices. The chyme produced from the stomach is highly acidic in nature; the pancreatic juices contain high levels of bicarbonate, an alkali that neutralizes the acidic chyme. Additionally, the pancreatic juices contain a large variety of enzymes that are required for the digestion of protein and carbohydrates.

The gallbladder, a small organ, aids the liver by storing bile and concentrating bile salts. When chyme containing fatty acids enters the duodenum, the bile is secreted from the gallbladder into the duodenum.

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Key Points

- The small intestine is the primary site of enzyme activity and nutrient absorption during digestion.
- Enzymes from the liver and pancreas are added to the duodenum of the small intestine to aid with chemical breakdown; the remaining chyme is moved via peristalsis through the jejunum and the ileum into the large intestine.
- The large intestine reabsorbs water from the remaining food material and compacts the waste for elimination from the body by way of the rectum and the anus.
- The liver creates and secretes bile, which breaks down lipids; the pancreas secretes enzymes to assist with protein digestion.

Key Terms

- **villus**: a small projection from a mucous membrane, particularly those found in the intestines
- **sphincter**: a ringlike band of muscle that surrounds a bodily opening, constricting and relaxing as required for normal physiological functioning
- **duodenum**: the first part of the small intestine, starting at the lower end of the stomach and extending to the jejunum
- **colon**: part of the large intestine; the final segment of the digestive system, after (distal to) the ileum and before (proximal to) the anus

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34.7: Nutrition and Energy Production - Food Requirements and Essential Nutrients

Learning Objectives

- Describe the essential nutrients required for cellular function that cannot be synthesized by the animal body

Food Requirements

What are the fundamental requirements of the animal diet? The animal diet should be well balanced and provide nutrients required for bodily function along with the minerals and vitamins required for maintaining structure and regulation necessary for good health and reproductive capability.

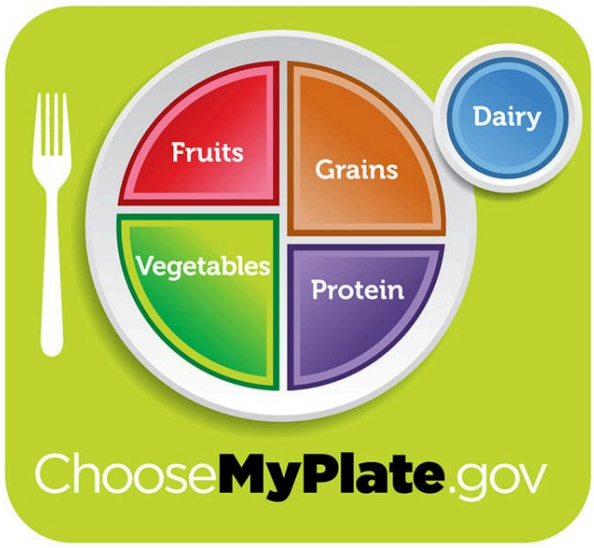


Figure 34.7.1: A balanced diet: For humans, a balanced diet includes fruits, vegetables, grains, and protein. Each of these food sources provides different nutrients the body cannot make for itself. These include vitamins, omega 3 fatty acids, and some amino acids.

Organic Precursors

The organic molecules required for building cellular material and tissues must come from food. Carbohydrates or sugars are the primary source of organic carbons in the animal body. During digestion, digestible carbohydrates are ultimately broken down into glucose and used to provide energy through metabolic pathways. The excess sugars in the body are converted into glycogen and stored in the liver and muscles for later use. Glycogen stores are used to fuel prolonged exertions, such as long-distance running, and to provide energy during food shortage. Excess digestible carbohydrates are stored by mammals in order to survive famine and aid in mobility.

Another important requirement is that of nitrogen. Protein catabolism provides a source of organic nitrogen. Amino acids are the building blocks of proteins and protein breakdown provides amino acids that are used for cellular function. The carbon and nitrogen derived from these become the building block for nucleotides, nucleic acids, proteins, cells, and tissues. Excess nitrogen must be excreted, as it is toxic. Fats add flavor to food and promote a sense of satiety or fullness. Fatty foods are also significant sources of energy because one gram of fat contains nine calories. Fats are required in the diet to aid the absorption of fat-soluble vitamins and the production of fat-soluble hormones.

Essential Nutrients

While the animal body can synthesize many of the molecules required for function from the organic precursors, there are some nutrients that need to be consumed from food. These nutrients are termed essential nutrients: they must be eaten as the body cannot produce them.

Vitamins and minerals are substances found in the food we eat. Your body needs them to be able to work properly and for growth and development. Each vitamin has its own special role to play. For example, vitamin D (added to whole milk or naturally-occurring in sardines), helps make bones strong, while vitamin A (found in carrots) helps with night vision. Vitamins fall into two categories: fat soluble and water soluble. The fat-soluble vitamins dissolve in fat and can be stored in your body, whereas the water-soluble vitamins need to dissolve in water before your body can absorb them; therefore, the body cannot store them.

Fat-soluble vitamins are found primarily in foods that contain fat and oil, such as animal fats, vegetable oils, dairy foods, liver, and fatty fish. Your body needs these vitamins every day to enable it to work properly. However, you do not need to eat foods containing these every day. If your body does not need these vitamins immediately, they will be stored in the liver and fat tissues for future use. This means that stores can build up; if you have more than you need, fat soluble vitamins can become harmful. Some fat-soluble vitamins include vitamin A, vitamin K, vitamin D, and vitamin E. Unlike the other fat-soluble vitamins, vitamin D is difficult to obtain in adequate quantities in a normal diet; therefore, supplementation may be necessary.

Water-soluble vitamins are not stored in the body; therefore, you need to have them more frequently. If you have more then you need, the body rids itself of the extra vitamins during urination. Because the body does not store these vitamins, they are generally not harmful. Water-soluble vitamins are found in foods that include fruits, vegetables, and grains. Unlike fat-soluble vitamins, they can be destroyed by heat. This means that sometimes these vitamins can often be lost during cooking. This is why it is better to steam or grill these foods rather then boil them. Some water-soluble vitamins include vitamin B6, vitamin B12, vitamin C, biotin, folic acid, niacin, and riboflavin.

The omega-3 alpha-linolenic acid and the omega-6 linoleic acid are essential fatty acids needed to synthesize some membrane phospholipids. Many people take supplements to ensure they are obtaining all the essential fatty acids they need. Sea buckthorn contains many of these fatty acids and is also high in vitamins. Sea buckthorn can be used to treat acne and promote weight loss and wound healing.



Figure 34.7.1: Sea buckthorn seed oil: Sea buckthorn seed oil contains many vital nutrients.

Minerals are inorganic essential nutrients that must also be obtained from food. Among their many functions, minerals help in cell structure and regulation; they are also considered co-factors. In addition to vitamins and minerals, certain amino acids must also be procured from food and cannot be synthesized by the body. These amino acids are the “essential” amino acids. The human body can synthesize only 11 of the 20 required amino acids. The rest must be obtained from food.

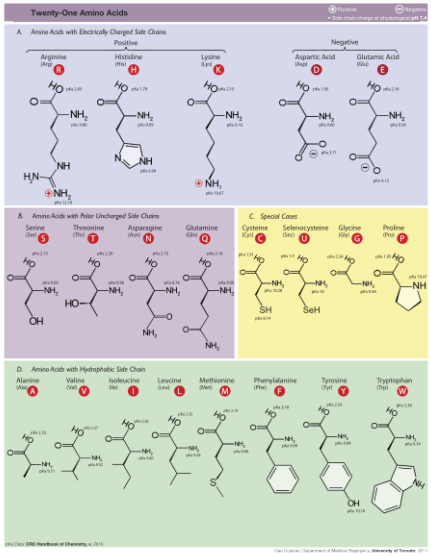


Figure 34.7.1: Amino Acids: There are 20 known amino acids. Animals can make only 11, so the others must be obtained through the diet. Meats are the best source of amino acids, although some amino acids can also be obtained from vegetables and grains.

Key Points

- The animal diet needs to be well-balanced in order to ensure that all necessary vitamins and minerals are being obtained.
- Vitamins are important for maintaining bodily health, making bones strong, and seeing in the dark.
- Water-soluble vitamins are not stored by the body and need to be consumed more regularly than fat-soluble vitamins, which build up within body tissues.
- Essential fatty acids need to be consumed through the diet and are important building blocks of cell membranes.
- Nine of the 20 amino acids cannot be synthesized by the body and need to be obtained from the diet.

Key Terms

- **nutrient**: a source of nourishment, such as food, that can be metabolized by an organism to give energy and build tissue
- **catabolism**: destructive metabolism, usually including the release of energy and breakdown of materials
- **vitamin**: any of a specific group of organic compounds essential in small quantities for healthy human growth, metabolism, development, and body function

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34.8: Nutrition and Energy Production - Food Energy and ATP

Learning Objectives

- Summarize the ways in which animals obtain, store, and use food energy

Food Energy and ATP

Animals need food to obtain energy and maintain homeostasis. Homeostasis is the ability of a system to maintain a stable internal environment even in the face of external changes to the environment. For example, the normal body temperature of humans is 37°C (98.6°F). Humans maintain this temperature even when the external temperature is hot or cold. The energy it takes to maintain this body temperature is obtained from food.

The primary source of energy for animals is carbohydrates, primarily glucose: the body's fuel. The digestible carbohydrates in an animal's diet are converted to glucose molecules and into energy through a series of catabolic chemical reactions.

Adenosine triphosphate, or ATP, is the primary energy currency in cells. ATP stores energy in phosphate ester bonds, releasing energy when the phosphodiester bonds are broken: ATP is converted to ADP and a phosphate group. ATP is produced by the oxidative reactions in the cytoplasm and mitochondrion of the cell, where carbohydrates, proteins, and fats undergo a series of metabolic reactions collectively called cellular respiration.

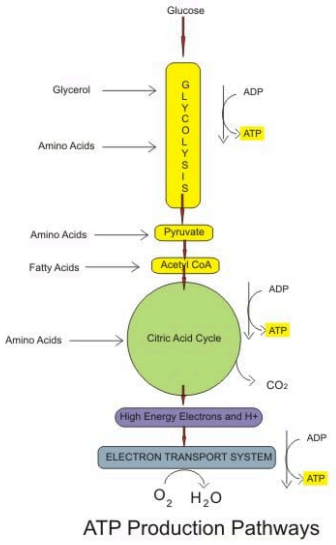


Figure 34.8.1: ATP production pathways: ATP is the energy molecule of the cell. It is produced through various pathways during the cellular respiration process, with each making different amounts of energy.

ATP is required for all cellular functions. It is used to build the organic molecules that are required for cells and tissues. It also provides energy for muscle contraction and for the transmission of electrical signals in the nervous system. When the amount of ATP available is in excess of the body's requirements, the liver uses the excess ATP and excess glucose to produce molecules called glycogen (a polymeric form of glucose) that is stored in the liver and skeletal muscle cells. When blood sugar drops, the liver releases glucose from stores of glycogen. Skeletal muscle converts glycogen to glucose during intense exercise. The process of converting glucose and excess ATP to glycogen and the storage of excess energy is an evolutionarily-important step in helping animals deal with mobility, food shortages, and famine.

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Key Points

- Animals obtain energy from the food they consume, using that energy to maintain body temperature and perform other metabolic functions.
- Glucose, found in the food animals eat, is broken down during the process of cellular respiration into an energy source called ATP.
- When excess ATP and glucose are present, the liver converts them into a molecule called glycogen, which is stored for later use.

Key Terms

- **glucose**: a simple monosaccharide (sugar) with a molecular formula of C6H12O6; it is a principal source of energy for cellular metabolism
- **adenosine triphosphate**: a multifunctional nucleoside triphosphate used in cells as a coenzyme, often called the “molecular unit of energy currency” in intracellular energy transfer
- **phosphodiester**: any of many biologically active compounds in which two alcohols form ester bonds with phosphate

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34.9: Digestive System Processes - Ingestion

Learning Objectives

- Describe the process of ingestion and its role in the digestive system

Obtaining nutrition and energy from food is a multi-step process. For animals, the first step is ingestion, the act of taking in food. The large molecules found in intact food cannot pass through the cell membranes. Food needs to be broken into smaller particles so that animals can harness the nutrients and organic molecules. The first step in this process is ingestion: taking in food through the mouth. Once in the mouth, the teeth, saliva, and tongue play important roles in mastication (preparing the food into bolus). Mastication, or chewing, is an extremely important part of the digestive process, especially for fruits and vegetables, as these have indigestible cellulose coats which must be physically broken down. Also, digestive enzymes only work on the surfaces of food particles, so the smaller the particle, the more efficient the digestive process. While the food is being mechanically broken down, the enzymes in saliva begin to chemically process the food as well. The combined action of these processes modifies the food from large particles to a soft mass that can be swallowed and can travel the length of the esophagus.



Figure 34.9.1: Mastication: The first step in obtaining nutrition is ingestion. Ingested food must be broken down into small pieces by mastication, or chewing.

Besides nutritional items, other substances may be ingested, including medications (where ingestion is termed oral administration) and substances considered inedible, such as insect shells. Ingestion is also a common route taken by pathogenic organisms and poisons entering the body.

Some pathogens transmitted via ingestion include viruses, bacteria, and parasites. Most commonly, this takes place via the fecal-oral route. An intermediate step is often involved, such as drinking water contaminated by feces or food prepared by workers who fail to practice adequate hand-washing. This is more common in regions where untreated sewage is prevalent. Diseases transmitted via the fecal-oral route include hepatitis A, polio, and cholera.

Key Points

- Food is ingested through the mouth and broken down through mastication (chewing).
- Food must be chewed in order to be swallowed and broken down by digestive enzymes.
- While food is being chewed, saliva chemically processes the food to aid in swallowing.
- Medications and harmful or inedible substances may be ingested as well.
- Pathogens, such as viruses, bacteria, and parasites, may be transmitted via ingestion, causing diseases like hepatitis A, polio,

and cholera.

Key Terms

- **ingestion**: consuming something orally, whether it be food, drink, medicine, or other substance; the first step of digestion
- **bolus**: a round mass of something, especially of chewed food in the mouth or alimentary canal
- **mastication**: the process of chewing

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34.10: Digestive System Processes - Digestion and Absorption

Learning Objectives

- Explain the processes of digestion and absorption

Digestion and Absorption

Digestion is the mechanical and chemical break down of food into small organic fragments. Mechanical digestion refers to the physical breakdown of large pieces of food into smaller pieces which can subsequently be accessed by digestive enzymes. In chemical digestion, enzymes break down food into the small molecules the body can use.

It is important to break down macromolecules into smaller fragments that are of suitable size for absorption across cell membranes. Large, complex molecules of proteins, polysaccharides, and lipids must be reduced to simpler particles before they can be absorbed by the digestive epithelial cells. Different organs play specific roles in the digestive process. The animal diet needs carbohydrates, protein, and fat, as well as vitamins and inorganic components for nutritional balance.

Digestive enzymes are enzymes that break down polymeric macromolecules into their smaller building blocks, in order to facilitate their absorption by the body. Digestive enzymes are found in the digestive tracts of animals. Digestive enzymes are diverse and are found in the saliva secreted by the salivary glands, in the stomach secreted by cells lining the stomach, in the pancreatic juice secreted by pancreatic exocrine cells, and in the intestinal (small and large) secretions, or as part of the lining of the gastrointestinal tract.

Intestinal microflora benefit the host by gleaning the energy from the fermentation of undigested carbohydrates and the subsequent absorption of short-chain fatty acids. Intestinal bacteria also play a role in synthesizing vitamin B and vitamin K as well as metabolizing bile acids, sterols and xenobiotics.

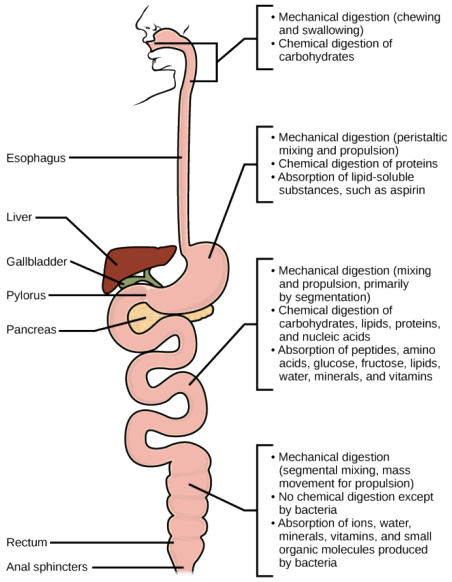


Figure 34.10.1: Mechanical and chemical digestion: Mechanical and chemical digestion of food takes place in many steps, beginning in the mouth and ending in the rectum.

Carbohydrates

The digestion of carbohydrates begins in the mouth. The salivary enzyme amylase begins the breakdown of food starches into maltose, a disaccharide. As the food travels through the esophagus to the stomach, no significant digestion of carbohydrates takes place. The acidic environment in the stomach stops amylase from continuing to break down the molecules.

The next step of carbohydrate digestion takes place in the duodenum. The chyme from the stomach enters the duodenum and mixes with the digestive secretions from the pancreas, liver, and gallbladder. Pancreatic juices also contain amylase, which continues the breakdown of starch and glycogen into maltose and other disaccharides. These disaccharides are then broken down into monosaccharides by enzymes called maltases, sucrases, and lactases. The monosaccharides produced are absorbed so that they can be used in metabolic pathways to harness energy. They are absorbed across the intestinal epithelium into the bloodstream to be transported to the different cells in the body.

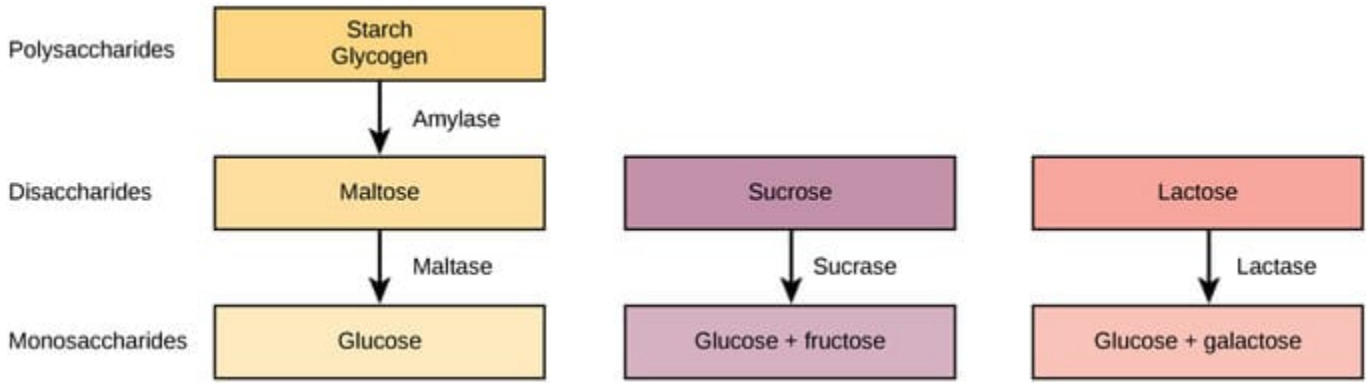


Figure 34.10.1: Digestion of carbohydrates: Digestion of carbohydrates is performed by several enzymes. Starch and glycogen are broken down into glucose by amylase and maltase. Sucrose (table sugar) and lactose (milk sugar) are broken down by sucrase and lactase, respectively.

Protein

A large part of protein digestion takes place in the stomach. The enzyme pepsin plays an important role in the digestion of proteins by breaking them down into peptides, short chains of four to nine amino acids. In the duodenum, other enzymes – trypsin, elastase, and chymotrypsin – act on the peptides, reducing them to smaller peptides. These enzymes are produced by the pancreas and released into the duodenum where they also act on the chyme. Further breakdown of peptides to single amino acids is aided by enzymes called peptidases (those that break down peptides). The amino acids are absorbed into the bloodstream through the small intestine.

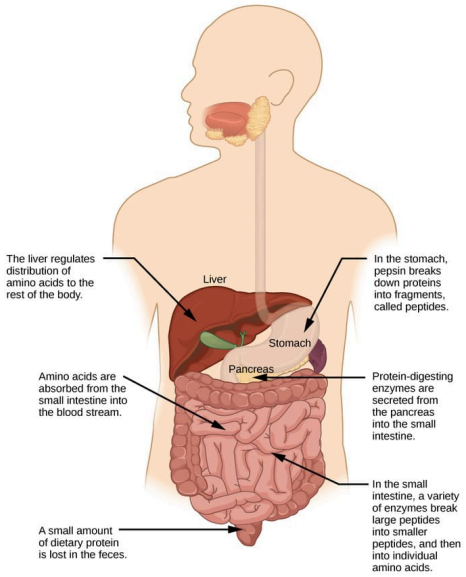


Figure 34.10.1: Protein digestion and absorption: Protein digestion is a multistep process that begins in the stomach and continues through the intestines. Proteins are absorbed into the blood stream by the small intestine.

Lipids

Lipid (fat) digestion begins in the stomach with the aid of lingual lipase and gastric lipase. However, the bulk of lipid digestion occurs in the small intestine due to pancreatic lipase. When chyme enters the duodenum, the hormonal responses trigger the release of bile, which is produced in the liver and stored in the gallbladder. Bile aids in the digestion of lipids, primarily triglycerides, through emulsification. Emulsification is a process in which large lipid globules are broken down into several small lipid globules. These small globules are widely distributed in the chyme rather than forming large aggregates. Lipids are hydrophobic substances. Bile contains bile salts, which have hydrophobic and hydrophilic sides. The bile salts' hydrophilic side can interface with water, while the hydrophobic side interfaces with lipids, thereby emulsifying large lipid globules into small lipid globules.

Emulsification is important for the digestion of lipids because lipases can only efficiently act on the lipids when they are broken into small aggregates. Lipases break down the lipids into fatty acids and glycerides. These molecules can pass through the plasma membrane of the cell, entering the epithelial cells of the intestinal lining. The bile salts surround long-chain fatty acids and monoglycerides, forming tiny spheres called micelles. The micelles move into the brush border of the small intestine absorptive cells where the long-chain fatty acids and monoglycerides diffuse out of the micelles into the absorptive cells, leaving the micelles behind in the chyme. The long-chain fatty acids and monoglycerides recombine in the absorptive cells to form triglycerides, which aggregate into globules, and are then coated with proteins. These large spheres are called chylomicrons. Chylomicrons contain triglycerides, cholesterol, and other lipids; they have proteins on their surface. The surface is also composed of the hydrophilic phosphate "heads" of phospholipids. Together, they enable the chylomicron to move in an aqueous environment without exposing the lipids to water. Chylomicrons leave the absorptive cells via exocytosis, entering the lymphatic vessels. From there, they enter the blood in the subclavian vein.

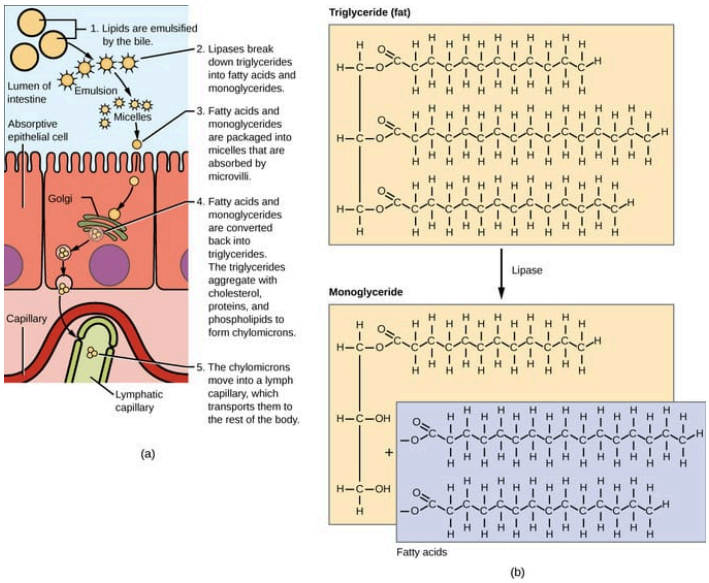


Figure 34.10.1: Lipid digestion and absorption: Lipids are digested and absorbed in the small intestine.

Vitamins

Vitamins can be either water-soluble or lipid-soluble. Fat-soluble vitamins are absorbed in the same manner as lipids. It is important to consume some amount of dietary lipid to aid the absorption of lipid-soluble vitamins. Water-soluble vitamins can be directly absorbed into the bloodstream from the intestine.

Key Points

- In the mouth, carbohydrates are broken down by amylase into maltose (a disaccharide) and then move down the esophagus, which produces mucus for lubrication, but no digestive enzymes.
- In the duodenum, disaccharides are broken down into monosaccharides by enzymes called maltases, sucrases, and lactases; the monosaccharides produced are then absorbed into the bloodstream and transported to cells to be used in metabolic pathways to harness energy.
- In the stomach, proteins are broken down into peptides, which are then broken down into single amino acids that are absorbed in the bloodstream though the small intestine.
- Lipids are digested mainly in the small intestine by bile salts through the process of emulsification, which allows lipases to divide lipids into fatty acids and monoglycerides.
- Monoglycerides and fatty acids enter absorptive cells in the small intestine through micelles; they leave micelles and recombine into chylomicrons, which then enter the bloodstream.
- Fat-soluble vitamins are absorbed in the same manner as lipids; water-soluble vitamins can be directly absorbed into the bloodstream from the intestine.

Key Terms

- **chemical digestion**: The process of enzymes breaking down food into small molecules the body can use.
- **lipase**: Enzymes in the pancreatic juices that break down lipids.
- **chylomicron**: A microscopic globule of triglycerids and other lipids coated with proteins, found in blood and lymphatic vessels, that is associated with the digestion of fats.
- **amylase**: Any of a class of digestive enzymes present in saliva that break down complex carbohydrates, such as starch, into simpler sugars like glucose.
- **mechanical digestion**: The physical breakdown of large pieces of food into smaller pieces which can subsequently be accessed by enzymes.

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34.11: Digestive System Processes - Elimination

Learning Objectives

- Describe the process of elimination and problems that can occur

The final step in digestion is the elimination of undigested food content and waste products. After food passes through the small intestine, the undigested food material enters the colon, where most of the water is reabsorbed. Recall that the colon is also home to the microflora called “intestinal flora” that aid in the digestion process. The semi-solid waste is moved through the colon by peristaltic movements of the muscle and is stored in the rectum. As the rectum expands in response to storage of fecal matter, it triggers the neural signals required to set up the urge to eliminate. The solid waste is eliminated through the anus using peristaltic movements of the rectum.

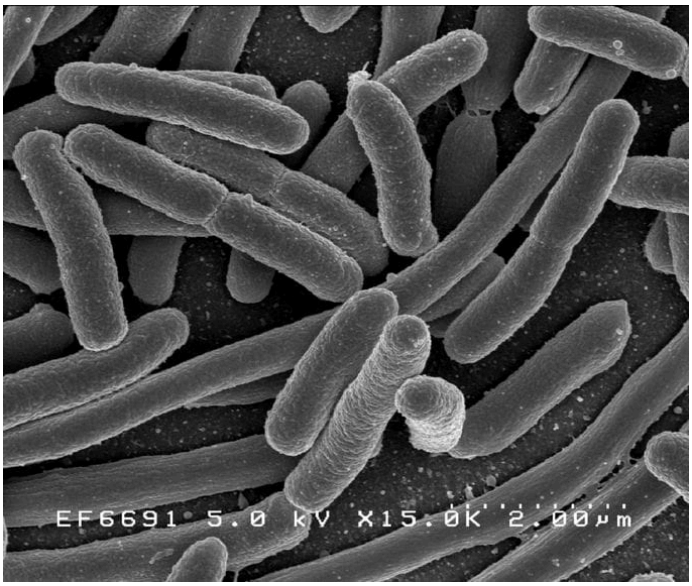


Figure 34.11.1: Intestinal flora: *Escherichia coli* is one of the many species of bacteria present in the human gut.

Common Problems with Elimination

Diarrhea and constipation are some of the most common health concerns that affect digestion. Constipation is a condition where the feces are hardened because of excess water removal in the colon. In contrast, if not enough water is removed from the feces, it results in diarrhea. Many bacteria, including the ones that cause cholera, affect the proteins involved in water reabsorption in the colon and result in excessive diarrhea.

Emesis

Emesis, or vomiting, is elimination of food by forceful expulsion through the mouth. It is often in response to an irritant that affects the digestive tract, including, but not limited to, viruses, bacteria, emotions, trauma, and food poisoning. This forceful expulsion of the food is due to the strong contractions produced by the stomach muscles. The process of emesis is regulated by the medulla.

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Key Points

- Water is reabsorbed in the colon after undigested food enters it from the small intestine.
- Waste is moved through the colon by peristaltic movements of the muscle and is stored in the rectum.
- The rectum expands in response to the storage of fecal matter; neural signals are triggered, and the waste is eliminated from the anus by peristaltic movements of the rectum.

- Constipation is a condition where the feces are hardened because of excess water removal in the colon.
- Diarrhea results when large amounts of water are not removed from the feces.
- Emesis, or vomiting, is elimination of food by forceful expulsion through the mouth caused by the strong contractions produced by the stomach muscles.

Key Terms

- **emesis**: the act or process of vomiting
- **intestinal flora**: the bacterial colonies that normally live in the digestive tract of animals
- **constipation**: condition where the feces are hardened because of excess water removal in the colon

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34.12: Digestive System Regulation - Neural Responses to Food

Learning Objectives

- Summarize the neural responses to food

In reaction to the smell, sight, or thought of food, the first hormonal response is that of salivation. The salivary glands secrete more saliva in response to the stimulus presented by food in preparation for digestion. Simultaneously, the stomach begins to produce hydrochloric acid to digest the food. Recall that the peristaltic movements of the esophagus and other organs of the digestive tract are under the control of the brain. The brain prepares these muscles for movement as well. When the stomach is full, the part of the brain that detects satiety signals fullness. There are three overlapping phases of gastric control: the cephalic phase, the gastric phase, and the intestinal phase. Each requires many enzymes and is under neural control as well.



Figure 34.12.1: Salivation: Seeing a plate of food triggers the secretion of saliva in the mouth and the production of hydrochloric acid in the stomach.

Digestive Phases

The response to food begins even before food enters the mouth. The first phase of ingestion, called the cephalic phase, is controlled by the neural response to the stimulus provided by food. All aspects, such as sight, sense, and smell, trigger the neural responses resulting in salivation and secretion of gastric juices. The gastric and salivary secretion in the cephalic phase can also take place at the thought of food. Right now, if you think about a piece of chocolate or a crispy potato chip, the increase in salivation is a cephalic phase response to the thought. The central nervous system prepares the stomach to receive food.

The gastric phase begins once the food arrives in the stomach. It builds on the stimulation provided during the cephalic phase. Gastric acids and enzymes process the ingested materials. The gastric phase is stimulated by (1) distension of the stomach, (2) a decrease in the pH of the gastric contents, and (3) the presence of undigested material. This phase consists of local, hormonal, and neural responses. These responses stimulate secretions and powerful contractions.

The intestinal phase begins when chyme enters the small intestine, triggering digestive secretions. This phase controls the rate of gastric emptying. In addition to gastric emptying, when chyme enters the small intestine, it triggers other hormonal and neural events that coordinate the activities of the intestinal tract, pancreas, liver, and gallbladder.

Key Points

- The cephalic phase is controlled by sight, sense, and smell, which trigger neural responses, including salivation and hydrochloric acid production, before food has even reached the mouth.
- Once food reaches the stomach, gastric acids and enzymes process the ingested materials in the gastric phase, which involves local, hormonal, and neural responses.
- The intestinal phase controls the rate of gastric emptying and the release of hormones needed to digest chyme in the small intestine.

Key Terms

- **neural**: of, or relating to the nerves, neurons or the nervous system
- **salivary gland**: any of several exocrine glands that produce saliva to break down carbohydrates in food enzymatically
- **peristaltic**: of, or pertaining to the rhythmic, wave-like contraction of the digestive tract that forces food through it

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34.13: Digestive System Regulation - Hormonal Responses to Food

Learning Objectives

- Describe hormonal responses to food

The endocrine system controls the response of the various glands in the body and the release of hormones at the appropriate times. The endocrine system's effects are slow to initiate, but prolonged in their response, lasting from a few hours up to weeks. The system is made of a series of glands that produce chemicals called hormones. These hormones are chemical mediators released from endocrine tissue into the bloodstream where they travel to target tissue and generate a response.

One of the important factors under hormonal control is the stomach acid environment. During the gastric phase, the hormone gastrin is secreted by G cells in the stomach in response to the presence of proteins. Gastrin stimulates the release of stomach acid, or hydrochloric acid (HCl), which aids in the digestion of the majority of proteins. However, when the stomach is emptied, the acidic environment need not be maintained and a hormone called somatostatin stops the release of hydrochloric acid. This is controlled by a negative feedback mechanism.

In the duodenum, digestive secretions from the liver, pancreas, and gallbladder play an important role in digesting chyme during the intestinal phase. In order to neutralize the acidic chyme, a hormone called secretin stimulates the pancreas to produce alkaline bicarbonate solution and deliver it to the duodenum. Secretin acts in tandem with another hormone called cholecystokinin (CCK). Not only does CCK stimulate the pancreas to produce the requisite pancreatic juices, it also stimulates the gallbladder to release bile into the duodenum.

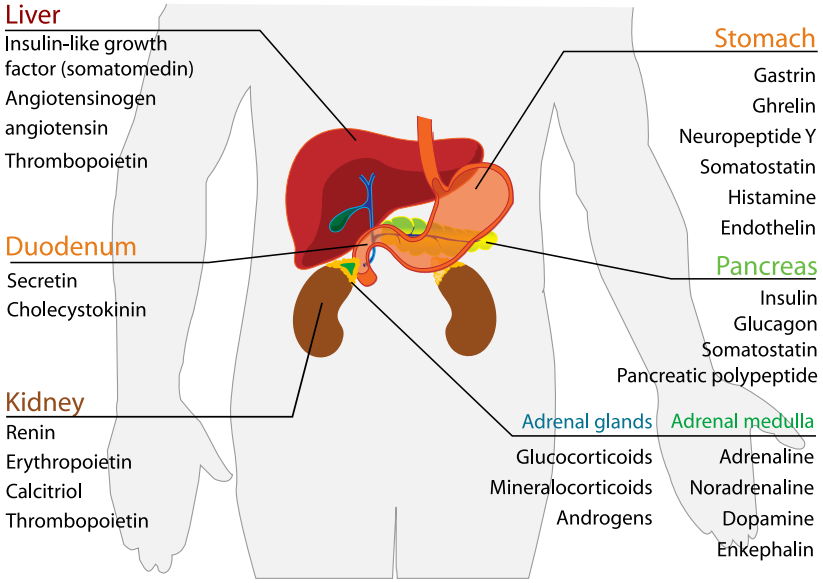


Figure 34.13.1: Digestive endocrine system: Hormones, such as secretin and cholecystokinin, play important roles in digestive processes. These hormones are released from endocrine tissue to generate specific controls in the digestion of chyme. As seen in the image, hormones are vital players in several bodily functions and processes.

Another level of hormonal control occurs in response to the composition of food. Foods high in lipids (fatty foods) take a long time to digest. A hormone called gastric inhibitory peptide is secreted by the small intestine to slow down the peristaltic movements of the intestine to allow fatty foods more time to be digested and absorbed.

Understanding the hormonal control of the digestive system is an important area of ongoing research. Scientists are exploring the role of each hormone in the digestive process and developing ways to target these hormones. Advances could lead to knowledge that may help to battle the obesity epidemic.

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Key Points

- The presence and absence of hormones that are released into the bloodstream generate specific digestive responses; they either stimulate or discontinue digestive processes.
- In hormone control, a negative feedback mechanism takes place when the stomach is empty and its acidic environment does not need to be maintained; as a result, a hormone is released to stop the release of hydrochloric acid, which was previously activated to aid digestion.
- In some cases, hormones work in tandem and sequentially to achieve important digestive functions, such as in the breakdown of acidic chyme, where hormones act in releasing the appropriate secretions in the appropriate stages of digestion.
- When digesting certain types of foods, such as ones high in fat, hormones can control the speed of food digestion and, therefore, absorption.

Key Terms

- **endocrine system**: a control system of ductless glands that secrete hormones which circulate via the bloodstream to affect cells within specific organs
- **chyme**: the thick semifluid mass of partly digested food that is passed from the stomach to the duodenum
- **secretin**: a peptide hormone, secreted by the duodenum, that serves to regulate its acidity
- **cholecystokinin**: any of several peptide hormones that stimulate the digestion of fat and protein
- **somatostatin**: a polypeptide hormone, secreted by the pancreas, that inhibits the production of certain other hormones
- **gastrin**: a hormone that stimulates the production of gastric acid in the stomach

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35: THE NERVOUS SYSTEM

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35.1: Neurons and Glial Cells - Introduction

Learning Objectives

- Recall the differences in structure and function between the central and peripheral nervous systems

The Nervous System: Introduction

The nervous system coordinates the body's voluntary and involuntary actions and transmits signals between different parts of the body. Nervous tissue first arose in wormlike organisms approximately 550 to 600 million years ago. In most types of vertebrate animals, it consists of two main parts: the central nervous system (CNS) and the peripheral nervous system (PNS). The CNS contains the brain and spinal cord. The PNS consists mainly of nerves, which are long fibers that connect the CNS to every other part of the body. The PNS includes motor neurons (mediating voluntary movement), the autonomic nervous system (comprising the sympathetic nervous system and the parasympathetic nervous system, which regulate involuntary functions), and the enteric nervous system (a semi-independent part of the nervous system whose function is to control the gastrointestinal system).

The nervous system performs several functions simultaneously. For example, as you are reading, the visual system is processing what is seen on the page; the motor system controls the turn of the pages (or click of the mouse); the prefrontal cortex maintains attention. Even fundamental functions, like breathing and regulation of body temperature, are controlled by the nervous system. A nervous system is an organism's control center: it processes sensory information from outside (and inside) the body and controls all behaviors, from eating to sleeping to finding a mate.



Figure 35.1.1: Nervous system at work: An athlete's nervous system is hard at work during the planning and execution of a movement as precise as a high jump. Parts of the nervous system are involved in determining how hard to push off and when to turn, as well as controlling the muscles throughout the body that make this complicated movement possible without knocking the bar down; all in just a few seconds.

Nervous systems throughout the animal kingdom vary in structure and complexity. Some organisms, such as sea sponges, lack a true nervous system. Others, such as jellyfish, lack a true brain. Instead, they have a system of separate-but-connected nerve cells (neurons) called a "nerve net." Echinoderms, such as sea stars, have nerve cells that are bundled into fibers called nerves. Flatworms of the phylum Platyhelminthes have both a central nervous system, made up of a small "brain" and two nerve cords, and a peripheral nervous system containing a system of nerves that extend throughout the body. The insect nervous system is more complex, but also fairly decentralized. It contains a brain, ventral nerve cord, and ganglia (clusters of connected neurons). These ganglia can control movements and behaviors without input from the brain. Octopuses may have the most complicated of invertebrate nervous systems. They have neurons that are organized in specialized lobes and eyes that are structurally similar to vertebrate species.

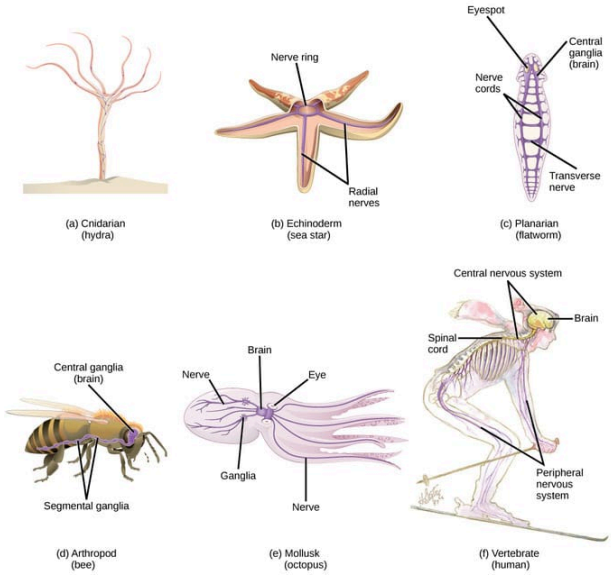


Figure 35.1.1: Various nervous systems: (a) In cnidarians, nerve cells form a decentralized nerve net. (b) In echinoderms, nerve cells are bundled into fibers called nerves. (c) In animals exhibiting bilateral symmetry, such as planarians, neurons cluster into an anterior brain that processes information. (d) In addition to a brain, arthropods have clusters of nerve cell bodies, called peripheral ganglia, located along the ventral nerve cord. Mollusks, such as squid and (e) octopuses, which must hunt to survive, have complex brains containing millions of neurons. In (f) vertebrates, the brain and spinal cord comprise the central nervous system, while neurons extending into the rest of the body comprise the peripheral nervous system.

Compared to invertebrates, vertebrate nervous systems are more complex, centralized, and specialized. While there is great diversity among different vertebrate nervous systems, they all share a basic structure: a CNS and a PNS. One interesting difference between the nervous systems of invertebrates and vertebrates is that the nerve cords of many invertebrates are located ventrally (near the abdomen), whereas the vertebrate spinal cords are located dorsally (near the back). There is debate among evolutionary biologists as to whether these different nervous system plans evolved separately or whether the invertebrate body plan arrangement somehow “flipped” during the evolution of vertebrates.

The nervous system is made up of neurons, specialized cells that can receive and transmit chemical or electrical signals, and glia, cells that provide support functions for the neurons by playing an information processing role that is complementary to neurons. A neuron can be compared to an electrical wire: it transmits a signal from one place to another. Glia can be compared to the workers at the electric company who make sure wires go to the right places, maintain the wires, and take down wires that are broken. Although glial cells support neurons, recent evidence suggests they also assume some of the signaling functions of neurons.

Key Points

- The central nervous system contains the brain and spinal cord; the peripheral nervous system consists of nerves, motor neurons, the autonomic nervous system, and the enteric nervous system.
- The nervous system coordinates the voluntary and involuntary actions of the body by transmitting signals from the brain to the other body parts and listening for feedback.
- Nervous systems vary across different animals; some invertebrates lack a true nervous system or true brain, while other invertebrates have a brain and a system of nerves.
- Unlike vertebrates, not all invertebrates have both a CNS and PNS; their nerve cords are located ventrally rather than dorsally.
- The functions of the nervous system are performed by two types of cells: neurons, which transmit signals between them and from one part of the body to another, and glia, which regulate homeostasis, providing support and protection to the function of neurons.

Key Terms

- **neuron**: cell of the nervous system that conducts nerve impulses; consisting of an axon and several dendrites
- **nervous system**: an organ system that coordinates the body’s voluntary and involuntary actions and transmits signals

between different parts of the body
- **glial cell**: cell in the nervous system that supports and protects neurons

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35.2: Neurons and Glial Cells - Neurons

Learning Objectives

- Describe the functions of the structural components of a neuron

The nervous system of the common laboratory fly, *Drosophila melanogaster*, contains around 100,000 neurons, the same number as a lobster. This number compares to 75 million in the mouse and 300 million in the octopus. A human brain contains around 86 billion neurons. Despite these very different numbers, the nervous systems of these animals control many of the same behaviors, from basic reflexes to more complicated behaviors such as finding food and courting mates. The ability of neurons to communicate with each other, as well as with other types of cells, underlies all of these behaviors.

Most neurons share the same cellular components. But neurons are also highly specialized: different types of neurons have different sizes and shapes that relate to their functional roles.

Parts of a Neuron

Each neuron has a cell body (or soma) that contains a nucleus, smooth and rough endoplasmic reticulum, Golgi apparatus, mitochondria, and other cellular components. Neurons also contain unique structures, relative to most cells, which are required for receiving and sending the electrical signals that make neuronal communication possible. Dendrites are tree-like structures that extend away from the cell body to receive messages from other neurons at specialized junctions called synapses. While some neurons have no dendrites, other types of neurons have multiple dendrites. Dendrites can have small protrusions called dendritic spines, which further increase surface area for possible synaptic connections.

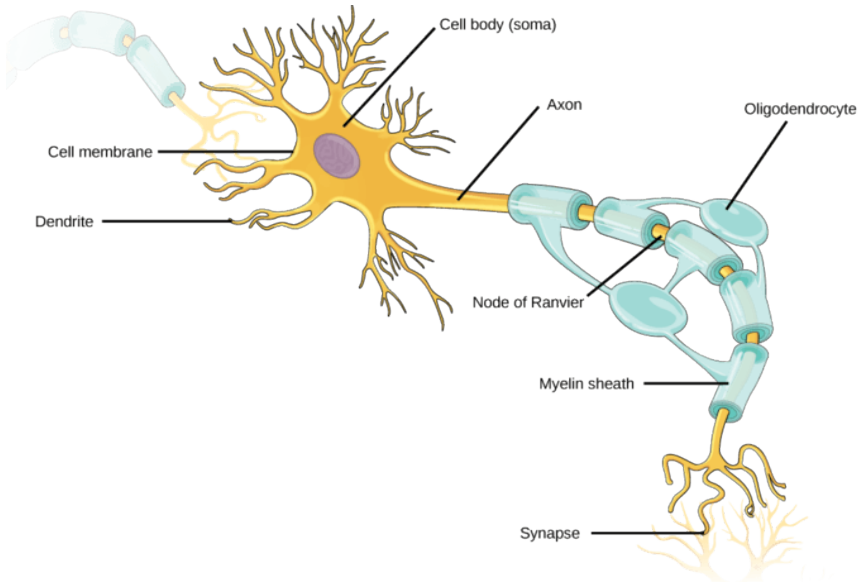


Figure 35.2.1: Cellular structure of neurons: Neurons contain organelles common to many other cells, such as a nucleus and mitochondria. They also have more specialized structures, including dendrites and axons.

Once a signal is received by the dendrite, it then travels passively to the cell body. The cell body contains a specialized structure, the axon hillock, that integrates signals from multiple synapses and serves as a junction between the cell body and an axon: a tube-like structure that propagates the integrated signal to specialized endings called axon terminals. These terminals, in turn, synapse on other neurons, muscles, or target organs. Chemicals released at axon terminals allow signals to be communicated to these other cells. Neurons usually have one or two axons, but some neurons, like amacrine cells in the retina, do not contain any axons. Some axons are covered with myelin, which acts as an insulator to minimize dissipation of the electrical signal as it travels down the axon, greatly increasing the speed on conduction. This insulation is important as the axon from a human motor neuron can be as long as a meter: from the base of the spine to the toes. The myelin sheath is not actually part of the neuron. Myelin

is produced by glial cells. Along these types of axons, there are periodic gaps in the myelin sheath. These gaps, called “nodes of Ranvier,” are sites where the signal is “recharged” as it travels along the axon.

It is important to note that a single neuron does not act alone. Neuronal communication depends on the connections that neurons make with one another (as well as with other cells, such as muscle cells). Dendrites from a single neuron may receive synaptic contact from many other neurons. For example, dendrites from a Purkinje cell in the cerebellum are thought to receive contact from as many as 200,000 other neurons.

Types of Neurons

There are different types of neurons; the functional role of a given neuron is intimately dependent on its structure. There is an amazing diversity of neuron shapes and sizes found in different parts of the nervous system (and across species).

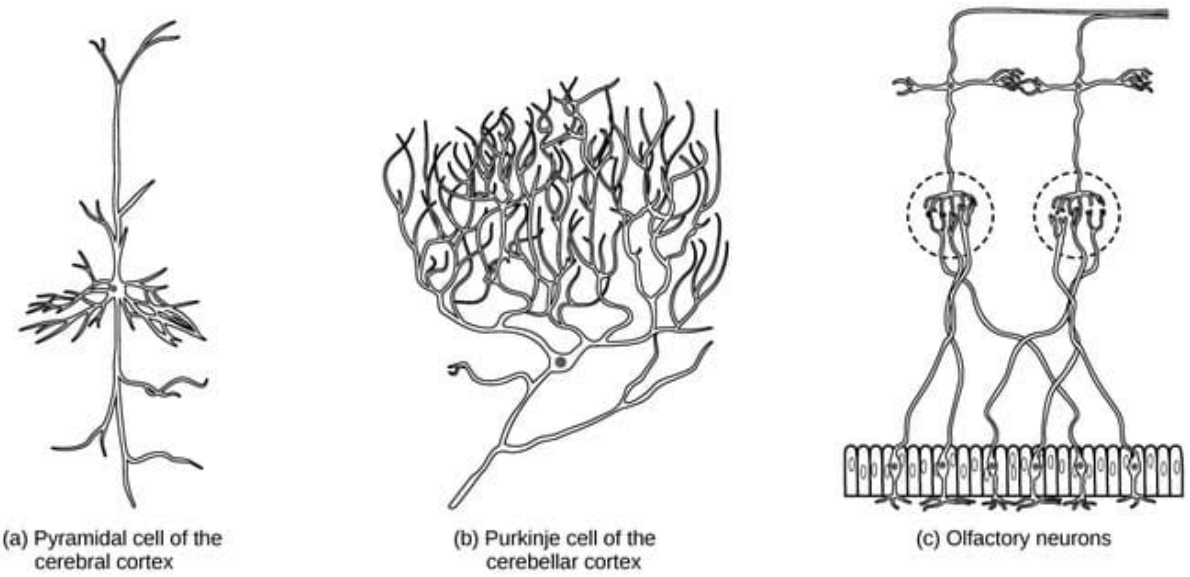


Figure 35.2.1: Neuron diversity: There is great diversity in the size and shape of neurons throughout the nervous system. Examples include (a) a pyramidal cell from the cerebral cortex, (b) a Purkinje cell from the cerebellar cortex, and (c) olfactory cells from the olfactory epithelium and olfactory bulb.

While there are many defined neuron cell subtypes, neurons are broadly divided into four basic types: unipolar, bipolar, multipolar, and pseudounipolar. Unipolar neurons have only one structure that extends away from the soma. These neurons are not found in vertebrates, but are found in insects where they stimulate muscles or glands. A bipolar neuron has one axon and one dendrite extending from the soma. An example of a bipolar neuron is a retinal bipolar cell, which receives signals from photoreceptor cells that are sensitive to light and transmits these signals to ganglion cells that carry the signal to the brain. Multipolar neurons are the most common type of neuron. Each multipolar neuron contains one axon and multiple dendrites. Multipolar neurons can be found in the central nervous system (brain and spinal cord). The Purkinje cell, a multipolar neuron in the cerebellum, has many branching dendrites, but only one axon. Pseudounipolar cells share characteristics with both unipolar and bipolar cells. A pseudounipolar cell has a single structure that extends from the soma (like a unipolar cell), which later branches into two distinct structures (like a bipolar cell). Most sensory neurons are pseudounipolar and have an axon that branches into two extensions: one connected to dendrites that receives sensory information and another that transmits this information to the spinal cord.

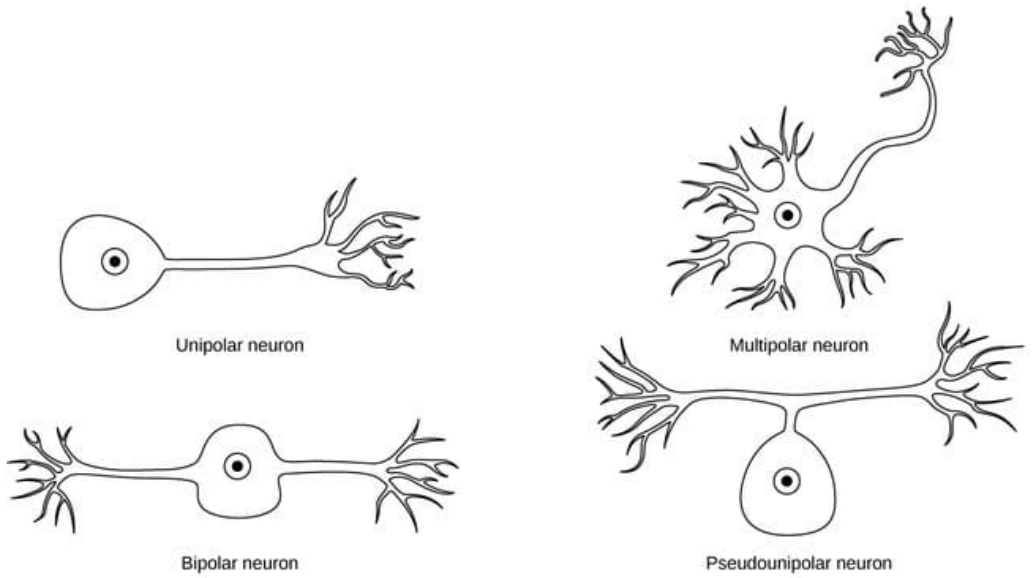


Figure 35.2.1: Types of Neurons: Neurons are broadly divided into four main types based on the number and placement of axons: (1) unipolar, (2) bipolar, (3) multipolar, and (4) pseudounipolar.

Key Points

- Dendrites are the tree-like structures in neurons that extend away from the cell body to receive messages from other neurons at synapses; not all neurons have dendrites.
- Synapses enable the dendrites from a single neuron to interact and receive signals from many other neurons.
- Axons are tube-like structures that send signals to other neurons, muscles, or organs; not all neurons have axons.
- Neurons are divided into four major types: unipolar, bipolar, multipolar, and pseudounipolar.
- Unipolar neurons have only one structure extending from the soma; bipolar neurons have one axon and one dendrite extending from the soma.
- Multipolar neurons contain one axon and many dendrites; pseudounipolar neurons have a single structure that extends from the soma, which later branches into two distinct structures.

Key Terms

- **dendrite**: branched projections of a neuron that conduct the impulses received from other neural cells to the cell body
- **axon**: long slender projection of a nerve cell that conducts nerve impulses away from the cell body to other neurons, muscles, and organs
- **synapse**: the junction between the terminal of a neuron and either another neuron or a muscle or gland cell, over which nerve impulses pass

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35.3: Neurons and Glial Cells - Glia

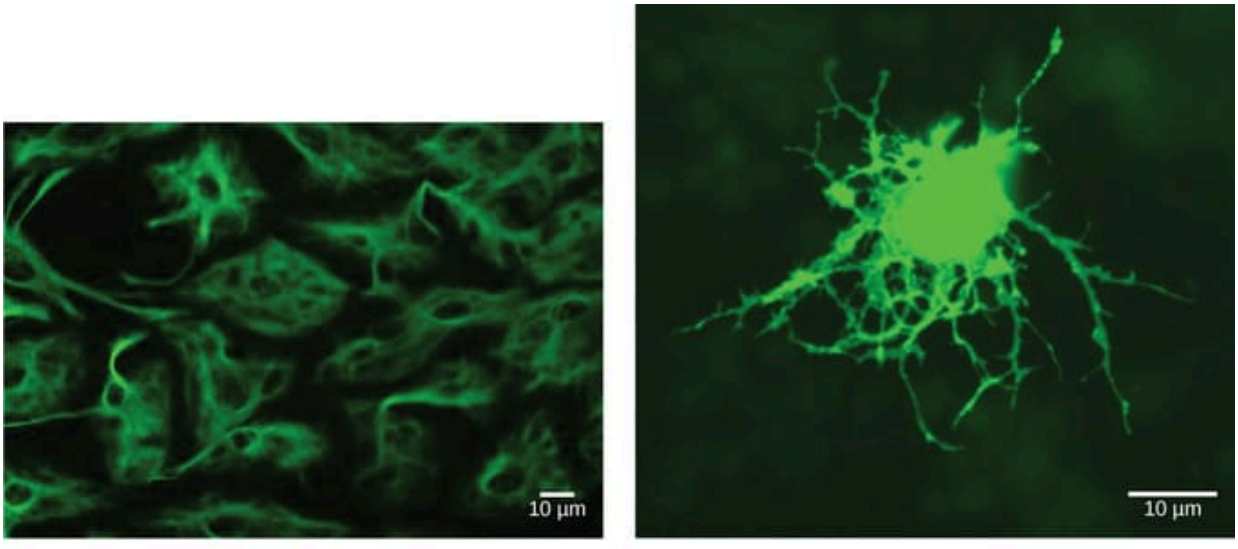
Learning Objectives

- Describe the specific roles that the seven types of glia play in the nervous systems

While glia (or glial cells) are often thought of as the supporting cast of the nervous system, the number of glial cells in the brain actually outnumbers the number of neurons by a factor of ten. Neurons would be unable to function without the vital roles that are fulfilled by these glial cells. Glia guide developing neurons to their destinations, buffer ions and chemicals that would otherwise harm neurons, and provide myelin sheaths around axons. Scientists have recently discovered that they also play a role in responding to nerve activity and modulating communication between nerve cells. When glia do not function properly, the result can be disastrous; most brain tumors are caused by mutations in glia.

Types of Glia

There are several different types of glia with different functions. Astrocytes make contact with both capillaries and neurons in the CNS. They provide nutrients and other substances to neurons, regulate the concentrations of ions and chemicals in the extracellular fluid, and provide structural support for synapses. Astrocytes also form the blood-brain barrier: a structure that blocks entrance of toxic substances into the brain. They have been shown, through calcium-imaging experiments, to become active in response to nerve activity, transmit calcium waves between astrocytes, and modulate the activity of surrounding synapses. Satellite glia provide nutrients and structural support for neurons in the PNS. Microglia scavenge and degrade dead cells, protecting the brain from invading microorganisms. Oligodendrocytes form myelin sheaths around axons in the CNS. One axon can be myelinated by several oligodendrocytes; one oligodendrocyte can provide myelin for multiple neurons. This is distinctive from the PNS where a single Schwann cell provides myelin for only one axon as the entire Schwann cell surrounds the axon. Radial glia serve as bridges for developing neurons as they migrate to their end destinations. Ependymal cells line fluid-filled ventricles of the brain and the central canal of the spinal cord. They are involved in the production of cerebrospinal fluid, which serves as a cushion for the brain, moves the fluid between the spinal cord and the brain, and is a component for the choroid plexus.



(a) Astrocyte (b) Oligodendrocyte

Figure 35.3.1: Images of glial cells: (a) Astrocytes and (b) oligodendrocytes are glial cells of the central nervous system.

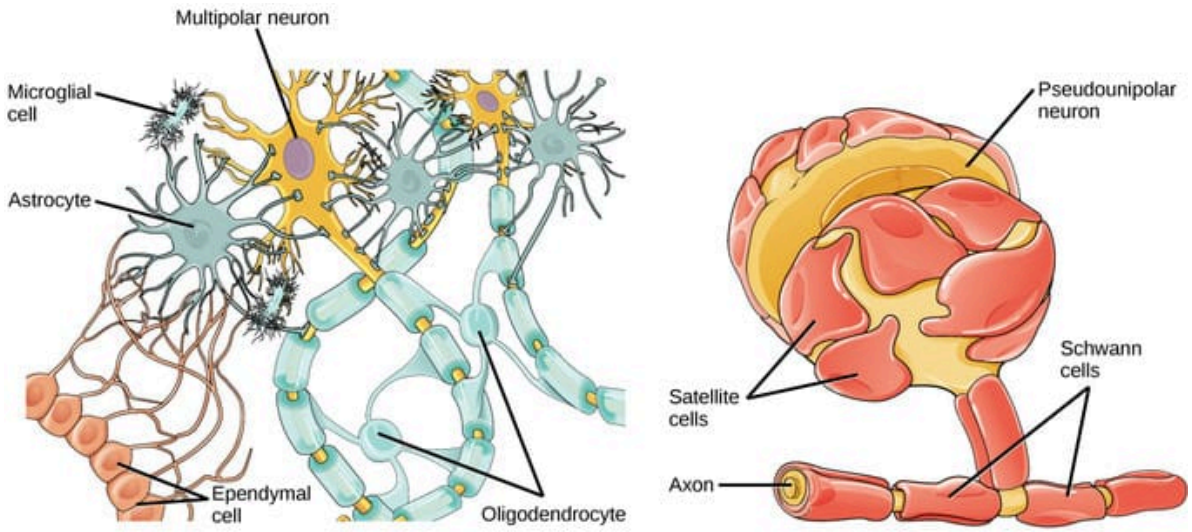


Figure 35.3.1: Glial cells: Glial cells support neurons and maintain their environment. Glial cells of the (a) central nervous system include oligodendrocytes, astrocytes, ependymal cells, and microglial cells. Oligodendrocytes form the myelin sheath around axons. Astrocytes provide nutrients to neurons, maintain their extracellular environment, and provide structural support. Microglia scavenge pathogens and dead cells. Ependymal cells produce cerebrospinal fluid that cushions the neurons. Glial cells of the (b) peripheral nervous system include Schwann cells, which form the myelin sheath, and satellite cells, which provide nutrients and structural support to neurons.

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Key Points

- Glia guide developing neurons to their destinations, buffer harmful ions and chemicals, and build the myelin sheaths around axons.
- In the CNS astrocytes provide nutrients to neurons, give synapses structural support, and block toxic substances from entering the brain; satellite glia provide nutrients and structural support for neurons in the PNS.
- Microglia scavenge and degrade dead cells, protecting the brain from invading microorganisms.
- Oligodendrocytes form myelin sheaths around axons in the CNS; Schwann cell forms myelin sheaths around axons in the PNS.
- Radial glia serve as bridges for developing neurons as they migrate to their end destinations.
- Ependymal cells line fluid-filled ventricles of the brain and central canal of the spinal cord which produce cerebrospinal fluid.

Key Terms

- **satellite glia**: glial cell that provides nutrients for neurons in the PNS
- **radial glia**: glial cell that serves as a bridge for developing neurons as they move to their end destinations
- **astrocyte**: a neuroglial cell, in the shape of a star, in the brain

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35.4: How Neurons Communicate - Nerve Impulse Transmission within a Neuron- Resting Potential

Learning Objectives

- Explain the formation of the resting potential in neurons

Nerve Impulse Transmission within a Neuron

For the nervous system to function, neurons must be able to send and receive signals. These signals are possible because each neuron has a charged cellular membrane (a voltage difference between the inside and the outside). The charge of this membrane can change in response to neurotransmitter molecules released from other neurons and environmental stimuli. Any voltage is a difference in electric potential between two points; for example, the separation of positive and negative electric charges on opposite sides of a resistive barrier. To understand how neurons communicate, one must first understand the basis of charged membranes and the baseline or 'resting' membrane charge.

Neuronal Charged Membranes

The lipid bilayer membrane that surrounds a neuron is impermeable to charged molecules or ions. To enter or exit the neuron, ions must pass through special proteins called ion channels that span the membrane. Ion channels have different configurations: open, closed, and inactive. Some ion channels need to be activated in order to open and allow ions to pass into or out of the cell. These ion channels are sensitive to the environment and can change their shape accordingly. Ion channels that change their structure in response to voltage changes are called voltage-gated ion channels. Voltage-gated ion channels regulate the relative concentrations of different ions inside and outside the cell. The difference in total charge between the inside and outside of the cell is called the membrane potential.

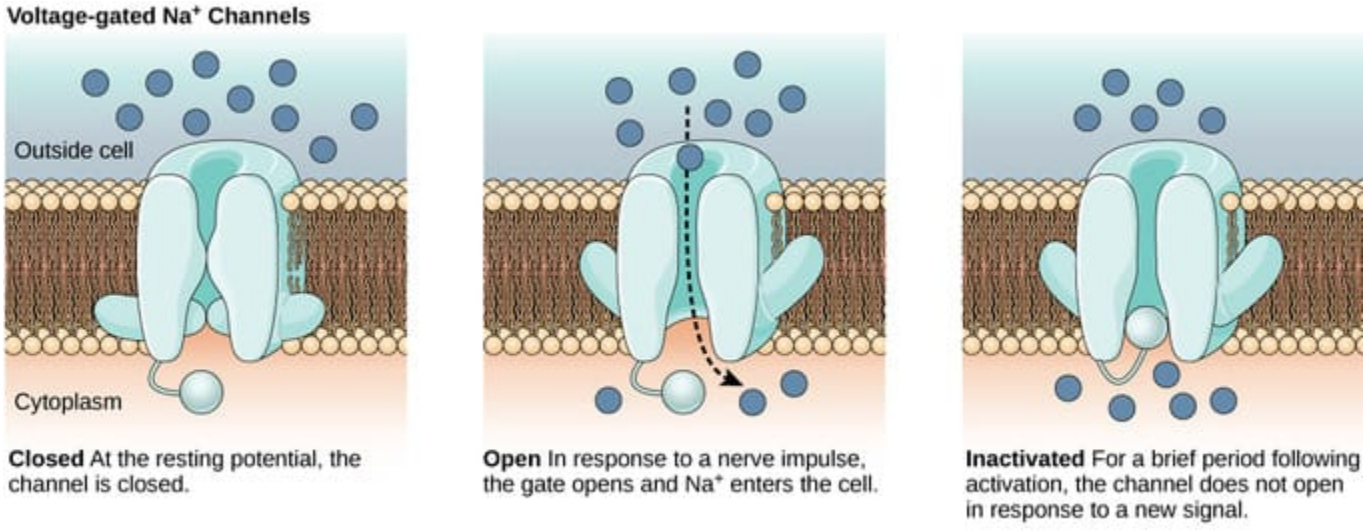


Figure 35.4.1: Ion channel configurations: Voltage-gated ion channels are closed at the resting potential and open in response to changes in membrane voltage. After activation, they become inactivated for a brief period and will no longer open in response to a signal.

Resting Membrane Potential

For quiescent cells, the relatively-static membrane potential is known as the resting membrane potential. The resting membrane potential is at equilibrium since it relies on the constant expenditure of energy for its maintenance. It is dominated by the ionic

species in the system that has the greatest conductance across the membrane. For most cells, this is potassium. As potassium is also the ion with the most-negative equilibrium potential, usually the resting potential can be no more negative than the potassium equilibrium potential.

A neuron at rest is negatively charged because the inside of a cell is approximately 70 millivolts more negative than the outside (–70 mV); this number varies by neuron type and by species. This voltage is called the resting membrane potential and is caused by differences in the concentrations of ions inside and outside the cell. If the membrane were equally permeable to all ions, each type of ion would flow across the membrane and the system would reach equilibrium. Because ions cannot simply cross the membrane at will, there are different concentrations of several ions inside and outside the cell. The difference in the number of positively-charged potassium ions (K^+) inside and outside the cell dominates the resting membrane potential. When the membrane is at rest, K^+ ions accumulate inside the cell due to a net movement with the concentration gradient. The negative resting membrane potential is created and maintained by increasing the concentration of cations outside the cell (in the extracellular fluid) relative to inside the cell (in the cytoplasm). The negative charge within the cell is created by the cell membrane being more permeable to K^+ movement than Na^+movement.

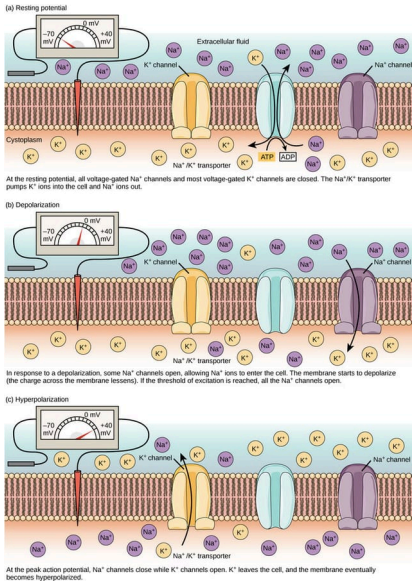


Figure 35.4.1: Membrane potential: The (a) resting membrane potential is a result of different concentrations of Na+ and K+ ions inside and outside the cell. A nerve impulse causes Na+ to enter the cell, resulting in (b) depolarization. At the peak action potential, K+ channels open and the cell becomes (c) hyperpolarized.

In neurons, potassium ions (K+) are maintained at high concentrations within the cell, while sodium ions (Na+) are maintained at high concentrations outside of the cell. The cell possesses potassium and sodium leakage channels that allow the two cations to diffuse down their concentration gradient. However, the neurons have far more potassium leakage channels than sodium leakage channels. Therefore, potassium diffuses out of the cell at a much faster rate than sodium leaks in. More cations leaving the cell than entering it causes the interior of the cell to be negatively charged relative to the outside of the cell. The actions of the sodium-potassium pump help to maintain the resting potential, once it is established. Recall that sodium-potassium pumps bring two K^+ ions into the cell while removing three Na+ ions per ATP consumed. As more cations are expelled from the cell than are taken in, the inside of the cell remains negatively charged relative to the extracellular fluid.

Key Points

- When the neuronal membrane is at rest, the resting potential is negative due to the accumulation of more sodium ions outside the cell than potassium ions inside the cell.
- Potassium ions diffuse out of the cell at a much faster rate than sodium ions diffuse into the cell because neurons have many more potassium leakage channels than sodium leakage channels.
- Sodium-potassium pumps move two potassium ions inside the cell as three sodium ions are pumped out to maintain the negatively-charged membrane inside the cell; this helps maintain the resting potential.

Key Terms

- **ion channel**: a protein complex or single protein that penetrates a cell membrane and catalyzes the passage of specific ions through that membrane
- **membrane potential**: the difference in electrical potential across the enclosing membrane of a cell
- **resting potential**: the nearly latent membrane potential of inactive cells

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35.5: How Neurons Communicate - Nerve Impulse Transmission within a Neuron- Action Potential

Learning Objectives

- Explain the formation of the action potential in neurons

Action Potential

A neuron can receive input from other neurons via a chemical called a neurotransmitter. If this input is strong enough, the neuron will pass the signal to downstream neurons. Transmission of a signal within a neuron (in one direction only, from dendrite to axon terminal) is carried out by the opening and closing of voltage-gated ion channels, which cause a brief reversal of the resting membrane potential to create an action potential. As an action potential travels down the axon, the polarity changes across the membrane. Once the signal reaches the axon terminal, it stimulates other neurons.

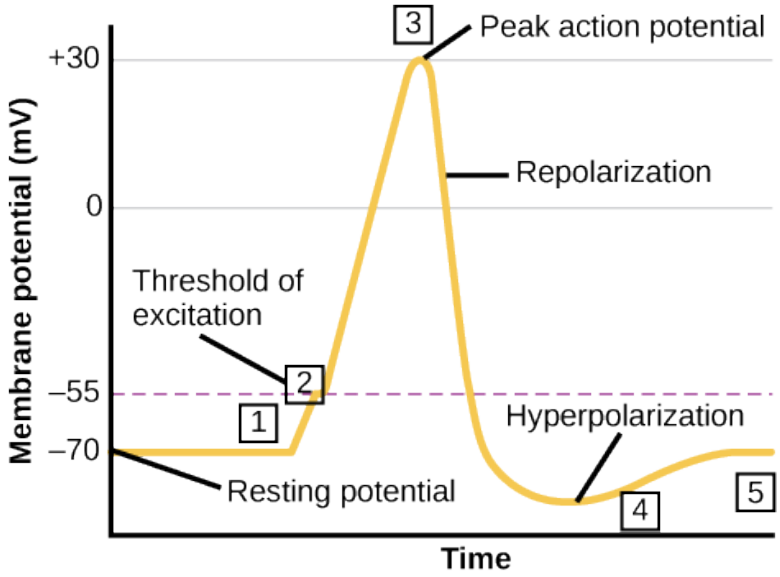


Figure 35.5.1: Formation of an action potential: The formation of an action potential can be divided into five steps. (1) A stimulus from a sensory cell or another neuron causes the target cell to depolarize toward the threshold potential. (2) If the threshold of excitation is reached, all Na+ channels open and the membrane depolarizes. (3) At the peak action potential, K+ channels open and K+ begins to leave the cell. At the same time, Na+ channels close. (4) The membrane becomes hyperpolarized as K+ ions continue to leave the cell. The hyperpolarized membrane is in a refractory period and cannot fire. (5) The K+ channels close and the Na+/K+ transporter restores the resting potential.

Depolarization and the Action Potential

When neurotransmitter molecules bind to receptors located on a neuron's dendrites, voltage-gated ion channels open. At excitatory synapses, positive ions flood the interior of the neuron and depolarize the membrane, decreasing the difference in voltage between the inside and outside of the neuron. A stimulus from a sensory cell or another neuron depolarizes the target neuron to its threshold potential (-55 mV), and Na^+ channels in the axon hillock open, starting an action potential. Once the sodium channels open, the neuron completely depolarizes to a membrane potential of about +40 mV. The action potential travels down the neuron as Na+ channels open.

Hyperpolarization and Return to Resting Potential

Action potentials are considered an “all-or nothing” event. Once the threshold potential is reached, the neuron completely depolarizes. As soon as depolarization is complete, the cell “resets” its membrane voltage back to the resting potential. The Na^+ channels close, beginning the neuron’s refractory period. At the same time, voltage-gated K^+ channels open, allowing K^+ to leave the cell. As K^+ ions leave the cell, the membrane potential once again becomes negative. The diffusion of K^+ out of the cell hyperpolarizes the cell, making the membrane potential more negative than the cell’s normal resting potential. At this point, the sodium channels return to their resting state, ready to open again if the membrane potential again exceeds the threshold potential. Eventually, the extra K^+ ions diffuse out of the cell through the potassium leakage channels, bringing the cell from its hyperpolarized state back to its resting membrane potential.

Myelin and Propagation of the Action Potential

For an action potential to communicate information to another neuron, it must travel along the axon and reach the axon terminals where it can initiate neurotransmitter release. The speed of conduction of an action potential along an axon is influenced by both the diameter of the axon and the axon’s resistance to current leak. Myelin acts as an insulator that prevents current from leaving the axon, increasing the speed of action potential conduction. Diseases like multiple sclerosis cause degeneration of the myelin, which slows action potential conduction because axon areas are no longer insulated so the current leaks.

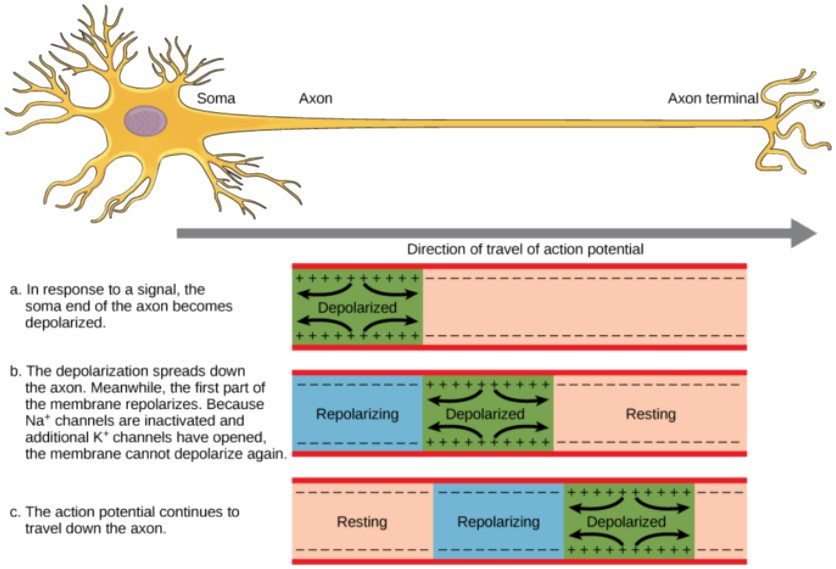


Figure 35.5.1: Action potential travel along a neuronal axon: The action potential is conducted down the axon as the axon membrane depolarizes, then repolarizes.

A node of Ranvier is a natural gap in the myelin sheath along the axon. These unmyelinated spaces are about one micrometer long and contain voltage gated Na^+ and K^+ channels. The flow of ions through these channels, particularly the Na^+ channels, regenerates the action potential over and over again along the axon. Action potential “jumps” from one node to the next in saltatory conduction. If nodes of Ranvier were not present along an axon, the action potential would propagate very slowly; Na^+ and K^+ channels would have to continuously regenerate action potentials at every point along the axon. Nodes of Ranvier also save energy for the neuron since the channels only need to be present at the nodes and not along the entire axon.

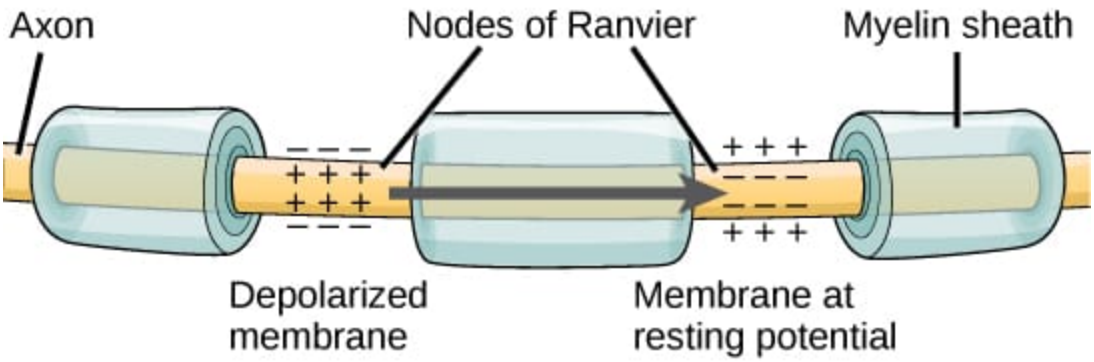


Figure 35.5.1: Nodes of Ranvier: Nodes of Ranvier are gaps in myelin coverage along axons. Nodes contain voltage-gated K+ and Na+ channels. Action potentials travel down the axon by jumping from one node to the next.

Key Points

- Action potentials are formed when a stimulus causes the cell membrane to depolarize past the threshold of excitation, causing all sodium ion channels to open.
- When the potassium ion channels are opened and sodium ion channels are closed, the cell membrane becomes hyperpolarized as potassium ions leave the cell; the cell cannot fire during this refractory period.
- The action potential travels down the axon as the membrane of the axon depolarizes and repolarizes.
- Myelin insulates the axon to prevent leakage of the current as it travels down the axon.
- Nodes of Ranvier are gaps in the myelin along the axons; they contain sodium and potassium ion channels, allowing the action potential to travel quickly down the axon by jumping from one node to the next.

Key Terms

- **action potential**: a short term change in the electrical potential that travels along a cell
- **depolarization**: a decrease in the difference in voltage between the inside and outside of the neuron
- **hyperpolarize**: to increase the polarity of something, especially the polarity across a biological membrane
- **node of Ranvier**: a small constriction in the myelin sheath of axons
- **saltatory conduction**: the process of regenerating the action potential at each node of Ranvier

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35.6: How Neurons Communicate - Synaptic Transmission

Learning Objectives

- Describe the process of synaptic transmission

Synaptic Transmission

In a chemical synapse, the pre and post synaptic membranes are separated by a synaptic cleft, a fluid filled space. The chemical event is involved in the transmission of the impulse via release, diffusion, receptor binding of neurotransmitter molecules and unidirectional communication between neurons.

Chemical Synapse

Neurotransmission at a chemical synapse begins with the arrival of an action potential at the presynaptic axon terminal. When an action potential reaches the axon terminal, it depolarizes the membrane and opens voltage-gated Na^+ channels. Na^+ ions enter the cell, further depolarizing the presynaptic membrane. This depolarization causes voltage-gated Ca^{2+} channels to open. Calcium ions entering the cell initiate a signaling cascade. A calcium sensing protein binds calcium and interacts with SNARE proteins. These SNARE proteins are involved in the membrane fusion. The synaptic vesicles fuse with the presynaptic axon terminal membrane and empty their contents by exocytosis into the synaptic cleft. Calcium is quickly removed from the terminal.

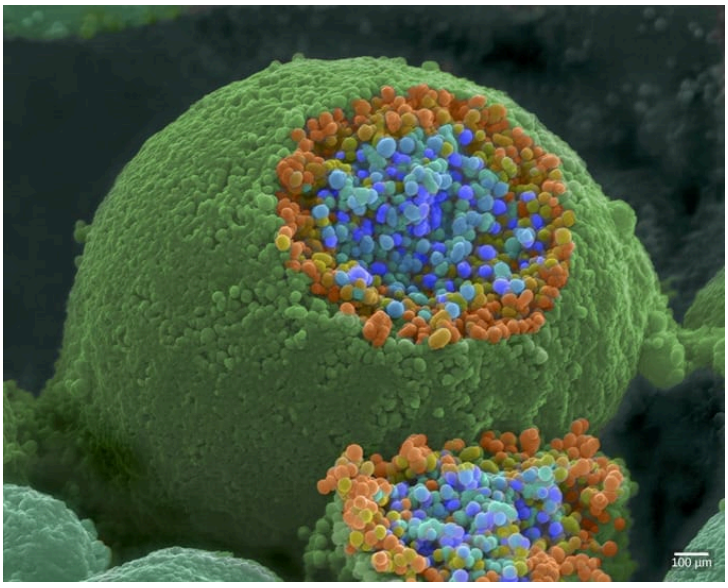


Figure 35.6.1: Synaptic vesicles inside a neuron: This pseudocolored image taken with a scanning electron microscope shows an axon terminal that was broken open to reveal synaptic vesicles (blue and orange) inside the neuron.

Fusion of a vesicle with the presynaptic membrane causes neurotransmitters to be released into the synaptic cleft. The neurotransmitter diffuses across the synaptic cleft, binding to receptor proteins on the postsynaptic membrane.

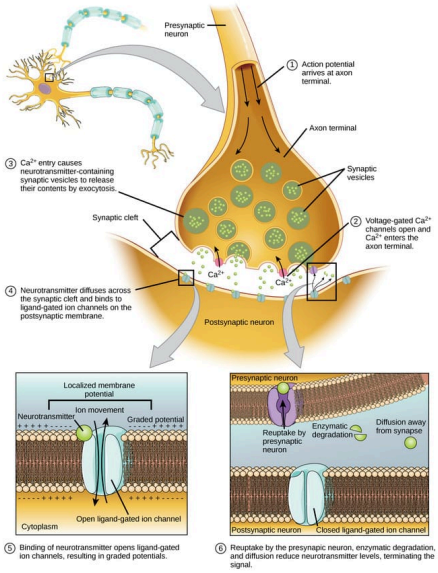


Figure 35.6.1: Communication at a chemical synapse: Communication at chemical synapses requires release of neurotransmitters. When the presynaptic membrane is depolarized, voltage-gated Ca2+ channels open and allow Ca2+ to enter the cell. The calcium entry causes synaptic vesicles to fuse with the membrane and release neurotransmitter molecules into the synaptic cleft. The neurotransmitter diffuses across the synaptic cleft and binds to ligand-gated ion channels in the postsynaptic membrane, resulting in a localized depolarization or hyperpolarization of the postsynaptic neuron.

The binding of a specific neurotransmitter causes particular ion channels, in this case ligand-gated channels, on the postsynaptic membrane to open. The binding of a neurotransmitter to its receptor is reversible. As long as it is bound to a post synaptic receptor, a neurotransmitter continues to affect membrane potential. The effects of the neurotransmitter generally lasts few milliseconds before being terminated. The neurotransmitter termination can occur in three ways. First, reuptake by astrocytes or presynaptic terminal where the neurotransmitter is stored or destroyed by enzymes. Second, degradation by enzymes in the synaptic cleft such as acetylcholinesterase. Third, diffusion of the neurotransmitter as it moves away from the synapse.

Key Points

- In a chemical synapse, the pre and post synaptic membranes are separated by a synaptic cleft, a fluid filled space.
- The chemical event is involved in the transmission of the impulse via release, diffusion, receptor binding of neurotransmitter molecules and unidirectional communication between neurons.
- The neurotransmitter termination can occur in three ways – reuptake, enzymatic degradation in the cleft and diffusion.

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35.7: How Neurons Communicate - Signal Summation

Learning Objectives

- Describe signal summation

Each neuron connects with numerous other neurons, often receiving multiple impulses from them. Sometimes, a single excitatory postsynaptic potential (EPSP) is strong enough to induce an action potential in the postsynaptic neuron, but often multiple presynaptic inputs must create EPSPs around the same time for the postsynaptic neuron to be sufficiently depolarized to fire an action potential. Summation, either spatial or temporal, is the addition of these impulses at the axon hillock. Together, synaptic summation and the threshold for excitation act as a filter so that random "noise" in the system is not transmitted as important information.

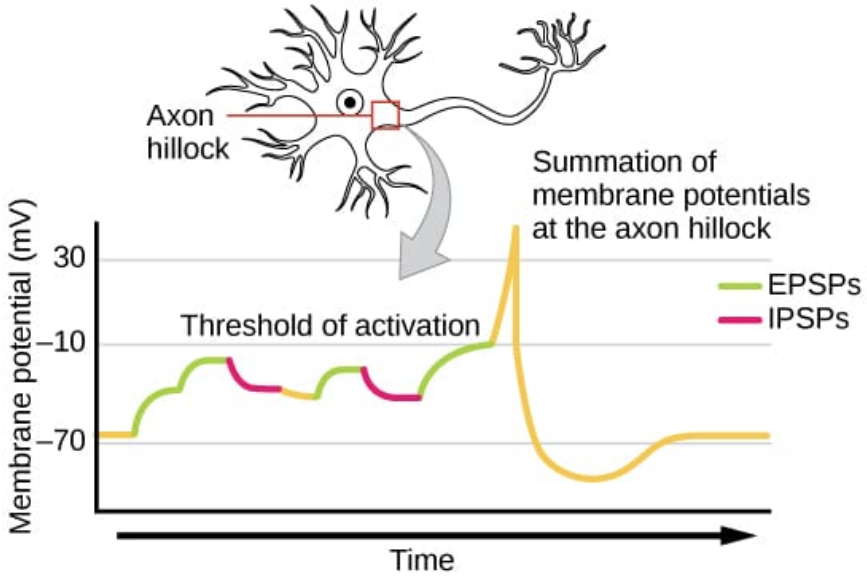


Figure 35.7.1: Signal summation at the axon hillock: A single neuron can receive both excitatory and inhibitory inputs from multiple neurons. All these inputs are added together at the axon hillock. If the EPSPs are strong enough to overcome the IPSPs and reach the threshold of excitation, the neuron will fire.

One neuron often has input from many presynaptic neurons, whether excitatory or inhibitory; therefore, inhibitory postsynaptic potentials (IPSPs) can cancel out EPSPs and vice versa. The net change in postsynaptic membrane voltage determines whether the postsynaptic cell has reached its threshold of excitation needed to fire an action potential. If the neuron only receives excitatory impulses, it will also generate an action potential. However, if the neuron receives as many inhibitory as excitatory impulses, the inhibition cancels out the excitation and the nerve impulse will stop there. Spatial summation means that the effects of impulses received at different places on the neuron add up so that the neuron may fire when such impulses are received simultaneously, even if each impulse on its own would not be sufficient to cause firing. Temporal summation means that the effects of impulses received at the same place can add up if the impulses are received in close temporal succession. Thus, the neuron may fire when multiple impulses are received, even if each impulse on its own would not be sufficient to cause firing.

Key Points

- Simultaneous impulses may add together from different places on the neuron to reach the threshold of excitation during spatial summation.
- When individual impulses cannot reach the threshold of excitation on their own, they can can add up at the same location on the neuron over a short time; this is known as temporal summation.
- The action potential of a neuron is fired only when the net change of excitatory and inhibitory impulses is non-zero.

Key Terms

- **temporal summation**: the effect when impulses received at the same place on the neuron add up
- **spatial summation**: the effect when simultaneous impulses received at different places on the neuron add up to fire the neuron
- **axon hillock**: the specialized part of the soma of a neuron that is connected to the axon and where impulses are added together

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35.8: How Neurons Communicate - Synaptic Plasticity

Learning Objectives

- Distinguish between long-term potentiation and long-term depression

Synaptic plasticity is the strengthening or weakening of synapses over time in response to increases or decreases in their activity. Plastic change also results from the alteration of the number of receptors located on a synapse. Synaptic plasticity is the basis of learning and memory, enabling a flexible, functioning nervous system. Synaptic plasticity can be either short-term (synaptic enhancement or synaptic depression) or long-term. Two processes in particular, long-term potentiation (LTP) and long-term depression (LTD), are important forms of synaptic plasticity that occur in synapses in the hippocampus: a brain region involved in storing memories.

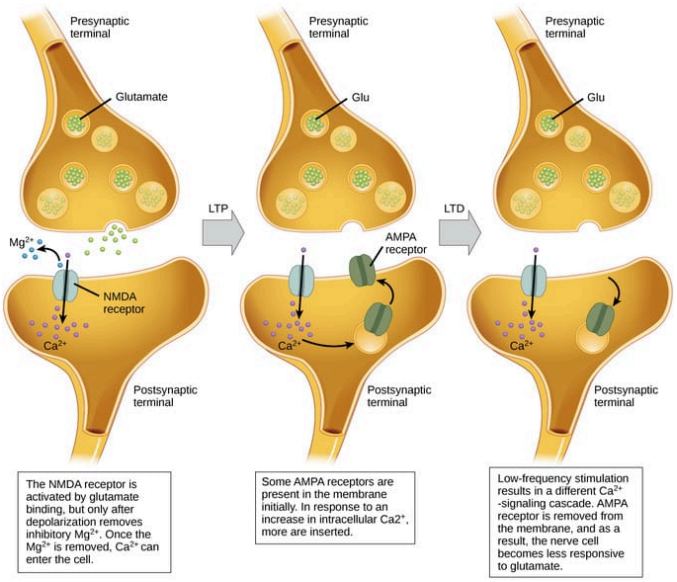


Figure 35.8.1: Long-term potentiation and depression: Calcium entry through postsynaptic NMDA receptors can initiate two different forms of synaptic plasticity: long-term potentiation (LTP) and long-term depression (LTD). LTP arises when a single synapse is repeatedly stimulated. This stimulation causes a calcium- and CaMKII-dependent cellular cascade, which results in the insertion of more AMPA receptors into the postsynaptic membrane. The next time glutamate is released from the presynaptic cell, it will bind to both NMDA and the newly-inserted AMPA receptors, thus depolarizing the membrane more efficiently. LTD occurs when few glutamate molecules bind to NMDA receptors at a synapse (due to a low firing rate of the presynaptic neuron). The calcium that does flow through NMDA receptors initiates a different calcineurin and protein phosphatase 1-dependent cascade, which results in the endocytosis of AMPA receptors. This makes the postsynaptic neuron less responsive to glutamate released from the presynaptic neuron.

Short-term Synaptic Enhancement and Depression

Short-term synaptic plasticity acts on a timescale of tens of milliseconds to a few minutes. Short-term synaptic enhancement results from more synaptic terminals releasing transmitters in response to presynaptic action potentials. Synapses will strengthen for a short time because of either an increase in size of the readily- releasable pool of packaged transmitter or an increase in the amount of packaged transmitter released in response to each action potential. Depletion of these readily-releasable vesicles causes synaptic fatigue. Short-term synaptic depression can also arise from post-synaptic processes and from feedback activation of presynaptic receptors.

Long-term Potentiation (LTP)

Long-term potentiation (LTP) is a persistent strengthening of a synaptic connection, which can last for minutes or hours. LTP is

based on the Hebbian principle: “cells that fire together wire together. ” There are various mechanisms, none fully understood, behind the synaptic strengthening seen with LTP.

One known mechanism involves a type of postsynaptic glutamate receptor: NMDA (N-Methyl-D-aspartate) receptors. These receptors are normally blocked by magnesium ions. However, when the postsynaptic neuron is depolarized by multiple presynaptic inputs in quick succession (either from one neuron or multiple neurons), the magnesium ions are forced out and Ca^{2+} ions pass into the postsynaptic cell. Next, Ca^{2+} ions entering the cell initiate a signaling cascade that causes a different type of glutamate receptor, AMPA (α-amino-3-hydroxy-5-methyl-4-isoxazolepropionic acid) receptors, to be inserted into the postsynaptic membrane. Activated AMPA receptors allow positive ions to enter the cell.

Therefore, the next time glutamate is released from the presynaptic membrane, it will have a larger excitatory effect (EPSP) on the postsynaptic cell because the binding of glutamate to these AMPA receptors will allow more positive ions into the cell. The insertion of additional AMPA receptors strengthens the synapse so that the postsynaptic neuron is more likely to fire in response to presynaptic neurotransmitter release. Some drugs co-opt the LTP pathway; this synaptic strengthening can lead to addiction.

Long-term Depression (LTD)

Long-term depression (LTD) is essentially the reverse of LTP: it is a long-term weakening of a synaptic connection. One mechanism known to cause LTD also involves AMPA receptors. In this situation, calcium that enters through NMDA receptors initiates a different signaling cascade, which results in the removal of AMPA receptors from the postsynaptic membrane. With the decrease in AMPA receptors in the membrane, the postsynaptic neuron is less responsive to the glutamate released from the presynaptic neuron. While it may seem counterintuitive, LTD may be just as important for learning and memory as LTP. The weakening and pruning of unused synapses trims unimportant connections, leaving only the salient connections strengthened by long-term potentiation.

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Key Points

- Short-term synaptic enhancement occurs when the amount of available neurotransmitter is increased, while short-term synaptic depression occurs when the amount of vesicles with neurotransmitters is decreased.
- Synapses are strengthened in long-term potentiation (LTP) when AMPA receptors (which bind to negatively-charged glutamate) are increased, allowing more calcium ions to enter the cell, causing a higher excitatory response.
- Long-term depression (LTD) occurs when the AMPA receptors are decreased, which decreases the amount of calcium ions entering the cell, weakening the synaptic response to the release of neurotransmitters.
- The strengthening and weakening of synapses over time controls learning and memory in the brain.

Key Terms

- **long-term potentiation**: a long-lasting (hours in vitro, weeks to months in vivo) increase, typically in amplitude, of the response of a postsynaptic neuron to a particular pattern of stimuli from a presynaptic neuron
- **long-term depression**: a long-term weakening of a synaptic connection
- **plasticity**: the property of neuron that allows it to be strengthened or weakened

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35.9: The Nervous System

Learning Objectives

- Summarize the nervous system

Introduction to the Nervous System

The nervous system of higher vertebrates (the group that includes humans) is a widely-distributed communication and processing network that serves controlling functions over other organ systems. It possesses a key function in the orientation of the individual; controls its behavior, motor function, and sensory processing; and contains mechanisms to store information. A classification of the nervous system can be performed under different aspects. The anatomical compartmentalization of its components defines the classical approach. Two major divisions of the nervous system are the central nervous system (CNS) and the peripheral nervous system (PNS).

Central Nervous System

The vertebrate central nervous system (CNS) contains the brain and the spinal cord. The brain contains structurally- and functionally-defined regions. In mammals, these include the cortex (which can be broken down into four primary functional lobes: frontal, temporal, occipital, and parietal), basal ganglia, thalamus, hypothalamus, limbic system, cerebellum, and brainstem; although structures in some of these designations overlap. While functions may be primarily localized to one structure in the brain, most complex functions, such as language and sleep, involve neurons in multiple brain regions. The spinal cord is the information superhighway, connecting the brain with the rest of the body through the peripheral nerves. It transmits sensory and motor input and also controls motor reflexes.

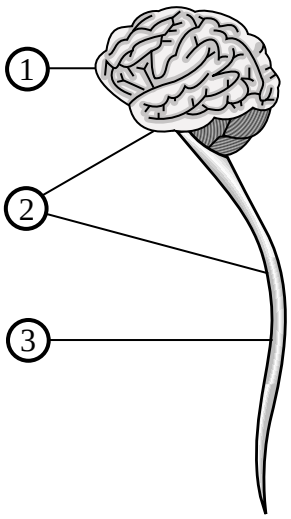


Figure 35.9.1: Central nervous system: The central nervous system (2) is a combination of the brain (1) and the spinal cord (3).

The CNS is covered with three layers of protective coverings called meninges (from the Greek word for membrane). The outermost layer is the dura mater (Latin for “hard mother”). As the Latin name suggests, the primary function for this thick layer is to protect the brain and spinal cord. The dura mater also contains vein-like structures that carry blood from the brain back to the heart. The middle layer is the web-like arachnoid mater. The last layer is the pia mater (Latin for “soft mother”), which directly contacts and covers the brain and spinal cord like plastic wrap. The space between the arachnoid and pia maters is filled with cerebrospinal fluid (CSF). CSF is produced by a tissue called the choroid plexus in fluid-filled compartments in the CNS called ventricles. The brain floats in CSF, which acts as a cushion and shock absorber, making the brain neutrally buoyant. CSF also functions to

circulate chemical substances throughout the brain and into the spinal cord.

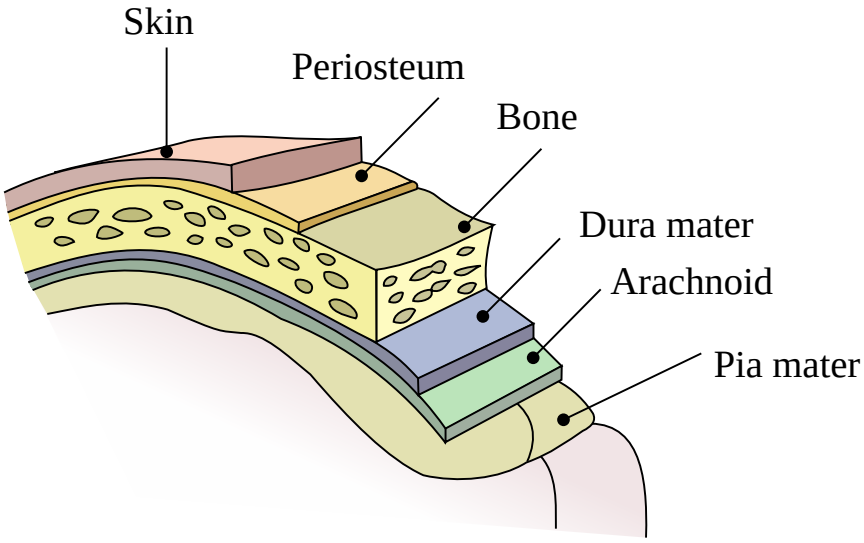


Figure 35.9.1: Meninges of the brain: The outermost layer of the meninges is the dura mater, which protects the brain and spinal cord. The innermost layer is the pia mater, which directly covers the brain and spinal cord. The arachnoid mater is found between the two.

Peripheral Nervous System

The peripheral nervous system consists of nerves that are connected to the brain (cranial nerves) and nerves that are connected to the spinal cord (spinal nerves). The main function of the PNS is to connect the central nervous system (CNS) to the limbs and organs, essentially serving as a communication relay between the brain and the extremities. Unlike the CNS, the PNS is not protected by the bone of spine and skull. Nor does it have a barrier between itself and the blood, leaving it exposed to toxins and mechanical injuries.

The autonomic nervous system, also part of the peripheral nervous system, controls internal body functions that are not under conscious control. For example, when a prey animal is chased by a predator, the autonomic nervous system automatically increases the rate of breathing and the heartbeat. It dilates the blood vessels that carry blood to the muscles, releases glucose from the liver, and makes other adjustments to provide for the sudden increase in activity. When the animal has escaped and is safe once again, the nervous system slows down all these processes and resumes all the normal body activities, such as the digestion of food.

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Key Points

- The central nervous system consists of the brain, which controls complex body functions, and the spinal cord, which transmits signals from the brain to the rest of the body.
- The brain and spinal cord are covered by three layers of meninges, or protective coverings: the dura mater, the arachnoid mater, and the pia mater.
- Cerebrospinal fluid surrounds the brain, cushioning it and providing shock absorption to prevent damage.
- The peripheral nervous system is made up of nerves that originate within the brain and spinal cord; it serves to relay information from the central nervous system to all parts of the body.
- The autonomic system controls involuntary bodily functions, such as heart rate, breathing, digestion, and blood vessel dilation.

Key Terms

- **central nervous system**: in vertebrates, that part of the nervous system comprising the brain and spinal cord
- **cerebrospinal fluid**: a clear bodily fluid that occupies the subarachnoid space in the brain (between the skull and the cerebral cortex), and which acts as a cushion or buffer for the cortex
- **meninges**: the three membranes that envelop the brain and spinal cord
- **autonomic nervous system**: the part of the nervous system that regulates the involuntary activity of the heart, intestines and glands
- **peripheral nervous system**: the part of the nervous system which is not the central nervous system

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35.10: The Central Nervous System - Cerebral Cortex and Brain Lobes

Learning Objectives

- Describe the structure and function of the cerebral cortex

The brain is the part of the central nervous system that is contained in the cranial cavity of the skull. It includes the cerebral cortex, limbic system, basal ganglia, thalamus, hypothalamus, and cerebellum.

Cerebral Cortex

The outermost part of the brain is a thick piece of nervous system tissue called the cerebral cortex, which is folded into hills called gyri (singular: gyrus) and valleys called sulci (singular: sulcus). The cortex is composed of two hemispheres, right and left, which are separated by a large sulcus. A thick fiber bundle, the corpus callosum, connects the two hemispheres, allowing information to be passed from one side to the other. Although there are some brain functions that are localized more to one hemisphere than the other, the functions of the two hemispheres are largely redundant. In fact, sometimes (very rarely) an entire hemisphere is removed to treat severe epilepsy. While patients do suffer some deficits following the surgery, they can have surprisingly few problems, especially when the surgery is performed on children who have relatively-undeveloped nervous systems.

In other surgeries to treat severe epilepsy, the corpus callosum is cut instead of removing an entire hemisphere. This causes a condition called split-brain syndrome, which gives insights into unique functions of the two hemispheres. For example, when an object is presented to patients' left visual fields, they may be unable to verbally name the object (and may claim not to have seen an object at all). This is because the visual input from the left visual field crosses and enters the right hemisphere and is unable to signal to the speech center, which generally is found in the left side of the brain. Remarkably, if a split-brain patient is asked to pick up a specific object out of a group of objects with the left hand, the patient will be able to do so, but will still be unable to vocally identify it.

The Four Brain Lobes

Each hemisphere of the mammalian cerebral cortex can be broken down into four functionally- and spatially-defined lobes: frontal, parietal, temporal, and occipital. The frontal lobe is located at the front of the brain, over the eyes. This lobe contains the olfactory bulb, which processes smells. The frontal lobe also contains the motor cortex, which is important for planning and implementing movement. Areas within the motor cortex map to different muscle groups; there is some organization to this map. For example, the neurons that control movement of the fingers are next to the neurons that control movement of the hand. Neurons in the frontal lobe also control cognitive functions such as maintaining attention, speech, and decision-making. Studies of humans who have damaged their frontal lobes show that parts of this area are involved in personality, socialization, and assessing risk.

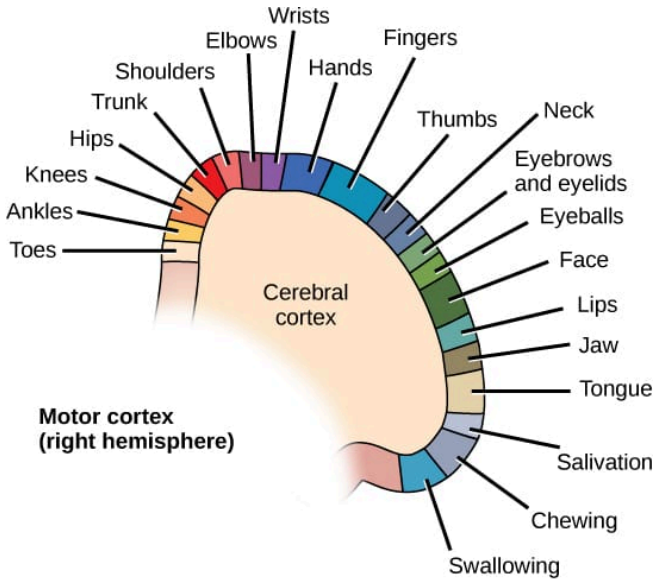


Figure 35.10.1: Motor cortex control of muscle movement: Different parts of the motor cortex control different muscle groups. Muscle groups that are neighbors in the body are generally controlled by neighboring regions of the motor cortex as well. For example, the neurons that control shoulder movement are near the neurons that control elbow movement, which are themselves next to those that control wrist movement.

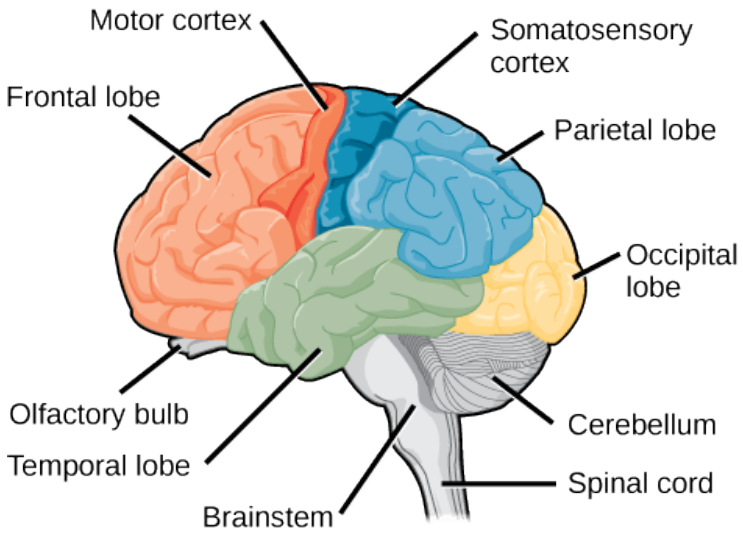


Figure 35.10.1: Lobes of the cerebral cortex: The human cerebral cortex includes the frontal, parietal, temporal, and occipital lobes, each of which is involved in a different higher function.

The parietal lobe is located at the top of the brain. Neurons in the parietal lobe are involved in speech and reading. Two of the parietal lobe's main functions are processing somatosensation (touch sensations such as pressure, pain, heat, cold) and processing proprioception (the sense of how parts of the body are oriented in space). The parietal lobe contains a somatosensory map of the body similar to the motor cortex.

The occipital lobe is located at the back of the brain. It is primarily involved in vision: seeing, recognizing, and identifying the visual world.

The temporal lobe is located at the base of the brain by the ears. It is primarily involved in processing and interpreting sounds. It also contains the hippocampus (Greek for "seahorse", which is what it resembles), a structure that processes memory formation. The role of the hippocampus in memory was partially determined by studying one famous epileptic patient, HM, who had both sides of his hippocampus removed in an attempt to cure his epilepsy. His seizures went away, but he could no longer form new memories (although he could remember some facts from before his surgery and could learn new motor tasks).

Key Points

- The cerebral cortex is the outermost layer of the brain; it is easily recognizable by the grooves (sulci) and “hills” (gyri).
- The brain contains two hemispheres, the left and the right, which are connected by a bundle of nerve fibers called the corpus callosum that transmits information between them.
- The frontal lobe houses the olfactory bulb, which processes smells; the motor cortex, which controls movement; and it controls cognitive functions such as attention, speech, and decision-making.
- The parietal lobe is involved in speech and reading, as well as interpreting touch sensations such as pressure, pain, heat, cold, along with sensing where each part of the body is in relation to the others and its environment.
- The occipital lobe interprets visual cues, such as what we see and recognition of faces and objects.
- The temporal lobe processes and interprets sounds and is also involved in forming new memories, a task for which the hippocampus, a structure inside the temporal lobe, is responsible.

Key Terms

- **corpus callosum**: in mammals, a broad band of nerve fibers that connects the left and right hemispheres of the brain
- **proprioception**: the sense of the position of parts of the body, relative to other neighbouring parts of the body
- **somatosensation**: general senses which respond to stimuli like temperature, pain, pressure, and vibration
- **gyrus**: a ridge or fold on the cerebral cortex
- **sulcus**: any of the grooves that mark the convolutions of the surface of the brain

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35.11: The Central Nervous System - Midbrain and Brain Stem

Learning Objectives

- Explain the structure and function of the non-cerebral cortex portions of the brain

Basal Ganglia

Interconnected brain areas called the basal ganglia (or basal nuclei) play important roles in movement control and posture. Damage to the basal ganglia, which occurs in Parkinson's disease, leads to motor impairments such as a shuffling gait when walking. The basal ganglia also regulate motivation. For example, when a wasp sting led to bilateral basal ganglia damage in a 25-year-old businessman, he began to spend all his days in bed and showed no interest in anything or anybody. But when he was externally stimulated, as when someone asked to play a card game with him, he was able to function normally. Interestingly, he and other similar patients do not report feeling bored or frustrated by their state.

Thalamus

The thalamus (Greek for "inner chamber") acts as a gateway to and from the cortex. It receives sensory and motor inputs from the body and also receives feedback from the cortex. This feedback mechanism can modulate conscious awareness of sensory and motor inputs depending on the attention and arousal state of the animal. The thalamus helps regulate consciousness, arousal, and sleep states. A rare genetic disorder, fatal familial insomnia, causes the degeneration of thalamic neurons and glia. This disorder prevents affected patients from being able to sleep, among other symptoms, and is eventually fatal.

Hypothalamus

Below the thalamus is the hypothalamus. The hypothalamus controls the endocrine system by sending signals to the pituitary gland, a pea-sized endocrine gland that releases several different hormones that affect other glands as well as other cells. This relationship means that the hypothalamus regulates important behaviors that are controlled by these hormones. The hypothalamus is the body's thermostat: it makes sure key functions like food and water intake, energy expenditure, and body temperature are kept at appropriate levels. Neurons within the hypothalamus also regulate circadian rhythms, sometimes called sleep cycles.

The limbic system is a connected set of structures that regulates emotion, as well as behaviors related to fear and motivation. It plays a role in memory formation and includes parts of the thalamus and hypothalamus as well as the hippocampus. One important structure within the limbic system is a temporal lobe structure called the amygdala (Greek for "almond"). The two amygdale are important both for the sensation of fear and for recognizing fearful faces. The cingulate gyrus helps regulate emotions and pain.

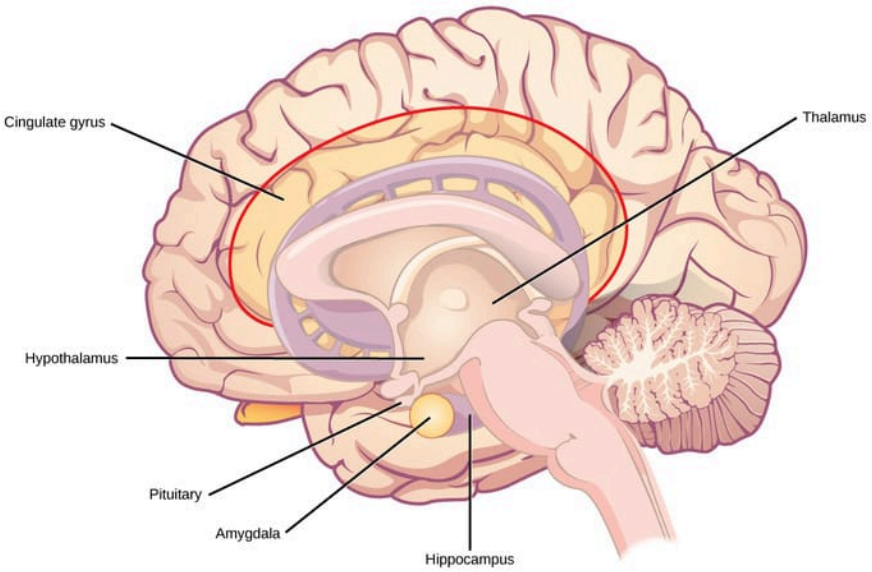


Figure 35.11.1: The limbic system: The limbic system regulates emotion and other behaviors. It includes parts of the cerebral cortex located near the center of the brain, including the cingulate gyrus and the hippocampus as well as the thalamus, hypothalamus, and amygdala.

Cerebellum

The cerebellum (Latin for “little brain”) sits at the base of the brain on top of the brainstem. The cerebellum controls balance and aids in coordinating movement and learning new motor tasks.

Brainstem

The brainstem connects the rest of the brain with the spinal cord. It consists of the midbrain, medulla oblongata, and the pons. Motor and sensory neurons extend through the brainstem, allowing for the relay of signals between the brain and spinal cord. Ascending neural pathways cross in this section of the brain, allowing the left hemisphere of the cerebrum to control the right side of the body and vice versa. The brainstem coordinates motor control signals sent from the brain to the body. It also controls several important functions of the body including alertness, arousal, breathing, blood pressure, digestion, heart rate, swallowing, walking, and sensory and motor information integration.

Key Points

- The basal ganglia control movement and posture; they also appear to be involved in self-motivation.
- The thalamus communicates information from the cerebral cortex to the rest of the body and also helps regulate the states of consciousness versus sleep.
- The hypothalamus regulates the pituitary gland, which controls the release of hormones throughout the body; it indirectly regulates functions such as water intake, body temperature, and sleep cycles.
- The limbic system includes the amygdala, the hippocampus, and parts of the thalamus and hypothalamus; it regulates emotion, fear, and motivation.
- The cerebellum controls motor reflexes and is, therefore, involved in balance and muscle coordination.
- The brainstem connects and transmits signals from the brain to the spinal cord, controlling functions such as breathing, heart rate, and alertness.

Key Terms

- **cingulate gyrus**: a section of the cerebral cortex, belonging to the fornicate gyrus, which arches over the corpus callosum
- **limbic system**: part of the human brain involved in emotion, motivation, and emotional association with memory
- **endocrine system**: a control system of ductless glands that secrete hormones which circulate via the bloodstream to affect cells within specific organs

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35.12: The Central Nervous System - Spinal Cord

Learning Objectives

- Describe the structure and function of the spinal cord

Connecting to the brainstem and extending down the body through the spinal column is the spinal cord: a thick bundle of nerve tissue that carries information about the body to the brain and from the brain to the body. The spinal cord is contained within the bones of the vertebral column, but is able to communicate signals to and from the body through its connections with spinal nerves (part of the peripheral nervous system). A cross-section of the spinal cord looks like a white oval containing a gray butterfly-shape. Myelinated axons (the part of neurons that send signals) compose the "white matter," while neuron and glial cell bodies (neuronal "support" cells) compose the "grey matter." Grey matter is also composed of interneurons, which connect two neurons, each located in different parts of the body. Axons and cell bodies in the dorsal (facing the back of the animal) spinal cord convey mostly sensory information from the body to the brain. Axons and cell bodies in the ventral (facing the front of the animal) spinal cord primarily transmit signals controlling movement from the brain to the body.

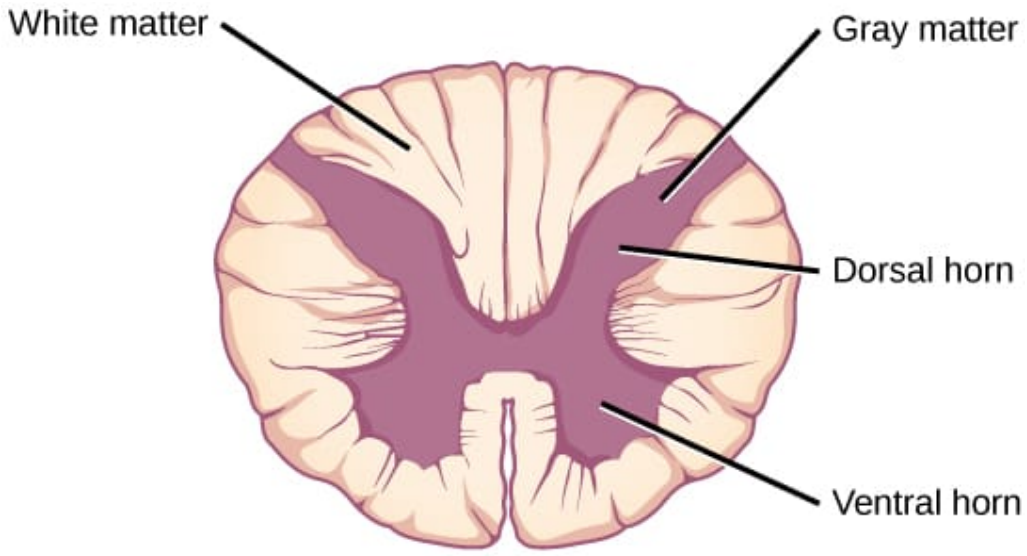


Figure 35.12.1: Spinal cord cross-section: A cross-section of the spinal cord shows grey matter (containing cell bodies and interneurons) and white matter (containing axons).

The spinal cord also controls motor reflexes. These reflexes are quick, unconscious movements, such as automatically removing a hand from a hot object. Reflexes are so fast because they involve local synaptic connections. For example, the knee reflex that a doctor tests during a routine physical is controlled by a single synapse between a sensory neuron and a motor neuron. While a reflex may only require the involvement of one or two synapses, synapses with interneurons in the spinal column transmit information to the brain to convey what happened (the knee jerked, or the hand was hot).

In the United States, there around 10,000 spinal cord injuries each year. Because the spinal cord is the information superhighway connecting the brain with the body, damage to the spinal cord can lead to paralysis. The extent of the paralysis depends on the location of the injury along the spinal cord and whether the spinal cord was completely severed. For example, if the spinal cord is damaged at the level of the neck, it can cause paralysis from the neck down, whereas damage to the spinal column further down may limit paralysis to the legs. Spinal cord injuries are notoriously difficult to treat because spinal nerves do not regenerate, although ongoing research suggests that stem cell transplants may be able to act as a bridge to reconnect severed nerves. Researchers are also looking at ways to prevent the inflammation that worsens nerve damage after injury. One such treatment is to pump the body with cold saline to induce hypothermia. This cooling can prevent swelling and other processes that are thought to worsen spinal cord injuries.

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Key Points

- The spinal cord consists of a butterfly-shaped area of grey matter, containing neuronal and glial cell bodies, surrounded by white matter that contains the axons of the neurons.
- Neurons at the back of the spinal cord (dorsal) generally transmit information from the body to the brain, while neurons at the front of the spinal cord (ventral) primarily transmit information from the brain to the body.
- The spinal cord controls reflexes, which are incredibly fast reactions to stimuli; the speed at which they operate is due to the

fact that they involve only a local connection between neurons and are not relayed through the brain.
- Spinal cord injuries often result in paralysis; they do not heal, as spinal nerves lack the ability to regenerate.

Key Terms

- **grey matter**: a collection of cell bodies and (usually) dendritic connections, in contrast to white matter
- **synapse**: the junction between the terminal of a neuron and either another neuron or a muscle or gland cell, over which nerve impulses pass
- **axon**: long slender projection of a nerve cell that conducts nerve impulses away from the cell body to other neurons, muscles, and organs
- **white matter**: a region of the central nervous system containing myelinated nerve fibers and no dendrites
- **interneuron**: a multipolar neuron that connects afferent and efferent neurons

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35.13: The Peripheral Nervous System - Autonomic Nervous System

Learning Objectives

- Explain the function of the autonomic nervous system

Autonomic Nervous System

The autonomic nervous system (ANS) serves as the relay between the central nervous system (CNS) and the internal organs. It controls the lungs, the heart, smooth muscle, and exocrine and endocrine glands, largely without conscious control. It can continuously monitor the conditions of these different systems and implement changes as needed. Signaling to the target tissue usually involves two synapses. A preganglionic neuron (originating in the CNS) synapses to a neuron in a ganglion that, in turn, synapses on the target organ. There are two divisions of the autonomic nervous system that often have opposing effects: the sympathetic nervous system and the parasympathetic nervous system.

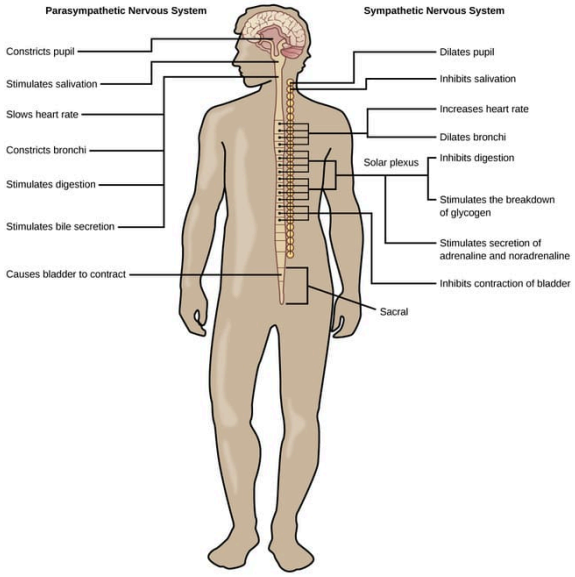


Figure 35.13.1: Actions of the SNS and PNS: The sympathetic and parasympathetic nervous systems often have opposing effects on target organs.

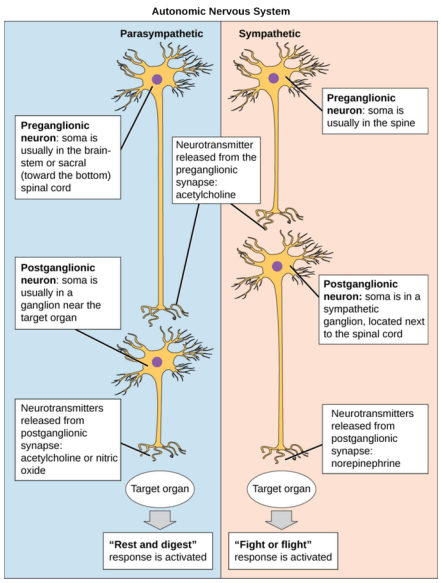


Figure 35.13.1: Autonomic nervous system: Autonomic responses are mediated by the sympathetic and the parasympathetic systems, which are antagonistic to one another. The sympathetic system activates the "fight or flight" response, while the parasympathetic system activates the "rest and digest" response. In the autonomic nervous system, a preganglionic neuron of the CNS synapses with a postganglionic neuron of the parasympathetic nervous system. The postganglionic neuron, in turn, acts on a target organ.

Sympathetic Nervous System

The sympathetic nervous system is responsible for the "fight or flight" response that occurs when an animal encounters a dangerous situation. One way to remember this is to think of the surprise a person feels when encountering a snake ("snake" and "sympathetic" both begin with "s"). Examples of functions controlled by the sympathetic nervous system include an accelerated heart rate and inhibited digestion, both of which help prepare an organism's body for the physical strain required to escape a potentially dangerous situation or to fend off a predator.

Most preganglionic neurons in the sympathetic nervous system originate in the spinal cord. The axons of these neurons release acetylcholine on postganglionic neurons within sympathetic ganglia (the sympathetic ganglia form a chain that extends alongside the spinal cord). The acetylcholine activates the postganglionic neurons. Postganglionic neurons then release norepinephrine onto target organs. As anyone who has ever felt a rush before a big test, speech, or athletic event can attest, the effects of the sympathetic nervous system are quite pervasive. This is both because one preganglionic neuron synapses on multiple postganglionic neurons, amplifying the effect of the original synapse, and because the adrenal gland also releases norepinephrine (and the closely-related hormone epinephrine) into the blood stream. The physiological effects of this norepinephrine release include dilating the trachea and bronchi (making it easier for the animal to breathe), increasing heart rate, and moving blood from the skin to the heart, muscles, and brain (so the animal can think and run). The strength and speed of the sympathetic response helps an organism avoid danger. Scientists have found evidence that it may also increase long term potentiation in neurons, allowing the animal to remember the dangerous situation and avoid it in the future.

Parasympathetic Nervous System

While the sympathetic nervous system is activated in stressful situations, the parasympathetic nervous system allows an animal to "rest and digest." One way to remember this is to think that during a restful situation like a picnic, the parasympathetic nervous system is in control ("picnic" and "parasympathetic" both start with "p"). Parasympathetic preganglionic neurons have cell bodies located in the brainstem and in the sacral (toward the bottom) spinal cord. The axons of the preganglionic neurons release acetylcholine on the postganglionic neurons, which are generally located very near the target organs.

The parasympathetic nervous system resets organ function after the sympathetic nervous system is activated (the common adrenaline dump you feel after a 'fight-or-flight' event). Effects of acetylcholine release on target organs include slowing of heart rate, lowered blood pressure, and stimulation of digestion.

Key Points

- The autonomic nervous system controls the workings of internal organs such as the heart, lungs, digestive system, and endocrine systems; it does so without conscious effort.
- The sympathetic nervous system controls the body's automatic response to danger, increasing the heart rate, dilating the blood vessels, slowing digestion, and moving blood flow to the heart, muscles, and brain.
- The parasympathetic nervous system works in opposition to the sympathetic; during periods of rest it slows the heart rate, lowers the blood pressure, stimulates digestion, and moves blood flow back to the skin.

Key Terms

- **preganglionic**: describing the nerve fibres that supply a ganglion
- **sympathetic nervous system**: the part of the autonomic nervous system that under stress raises blood pressure and heart rate, constricts blood vessels and dilates the pupils
- **parasympathetic nervous system**: one of the divisions of the autonomic nervous system, based between the brain and the spinal cord, that slows the heart and relaxes muscles
- **acetylcholine**: a neurotransmitter in humans and other animals, which is an ester of acetic acid and choline

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35.14: The Peripheral Nervous System - The Sensory-Somatic Nervous System

Learning Objectives

- Explain the role of the cranial and spinal nerves in the sensory-somatic nervous system

The sensory-somatic nervous system is composed of cranial and spinal nerves and contains both sensory and motor neurons. Sensory neurons transmit sensory information from the skin, skeletal muscle, and sensory organs to the central nervous system (CNS). Motor neurons transmit messages about desired movement from the CNS to the muscles, causing them to contract. Without its sensory-somatic nervous system, an animal would be unable to process any information about its environment (what it sees, feels, hears, etc.) and could not control motor movements. Unlike the autonomic nervous system, which has two synapses between the CNS and the target organ, sensory and motor neurons have only one synapse: one ending of the neuron is at the organ and the other directly contacts a CNS neuron. Acetylcholine is the main neurotransmitter released at these synapses.

Cranial Nerves

Humans have 12 cranial nerves, nerves that emerge from or enter the skull (cranium), as opposed to the spinal nerves, which emerge from the vertebral column. Each cranial nerve has a name. Some cranial nerves transmit only sensory information. For example, the olfactory nerve transmits information about smells from the nose to the brainstem. Other cranial nerves transmit almost solely motor information. The oculomotor nerve controls the opening and closing of the eyelid and some eye movements. Other cranial nerves contain a mix of sensory and motor fibers. For example, the glossopharyngeal nerve has a role in both taste (sensory) and swallowing (motor).

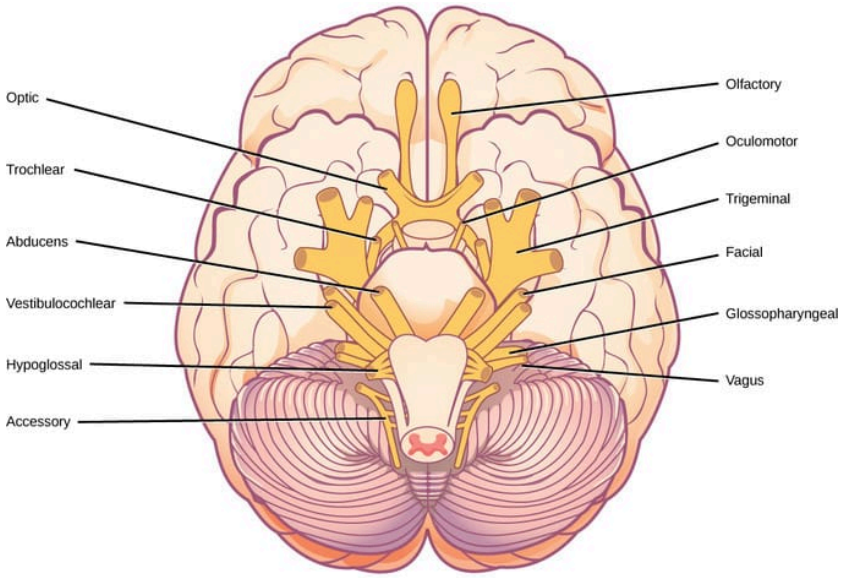


Figure 35.14.1: Cranial nerves: The human brain contains 12 cranial nerves that receive sensory input and control motor output for the head and neck.

Spinal Nerves

Spinal nerves transmit sensory and motor information between the spinal cord and the rest of the body. Each of the 31 spinal nerves (in humans) contains both sensory and motor axons. The sensory neuron cell bodies are grouped in structures called dorsal root ganglia. Each sensory neuron has one projection with a sensory receptor ending in skin, muscle, or sensory organs, and another that synapses with a neuron in the dorsal spinal cord. Motor neurons have cell bodies in the ventral gray matter of

the spinal cord that project to muscle through the ventral root. These neurons are usually stimulated by interneurons within the spinal cord, but are sometimes directly stimulated by sensory neurons.

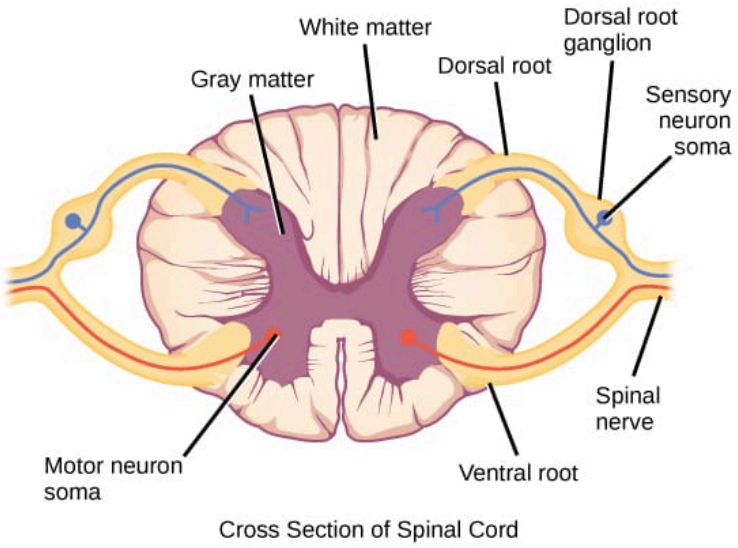


Figure 35.14.1: Spinal nerves: Spinal nerves contain both sensory and motor axons. The cell bodies of sensory neurons are located in dorsal root ganglia. The cell bodies of motor neurons are found in the ventral portion of the gray matter of the spinal cord.

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Key Points

- The sensory and motor neurons of the sensory-somatic system have only one synapse between the organ and a neuron of the CNS; these synapses utilize acetylcholine to transmit signals across this synapse.
- The twelve cranial nerves either enter or exit from the skull; some transmit only sensory information, some transmit only motor information, and some transmit both.
- There are 31 spinal nerves that convey both sensory and motor signals between the spinal cord and the rest of the body.

Key Terms

- **cranial nerve**: any of the twelve paired nerves that originate from the brainstem instead of the spinal cord
- **spinal nerve**: one of 31 pairs of nerves that carry motor, sensory, and autonomic signals between the spinal cord and the body
- **acetylcholine**: a neurotransmitter in humans and other animals, which is an ester of acetic acid and choline

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35.15: Neurodegenerative Disorders - Introduction

Learning Objectives

- Distinguish between the neurodegenerative disorders of Alzheimer's disease and Parkinson's disease

Neurodegenerative disorders are illnesses characterized by a loss of nervous system functioning that are usually caused by neuronal death. These diseases generally worsen over time as more and more neurons die. The symptoms of a particular neurodegenerative disease are related to where in the nervous system the death of neurons occurs. Spinocerebellar ataxia, for example, leads to neuronal death in the cerebellum. The death of these neurons causes problems in balance and walking. Neurodegenerative disorders include Huntington's disease, amyotrophic lateral sclerosis (ALS), Alzheimer's disease, other dementia disorders, and Parkinson's disease. In this section, Alzheimer's and Parkinson's disease will be discussed in more depth.

Alzheimer's Disease

Alzheimer's disease is the most common cause of dementia in the elderly. In 2012, an estimated 5.4 million Americans suffered from Alzheimer's disease. Payments for their care are estimated at $200 billion. Roughly one in every eight people age 65 or older has the disease. Due to the aging of the baby-boomer generation, there are projected to be as many as 13 million Alzheimer's patients in the United States in the year 2050.

Symptoms of Alzheimer's disease include disruptive memory loss, confusion about time or place, difficulty planning or executing tasks, poor judgement, and personality changes. Problems smelling certain scents can also be indicative of Alzheimer's disease and may serve as an early warning sign. Many of these symptoms are also common in people who are aging normally, so it is the severity and longevity of the symptoms that determine whether a person is suffering from Alzheimer's.

Alzheimer's disease was named for Alois Alzheimer, a German psychiatrist who published a report in 1911 about a woman who showed severe dementia symptoms. Along with his colleagues, he examined the woman's brain following her death and reported the presence of abnormal clumps, which are now called amyloid plaques, along with tangled brain fibers called neurofibrillary tangles. Amyloid plaques, neurofibrillary tangles, and an overall shrinking of brain volume are commonly seen in the brains of Alzheimer's patients. Loss of neurons in the hippocampus is especially severe in advanced Alzheimer's patients. Many research groups are examining the causes of these hallmarks of the disease.

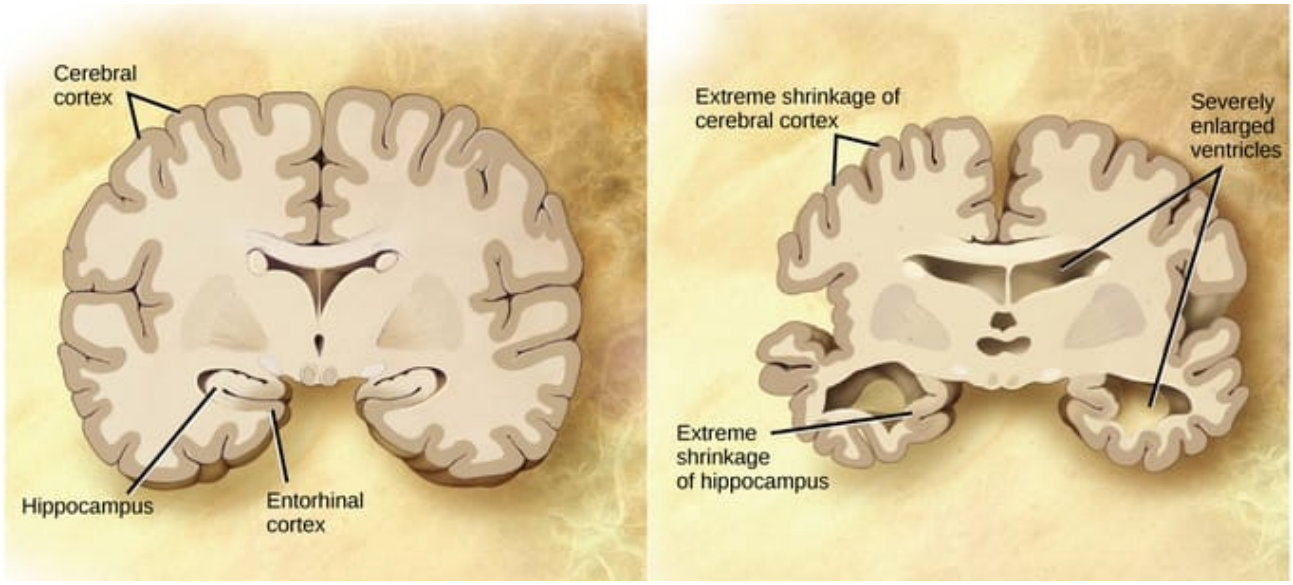


Figure 35.15.1: Alzheimer's disease: Compared to a normal brain (left), the brain from a patient with Alzheimer's disease (right) shows a dramatic neurodegeneration, particularly within the ventricles and hippocampus.

One form of the disease is usually caused by mutations in one of three known genes. This rare form of early-onset Alzheimer's disease affects fewer than five percent of patients with the disease and causes dementia beginning between the ages of 30 and 60. The more prevalent, late-onset form of the disease probably also has a genetic component. One particular gene, apolipoprotein E (APOE) has a variant (E4) that increases a carrier 's probability of developing the disease. Many other genes have been identified that may be involved in the pathology.

Unfortunately, there is no cure for Alzheimer's disease. Current treatments focus on managing the symptoms of the disease. Because decrease in the activity of cholinergic neurons (neurons that use the neurotransmitter acetylcholine) is common in Alzheimer's disease, several drugs used to treat the disease work by increasing acetylcholine neurotransmission, often by inhibiting the enzyme that breaks down acetylcholine in the synaptic cleft. Other clinical interventions focus on behavioral therapies such as psychotherapy, sensory therapy, and cognitive exercises. Since Alzheimer's disease appears to hijack the normal aging process, research into prevention is prevalent.

Parkinson's Disease

Parkinson's disease is also a neurodegenerative disease. It was first characterized by James Parkinson in 1817. Each year, 50,000-60,000 people in the United States are diagnosed with the disease. Parkinson's disease causes the loss of dopamine neurons in the substantia nigra, a midbrain structure that regulates movement. Loss of these neurons causes many symptoms including tremor (shaking of fingers or a limb), slowed movement, speech changes, balance and posture problems, and rigid muscles. The combination of these symptoms often causes a characteristic slow, hunched, shuffling walk. Patients with Parkinson's disease can also exhibit psychological symptoms, such as dementia or emotional problems.



Figure 35.15.1: Parkinson's disease: Parkinson's patients often have a characteristic hunched walk. The disease is likely the result of a combination of genetic and environmental factors.

Although some patients have a form of the disease known to be caused by a single mutation, for most patients, the exact causes of Parkinson's disease remain unknown. The disease probably results from a combination of genetic and environmental factors, similar to Alzheimer's disease. Post-mortem analysis of brains from Parkinson's patients shows the presence of Lewy bodies, abnormal protein clumps, in dopaminergic neurons. The prevalence of these Lewy bodies often correlates with the severity of the disease.

There is no cure for Parkinson's disease; treatment is focused on easing symptoms. One of the most-commonly prescribed drugs for Parkinson's is L-DOPA, which is a chemical that is converted into dopamine by neurons in the brain. This conversion increases the overall level of dopamine neurotransmission and can help compensate for the loss of dopaminergic neurons in the substantia nigra. Other drugs work by inhibiting the enzyme that breaks down dopamine.

Key Points

- Neural death is the main cause behind neurodegenerative disorders.
- Symptoms of neurodegenerative disorders usually depend on the area within the nervous system where neuron deaths take place.
- Alzheimer's disease, characterized by severe dementia, can appear in the form of disruptive memory loss, confusion, difficulty planning or executing tasks, poor judgement, and personality changes.
- A decrease in the activity of cholinergic neurons is commonly seen in patients with Alzheimer's disease.
- In Parkinson's disease, the loss of dopamine neurons results in symptoms that include tremors, slowed movement, speech changes, balance and posture problems, and rigid muscles.
- Neither Alzheimer's nor Parkinson's disease have cures, but there are drug treatments available to control symptoms.

Key Terms

- **neurodegenerative**: of, pertaining to, or resulting in the progressive loss of nerve cells and of neurologic function
- **dementia**: a progressive decline in cognitive function due to damage or disease in the brain beyond what might be expected from normal aging
- **Parkinson's disease**: a degenerative disorder of the central nervous system
- **Alzheimer's disease**: a disorder involving loss of mental functions resulting from brain tissue changes; senile dementia

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35.16: Nervous System Disorders - Neurodevelopmental Disorders - Autism and ADHD

Learning Objectives

- Distinguish between the neurodevelopmental disorders of autism and ADHD

Neurodevelopmental disorders occur when the development of the nervous system is disturbed. There are several different classes of neurodevelopmental disorders. Some, like Down Syndrome, cause intellectual deficits, while others specifically affect communication, learning, or the motor system. Some disorders, such as autism spectrum disorder and attention deficit/hyperactivity disorder, have complex symptoms.

Autism

Autism spectrum disorder (ASD, sometimes just “autism”) is a neurodevelopmental disorder in which severity differs from person to person. Estimates for the prevalence of the disorder have changed rapidly in the past few decades. Current estimates suggest that one in 88 children will develop the disorder. ASD is four times more prevalent in males than females.

A characteristic symptom of ASD is impaired social skills. Children with autism may have difficulty making and maintaining eye contact and reading social cues. They also may have problems feeling empathy for others. Other symptoms of ASD include repetitive motor behaviors (such as rocking back and forth), preoccupation with specific subjects, strict adherence to certain rituals, and unusual language use. Up to 30 percent of patients with ASD develop epilepsy. Patients with some forms of the disorder (e.g., Fragile X syndrome) also have intellectual disability. Because it is a spectrum disorder, other ASD patients are very functional and have good-to-excellent language skills. Many of these patients do not feel that they suffer from a disorder and instead just believe that they process information differently.

Except for some well-characterized, clearly-genetic forms of autism (e.g., Fragile X and Rett Syndrome), the causes of ASD are largely unknown. Variants of several genes correlate with the presence of ASD, but for any given patient, many different mutations in different genes may be required for the disease to develop. At a general level, ASD is thought to be a disease of “incorrect” wiring. Accordingly, brains of some ASD patients lack the same level of synaptic pruning that occurs in non-affected people. There has been some unsubstantiated controversy linking vaccinations and autism. In the 1990s, a research paper linked autism to a common vaccine given to children. This paper was retracted when it was discovered that the author falsified data; follow-up studies showed no connection between vaccines and autism.

Treatment for autism usually combines behavioral therapies and interventions, along with medications to treat other disorders common to people with autism (depression, anxiety, obsessive compulsive disorder). Although early interventions can help mitigate the effects of the disease, there is currently no cure for ASD.

Attention Deficit Hyperactivity Disorder (ADHD)

Approximately three to five percent of children and adults are affected by attention deficit/hyperactivity disorder (ADHD). Like ASD, ADHD is more prevalent in males than females. Symptoms of the disorder include inattention (lack of focus), executive functioning difficulties, impulsivity, and hyperactivity beyond what is characteristic of the normal developmental stage. Some patients do not have the hyperactive component of symptoms and are diagnosed with a subtype of ADHD: attention deficit disorder (ADD). Many people with ADHD also show comorbidity: they develop secondary disorders in addition to ADHD. Examples include depression or obsessive compulsive disorder (OCD).



Figure 35.16.1: Comorbidity with ADHD: Many people with ADHD have one or more other psychological or neurological disorders.

The cause of ADHD is unknown, although research points to a delay and dysfunction in the development of the prefrontal cortex and disturbances in neurotransmission. According to some twin studies, the disorder has a strong genetic component. There are several candidate genes that may contribute to the disorder, but no definitive links have been discovered. Environmental factors, including exposure to certain pesticides, may also contribute to the development of ADHD in some patients. Treatment for ADHD often involves behavioral therapies and the prescription of stimulant medications, which, paradoxically, cause a calming effect in these patients.

Key Points

- Disturbances in the development of the nervous system, genetic or environmental, may lead to neurodevelopmental diseases.
- Individuals affected by autism are believed to have one of many different mutations in genes required for the disease to cause disruptions in the nervous system that are generally observed; however, studies on specifics are still inconclusive.
- In ADHD, a strong genetic component may contribute to the disorder; however, no definitive links have been found.
- Individuals with ADHD may experience other psychological or neurological disorders in addition to their ADHD symptoms; this experience of having more than one disorder is termed comorbidity.
- The cause of both autism and ADHD are unknown and cures are unavailable; however, treatments to alleviate symptoms are accessible.

Key Terms

- **autism**: disorder observed in early childhood with symptoms of abnormal self-absorption, characterised by lack of response to other humans and a limited ability or disinclination to communicate and socialize
- **attention deficit hyperactivity disorder**: a developmental disorder in which a person has a persistent pattern of impulsiveness and inattention, with or without a component of hyperactivity
- **fragile X syndrome**: a particular, genetic syndrome, caused by the excessive repetition of a particular trinucleotide
- **rett syndrome**: a neurodevelopmental disorder of the grey matter of the brain that almost exclusively affects females, but has also been found in male patients
- **comorbidity**: the presence of one or more disorders (or diseases) in addition to a primary disease or disorder
- **neurodevelopmental disorder**: a disorder of brain function that affects emotion, learning ability and memoryand that unfolds as the individual grows

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35.17: Nervous System Disorders - Neurodevelopmental Disorders - Mental Illnesses

Learning Objectives

- Distinguish between the disorders of schizophrenia and depression

Mental illnesses are nervous system disorders that result in problems with thinking, mood, or relating with other people. These disorders are severe enough to affect a person's quality of life and often make it difficult for people to perform the routine tasks of daily living. Debilitating mental disorders plague approximately 12.5 million Americans (about 1 in 17 people) at an annual cost of more than $300 billion. There are several types of mental disorders including schizophrenia, major depression, bipolar disorder, anxiety disorders, post-traumatic stress disorder, and many others. The American Psychiatric Association publishes the Diagnostic and Statistical Manual of Mental Disorders (or DSM), which describes the symptoms required for a patient to be diagnosed with a particular mental disorder. Each newly-released version of the DSM contains different symptoms and classifications as researchers learn more about these disorders, their causes, and how they relate to each other. A more detailed discussion of two mental illnesses, schizophrenia and major depression, is given below.

Schizophrenia

Schizophrenia is a serious and often-debilitating mental illness affecting one percent of the population in the United States. Symptoms of the disease include the inability to differentiate between reality and imagination, inappropriate and unregulated emotional responses, difficulty thinking, and problems with social situations. Symptoms of schizophrenia may be characterized as either "negative" (deficit symptoms) or "positive". Positive symptoms are those that most individuals do not normally experience, but are present in people with schizophrenia. They can include delusions, disordered thoughts and speech, and tactile, auditory, visual, olfactory and gustatory hallucinations, typically regarded as manifestations of psychosis. Negative symptoms are deficits of normal emotional responses or of other thought processes, and commonly include flat or blunted affect and emotion, poverty of speech, inability to experience pleasure, lack of desire to form relationships, and lack of motivation.

Many schizophrenic patients are diagnosed in their late adolescence or early 20s. The development of schizophrenia is thought to involve malfunctioning dopaminergic neurons and may also involve problems with glutamate signaling. Treatment for the disease usually requires anti-psychotic medications that work by blocking dopamine receptors and decreasing dopamine neurotransmission in the brain. This decrease in dopamine can cause Parkinson's disease-like symptoms in some patients. While some classes of anti-psychotics can be quite effective at treating the disease, they are not a cure; most patients must remain medicated for the rest of their lives.

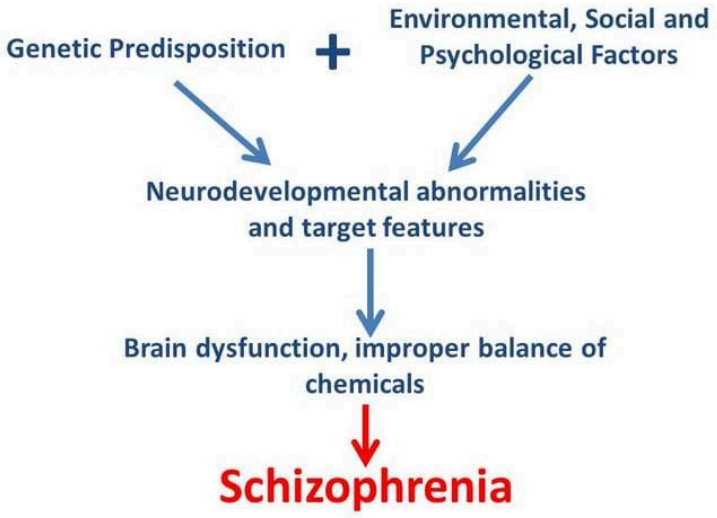


Figure 35.17.1: Schizophrenia: The development of schizophrenia is thought to be caused by malfunctioning dopaminergic neurons, which causes brain dysfunction and an imbalance of chemicals in the brain.

Depression

Major depression (also referred to as just “depression” or “major depressive disorder”) affects approximately 6.7 percent of the adults in the United States each year and is one of the most common mental disorders. To be diagnosed with major depressive disorder, a person must have experienced a severely-depressed mood lasting longer than two weeks along with other symptoms that may include a loss of enjoyment in activities that were previously enjoyed, changes in appetite and sleep schedules, difficulty concentrating, feelings of worthlessness, and suicidal thoughts. The exact causes of major depression are unknown and probably include both genetic and environmental risk factors. Some research supports the “classic monoamine hypothesis,” which suggests that depression is caused by a decrease in norepinephrine and serotonin neurotransmission. One argument against this hypothesis is the fact that some antidepressant medications cause an increase in norepinephrine and serotonin release within a few hours of beginning treatment, but clinical results of these medications are not seen until weeks later. This has led to alternative hypotheses. For example, dopamine may also be decreased in depressed patients, or it may actually be an increase in norepinephrine and serotonin that causes the disease, and antidepressants force a feedback loop that decreases this release.

Treatments for depression include psychotherapy, electroconvulsive therapy, deep-brain stimulation, and prescription medications. Most commonly, individuals undergo some combination of psychotherapy and medication. There are several classes of antidepressant medications that work through different mechanisms. For example, monoamine oxidase inhibitors (MAO inhibitors) block the enzyme that degrades many neurotransmitters (including dopamine, serotonin, norepinephrine), resulting in increased neurotransmitter in the synaptic cleft. Selective serotonin reuptake inhibitors (SSRIs) block the reuptake of serotonin into the presynaptic neuron. This blockage results in an increase in serotonin in the synaptic cleft. Other types of drugs, such as norepinephrine-dopamine reuptake inhibitors and norepinephrine-serotonin reuptake inhibitors, are also used to treat depression.

Key Points

- Complications with thinking, mood, or problems relating to other people are issues that are commonly associated with those affected with neurodevelopmental disorders.
- Malfunctioning dopaminergic neurons and problems with glutamate signaling are thought to be potential causes of schizophrenia.
- Although no definitive answer yet exists, genetic and environmental risk factors are believed to be the main causes of depression.
- Exact cures do not exist for either schizophrenia or depression; however, schizophrenia may be treated with anti-psychotic medications while depression treatments include psychotherapy, electroconvulsive therapy, deep-brain stimulation, and prescription medications.

Key Terms

- **norepinephrine**: a neurotransmitter found in the locus coeruleus which is synthesized from dopamine
- **serotonin**: an indoleamine neurotransmitter that is involved in depression, appetite, etc., and is crucial in maintaining a sense of well-being, security, etc.
- **mental disorder**: any of the various diseases affecting the mind onset by brain damage or genetics
- **schizophrenia**: a psychiatric diagnosis denoting a persistent, often chronic, mental illness variously affecting behavior, thinking, and emotion
- **depression**: in psychotherapy and psychiatry, a period of unhappiness or low morale which lasts longer than several weeks and may include ideation of self-inflicted injury or suicide
- **dopamine**: a neurotransmitter associated with movement, attention, learning, and the brain's pleasure and reward system

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35.18: Nervous System Disorders - Other Neurological Disorders

Learning Objectives

- Distinguish between the neurological disorders of epilepsy and stroke

There are several other neurological disorders that cannot be easily placed into clean-cut categories. These include chronic pain conditions, cancers of the nervous system, epilepsy disorders, and stroke. Epilepsy and stroke are discussed below.

Epilepsy

Estimates suggest that up to three percent of people in the United States will be diagnosed with epilepsy in their lifetime. While there are several different types of epilepsy, all are characterized by recurrent seizures. Epilepsy itself can be a symptom of a brain injury, disease, or other illness. For example, people who have intellectual disability or autism spectrum disorder can experience seizures, presumably because the developmental wiring malfunctions that caused their disorders also put them at risk for epilepsy. For many patients, however, the cause of their epilepsy is never identified and is probably a combination of genetic and environmental factors. Often, seizures can be controlled with anti-convulsant medications. However, for very severe cases, patients may undergo brain surgery to remove the brain area where seizures originate.

Stroke

A stroke results when blood fails to reach a portion of the brain for a long enough time to cause damage. Without the oxygen supplied by blood flow, neurons in this brain region die. This neuronal death can cause many different symptoms, depending on the brain area affected, including headache, muscle weakness or paralysis, speech disturbances, sensory problems, memory loss, and confusion. Stroke is often caused by blood clots, but can also be caused by the bursting of a weak blood vessel. Strokes are extremely common; they are the third most-common cause of death in the United States. On average one person experiences a stroke every 40 seconds in the United States. Approximately 75 percent of strokes occur in people older than 65. Risk factors for stroke include high blood pressure, diabetes, high cholesterol, and a family history of stroke. Smoking doubles the risk of stroke. Treatment following a stroke can include blood pressure medication (to prevent future strokes) and (sometimes intense) physical therapy.

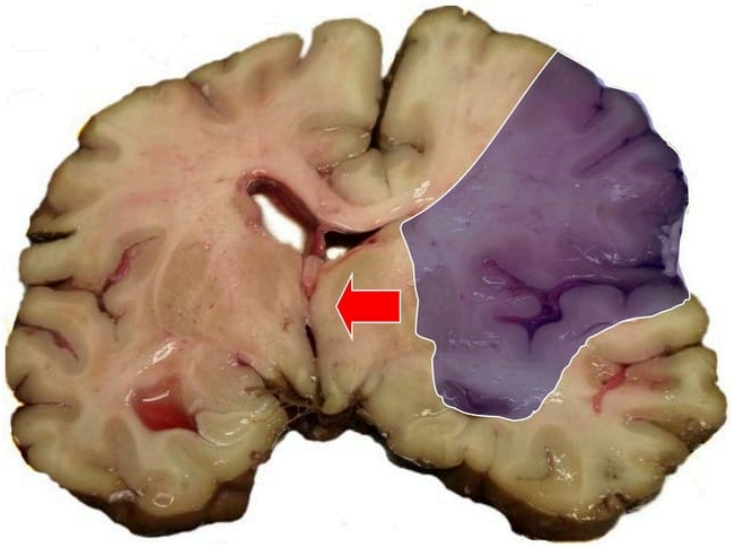


Figure 35.18.1: Stroke effects on the brain: A cerebral infarction, shaded in blue, occurs after a stroke when blood fails to reach a portion of the brain long enough to cause damage. The red arrow depicts the midline shift that occurs in the brain, which is also caused by a stroke.

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Key Points

- Although all types of epilepsy are characterized by recurrent seizures, the disorder itself can be a symptom of various factors, both genetic and environmental; the specific causes of epilepsy remain to be identified.
- Neural death, caused by a lack of oxygen for a prolonged period of time, is the main cause of stroke.
- Anti-convulsant medications and brain removal surgery are treatments for epilepsy, while anti-clotting medication and physical therapy are used in the treatment of stroke.
- Anti-convulsant medications and brain removal surgery are treatments for epilepsy while anti-clotting medication and physical therapy are used in the treatment of stroke.

Key Terms

- **epilepsy**: a medical condition in which the sufferer experiences seizures (or convulsions) and blackouts
- **stroke**: the loss of brain function arising when the blood supply to the brain is suddenly interrupted

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36: SENSORY SYSTEMS

36.1: Sensory Processes - Reception

36.2: Sensory Processes - Transduction and Perception

36.3: Somatosensation - Somatosensory Receptors

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36.8: Hearing and Vestibular Sensation - Sound

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36.11: Hearing and Vestibular Sensation - Balance and Determining Equilibrium

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36.13: Vision - Anatomy of the Eye

36.14: Vision - Transduction of Light

36.15: Vision - Visual Processing

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36.1: Sensory Processes - Reception

Learning Objectives

- Explain the process of sensory reception

Introduction to Sensation

In more advanced animals, the senses are constantly at work, making the animal aware of stimuli, such as light or sound or the presence of a chemical substance in the external environment, while monitoring information about the organism's internal environment. All bilaterally symmetric animals have a sensory system. The development of any species ' sensory system has been driven by natural selection; thus, sensory systems differ among species according to the demands of their environments. For example, the shark, unlike most fish predators, is electrosensitive (i.e., sensitive to electrical fields produced by other animals in its environment). While it is helpful to this underwater predator, electrosensitivity is a sense not found in most land animals.

Senses provide information about the body and its environment. Humans have five special senses: olfaction (smell), gustation (taste), equilibrium (balance and body position), vision, and hearing. Additionally, we possess general senses, also called somatosensation, which respond to stimuli like temperature, pain, pressure, and vibration. Vestibular sensation, which is an organism's sense of spatial orientation and balance, proprioception (position of bones, joints, and muscles), and the sense of limb position that is used to track kinesthesia (limb movement) are part of somatosensation. Although the sensory systems associated with these senses are very different, all share a common function: to convert a stimulus (light, sound, or the position of the body) into an electrical signal in the nervous system. This process is called sensory transduction.

There are two broad types of cellular systems that perform sensory transduction. In one, a neuron works with a sensory receptor, a cell, or cell process that is specialized to engage with and detect a specific stimulus. Stimulation of the sensory receptor activates the associated afferent neuron, which carries information about the stimulus to the central nervous system. In the second type of sensory transduction, a sensory nerve ending responds to a stimulus in the internal or external environment; this neuron constitutes the sensory receptor. Free nerve endings can be stimulated by several different stimuli, thus showing little receptor specificity. For example, pain receptors in your gums and teeth may be stimulated by temperature changes, chemical stimulation, or pressure.

Reception

The first step in sensation is reception: the activation of sensory receptors by stimuli such as mechanical stimuli (being bent or squished, for example), chemicals, or temperature. The receptor can then respond to the stimuli. The region in space in which a given sensory receptor can respond to a stimulus, be it far away or in contact with the body, is that receptor's receptive field. Think for a moment about the differences in receptive fields for the different senses. For the sense of touch, a stimulus must come into contact with body. For the sense of hearing, a stimulus can be a moderate distance away. For vision, a stimulus can be very far away; for example, the visual system perceives light from stars at enormous distances.

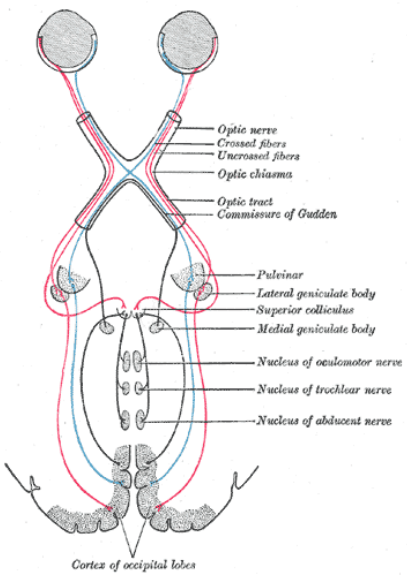


Figure 36.1.1: Visual sensory system: This scheme shows the flow of information from the eyes to the central connections of the optic nerves and optic tracts, to the visual cortex. Area V1 is the region of the brain which is engaged in vision.

Key Points

- Reception is the process of activating a sensory receptor by a stimuli.
- Sensory transduction is the process of converting that sensory signal to an electrical signal in the sensory neuron.
- The process of reception is dependent on the stimuli itself, the type of receptor, receptor specificity, and the receptive field, which can vary depending on the receptor type.

Key Terms

- **somatosensation**: general senses which respond to stimuli like temperature, pain, pressure, and vibration
- **reception**: the act or ability to receive signals from stimuli

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36.2: Sensory Processes - Transduction and Perception

Learning Objectives

- Explain how stimuli are converted to signals that are carried to the central nervous system

Transduction

The most fundamental function of a sensory system is the translation of a sensory signal to an electrical signal in the nervous system. This takes place at the sensory receptor. The change in electrical potential that is produced is called the receptor potential. How is sensory input, such as pressure on the skin, changed to a receptor potential? As an example, a type of receptor called a mechanoreceptor possesses specialized membranes that respond to pressure. Disturbance of these dendrites by compressing them or bending them opens gated ion channels in the plasma membrane of the sensory neuron, changing its electrical potential. In the nervous system, a positive change of a neuron's electrical potential (also called the membrane potential), depolarizes the neuron. Receptor potentials are graded potentials: the magnitude of these graded (receptor) potentials varies with the strength of the stimulus. If the magnitude of depolarization is sufficient (that is, if membrane potential reaches a threshold), the neuron will fire an action potential. In most cases, the correct stimulus impinging on a sensory receptor will drive membrane potential in a positive direction, although for some receptors, such as those in the visual system, this is not always the case.

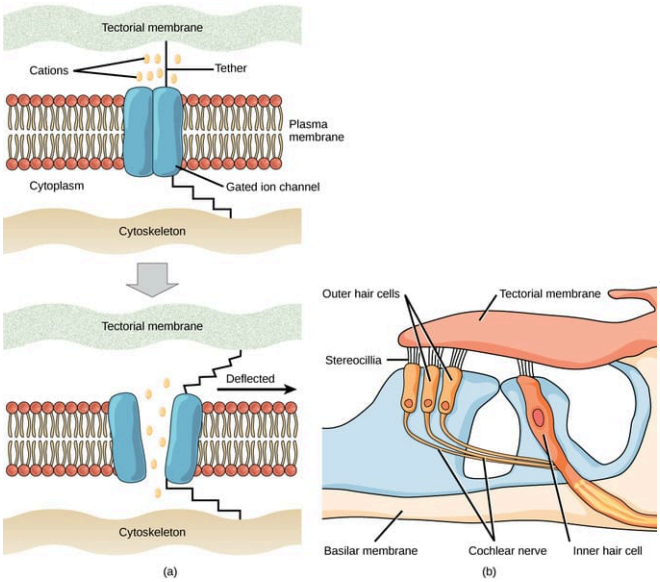


Figure 36.2.1: Mechanoreceptor activation: (a) Mechanosensitive ion channels are gated ion channels that respond to mechanical deformation of the plasma membrane. A mechanosensitive channel is connected to the plasma membrane and the cytoskeleton by hair-like tethers. When pressure causes the extracellular matrix to move, the channel opens, allowing ions to enter or exit the cell. (b) Stereocilia in the human ear are connected to mechanosensitive ion channels. When a sound causes the stereocilia to move, mechanosensitive ion channels transduce the signal to the cochlear nerve.

Sensory receptors for the various senses work differently from each other. They are specialized according to the type of stimulus they sense; thus, they have receptor specificity. For example, touch receptors, light receptors, and sound receptors are each activated by different stimuli. Touch receptors are not sensitive to light or sound; they are sensitive only to touch or pressure. However, stimuli may be combined at higher levels in the brain, as happens with olfaction, contributing to our sense of taste.

Encoding and Transmission of Sensory Information

Four aspects of sensory information are encoded by sensory systems: the type of stimulus, the location of the stimulus in the

receptive field, the duration of the stimulus, and the relative intensity of the stimulus. Thus, action potentials transmitted over a sensory receptor's afferent axons encode one type of stimulus. This segregation of the senses is preserved in other sensory circuits. For example, auditory receptors transmit signals over their own dedicated system. The electrical activity in the axons of the auditory receptors will be interpreted by the brain as an auditory stimulus: a sound.

The intensity of a stimulus is often encoded in the rate of action potentials produced by the sensory receptor. Thus, an intense stimulus will produce a more rapid train of action potentials. Reducing the stimulus will likewise slow the rate of production of action potentials. A second way in which intensity is encoded is by the number of receptors activated. An intense stimulus might initiate action potentials in a large number of adjacent receptors, while a less intense stimulus might stimulate fewer receptors. Integration of sensory information begins as soon as the information is received in the central nervous system.

Perception

Perception is an individual's interpretation of a sensation. Although perception relies on the activation of sensory receptors, perception happens, not at the level of the sensory receptor, but at the brain level. The brain distinguishes sensory stimuli through a sensory pathway: action potentials from sensory receptors travel along neurons that are dedicated to a particular stimulus.

All sensory signals, except those from the olfactory system, are transmitted though the central nervous system: they are routed to the thalamus and to the appropriate region of the cortex. The thalamus is a structure in the forebrain that serves as a clearinghouse and relay station for sensory (as well as motor) signals. When the sensory signal exits the thalamus, it is conducted to the specific area of the cortex dedicated to processing that particular sense.

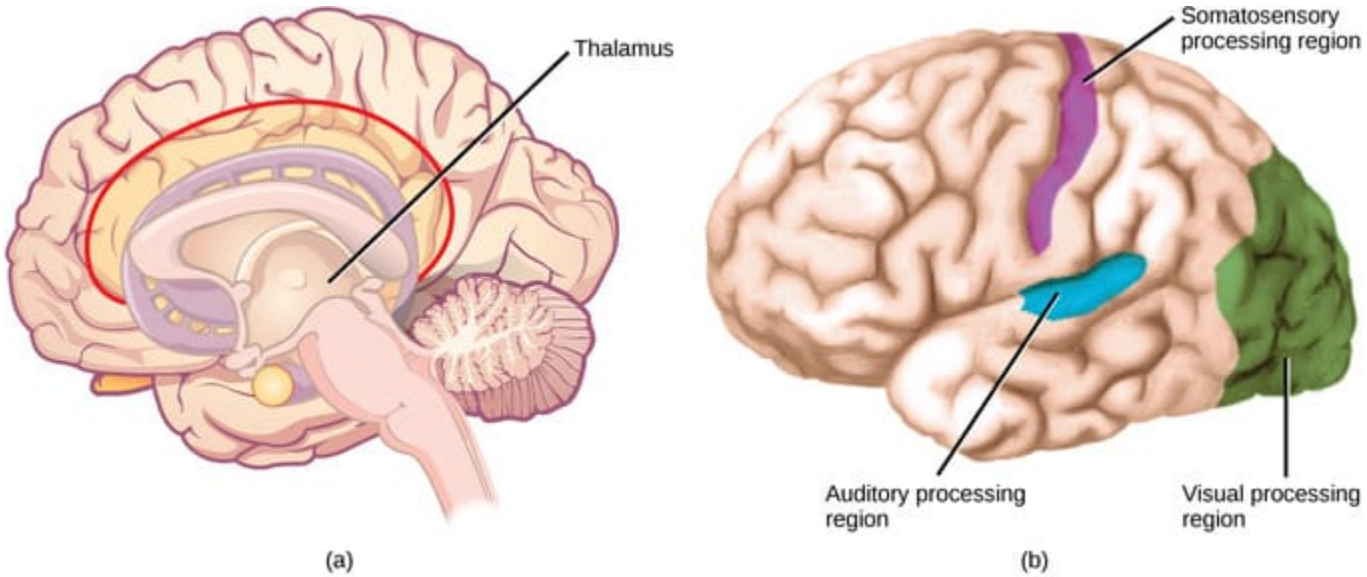


Figure 36.2.1: Sensation processing: The brain has dedicated areas to the processing of stimuli, including: (a) thalamus and (b) the auditory, visual and somatosensory processing regions.

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Key Points

- Sensory signals are converted to electrical signals via depolarization of sensory neuron membranes upon stimulus of the receptor, which causes opening of gated ion channels that cause the membrane potential to reach its threshold.
- The receptor potentials are classified as graded potentials; the magnitude of these potentials is dependent on the strength of the stimulus.
- The sensory system shows receptor specificity; although stimuli can be combined in processing regions of the brain, a specific receptor will only be activated by its specific stimulus.
- The brain contains specific processing regions (such as the somatosensory, visual, and auditory regions) that are dedicated to processing the information which has previously passed through the thalamus, the 'clearinghouse and relay station' for both sensory and motor signals.
- The four major components of encoding and transmitting sensory information include: the type of stimulus, the stimulus location within the receptive field, the duration, and the intensity of the stimulus.

Key Terms

- **membrane potential**: the difference in electrical potential across the enclosing membrane of a cell
- **action potential**: a short term change in the electrical potential that travels along a cell
- **transduction**: the translation of a sensory signal in the sensory system to an electrical signal in the nervous system

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36.3: Somatosensation - Somatosensory Receptors

Learning Objectives

- Describe the structure and function of mechanoreceptors

Somatosensory Receptors

Sensory receptors are classified into five categories: mechanoreceptors, thermoreceptors, proprioceptors, pain receptors, and chemoreceptors. These categories are based on the nature of the stimuli that each receptor class transduces. Mechanoreceptors in the skin are described as encapsulated or unencapsulated. A free nerve ending is an unencapsulated dendrite of a sensory neuron; they are the most common nerve endings in skin. Free nerve endings are sensitive to painful stimuli, to hot and cold, and to light touch. They are slow to adjust to a stimulus and so are less sensitive to abrupt changes in stimulation.

Mechanoreceptors

There are three classes of mechanoreceptors: tactile, proprioceptors, and baroreceptors. Mechanoreceptors sense stimuli due to physical deformation of their plasma membranes. They contain mechanically-gated ion channels whose gates open or close in response to pressure, touch, stretching, and sound. There are four primary tactile mechanoreceptors in human skin: Merkel's disks, Meissner's corpuscles, Ruffini endings, and Pacinian corpuscle; two are located toward the surface of the skin and two are located deeper. A fifth type of mechanoreceptor, Krause end bulbs, are found only in specialized regions.

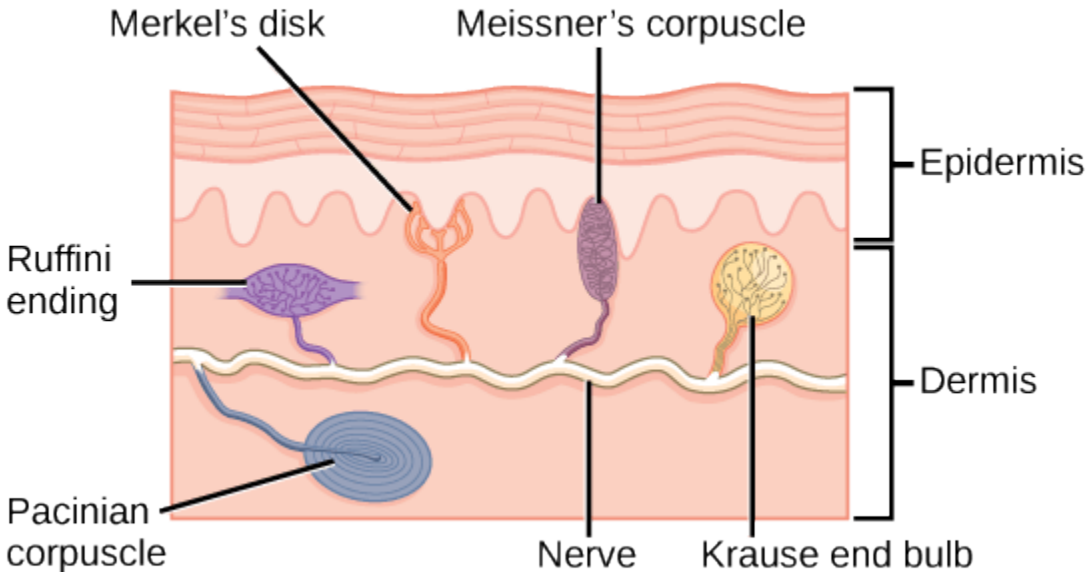


Figure 36.3.1: Primary mechanoreceptors: Four of the primary mechanoreceptors in human skin are shown. Merkel's disks, which are unencapsulated, respond to light touch. Meissner's corpuscles, Ruffini endings, Pacinian corpuscles, and Krause end bulbs are all encapsulated. Meissner's corpuscles respond to touch and low-frequency vibration. Ruffini endings detect stretch, deformation within joints, and warmth. Pacinian corpuscles detect transient pressure and high-frequency vibration. Krause end bulbs detect cold.

Merkel's disks are found in the upper layers of skin near the base of the epidermis, both in skin that has hair and on glabrous skin; that is, the hairless skin found on the palms and fingers, the soles of the feet, and the lips of humans and other primates. Merkel's disks are densely distributed in the fingertips and lips. They are slow-adapting, unencapsulated nerve endings, which respond to light touch. Light touch, also known as discriminative touch, is a light pressure that allows the location of a stimulus to be pinpointed. The receptive fields of Merkel's disks are small, with well-defined borders. That makes them very sensitive to edges; they come into use in tasks such as typing on a keyboard.

Meissner's corpuscles, also known as tactile corpuscles, are found in the upper dermis, but they project into the epidermis. They are found primarily in the glabrous skin on the fingertips and eyelids. They respond to fine touch and pressure, but they also respond to low-frequency vibration or flutter. They are rapidly- adapting, fluid-filled, encapsulated neurons with small, well-defined borders which are responsive to fine details. Merkel's disks and Meissner's corpuscles are not as plentiful in the palms as they are in the fingertips.

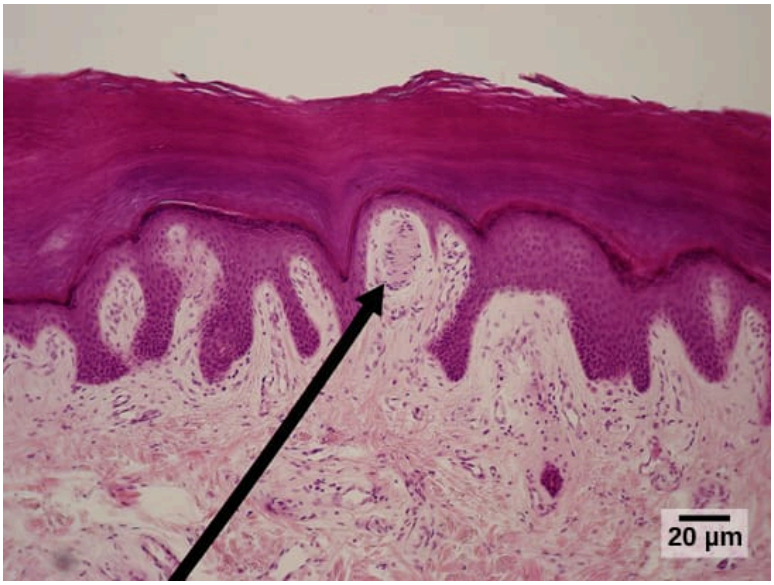


Figure 36.3.1: Meissner corpuscles: Meissner corpuscles in the fingertips, such as the one viewed here using bright field light microscopy, allow for touch discrimination of fine detail.

Deeper in the dermis, near the base, are Ruffini endings, which are also known as bulbous corpuscles. They are found in both glabrous and hairy skin. These are slow-adapting, encapsulated mechanoreceptors that detect skin stretch and deformations within joints; they provide valuable feedback for gripping objects and controlling finger position and movement. Thus, they also contribute to proprioception and kinesthesia. Ruffini endings also detect warmth. Note that these warmth detectors are situated deeper in the skin than are the cold detectors. It is not surprising, then, that humans detect cold stimuli before they detect warm stimuli.

Pacinian corpuscles, located deep in the dermis of both glabrous and hairy skin, are structurally similar to Meissner's corpuscles. They are found in the bone periosteum, joint capsules, pancreas and other viscera, breast, and genitals. They are rapidly-adapting mechanoreceptors that sense deep, transient (not prolonged) pressure, and high-frequency vibration. Pacinian receptors detect pressure and vibration by being compressed which stimulates their internal dendrites. There are fewer Pacinian corpuscles and Ruffini endings in skin than there are Merkel's disks and Meissner's corpuscles.

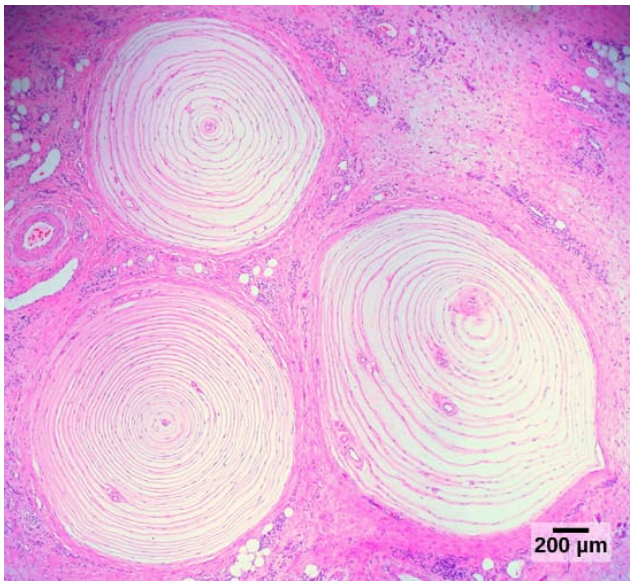


Figure 36.3.1: Pacinian corpuscles: Pacinian corpuscles, such as these visualized using bright field light microscopy, detect pressure (touch) and high-frequency vibration.

Key Points

- The four major types of tactile mechanoreceptors include: Merkel's disks, Meissner's corpuscles, Ruffini endings, and Pacinian corpuscles.
- Merkel's disk are slow-adapting, unencapsulated nerve endings that respond to light touch; they are present in the upper layers of skin that has hair or is glabrous.
- Meissner's corpuscles are rapidly-adapting, encapsulated neurons that responds to low-frequency vibrations and fine touch; they are located in the glabrous skin on fingertips and eyelids.
- Ruffini endings are slow adapting, encapsulated receptors that respond to skin stretch and are present in both the glabrous and hairy skin.
- -Pacinian corpuscles are rapidly-adapting, deep receptors that respond to deep pressure and high-frequency vibration.

Key Terms

- **dendrite**: branched projections of a neuron that conduct the impulses received from other neural cells to the cell body
- **glabrous**: smooth, hairless, bald

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36.4: Somatosensation - Integration of Signals from Mechanoreceptors

Learning Objectives

- Describe how the density of mechanoreceptors affects the receptive field

Integration of Signals from Mechanoreceptors

The configuration of the different types of receptors working in concert in the human skin results in a very refined sense of touch. The nociceptive receptors (those that detect pain) are located near the surface. Small, finely-calibrated mechanoreceptors (Merkel's disks and Meissner's corpuscles) are located in the upper layers and can precisely localize even gentle touch. The large mechanoreceptors (Pacinian corpuscles and Ruffini endings) are located in the lower layers and respond to deeper touch. Consider that the deep pressure that reaches those deeper receptors would not need to be finely localized. Both the upper and lower layers of the skin hold rapidly- and slowly-adapting receptors. Both primary somatosensory cortex and secondary cortical areas are responsible for processing the complex picture of stimuli transmitted from the interplay of mechanoreceptors.

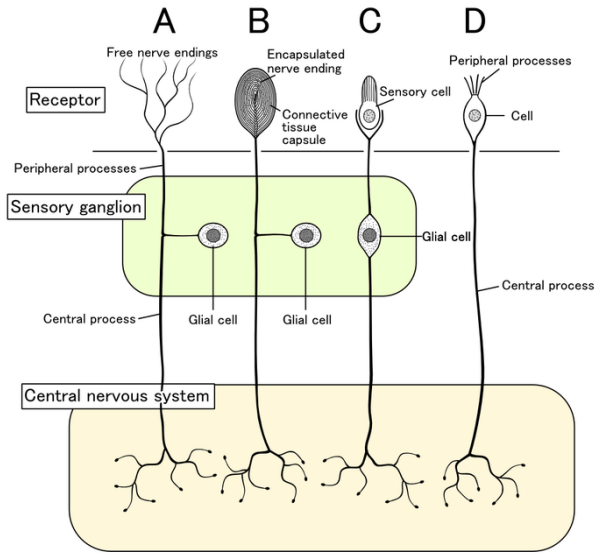


Figure 36.4.1: Sensory receptor structure: Structure of four different types of sensory receptors found within the sensory system.

Density of Mechanoreceptors

In the somatosensory system, receptive fields are regions of the skin or of internal organs. During the transmission of sensory information from these fields, the signals must be conveyed to the nervous system. The mechanoreceptors are activated, the signal is conveyed, and then processed. Some types of mechanoreceptors have large receptive fields, while others have smaller ones. Large receptive fields allow the cell to detect changes over a wider area, but lead to a less-precise perception. Touch receptors are denser in glabrous skin (the type found on human fingertips and lips, for example), which is typically more sensitive and is thicker than hairy skin (4 to 5 mm versus 2 to 3 mm). Thus, the fingers, which require the ability to detect fine detail, have many, densely-packed (up to 500 per cubic cm) mechanoreceptors with small receptive fields (around 10 square mm), while the back and legs, for example, have fewer receptors with large receptive fields. Receptors with large receptive fields usually have a "hot spot": an area within the receptive field (usually in the center, directly over the receptor) where stimulation produces the most intense response. Tactile-sense-related cortical neurons have receptive fields on the skin that can be modified by experience or by injury to sensory nerves, resulting in changes in the field's size and position. In general, these neurons have relatively large receptive fields (much larger than those of dorsal root ganglion cells). However, the neurons are able to discriminate fine detail

due to patterns of excitation and inhibition relative to the field, which leads to spatial resolution.

The relative density of pressure receptors in different locations on the body can be demonstrated experimentally using a two-point discrimination test. In this demonstration, two sharp points, such as two thumbtacks, are brought into contact with the subject's skin (though not hard enough to cause pain or break the skin). The subject reports if they feel one point or two points. If the two points are felt as one point, it can be inferred that the two points are both in the receptive field of a single sensory receptor. If two points are felt as two separate points, each is in the receptive field of two separate sensory receptors. The points could then be moved closer and re-tested until the subject reports feeling only one point. The size of the receptive field of a single receptor could be estimated from that distance.

Key Points

- The various types of receptors, nociceptors, mechanoreceptors (both small and large), thermoreceptors, chemoreceptors, and proprioreceptors, work together to ensure that complex stimuli are transmitted properly to the brain for processing.
- The distribution of mechanoreceptors within the body can affect how stimuli are perceived; this is dependent on the size of the receptive field and whether single or multiple sensory receptors are activated.
- A large receptive field allows for detection of stimuli over a wide area, but can result in less precise detection; a small receptive field allows for detection of stimuli over a small area, which results in more precise detection.
- The two-point discrimination test can be used to determine the density of receptors within various locations by measuring whether a two-point stimulus (such as thumb tacks) is detected as one or two points.

Key Terms

- **mechanoreceptor**: any receptor that provides an organism with information about mechanical changes in its environment, such as movement, tension and pressure

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36.5: Somatosensation - Thermoreception

Learning Objectives

- Describe the various types of receptors used for thermoreception: Krause end bulbs, Ruffini endings, free nerve endings

Thermoreception

Thermoception or thermoreception is the sense by which an organism perceives temperatures. The details of how temperature receptors work are still being investigated. Mammals have at least two types of sensors: those that detect heat (i.e., temperatures above body temperature) and those that detect cold (i.e., temperatures below body temperature). A thermoreceptor is a sensory receptor or, more accurately, the receptive portion of a sensory neuron that codes absolute and relative changes in temperature, primarily within the innocuous range. The adequate stimulus for a warm receptor is warming, which results in an increase in their action potential discharge rate; cooling results in a decrease in warm receptor discharge rate. For cold receptors, their firing rate increases during cooling and decreases during warming. The types of receptors capable of detecting changes in temperature can vary.

Types of Thermoreceptors: Capsule Receptors

Some of the receptors that exhibit the ability to detect changes in temperature include Krause end bulbs and Ruffini endings. Krause end bulbs are defined by cylindrical or oval bodies consisting of a capsule that is formed by the expansion of the connective-tissue sheath, containing an axis-cylinder core. End-bulbs are found in the conjunctiva of the eye, in the mucous membrane of the lips and tongue, and in the epineurium of nerve trunks. They are also found in the penis and the clitoris; hence, the name of genital corpuscles. In these locations, they have a mulberry-like appearance, being constricted by connective-tissue septa into two to six knob-like masses.

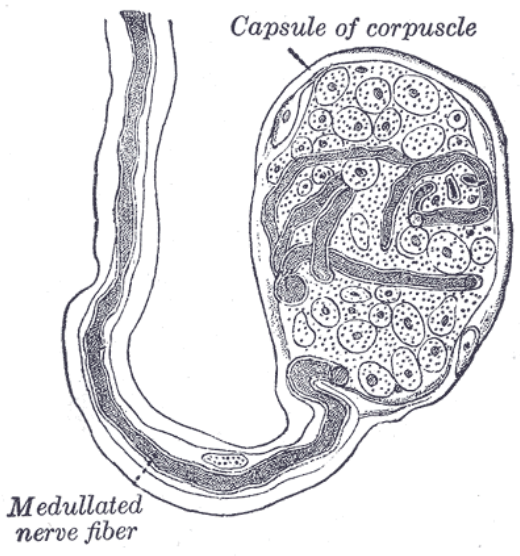


Figure 36.5.1: Krause end bulb: A drawing of a Krause end bulb receptor which can detect cold.

The Ruffini endings, enlarged dendritic endings with elongated capsules, can act as thermoreceptors. This spindle-shaped receptor is sensitive to skin stretch, contributing to the kinesthetic sense of and control of finger position and movement. Ruffini corpuscles respond to sustained pressure and show very little adaptation. Ruffinian endings are located in the deep layers of the skin where they register mechanical deformation within joints as well as continuous pressure states.They also act as thermoreceptors that respond for an extended period; in case of deep burn, there will be no pain as these receptors will be burned off.

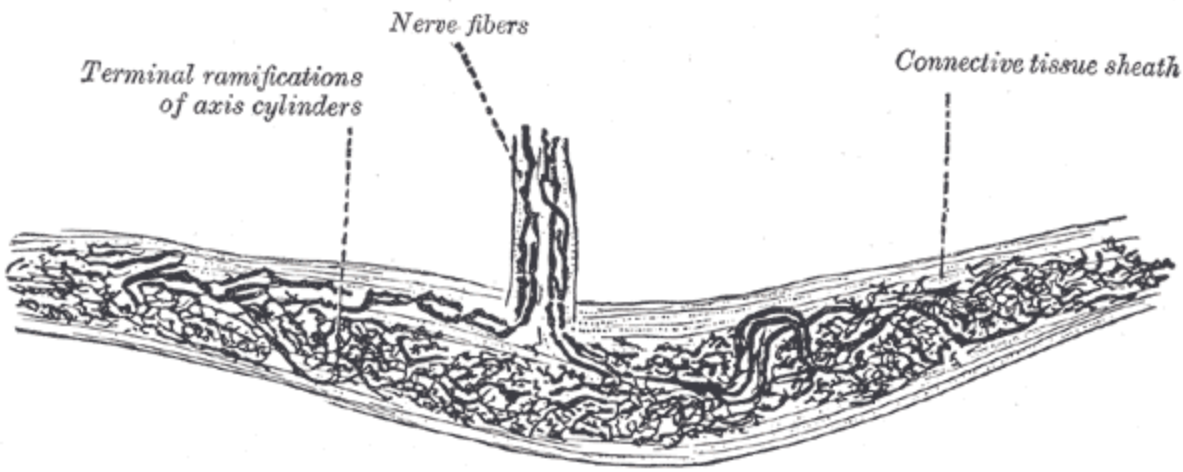


Figure 36.5.1: Ruffini endings: A drawing of a Ruffini ending receptor which can detect warmth.

In addition to Krause end bulbs that detect cold and Ruffini endings that detect warmth, there are different types of cold receptors on free nerve endings.

Types of Thermoreceptors: Free Nerve Endings

There are thermoreceptors that are located in the dermis, skeletal muscles, liver, and hypothalamus that are activated by different temperatures. These thermoreceptors, which have free nerve endings, include only two types of thermoreceptors that signal innocuous warmth and cooling respectively in our skin. The warm receptors show a maximum sensitivity at ~ 45°C, signal temperatures between 30 and 45°C, and cannot unambiguously signal temperatures higher than 45°C; they are unmyelinated. The cold receptors have their maximum sensitivity at ~ 27°C, signal temperatures above 17°C, and some consist of lightly-myelinated fibers, while others are unmyelinated. Our sense of temperature comes from the comparison of the signals from the warm and cold receptors. Thermoreceptors are poor indicators of absolute temperature, but are very sensitive to changes in skin temperature.

The Thermoreceptor Pathway

The thermoreceptor pathway in the brain runs from the spinal cord through the thalamus to the primary somatosensory cortex. Warmth and cold information from the face travels through one of the cranial nerves to the brain. You know from experience that a tolerably cold or hot stimulus can quickly progress to a much more intense stimulus that is no longer tolerable. Any stimulus that is too intense can be perceived as pain because temperature sensations are conducted along the same pathways that carry pain sensations.

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Key Points

- Thermoreceptors can include: Krause end bulbs, which detect cold and are defined by capsules; Ruffini endings, which detect warmth and are defined by enlarged dendritic endings; and warm and cold receptors present on free nerve endings which can detect a range of temperature.
- The cold receptors present on free nerve endings, that can be either lightly-myelinated or unmyelinated, have a maximum sensitivity at ~ 27°C and will signal temperatures above 17°C.
- The warm receptors present on free nerve endings are unmyelinated fibers that have a maximum senstivity of ~45°C and will signal temperature above 30°C.

Key Terms

- **thermoreceptor**: a nerve cell that is sensitive to changes in temperature
- **somatosensory**: of or pertaining to the perception of sensory stimuli produced by the skin or internal organs

- **epineurium**: the connective tissue framework and sheath of a nerve which bind together the nerve bundles, each of which has its own special sheath, or perineurium

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36.6: Taste and Smell - Tastes and Odors

Learning Objectives

- Explain the interaction of taste and odor

Tastes and Odors

Both taste and odor stimuli are molecules taken in from the environment. The primary tastes detected by humans are sweet, sour, bitter, salty, and umami. The first four tastes need little explanation. The identification of umami as a fundamental taste occurred fairly recently. It was identified in 1908 by Japanese scientist Kikunae Ikeda while he worked with seaweed broth, but it was not widely accepted as a taste that could be physiologically distinguished until many years later. The taste of umami, also known as savoriness, is attributable to the taste of the amino acid L-glutamate. In fact, monosodium glutamate, or MSG, is often used in cooking to enhance the savory taste of certain foods. The adaptive value of being able to distinguish umami is that savory substances tend to be high in protein.

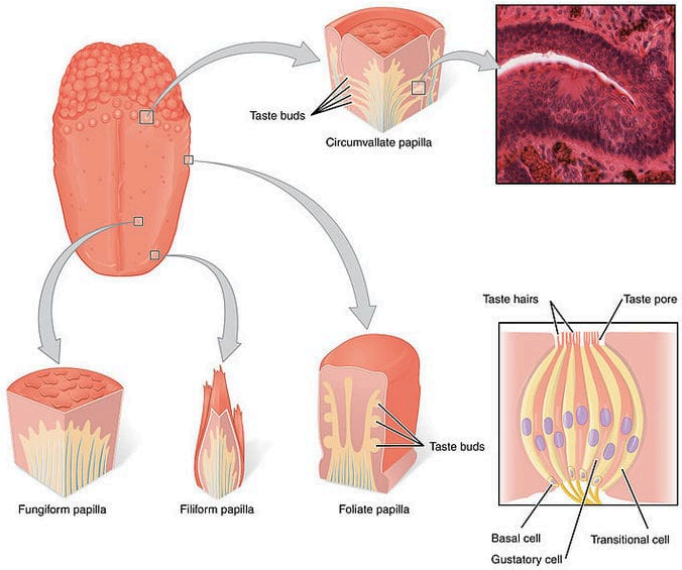


Figure 36.6.1: Uniform Distribution of Taste Receptors: Humans detect taste using receptors called taste buds. Each of these receptors is specially adapted to determine one type of taste sensation. Recent evidence suggests that taste receptors are uniformly distributed across the tongue; thus, the traditional tongue map is no longer valid.

All odors that we perceive are molecules in the air we breathe. If a substance does not release molecules into the air from its surface, it has no smell. If a human or other animal does not have a receptor that recognizes a specific molecule, then that molecule has no smell. Humans have about 350 olfactory receptor subtypes that work in various combinations to allow us to sense about 10,000 different odors. Compare that to mice, for example, which have about 1,300 olfactory receptor types and, therefore, probably sense many more odors.

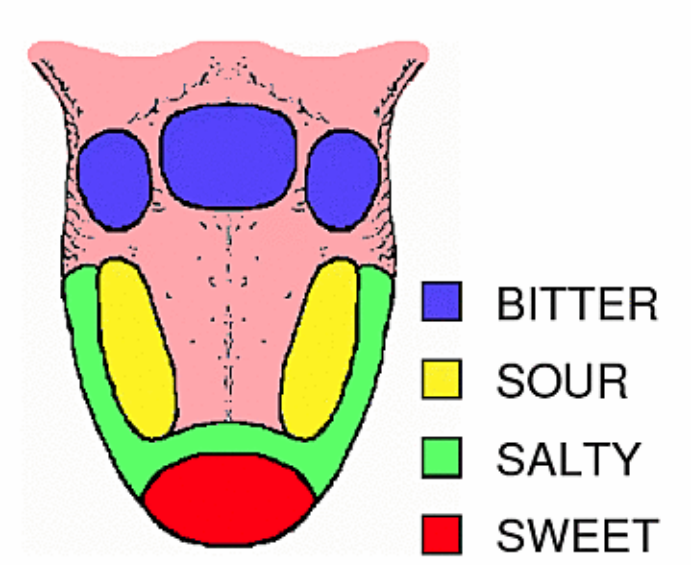


Figure 36.6.1: Uniform distribution of taste receptors (the myth of the tongue map): Humans detect taste using receptors called taste buds. Each of these receptors is specially adapted to determine one type of taste sensation. Recent evidence suggests that taste receptors are uniformly distributed across the tongue; thus, this traditional tongue map is no longer valid.

The senses of smell and taste combine at the back of the throat. When you taste something before you smell it, the smell lingers internally up to the nose causing you to smell it. Both smell and taste use chemoreceptors, which essentially means they are both sensing the chemical environment. This chemoreception in regards to taste, occurs via the presence of specialized taste receptors within the mouth that are referred to as taste cells and are bundled together to form taste buds. These taste buds, located in papillae which are found across the tongue, are specific for the five modalities: salt, sweet, sour, bitter and umami. These receptors are activated when their specific stimulus (i.e. sweet or salt molecules) is present and signals to the brain.

In addition to the activation of the taste receptors, there are similar receptors within the nose that coordinates with activation of the taste receptors. When you eat something, you can tell the difference between sweet and bitter. It is the sense of smell that is used to distinguish the difference. Although humans commonly distinguish taste as one sense and smell as another, they work together to create the perception of flavor. A person's perception of flavor is reduced if he or she has congested nasal passages.

Key Points

- Humans can taste sweet, sour, bitter, salty, and umami; umami is the savoriness of certain foods that are commonly high in protein.
- Odors come from molecules in the air that stimulate receptors in the nose; if an organism does not have a receptor for that particular odor molecule, for that organism, the odor has no smell.
- The senses of smell and taste are directly related because they both use the same types of receptors.
- If one's sense of smell is not functional, then the sense of taste will also not function because of the relationship of the receptors.

Key Terms

- **umami**: one of the five basic tastes, the savory taste of foods such as seaweed, cured fish, aged cheeses and meats
- **olfactory**: concerning the sense of smell
- **receptor**: a protein on a cell wall that binds with specific molecules so that they can be absorbed into the cell in order to control certain functions

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36.7: Taste and Smell - Reception and Transduction

Learning Objectives

- Describe the process by which tastes and odors are sensed

Reception and Transduction

Odorants (odor molecules) enter the nose and dissolve in the olfactory epithelium, the mucosa at the back of the nasal cavity. The olfactory epithelium is a collection of specialized olfactory receptors in the back of the nasal cavity that spans an area about 5 cm^2 in humans. Recall that sensory cells are neurons. An olfactory receptor, which is a dendrite of a specialized neuron, responds when it binds certain molecules inhaled from the environment by sending impulses directly to the olfactory bulb of the brain. Humans have about 12 million olfactory receptors distributed among hundreds of different receptor types that respond to different odors. Twelve million seems like a large number of receptors, but compare that to other animals: rabbits have about 100 million, most dogs have about 1 billion, and bloodhounds (dogs selectively bred for their sense of smell) have about 4 billion.

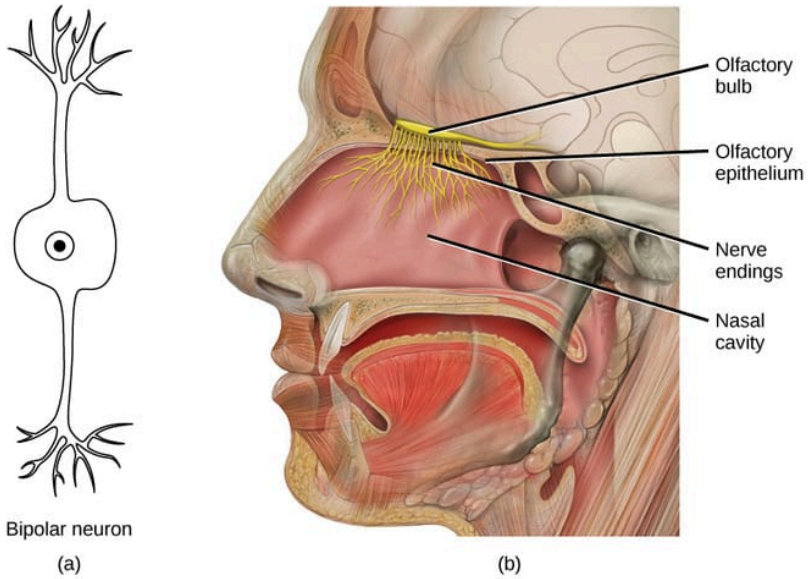


Figure 36.7.1: Human olfactory system: In the human olfactory system, (a) bipolar olfactory neurons extend from (b) the olfactory epithelium, where olfactory receptors are located, to the olfactory bulb.

Olfactory neurons are bipolar neurons (neurons with two processes from the cell body). Each neuron has a single dendrite buried in the olfactory epithelium; extending from this dendrite are 5 to 20 receptor-laden, hair-like cilia that trap odorant molecules. The sensory receptors on the cilia are proteins. It is the variations in their amino acid chains that make the receptors sensitive to different odorants. Each olfactory sensory neuron has only one type of receptor on its cilia. The receptors are specialized to detect specific odorants, so the bipolar neurons themselves are specialized. When an odorant binds with a receptor that recognizes it, the sensory neuron associated with the receptor is stimulated. Olfactory stimulation is the only sensory information that directly reaches the cerebral cortex, whereas other sensations are relayed through the thalamus.

Taste and Smell

Detecting a taste (gustation) is fairly similar to detecting an odor (olfaction), given that both taste and smell rely on chemical receptors being stimulated by certain molecules. The primary organ of taste is the taste bud. A taste bud is a cluster of gustatory receptors (taste cells) that are located within the bumps on the tongue called papillae (singular: papilla). There are several structurally-distinct papillae. Filiform papillae, which are located across the tongue, are tactile, providing friction that helps the tongue move substances; they contain no taste cells. In contrast, fungiform papillae, which are located mainly on the anterior

two-thirds of the tongue, each contain one to eight taste buds; they also have receptors for pressure and temperature. The large circumvallate papillae contain up to 100 taste buds and form a V near the posterior margin of the tongue.

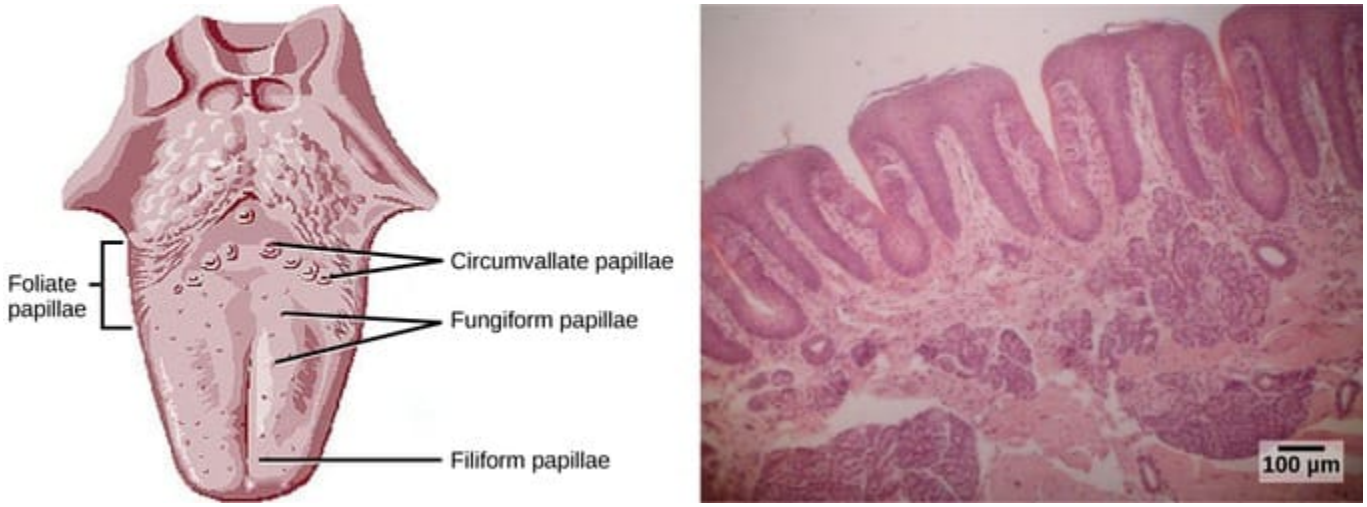


Figure 36.7.1: Taste buds: (a) Foliate, circumvallate, and fungiform papillae are located on different regions of the tongue. (b) Foliate papillae are prominent protrusions on this light micrograph.

In humans, there are five primary tastes; each taste has only one corresponding type of receptor. Thus, like olfaction, each receptor is specific to its stimulus (tastant). Transduction of the five tastes happens through different mechanisms that reflect the molecular composition of the tastant. A salty tastant (containing NaCl) provides the sodium ions (Na^+) that enter the taste neurons, exciting them directly. Sour tastants are acids which belong to the thermoreceptor protein family. Binding of an acid or other sour-tasting molecule triggers a change in the ion channel which increases hydrogen ion (H^+) concentrations in the taste neurons; thus, depolarizing them. Sweet, bitter, and umami tastants require a G-protein-coupled receptor. These tastants bind to their respective receptors, thereby exciting the specialized neurons associated with them.

Both tasting abilities and sense of smell change with age. In humans, the senses decline dramatically by age 50 and continue to decline. A child may find a food to be too spicy, whereas an elderly person may find the same food to be bland and unappetizing.

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Key Points

- Odorants are received by receptors in the nose, which send signals to the olfactory bulb of the brain to create an appropriate response; humans have about 12 million receptors.
- Taste results when molecules are dissolved in fluid and reach the gustatory receptors on the tongue; the signals are sent to the brain to determine which flavor (bitter, sour, sweet, salty, umami) is being consumed.
- Taste buds are found on the tongue and contain clusters of gustatory receptors on bumps called papillae; fungiform papillae each contain one to eight taste buds; they also have receptors for pressure and temperature.
- The ability to smell and taste declines with age.

Key Terms

- **tastant**: any substance that stimulates the sense of taste
- **papilla**: a nipple-like anatomical structure
- **odorant**: any substance that has a distinctive smell, especially one added to something (such as household gas) for safety purposes

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36.8: Hearing and Vestibular Sensation - Sound

Learning Objectives

- Describe the relationship of amplitude and frequency of a sound wave to attributes of sound

Sound

Auditory stimuli are sound waves, which are mechanical pressure waves that move through a medium, such as air or water. There are no sound waves in a vacuum since there are no air molecules for the waves to move through. The speed of sound waves differs based on altitude, temperature, and medium. At sea level and a temperature of 20° C (68° F), sound waves travel in the air at about 343 meters per second.

As is true for all waves, there are four main characteristics of a sound wave: frequency, wavelength, period, and amplitude. Frequency is the number of waves per unit of time; in sound, it is heard as pitch. High-frequency (≥15.000Hz) sounds are higher-pitched (short wavelength) than low-frequency (long wavelengths; ≤100Hz) sounds. Frequency is measured in cycles per second. For sound, the most-commonly used unit is hertz (Hz), or cycles per second. Most humans can perceive sounds with frequencies between 30 and 20,000 Hz. Women are typically better at hearing high frequencies, but everyone's ability to hear high frequencies decreases with age. Dogs detect up to about 40,000 Hz; cats, 60,000 Hz; bats, 100,000 Hz; dolphins, 150,000 Hz; and the American shad (*Alosa sapidissima*), a fish, can hear 180,000 Hz. Those frequencies above the human range are called ultrasound.

Amplitude, or the dimension of a wave from peak to trough, in sound is heard as volume. The sound waves of louder sounds have greater amplitude than those of softer sounds. For sound, volume is measured in decibels (dB). The softest sound that a human can hear is the zero point. Humans speak normally at 60 decibels.

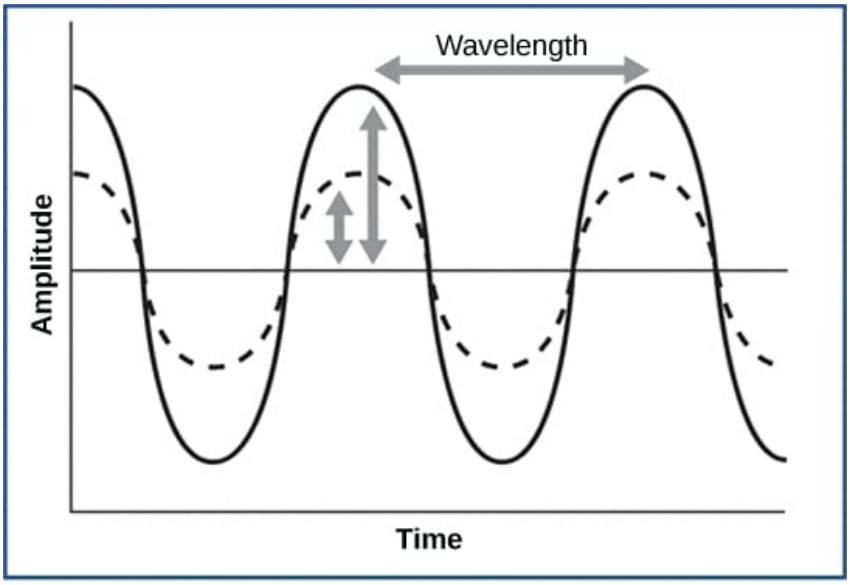


Figure 36.8.1: Amplitude: For sound waves, wavelength corresponds to pitch. The amplitude of the wave corresponds to volume. The sound wave shown with a dashed line is softer in volume than the sound wave shown with a solid line.

Key Points

- Sound waves are mechanical pressure waves that must travel through a medium and cannot exist in a vacuum.
- There are four main characteristics of a sound wave: frequency, wavelength, period, and amplitude.
- Frequency is the number of waves per unit of time and is heard as pitch; high-frequency sounds are high-pitched, and low-

frequency sounds are low-pitched.
- Most humans can perceive sounds with frequencies between 30 and 20,000 Hz; other animals, such as dolphins, can detect sounds at far higher frequencies.
- Amplitude, the dimension of a wave from peak to trough, is heard as volume; louder sounds have greater amplitudes than those of softer sounds.

Key Terms

- **frequency**: characterized as a periodic vibration that is audible; property of sound that most determines pitch and is measured in hertz
- **amplitude**: measure of a wave from its highest point to its lowest point; heard as volume
- **ultrasound**: sound frequencies above the human detectable ceiling of approximately 20,000 Hz

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36.9: Hearing and Vestibular Sensation - Reception of Sound

Learning Objectives

- Explain how animals sense sound

Reception of Sound

In order to hear a sound, the auditory system must accomplish three basic tasks. First, it must deliver the acoustic stimulus to the receptors; second, it must convert the stimulus from pressure changes into electrical signals; and third, it must process these electrical signals so that they can efficiently indicate the qualities of the sound source, such as frequency (pitch), amplitude (loudness, volume), and location.

The human ear can be divided into three functional segments:

- the outer ear: collects sound energy from the environment and sends it to the eardrum
- the middle ear: transduces the mechanical pressure signals from the ear drum into electrical signals
- the inner ear: interprets the electrical signals from the middle ear using hair cells

In mammals, sound waves are collected by the external, cartilaginous outer part of the ear called the pinna. They then travel through the auditory canal, causing vibration of the thin diaphragm called the tympanum, or ear drum, the innermost part of the outer ear. Interior to the tympanum is the middle ear, which holds three small bones called the ossicles (“little bones”), that transfer energy from the moving tympanum to the inner ear. The three ossicles are the malleus (also known as the hammer), the incus (the anvil), and stapes (the stirrup). The three ossicles are unique to mammals; each plays a role in hearing. The malleus attaches at three points to the interior surface of the tympanic membrane. The incus attaches the malleus to the stapes. In humans, the stapes is not long enough to reach the tympanum. If we did not have the malleus and the incus, then the vibrations of the tympanum would never reach the inner ear. These bones also function to collect force and amplify sounds. The ear ossicles are homologous to bones in a fish mouth; the bones that support gills in fish are thought to be adapted for use in the vertebrate ear over evolutionary time. Many animals (frogs, reptiles, and birds, for example) use the stapes of the middle ear to transmit vibrations to it.

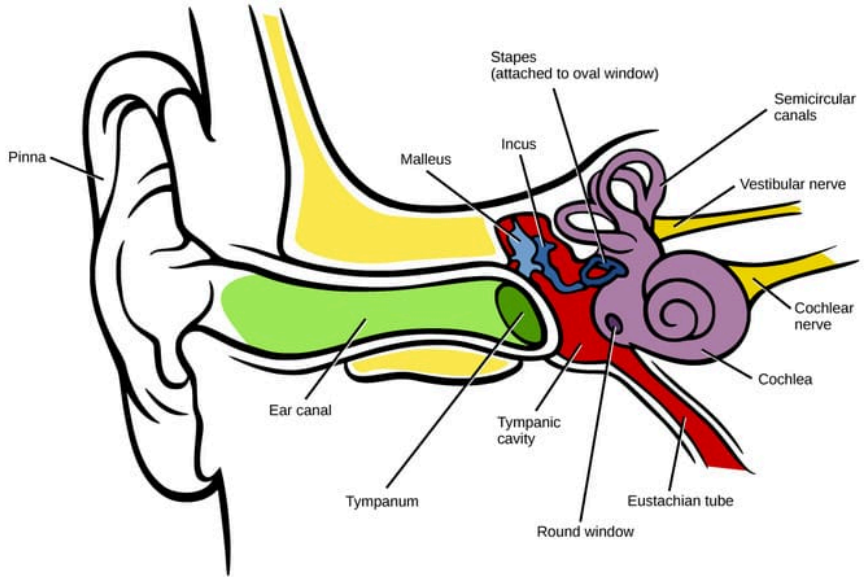


Figure 36.9.1: Human ear: Sound travels through the outer ear to the middle ear, which is bounded on its exterior by the tympanic membrane. The middle ear contains three bones called ossicles that transfer the sound wave to the oval window, the exterior boundary of the inner ear.

Key Points

- The human ear can be divided into three functional segments: the outer ear, the middle ear, and the inner ear.
- Sound waves are collected by the pinna, travel through the auditory canal, and cause vibration of the tympanum (ear drum).
- The three ossicles of the middle ear (malleus, incus, and stapes) transfer energy from the vibrating ear drum to the inner ear.
- The incus connects the malleus to the stapes, which allows vibrations to reach the inner ear.

Key Terms

- **malleus**: small hammer-shaped bone of the middle ear
- **incus**: small anvil-shaped bone in the middle ear; connects the malleus to the stapes
- **stapes**: small stirrup-shaped bone of the middle ear
- **pinna**: the visible, cartilaginous part of the ear that resides outside of the head and collects sound waves
- **tympanum**: innermost part of the outer ear; the eardrum

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36.10: Hearing and Vestibular Sensation - The Vestibular System

Learning Objectives

- Identify the structures of the vestibular system that respond to gravity

Vestibular Information

The stimuli associated with the vestibular system are linear acceleration (gravity) and angular acceleration/deceleration. Gravity, acceleration, and deceleration are detected by evaluating the inertia on receptive cells in the vestibular system. Gravity is detected through head position, while angular acceleration and deceleration are expressed through turning or tilting of the head.

The vestibular system has some similarities with the auditory system. It utilizes hair cells just like the auditory system, but it excites them in different ways. There are five vestibular receptor organs in the inner ear, all of which help to maintain balance: the utricle, the saccule, and three semicircular canals. Together, they make up what is known as the vestibular labyrinth. The utricle and saccule are most responsive to acceleration in a straight line, such as gravity. The roughly 30,000 hair cells in the utricle and 16,000 hair cells in the saccule lie below a gelatinous layer, with their stereocilia (singular: stereocilium) projecting into the gelatin. Embedded in this gelatin are calcium carbonate crystals, similar to tiny rocks. When the head is tilted, the crystals continue to be pulled straight down by gravity, but the new angle of the head causes the gelatin to shift, thereby bending the stereocilia. The bending of the stereocilia stimulates specific neurons that signal to the brain that the head is tilted, allowing the maintenance of balance. It is the vestibular branch of the vestibulocochlear cranial nerve that deals with balance.

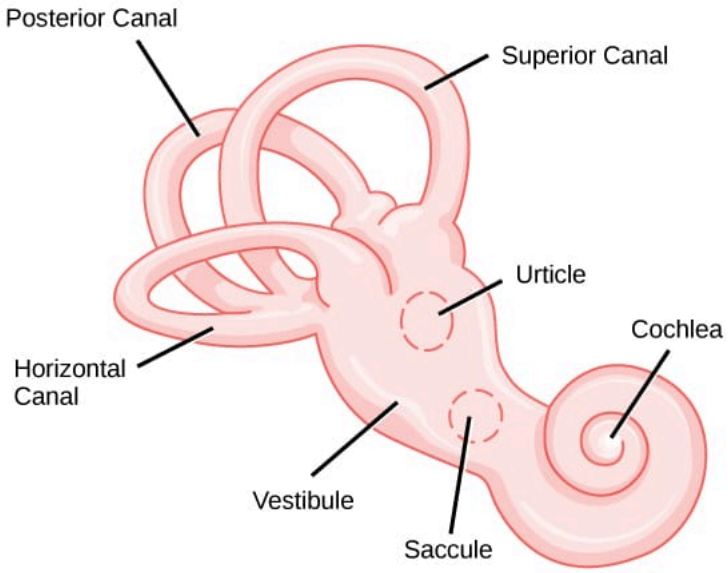


Figure 36.10.1: Vestibular labrynth: The structure of the vestibular labyrinth is made up of five vestibular receptor organs in the inner ear: the utricle, the saccule, and three semicircular canals.

The fluid-filled semicircular canals are tubular loops set at oblique angles, arranged in three spatial planes. The base of each canal has a swelling that contains a cluster of hair cells. The hairs project into a gelatinous cap, the cupula, where they monitor angular acceleration and deceleration from rotation. They would be stimulated by driving your car around a corner, turning your head, or falling forward. One canal lies horizontally, while the other two lie at about 45 degree angles to the horizontal axis. When the brain processes input from all three canals together, it can detect angular acceleration or deceleration in three dimensions. When the head turns, the fluid in the canals shifts, thereby bending stereocilia and sending signals to the brain. Upon cessation of acceleration or deceleration, the movement of the fluid within the canals slows or stops. For example, imagine holding a glass of water. When moving forward, water may splash backwards onto the hand; when motion has stopped, water may splash forward

onto the fingers. While in motion, the water settles in the glass and does not splash. Note that the canals are not sensitive to velocity itself, but to changes in velocity. In this way, moving forward at 60 mph with your eyes closed would not give the sensation of movement, but suddenly accelerating or braking would stimulate the receptors.

Higher Processing

Hair cells from the utricle, saccule, and semicircular canals also communicate through bipolar neurons to the cochlear nucleus in the medulla. Cochlear neurons send descending projections to the spinal cord and ascending projections to the pons, thalamus, and cerebellum. Connections to the cerebellum are important for coordinated movements. There are also projections to the temporal cortex, which account for feelings of dizziness; projections to autonomic nervous system areas in the brainstem, which account for motion sickness; and projections to the primary somatosensory cortex, which monitors subjective measurements of the external world and self-movement. People with lesions in the vestibular area of the somatosensory cortex see vertical objects in the world as being tilted. Finally, the vestibular signals project to certain optic muscles to coordinate eye and head movements.

Key Points

- The vestibular system uses hair cells, as does the auditory system, but it excites them in different ways.
- There are five vestibular receptor organs in the inner ear (the vestibular labyrinth): the utricle, the saccule, and three semicircular canals; the utricle and saccule respond to acceleration in a straight line, such as gravity.
- The bending of the stereocilia stimulates specific neurons that signal to the brain that the head is tilted, allowing the maintenance of balance.
- The fluid-filled semicircular canals are tubular loops set at oblique angle, arranged in three spatial planes; the base of each canal contains a cluster of hair cells that monitor angular acceleration and deceleration from rotation.
- Neuronal projections to the temporal cortex account for feelings of dizziness; projections to autonomic nervous system areas in the brainstem account for motion sickness; and projections to the primary somatosensory cortex monitor subjective measurements of the external world and self-movement.

Key Terms

- **vestibulocochlear**: of or pertaining to the vestibular and cochlear nerves
- **vestibular system**: the sensory system in mammals that contributes to movement, sense of balance, and spatial orientation
- **stereocilium**: any of many nonmotile cellular structures resembling long microvilli; those of the inner ear are responsible for auditory transduction

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36.11: Hearing and Vestibular Sensation - Balance and Determining Equilibrium

Learning Objectives

- Describe the anatomy that enables equilibrium and balance

Equilibrium

Along with audition, the inner ear is responsible for encoding information about equilibrium, or the sense of balance. A similar mechanoreceptor—a hair cell with stereocilia —senses head position, head movement, and whether our bodies are in motion. These cells are located within the vestibule of the inner ear. Head position is sensed by the utricle and saccule, whereas head movement is sensed by the semicircular canals. The neural signals generated in the vestibular ganglion are transmitted through the vestibulocochlear nerve to the brain stem and cerebellum. Together, these components make up the vestibular system.

Linear acceleration

The utricle and saccule are both largely composed of macula tissue (plural = maculae). The macula is composed of hair cells surrounded by support cells. The stereocilia of the hair cells extend into a viscous gel called the otolith. The otolith contains calcium carbonate crystals, making it denser and giving it greater inertia than the macula. Therefore, gravity will cause the otolith to move separately from the macula in response to head movements. Tilting the head causes the otolith to slide over the macula in the direction of gravity. The moving otolith layer, in turn, bends the sterocilia to cause some hair cells to depolarize as others hyperpolarize. The exact tilt of the head is interpreted by the brain on the basis of the pattern of hair-cell depolarization.

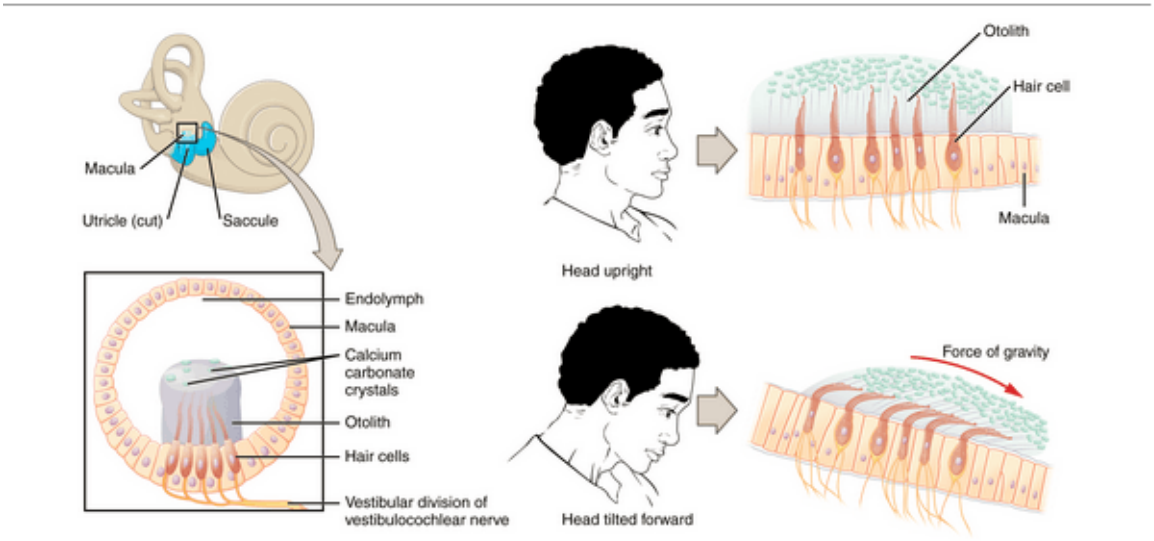


Figure 36.11.1: Linear acceleration coding by maculae: The maculae are specialized for sensing linear acceleration, such as when gravity acts on the tilting head, or if the head starts moving in a straight line. The difference in inertia between the hair cell stereocilia and the otolith in which they are embedded leads to a force that causes the stereocilia to bend in the direction of that linear acceleration.

Rotational movement

The semicircular canals are three ring-like extensions of the vestibule. One is oriented in the horizontal plane, whereas the other two are oriented in the vertical plane. The anterior and posterior vertical canals are oriented at approximately 45 degrees relative

to the sagittal plane. The base of each semicircular canal, where it meets with the vestibule, connects to an enlarged region known as the ampulla. The ampulla contains the hair cells that respond to rotational movement, such as turning your head from side to side when saying “no.” The stereocilia of these hair cells extend into the cupula, a membrane that attaches to the top of the ampulla. As the head rotates in a plane parallel to the semicircular canal, the fluid lags, deflecting the cupula in the direction opposite to the head movement. The semicircular canals contain several ampullae, with some oriented horizontally and others oriented vertically. By comparing the relative movements of both the horizontal and vertical ampullae, the vestibular system can detect the direction of most head movements within three-dimensional (3-D) space.

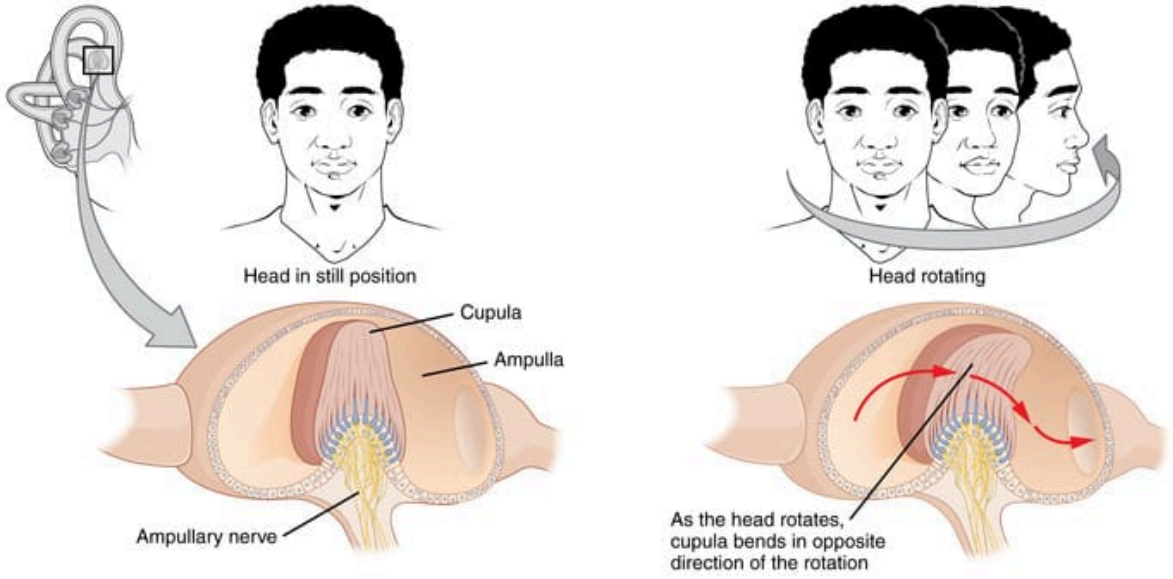


Figure 36.11.1: Rotational coding by semicircular canals: Rotational movement of the head is encoded by the hair cells in the base of the semicircular canals. As one of the canals moves in an arc with the head, the internal fluid moves in the opposite direction, causing the cupula and stereocilia to bend. The movement of two canals within a plane results in information about the direction in which the head is moving, and activation of all six canals can give a very precise indication of head movement in three dimensions.

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Key Points

- The hair cells of the utricle and saccule of the inner ear extend into the otolith, a dense viscous substance with calcium carbonate crystals.
- The otolith slides over the macula, tissue supporting the hair cells, in the direction of gravity when the head is moved due to its greater inertia, causing a pattern of hair cell depolarization interpreted by the brain as tilting.
- The three semicircular canals of the inner ear are ring-like structures with one ring oriented in the horizontal plane and the other two rings oriented at approximately 45 degrees relative to the sagittal plane.
- The ampulla, found at the base of each semicircular canal, contains hair cells that extend into the membrane that attaches to the top of the ampulla to an area called the cupula.
- A head rotation causes the fluid in the semicircular canal to move, but with a lag which produces a deflection of the cupula in the direction opposite to the head rotation which in turn causes the hair cells to depolarize.
- Using the hair cell depolarization information from all three ampullae, the direction and speed of head movements in all three dimensions can be detected by the vestibular system.

Key Terms

- **stereocilium**: any of many nonmotile cellular structures resembling long microvilli; those of the inner ear are responsible for auditory transduction
- **equilibrium**: the condition of a system in which competing influences are balanced, resulting in no net change
- **otolith**: a small particle, comprised mainly of calcium carbonate, found in the inner ear of vertebrates, being part of the balance sense

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36.12: Vision - Light

Learning Objectives

- Describe the characteristics of light

Light

As with auditory stimuli, light travels in waves. While the compression waves that compose sound must travel in a medium (consisting of a gas, a liquid, or a solid), light is composed of electromagnetic waves and needs no medium. Light can, in fact, travel in a vacuum. The behavior of light can be described in terms of the behavior of waves and the behavior of the fundamental unit of light, the photon: a packet of electromagnetic radiation. A glance at the electromagnetic spectrum shows that visible light for humans is just a small slice of the entire spectrum, which includes radiation that we cannot see as light because it is below the frequency of visible red light and above the frequency of visible violet light.

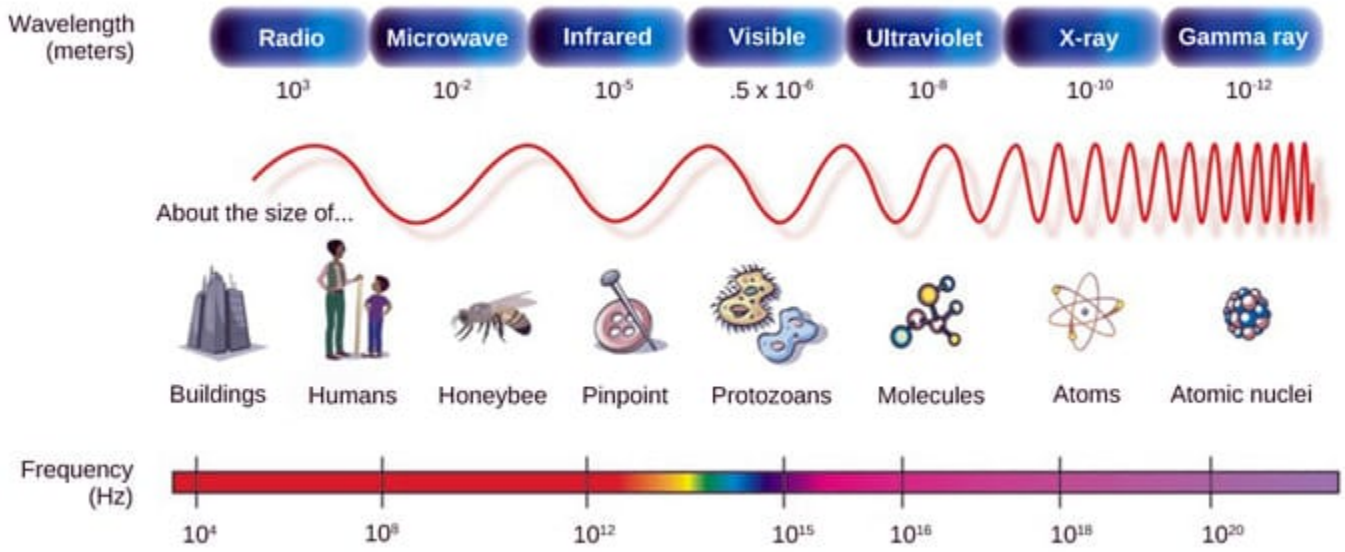


Figure 36.12.1: Electromagnetic spectrum: A glance at the electromagnetic spectrum shows that visible light for humans is just a small slice of the entire spectrum.

Certain variables are important when discussing perception of light. A wavelength (which varies inversely with frequency) manifests itself as color. Light at the red end of the visible spectrum has longer wavelengths (and is lower frequency), while light at the violet end has shorter wavelengths (and is higher frequency). The wavelength of light is expressed in nanometers (nm); one nanometer is one billionth of a meter. Humans perceive light that ranges between approximately 380 nm and 740 nm. However, some other animals can detect wavelengths outside of the human range. For example, bees see near-ultraviolet light in order to locate nectar guides on flowers. Some non-avian reptiles sense infrared light (such as heat that prey gives off).

Wave amplitude is perceived as luminous intensity or brightness. The standard unit of intensity of light is the candela, which is approximately the luminous intensity of one common candle.

Light waves travel 299,792 km per second in a vacuum and somewhat slower in various media such as air and water. Those waves arrive at the eye as long (red), medium (green), and short (blue) waves. The term “white light” is light that is perceived as white by the human eye. This effect is produced by light that stimulates the color receptors in the human eye equally. The apparent color of an object is actually the color (or colors) the object reflects. Thus a red object reflects the red wavelengths in mixed (white) light and absorbs all other wavelengths of light.

Key Points

- Light is composed of electromagnetic waves that can travel without a medium, unlike sound.
- The behavior of light can be seen in the behavior of waves and photons, the basic unit of light.
- A wavelength (which varies inversely with frequency) manifests itself as color, while wave amplitude is perceived as luminous intensity or brightness; it is measured by the standard unit of a candela.
- Humans can see light that ranges between 380 nm and 740 nm, but cannot see light that is below the frequency of visible red light or above the frequency of visible violet light.
- Light at the red end of the visible spectrum has long wavelengths (and is lower frequency), while light at the violet end has short wavelengths (and is higher frequency).
- Light waves enter the eye as long (red), medium (green), and short (blue) waves; the color of an object is the color the object reflects.

Key Terms

- **photon**: the quantum of light and other electromagnetic energy, regarded as a discrete particle having zero rest mass, no electric charge, and an indefinitely long lifetime
- **nanometer**: one billionth of a meter; used to express wavelength of light
- **electromagnetic spectrum**: the entire range of wavelengths of all known radiations consisting of oscillating electric and magnetic fields, including gamma rays, visible light, infrared, radio waves, and X-rays
- **wavelength**: the length of a single cycle of a wave, as measured by the distance between one peak or trough of a wave and the next; it corresponds to the velocity of the wave divided by its frequency

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36.13: Vision - Anatomy of the Eye

Learning Objectives

- Explain how eyes have evolved to benefit organisms

Anatomy of the Eye

The retina, a thin layer of cells located on the inner surface of the back of the eye, consists of photoreceptive cells, which are responsible for the transduction of light into nervous impulses. However, light does not enter the retina unaltered; it must first pass through other layers that process it so that it can be interpreted by the retina.

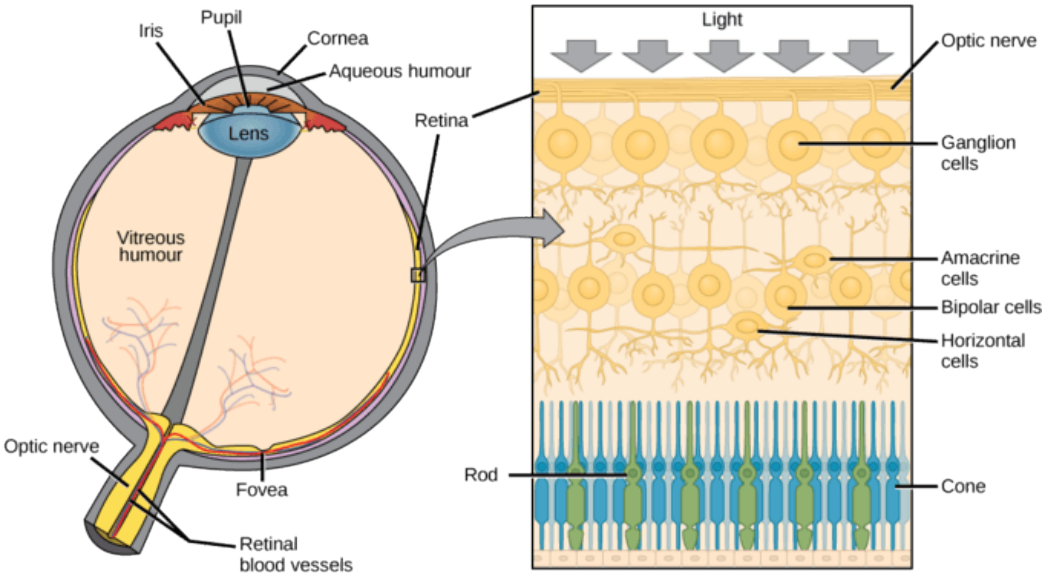


Figure 36.13.1: Retina: (a) The human eye is shown in cross section. The human eye contains structures, such as the cornea, iris, lens, and fovea, that process light so it can be deciphered by the retina. Other structures like the aqueous humor and the vitreous humor help maintain the shape of the eye. (b) A blowup shows the layers of the retina. The retina contains photoreceptive cells. In the retina, light is converted into neural signals sent to the brain.

The cornea, the front transparent layer of the eye, along with the crystalline lens, refract (bend) light to focus the image on the retina. After passing through the cornea, light passes through the aqueous humour, which connects the cornea to the lens. This clear gelatinous mass also provides the corneal epithelium with nutrients and helps maintain the convex shape of the cornea. The iris, which is visible as the colored part of the eye, is a circular muscular ring lying between the lens and the aqueous humour that regulates the amount of light entering the eye. Light passes through the center of the iris, the pupil, which actively adjusts its size to maintain a constant level of light entering the eye. In conditions of high ambient light, the iris contracts, reducing the size of the pupil. In conditions of low light, the iris relaxes and the pupil enlarges.

The main function of the lens is to focus light on the retina and fovea centralis. The lens is a transparent, convex structure located behind the cornea. On the other side of the lens is the vitreous humour, which lets light through without refraction, maintains the shape of the eye, and suspends the delicate lens. The lens focuses and re-focuses light as the eye rests on near and far objects in the visual field. The lens is operated by muscles that stretch it flat or allow it to thicken, changing the focal length of light coming through to focus it sharply on the retina. With age comes the loss of the flexibility of the lens; a form of farsightedness called presbyopia results. Presbyopia occurs because the image focuses behind the retina. It is a deficit similar to a different type of farsightedness, hyperopia, caused by an eyeball that is too short. For both defects, images in the distance are clear, but images nearby are blurry. Myopia (nearsightedness) occurs when an eyeball is elongated and the image focus falls in front of the retina. In this case, images in the distance are blurry, but images nearby are clear.

There are two types of photoreceptors in the retina: rods and cones. Both are named for their general appearance. Rods, strongly photosensitive, are located in the outer edges of the retina. They detect dim light and are used primarily for peripheral and nighttime vision. Cones, weakly photosensitive, are located near the center of the retina. They respond to bright light; their primary role is in daytime, color vision.

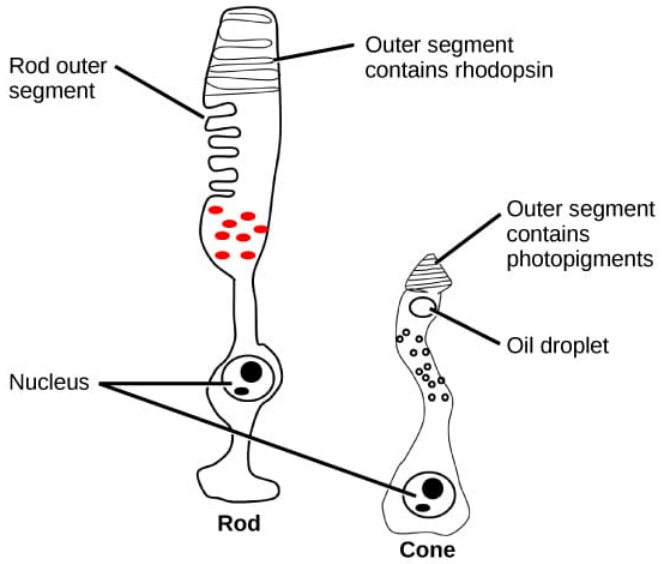


Figure 36.13.1: Rods and cones: Rods and cones are photoreceptors in the retina. Rods respond in low light and can detect only shades of gray. Cones respond in intense light and are responsible for color vision.

The fovea is the region in the center back of the eye that is responsible for acute (central) vision. The fovea has a high density of cones. When you bring your gaze to an object to examine it intently in bright light, the eyes orient so that the object's image falls on the fovea. However, when looking at a star in the night sky or other object in dim light, the object can be better viewed by the peripheral vision because it is the rods at the edges of the retina, rather than the cones at the center, that operate better in low light. In humans, cones far outnumber rods in the fovea.

Key Points

- The cornea and the lens bend light to focus the image on the retina; the iris and pupil regulate the amount of light entering the eye.
- The aqueous humour maintains the convex shape of the cornea; the vitreous humour supports the lens and maintains the shape of the entire eye.
- Presbyopia occurs because the image focuses behind the retina; it is similar to hyperopia (farsightedness), which is caused by an eyeball that is too short.
- Myopia (nearsightedness) occurs when an eyeball is elongated; images in the distance appear blurry, but images nearby are clear.
- Rods are used for peripheral and nighttime vision; cones are used for daytime and color vision.
- The fovea is responsible for acute vision because it has a high density of cones.

Key Terms

- **rod**: a rod-shaped cell located in the outer retina of the eye that is extremely sensitive to light
- **retina**: the thin layer of cells at the back of the eyeball where light is converted into neural signals sent to the brain
- **cone**: cell located near the center of the retina that is weakly photosensitive and is responsible for color vision in relatively bright light

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36.14: Vision - Transduction of Light

Learning Objectives

- Explain retinal processing and the process of transduction of light

Transduction of Light

The rods and cones are the site of transduction of light into a neural signal. Both rods and cones contain photopigments, which are pigments that undergo a chemical change when they absorb light. In vertebrates, the main photopigment, rhodopsin, has two main parts: an opsin, which is a membrane protein (in the form of a cluster of α-helices that span the membrane); and retinal, a molecule that absorbs light. When light hits a photoreceptor, it causes a shape change in the retinal, altering its structure from a bent (cis) form of the molecule to its linear (trans) isomer. This isomerization of retinal activates the rhodopsin, starting a cascade of events that ends with the closing of Na^+ channels in the membrane of the photoreceptor. Thus, unlike most other sensory neurons (which become depolarized by exposure to a stimulus), visual receptors become hyperpolarized and are driven away from the threshold.

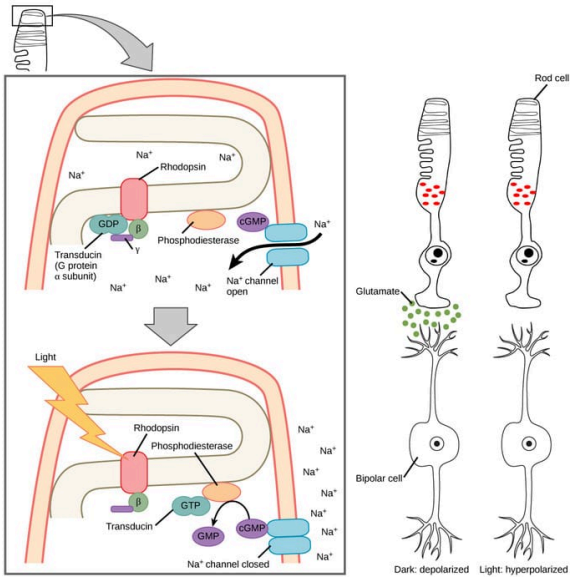


Figure 36.14.1: Hyperpolarized visual receptors: When light strikes rhodopsin, the G-protein transducin is activated, which in turn activates phosphodiesterase. Phosphodiesterase converts cGMP to GMP, thereby closing sodium channels. As a result, the membrane becomes hyperpolarized. The hyperpolarized membrane does not release glutamate to the bipolar cell.

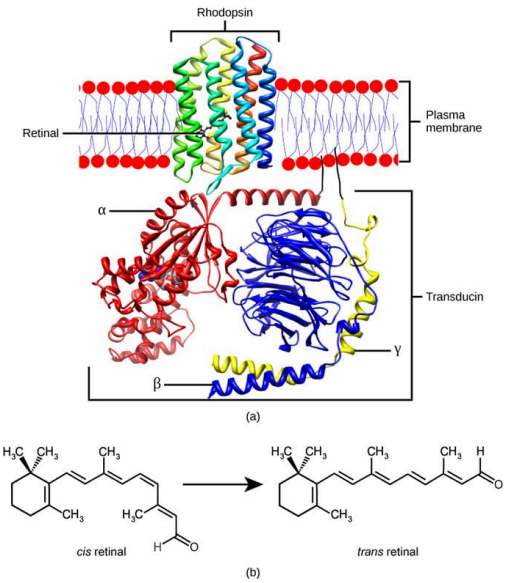


Figure 36.14.1: Rhodopsin: (a) Rhodopsin, the photoreceptor in vertebrates, has two parts: the trans-membrane protein opsin and retinal. When light strikes the retinal, it changes shape from (b) a cis to a trans form. The signal is passed to a G-protein called transducin, triggering a series of downstream events.

Trichromatic Coding

There are three types of cones (with different photopsins) that differ in the wavelength to which they are most responsive. Some cones are maximally responsive to short light waves of 420 nm; they are called S cones (“S” for “short”). Other cones (M cones, for “medium”) respond maximally to waves of 530 nm. A third group (L cones, or “long” cones) responds maximally to light of longer wavelengths at 560 nm. With only one type of cone, color vision would not be possible; a two-cone (dichromatic) system has limitations. Primates use a three-cone (trichromatic) system, resulting in full color vision.

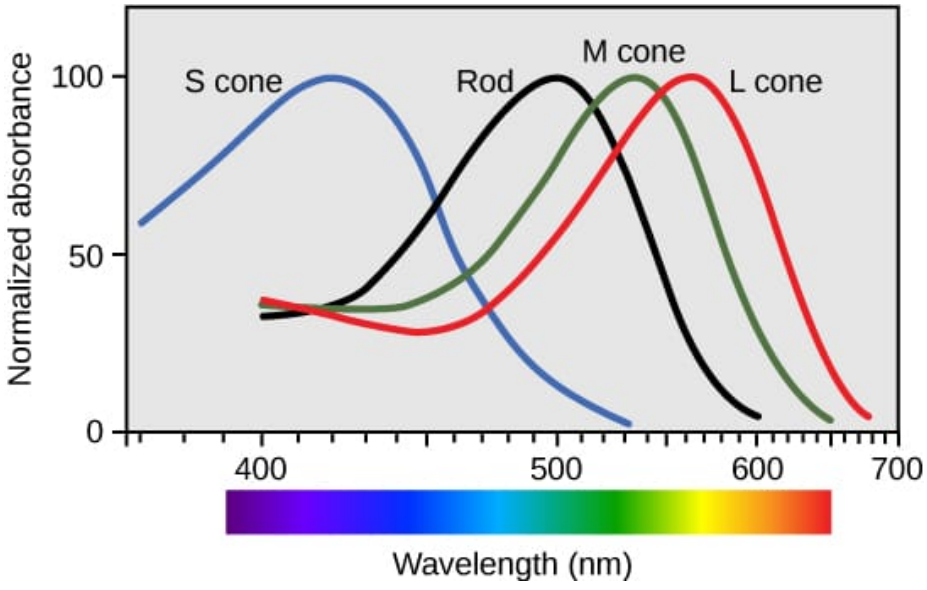


Figure 36.14.1: Rod and cone cells: Human rod cells and the different types of cone cells each have an optimal wavelength. However, there is considerable overlap in the wavelengths of light detected.

The color we perceive is a result of the ratio of activity of our three types of cones. The colors of the visual spectrum, running from long-wavelength light to short are:

- red (700 nm)
- orange (600 nm)

- yellow (565 nm)
- green (497 nm)
- blue (470 nm)
- indigo (450 nm)
- violet (425 nm).

Humans have very sensitive perception of color and can distinguish about 500 levels of brightness, 200 different hues, and 20 steps of saturation; in all, about 2 million distinct colors.

Retinal Processing

Visual signals leave the cones and rods, travel to the bipolar cells, and then to ganglion cells. A large degree of processing of visual information occurs in the retina itself, before visual information is sent to the brain.

Photoreceptors in the retina continuously undergo tonic activity. That is, they are always slightly active even when not stimulated by light. In neurons that exhibit tonic activity, the absence of stimuli maintains a firing rate at an equilibrium; while some stimuli increase firing rate from the baseline, other stimuli decrease firing rate. In the absence of light, the bipolar neurons that connect rods and cones to ganglion cells are continuously and actively inhibited by the rods and cones. Exposure of the retina to light hyperpolarizes the rods and cones, removing the inhibition of their bipolar cells. The now-active bipolar cells in turn stimulate the ganglion cells, which send action potentials along their axons (which leave the eye as the optic nerve). Thus, the visual system relies on changein retinal activity, rather than the absence or presence of activity, to encode visual signals for the brain. Sometimes horizontal cells carry signals from one rod or cone to other photoreceptors and to several bipolar cells. When a rod or cone stimulates a horizontal cell, the horizontal cell inhibits more-distant photoreceptors and bipolar cells, creating lateral inhibition. This inhibition sharpens edges and enhances contrast in the images by making regions receiving light appear lighter and dark surroundings appear darker. Amacrine cells can distribute information from one bipolar cell to many ganglion cells.

Key Points

- When light hits the photoreceptor, the retinal changes shape, which activates the photopigment rhodoposin.
- Primates have full color vision because of the three- cone (trichromatic) system; color is a result of the ratio of activity of the three types of cones.
- There are three types of cones with different photopsins: S cones respond to short waves; M cones respond to medium waves; L cones respond to light to long waves.
- If light is not present, neurons are inhibited by rods and cones; once light is introduced, rods and cones are hyperpolarized, which activates the neurons.
- Activated neurons stimulate ganglion cells, which send action potentials via the optic nerve.
- Horizontal cells can create lateral inhibition, which enhances light and dark contrast in images.

Key Terms

- **tonic activity**: when photoreceptors become slightly active even when not stimulated by light
- **rhodopsin**: a light-sensitive pigment in the rod cells of the retina; it consists of an opsin protein bound to the carotenoid retinal

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36.15: Vision - Visual Processing

Learning Objectives

- Describe the complexity of visual processing in the brain

Higher Processing

The myelinated axons of ganglion cells make up the optic nerves. Within the nerves, different axons carry different parts of the visual signal. Some axons constitute the magnocellular (big cell) pathway, which carries information about form, movement, depth, and differences in brightness. Other axons constitute the parvocellular (small cell) pathway, which carries information on color and fine detail. Some visual information projects directly back into the brain, while other information crosses to the opposite side of the brain. This crossing of optical pathways produces the distinctive optic chiasma (Greek, for "crossing") found at the base of the brain and allows us to coordinate information from both eyes.

Once in the brain, visual information is processed in several places. Its routes reflect the complexity and importance of visual information to humans and other animals. One route takes the signals to the thalamus, which serves as the routing station for all incoming sensory impulses except smell. In the thalamus, the magnocellular and parvocellular distinctions remain intact; there are different layers of the thalamus dedicated to each. When visual signals leave the thalamus, they travel to the primary visual cortex at the rear of the brain. From the visual cortex, the visual signals travel in two directions. One stream that projects to the parietal lobe, in the side of the brain, carries magnocellular ("where") information. A second stream projects to the temporal lobe and carries both magnocellular ("where") and parvocellular ("what") information.

Another important visual route is a pathway from the retina to the superior colliculus in the midbrain, where eye movements are coordinated and integrated with auditory information. Finally, there is the pathway from the retina to the suprachiasmatic nucleus (SCN) of the hypothalamus. The SCN is a cluster of cells that is considered to be the body's internal clock, which controls our circadian (day-long) cycle. The SCN sends information to the pineal gland, which is important in sleep/wake patterns and annual cycles.

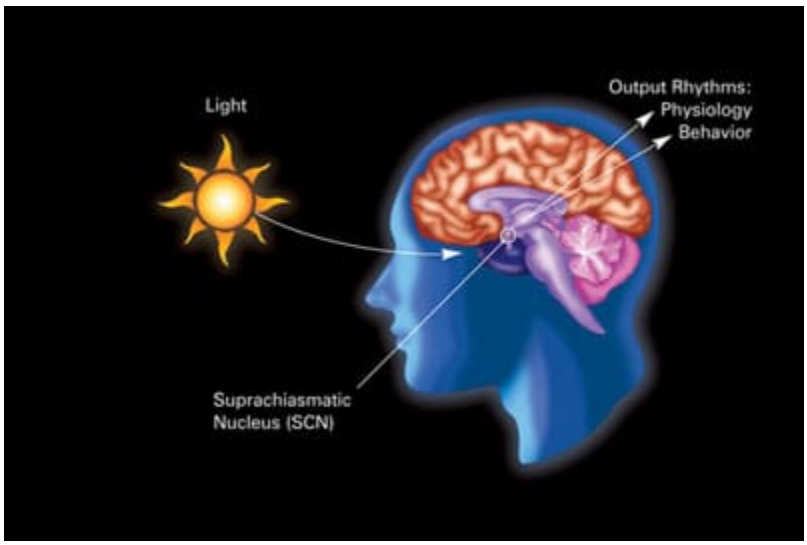


Figure 36.15.1: The suprachiasmatic nucleus (SNC): The presence of light and darkness influences circadian rhythms and related physiology and behavior through the SCN.

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Key Points

- The magnocellular pathway carries information about form, movement, depth, and differences in brightness; the parvocellular pathway carries information on color and fine detail.
- The optic chiasma allows us to coordinate information between both eyes and is produced by crossing optical information across the brain.
- Visual signals move from the visual cortex to either the parietal lobe or the temporal lobe.
- Some signals move to the thalamus, which sends the visual signals to the primary cortex.
- Visual signals can also travel from the retina to the superior colliculus, where eye movements are coordinated with auditory information.
- Visual signals can move from the retina to the suprachiasmatic nucleus (SCN), the body's internal clock, which is involved in sleep/wake patterns and annual cycles.

Key Terms

- **superior colliculus**: the primary area of the brain where eye movements are coordinated and integrated with auditory information
- **optic chiasma**: found at the base of the brain and coordinates information from both eyes
- **suprachiasmatic nucleus**: cluster of cells that is considered to be the body's internal clock, which controls our circadian (day-long) cycle

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37: THE ENDOCRINE SYSTEM

37.1: Types of Hormones - Hormone Functions

37.2: Types of Hormones - Lipid-Derived, Amino Acid-Derived, and Peptide Hormones

37.3: How Hormones Work - Introduction

37.4: How Hormones Work - Intracellular Hormone Receptors

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37.8: Regulation of Body Processes - Hormonal Regulation of Metabolism

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37.1: Types of Hormones - Hormone Functions

Learning Objectives

- Evaluate hormones and their purpose in the body

An animal's endocrine system controls body processes through the production, secretion, and regulation of hormones. Hormones serve as chemical "messengers" that function in cellular and organ activity to maintain the body's homeostasis. Maintaining homeostasis within the body requires the coordination of many different systems and organs. Communication between neighboring cells and between cells and tissues in distant parts of the body occurs through the release of hormones into body fluids (usually blood), which carry them to their target cells. Target cells, those having a receptor for a signal, respond to a hormone when they express a specific receptor for that hormone. Cellular recipients of a particular hormonal signal may be one of several cell types that reside within a number of different tissues, as is the case for insulin, which triggers a diverse range of systemic physiological effects. Different tissue types may also respond differently to the same hormonal signal.

By releasing hormones, the endocrine system plays a role in growth, metabolism, and sexual development. Hormones also play a role in induction or suppression of cell death, activation or inhibition of the immune system, mood swings, and hunger cravings. In humans, common endocrine system diseases include thyroid disease and diabetes mellitus.

Examples of endocrine glands include the adrenal glands, which produce hormones, such as epinephrine and norepinephrine that regulate responses to stress, and the thyroid gland, which produces thyroid hormones that regulate metabolic rates. In organisms that undergo metamorphosis, the process is controlled by the endocrine system. The transformation from tadpole to frog, for example, is complex and nuanced to adapt to specific environments and ecological circumstances.



Figure 37.1.1: Hormones in metamorphosis: The process of amphibian metamorphosis, as seen in the tadpole-to-frog stages shown here, is driven by hormones.

Key Points

- Hormones serve as chemical messengers in the body and help maintain homeostasis.
- Hormones are released into bodily fluids, like blood, which carry them to target cells.
- Target cells respond to a hormone when they express a specific receptor for that hormone.
- Hormones also play a role in the regulation of cell death, the immune system, reproductive development, mood swings, and hunger cravings.
- In the adrenal gland, epinephrine and norepinephrine regulate responses to stress; in the thyroid gland, thyroid hormones regulates metabolic rates.

Key Terms

- **target cell**: any cell having a specific receptor for a hormone
- **hormone**: any substance produced by one tissue and conveyed by the bloodstream to another to affect physiological activity
- **endocrine system**: a control system of ductless glands that secrete hormones which circulate via the bloodstream to affect cells within specific organs

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37.2: Types of Hormones - Lipid-Derived, Amino Acid-Derived, and Peptide Hormones

Learning Objectives

- Recognize characteristics associated with lipid-derived, amino acid-derived, and peptide hormones

Types of Hormones

Although there are many different hormones in the human body, they can be divided into three classes based on their chemical structure: lipid-derived, amino acid-derived, and peptide hormones (which includes peptides and proteins). One of the key, distinguishing features of lipid-derived hormones is that they can diffuse across plasma membranes whereas the amino acid-derived and peptide hormones cannot.

Lipid-Derived Hormones (or Lipid-soluble Hormones)

Most lipid hormones are derived from cholesterol, so they are structurally similar to it. The primary class of lipid hormones in humans is the steroid hormones. Chemically, these hormones are usually ketones or alcohols; their chemical names will end in "-ol" for alcohols or "-one" for ketones. Examples of steroid hormones include estradiol, which is an estrogen, or female sex hormone, and testosterone, which is an androgen, or male sex hormone. These two hormones are released by the female and male reproductive organs, respectively. Other steroid hormones include aldosterone and cortisol, which are released by the adrenal glands along with some other types of androgens. Steroid hormones are insoluble in water; they are carried by transport proteins in blood. As a result, they remain in circulation longer than peptide hormones. For example, cortisol has a half-life of 60 to 90 minutes, whereas epinephrine, an amino acid derived-hormone, has a half-life of approximately one minute.

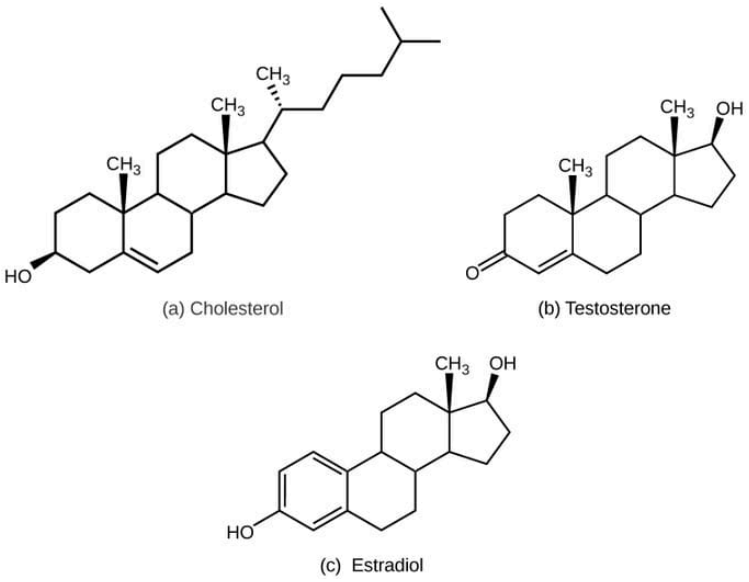


Figure 37.2.1: Lipid-derived hormones: The structures shown here represent (a) cholesterol, plus the steroid hormones (b) testosterone and (c) estradiol.

Amino Acid-Derived Hormones

The amino acid-derived hormones are relatively small molecules derived from the amino acids tyrosine and tryptophan. If a hormone is amino acid-derived, its chemical name will end in "-ine". Examples of amino acid-derived hormones include

epinephrine and norepinephrine, which are synthesized in the medulla of the adrenal glands, and thyroxine, which is produced by the thyroid gland. The pineal gland in the brain makes and secretes melatonin, which regulates sleep cycles.

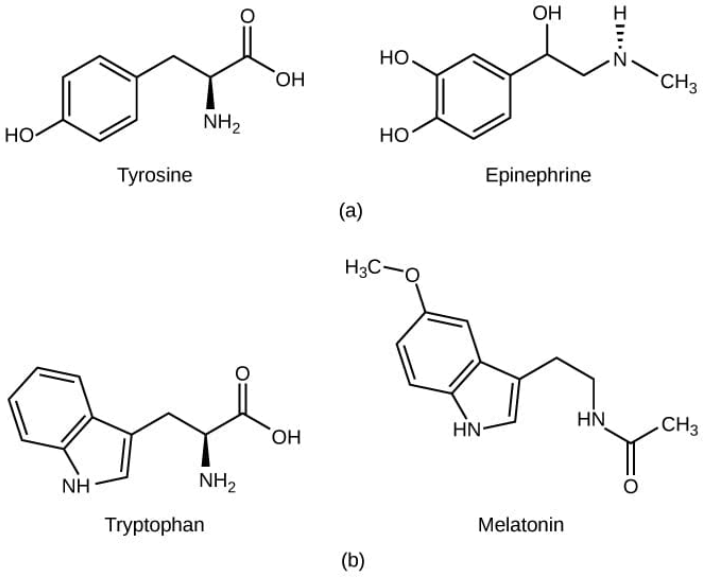


Figure 37.2.1: Amino acid-derived hormones: (a) The hormone epinephrine, which triggers the fight-or-flight response, is derived from the amino acid tyrosine. (b) The hormone melatonin, which regulates circadian rhythms, is derived from the amino acid tryptophan.

Peptide Hormones

The structure of peptide hormones is that of a polypeptide chain (chain of amino acids). The peptide hormones include molecules that are short polypeptide chains, such as antidiuretic hormone and oxytocin produced in the brain and released into the blood in the posterior pituitary gland. This class also includes small proteins, such as growth hormones produced by the pituitary, and large glycoproteins, such as follicle-stimulating hormone produced by the pituitary.

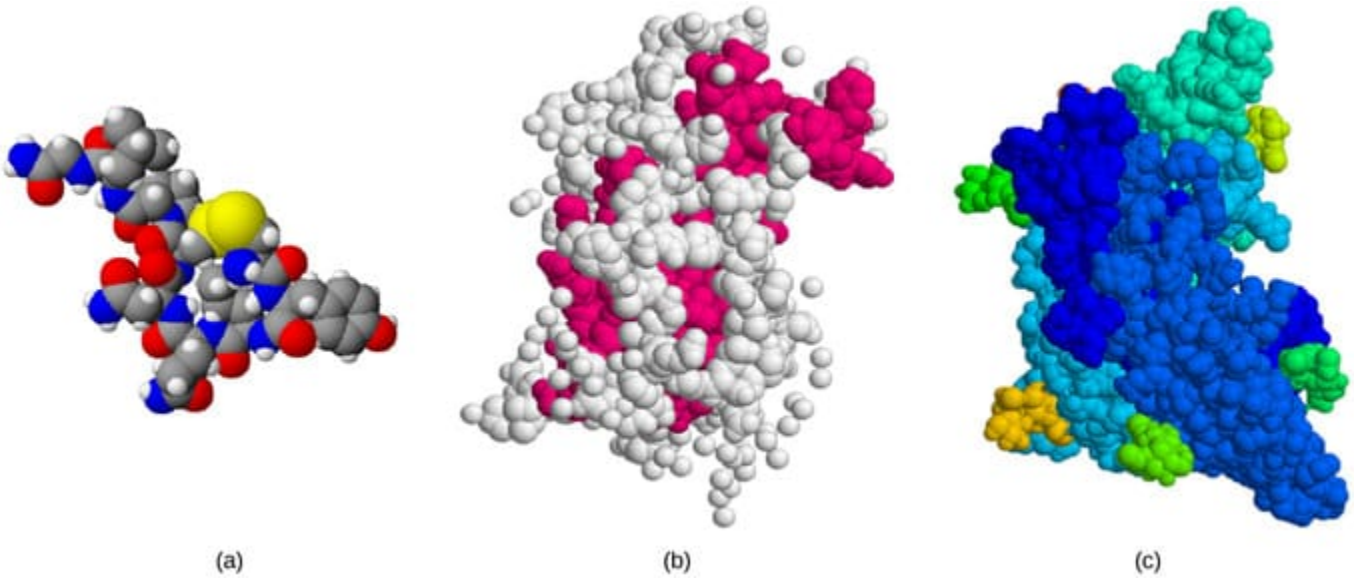


Figure 37.2.1: Peptide hormones: The structures of peptide hormones (a) oxytocin, (b) growth hormone, and (c) follicle-stimulating hormone are shown. These peptide hormones are much larger than those derived from cholesterol or amino acids.

Secreted peptides, such as insulin, are stored within vesicles in the cells which synthesize them. They are then released in response to stimuli (e.g., as high blood glucose levels in the case of insulin). Amino acid-derived and polypeptide hormones are water-soluble and insoluble in lipids. These hormones cannot pass through plasma membranes of cells; therefore, their receptors are found on the surface of the target cells.

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Key Points

- Most lipid hormones are steroid hormones, which are usually ketones or alcohols and are insoluble in water.
- Steroid hormones (ending in '-ol' or '-one') include estradiol, testosterone, aldosterone, and cortisol.
- The amino acid – derived hormones (ending in '-ine') are derived from tyrosine and tryptophan and include epinephrine and norepinephrine (produced by the adrenal medulla).
- Amino acid-derived hormones also include thyroxine (produced by the thryoid gland) and melatonin (produced by the pineal gland).
- Peptide hormones consist of a polypeptide chain; they include molecules such as oxytocin (short polypeptide chain) or growth hormones (proteins).
- Amino acid-derived hormones and protein hormones are water-soluble and insoluble in lipids.

Key Terms

- **oxytocin**: a hormone that stimulates contractions during labor, and then the production of milk
- **epinephrine**: (adrenaline) an amino acid-derived hormone secreted by the adrenal gland in response to stress
- **estrogen**: any of a group of steroids (lipid-hormones) that are secreted by the ovaries and function as female sex hormones

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37.3: How Hormones Work - Introduction

Learning Objectives

- Explain the ways in which hormones work

Hormones

A hormone is a chemical released by a cell or a gland in one part of the body that sends out messages that affect cells in other parts of the organism. Only a small amount of hormone is required to alter cell metabolism. In essence, it is a chemical messenger that transports a signal from one cell to another. All multicellular organisms produce hormones; plant hormones are also called phytohormones. Hormones in animals are often transported in the blood.

How Hormones Work

Hormones mediate changes in target cells by binding to specific hormone receptors. In this way, even though hormones circulate throughout the body and come into contact with many different cell types, they only affect cells that possess the necessary receptors. Receptors for a specific hormone may be found on many different cells or may be limited to a small number of specialized cells. For example, thyroid hormones act on many different tissue types, stimulating metabolic activity throughout the body. Cells can have many receptors for the same hormone, but often also possess receptors for different types of hormones. The number of receptors that respond to a hormone determines the cell's sensitivity to that hormone and the resulting cellular response. Additionally, the number of receptors that respond to a hormone can change over time, resulting in increased or decreased cell sensitivity. In up-regulation, the number of receptors increases in response to rising hormone levels, making the cell more sensitive to the hormone, allowing for more cellular activity. When the number of receptors decreases in response to rising hormone levels, called down-regulation, cellular activity is reduced.

Cells respond to a hormone when they express a specific receptor for that hormone. The hormone binds to the receptor protein, resulting in the activation of a signal transduction mechanism that ultimately leads to cell type-specific responses. Receptor binding alters cellular activity, resulting in an increase or decrease in normal body processes. Depending on the location of the protein receptor on the target cell and the chemical structure of the hormone, hormones can mediate changes directly by binding to intracellular hormone receptors and modulating gene transcription, or indirectly by binding to cell surface receptors and stimulating signaling pathways.

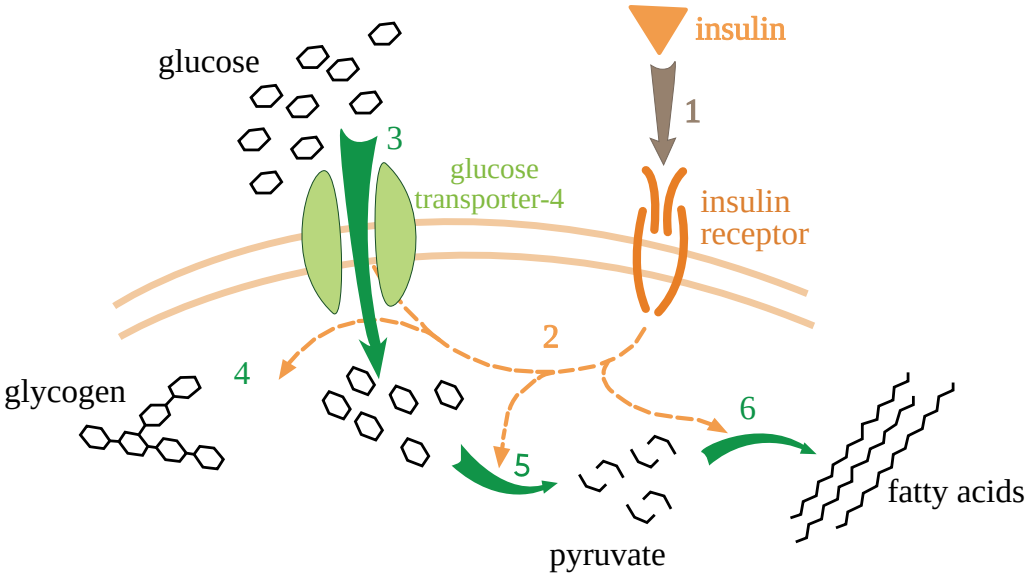


Figure 37.3.1: Hormone functioning: The hormone insulin binds to its receptor (1), which starts many protein activation cascades (2). These include translocation of Glut-4 transporter to the plasma membrane and influx of glucose (3), glycogen synthesis (4), glycolysis (5), and triglyceride (6).

Key Points

- Hormones can only affect cells that display receptors that are specific to them; cells can display receptors for many different hormones at once.
- The more receptors for a particular hormone that a cell displays, the more sensitive to that hormone it will be.
- When a cell displays more receptors in response to a hormone, this is called up-regulation, but when a cell reduces its number of receptors for a particular hormone, this is called down-regulation.
- A hormone can make changes directly to a cell by changing what genes are activated, or make changes indirectly to a cell by stimulating particular signaling pathways inside the cell that affect other processes.

Key Terms

- **phytohormone**: a plant hormone
- **hormone**: any substance produced by one tissue and conveyed by the bloodstream to another to affect physiological activity
- **receptor**: a protein on a cell wall that binds with specific molecules so that they can be absorbed into the cell in order to control certain functions

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37.4: How Hormones Work - Intracellular Hormone Receptors

Learning Objectives

- Describe how hormones alter cellular activity by binding to intracellular receptors

Intracellular Hormone Receptors

Lipid-derived (soluble) hormones such as steroid hormones diffuse across the lipid bilayer membranes of the endocrine cell. Once outside the cell, they bind to transport proteins that keep them soluble in the bloodstream. At the target cell, the hormones are released from the carrier protein and diffuse across the lipid bilayer of the plasma membrane of the target cells. They then adhere to intracellular receptors residing in the cytoplasm or in the nucleus. The cell signaling pathways induced by the steroid hormones regulate specific genes within the cell's DNA. The hormones and receptor complex act as transcription regulators by increasing or decreasing the synthesis of mRNA molecules from specific genes. This, in turn, determines the amount of corresponding protein that is synthesized from this RNA; this is known as altering gene expression. This protein can be used either to change the structure of the cell or to produce enzymes that catalyze chemical reactions. In this way, the steroid hormone regulates specific cell processes.

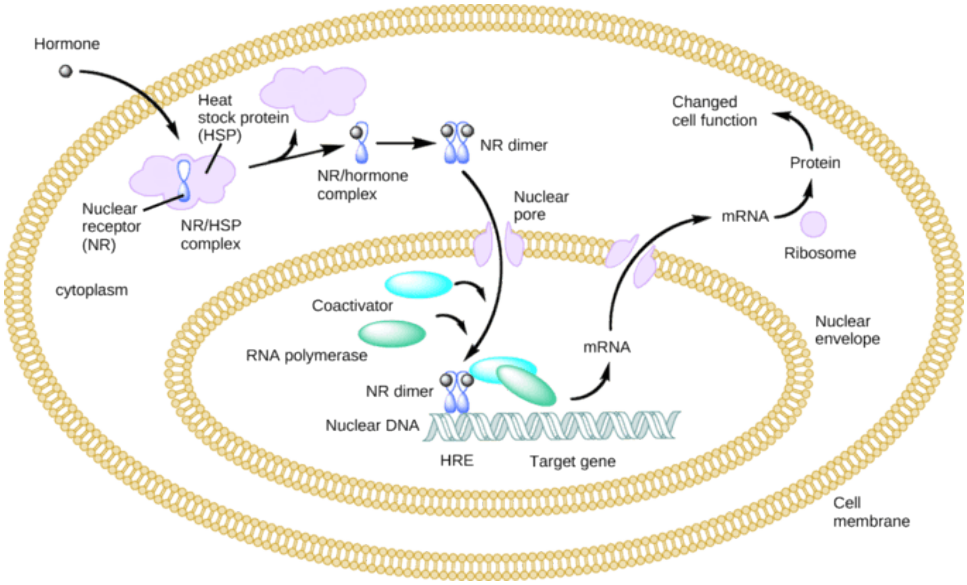


Figure 37.4.1: Hormone regulation of gene expression: An intracellular nuclear receptor (NR) is located in the cytoplasm bound to a heat shock protein (HSP). Upon hormone binding, the receptor dissociates from the heat shock protein and translocates to the nucleus. In the nucleus, the hormone-receptor complex binds to a DNA sequence called a hormone response element (HRE), which triggers gene transcription and translation. The corresponding protein product can then mediate changes in cell function.

Other lipid-soluble hormones that are not steroid hormones, such as vitamin D and thyroxine, have receptors located in the nucleus. The hormones diffuse across both the plasma membrane and the nuclear envelope, then bind to receptors in the nucleus. The hormone-receptor complex stimulates transcription of specific genes in the same way that steroid hormones do. For example, the active vitamin D metabolite, calcitriol, mediates its biological effects by binding to the vitamin D receptor (VDR), which is principally located in the nuclei of target cells. The binding of calcitriol to the VDR allows the VDR to act as a transcription factor that modulates the gene expression of transport proteins that are involved in calcium absorption in the intestine. VDR activation in the intestine, bone, kidney, and parathyroid gland cells leads to the maintenance of calcium and phosphorus levels in the blood and to the maintenance of bone content.

Key Points

- Lipid -soluble hormones are able to diffuse directly across the membranes of both the endocrine cell where they are produced and that of the target cell, as the cell membranes are made of a lipid bilayer.
- These hormones can bind to receptors that are located either in the cytoplasm of the cell or within the nucleus of the cell.
- When these hormones bind to their receptors, this signals the cell to synthesize more or less mRNA from a gene or genes, which then results in more or less protein being created from those mRNA molecules.
- The increase or decrease in protein production can alter the cell structurally or alter how and when it catalyzes chemical reactions.

Key Terms

- **gene expression**: the transcription and translation of a gene into messenger RNA and, thus, into a protein
- **transcription**: the synthesis of RNA under the direction of DNA
- **steroid**: a class of organic compounds having a structure of 17 carbon atoms arranged in four rings; they are lipids, and occur naturally as sterols, bile acids, adrenal and sex hormones, and some vitamins

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37.5: How Hormones Work - Plasma Membrane Hormone Receptors

Learning Objectives

- Describe the events that occur when a hormone binds to a plasma hormone receptor

Plasma Membrane Hormone Receptors

Amino acid-derived hormones and polypeptide hormones are not lipid-derived (lipid-soluble or fat-soluble); therefore, they cannot diffuse through the plasma membrane of cells. Lipid-insoluble hormones bind to receptors on the outer surface of the plasma membrane, via plasma membrane hormone receptors. Unlike steroid hormones, lipid-insoluble hormones do not directly affect the target cell because they cannot enter the cell and act directly on DNA. Binding of these hormones to a cell surface receptor results in activation of a signaling pathway; this triggers intracellular activity to carry out the specific effects associated with the hormone. In this way, nothing passes through the cell membrane; the hormone that binds at the surface remains at the surface of the cell while the intracellular product remains inside the cell. The hormone that initiates the signaling pathway is called a first messenger, which activates a second messenger in the cytoplasm.

One very important second messenger is cyclic adenosine monophosphate (cAMP). When a hormone binds to its membrane receptor, a G protein that is associated with the receptor is activated. G proteins are proteins separate from receptors that are found in the cell membrane. When a hormone is not bound to the receptor, the G protein is inactive and is bound to guanosine diphosphate, or GDP. When a hormone binds to the receptor, the G protein is activated by binding guanosine triphosphate, or GTP, in place of GDP. After binding, GTP is hydrolyzed by the G protein into GDP and becomes inactive.

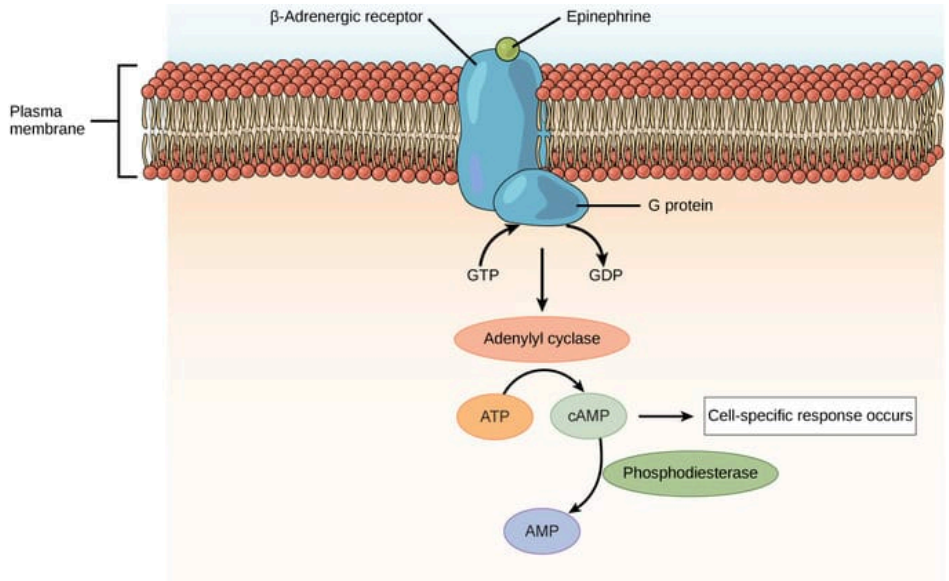


Figure 37.5.1: Second messenger systems: The amino acid-derived hormones epinephrine and norepinephrine bind to beta-adrenergic receptors on the plasma membrane of cells. Hormone binding to receptor activates a G protein, which in turn activates adenylyl cyclase, converting ATP to cAMP. cAMP is a second messenger that mediates a cell-specific response. An enzyme called phosphodiesterase breaks down cAMP, terminating the signal.

The activated G protein in turn activates a membrane-bound enzyme called adenylyl cyclase. Adenylyl cyclase catalyzes the conversion of ATP to cAMP. cAMP, in turn, activates a group of proteins called protein kinases, which transfer a phosphate group from ATP to a substrate molecule in a process called phosphorylation. The phosphorylation of a substrate molecule changes its structural orientation, thereby activating it. These activated molecules can then mediate changes in cellular processes.

The effect of a hormone is amplified as the signaling pathway progresses. The binding of a hormone at a single receptor causes the activation of many G-proteins, which activates adenylyl cyclase. Each molecule of adenylyl cyclase then triggers the formation of many molecules of cAMP. Further amplification occurs as protein kinases, once activated by cAMP, can catalyze many reactions. In this way, a small amount of hormone can trigger the formation of a large amount of cellular product. To stop hormone activity, cAMP is deactivated by the cytoplasmic enzyme phosphodiesterase, or PDE. PDE is always present in the cell, breaking down cAMP to control hormone activity; thus, preventing overproduction of cellular products.

The specific response of a cell to a lipid-insoluble hormone depends on the type of receptors that are present on the cell membrane and the substrate molecules present in the cell cytoplasm. Cellular responses to hormone binding of a receptor include altering membrane permeability and metabolic pathways, stimulating synthesis of proteins and enzymes, and activating hormone release.

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Key Points

- When a lipid (fat) insoluble hormone binds to a plasma membrane hormone receptor, this triggers specific actions inside the cell that alter the cell's activities, such as gene expression.
- Because the first event in this sequence is the binding of the hormone to the plasma membrane receptor, the hormone is called the "first messenger", while the molecule that is activated within the cell and carries out intracellular change is called the " second messenger ".
- In many cases, a hormone binding to a plasma membrane receptor activates a special kind of protein called a G protein, which in turn activates an enzyme that generates cAMP, a second messenger.
- cAMP activates another group of proteins called protein kinases, which can change the structure of other molecules by adding a phosphate group to them; these activated molecules can then affect changes within the cell.

Key Terms

- **second messenger**: any substance used to transmit a signal within a cell, especially one which triggers a cascade of events by activating cellular components
- **cyclic adenosine monophosphate**: cAMP, a second messenger derived from ATP that is involved in the activation of protein kinases and regulates the effects of adrenaline
- **G protein**: any of a class of proteins, found in cell membranes, that pass signals between hormone receptors and effector enzymes

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37.6: Regulation of Body Processes - Hormonal Regulation of the Excretory System

Learning Objectives

- Explain how the actions of different hormones regulate the excretory system

Hormonal Regulation of the Excretory System

Maintaining a proper water balance in the body is important to avoid dehydration or over-hydration (hyponatremia). The water concentration of the body is monitored by osmoreceptors in the hypothalamus, which detect the concentration of electrolytes in the extracellular fluid. The concentration of electrolytes in the blood rises when there is water loss caused by excessive perspiration, inadequate water intake, or low blood volume due to blood loss. An increase in blood electrolyte levels results in a neuronal signal being sent from the osmoreceptors in hypothalamic nuclei. The anterior pituitary is composed of glandular cells that secrete protein hormones. The pituitary gland has two components: anterior and posterior. The posterior pituitary is an extension of the hypothalamus. It is composed largely of neurons that are continuous with the hypothalamus.

Antidiuretic Hormone (ADH)

The hypothalamus produces a polypeptide hormone known as antidiuretic hormone (ADH), which is transported to and released from the posterior pituitary gland. The principal action of ADH is to regulate the amount of water excreted by the kidneys. As ADH (which is also known as vasopressin) causes direct water reabsorption from the kidney tubules, salts and wastes are concentrated in what will eventually be excreted as urine. The hypothalamus controls the mechanisms of ADH secretion, either by regulating blood volume or the concentration of water in the blood. Dehydration or physiological stress can cause an increase of osmolarity above threshold levels, which, in turn, raises ADH secretion and water retention, causing an increase in blood pressure. ADH travels in the bloodstream to the kidneys where it changes the kidneys to become more permeable to water by temporarily inserting water channels, aquaporins, into the kidney tubules. Water moves out of the kidney tubules through the aquaporins, reducing urine volume. The water is reabsorbed into the capillaries, lowering blood osmolarity back toward normal. As blood osmolarity decreases, a negative feedback mechanism reduces osmoreceptor activity in the hypothalamus; ADH secretion is reduced. ADH release can be reduced by certain substances, including alcohol, which can cause increased urine production and dehydration.

Chronic underproduction of ADH or a mutation in the ADH receptor results in diabetes insipidus. If the posterior pituitary does not release enough ADH, water cannot be retained by the kidneys and is lost as urine. This causes increased thirst, but water taken in is lost again and must be continually consumed. If the condition is not severe, dehydration may not occur, but severe cases can lead to electrolyte imbalances due to dehydration.

Another hormone responsible for maintaining electrolyte concentrations in extracellular fluids is aldosterone, a steroid hormone that is produced by the adrenal cortex. In contrast to ADH, which promotes the reabsorption of water to maintain proper water balance, aldosterone maintains proper water balance by enhancing Na^+ reabsorption and K^+ secretion from extracellular fluid of the cells in kidney tubules. Because it is produced in the cortex of the adrenal gland and affects the concentrations of minerals Na^+ and K^+, aldosterone is referred to as a mineralocorticoid, a corticosteroid that affects ion and water balance. Aldosterone release is stimulated by a decrease in blood sodium levels, blood volume, or blood pressure, or an increase in blood potassium levels. It also prevents the loss of Na^+ from sweat, saliva, and gastric juice. The reabsorption of Na^+ also results in the osmotic reabsorption of water, which alters blood volume and blood pressure.

Aldosterone production can be stimulated by low blood pressure, which triggers a sequence of chemical release. When blood pressure drops, the renin-angiotensin-aldosterone system (RAAS) is activated. Cells in the juxtaglomerular apparatus, which regulates the functions of the nephrons of the kidney, detect this and release renin. Renin, an enzyme, circulates in the blood, reacting with a plasma protein produced by the liver called angiotensinogen. When angiotensinogen is cleaved by renin, it produces angiotensin I, which is then converted into angiotensin II in the lungs. Angiotensin II functions as a hormone, causing

the release of the hormone aldosterone by the adrenal cortex, resulting in increased Na^+ reabsorption, water retention, and an increase in blood pressure. Angiotensin II, in addition to being a potent vasoconstrictor, also causes an increase in ADH and increased thirst, both of which help to raise blood pressure.

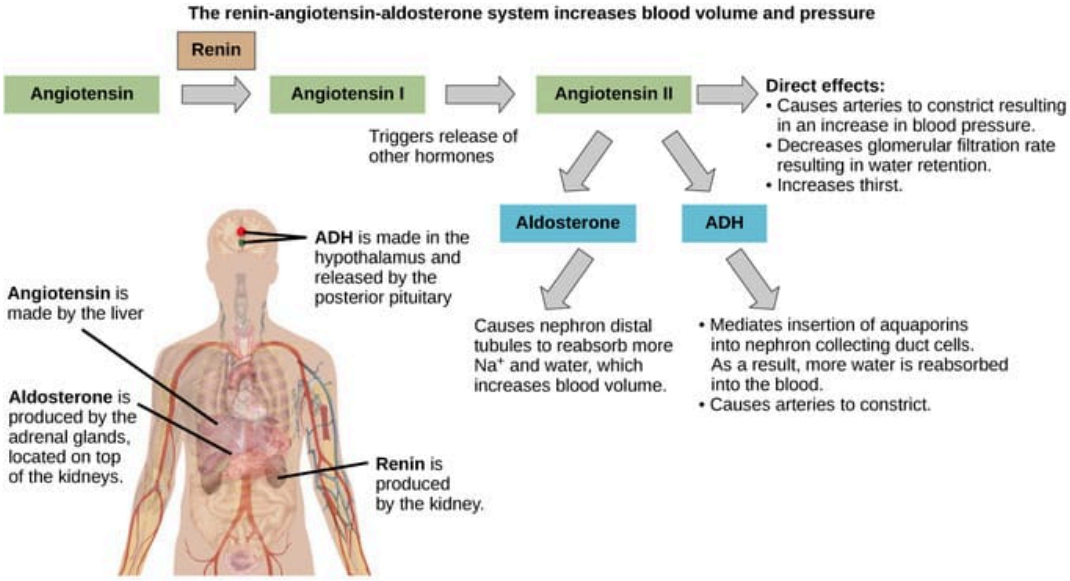


Figure 37.6.1: Action of aldosterone: ADH and aldosterone increase blood pressure and volume. Angiotensin II stimulates release of these hormones. Angiotensin II, in turn, is formed when renin cleaves angiotensin. This increases water retention and blood pressure.

Key Points

- The hypothalamus monitors the amount of water in the body by sensing the concentration of electrolytes in the blood; a high concentration of electrolytes means that the level of water in the body is low.
- Antidiuretic hormone (ADH), produced by the hypothalamus and released by the posterior pituitary, causes more water to be retained by the kidneys when water levels in the body are low.
- ADH effects water retention by creating special channels for water, called aquaporins, inside the kidneys so that more water can be reabsorbed before it is excreted.
- Aldosterone, produced by the adrenal cortex, causes the retention of water in the body by increasing the levels of sodium and potassium ions in the blood, which causes the body to reabsorb more water.
- When blood pressure is low, the enzyme renin is released, which cleaves the protein angiotensinogen into angiotensin I, which is further converted into angiotensin II.
- Angiotensin II signals the adrenal cortex to release aldosterone, which then increases the retention of sodium ions, enhancing the secretion of postassium ions, resulting in water retention and an increase in blood pressure.

Key Terms

- **renin**: a circulating enzyme released by mammalian kidneys that converts angiotensinogen to angiotensin-I that plays a role in maintaining blood pressure
- **mineralocorticoid**: any of a group of steroid hormones, characterised by their similarity to aldosterone and their influence on salt and water metabolism
- **electrolyte**: any of the various ions (such as sodium or chloride) that regulate the electric charge on cells and the flow of water across their membranes
- **aquaporin**: any of a class of proteins that form pores in the membrane of biological cells
- **aldosterone**: a mineralocorticoid hormone, secreted by the adrenal cortex, that regulates the balance of sodium and potassium in the body
- **osmoreceptor**: a sensory receptor primarily found in the hypothalamus of most homeothermic organisms that detects changes in osmotic pressure
- **antidiuretic hormone**: a hormone secreted by the posterior pituitary gland that regulates the amount of water excreted by the kidneys

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37.7: Regulation of Body Processes - Hormonal Regulation of the Reproductive System

Learning Objectives

- Explain the regulation of the male and female reproductive systems

Hormonal Regulation of the Reproductive System

Regulation of the reproductive system is a process that requires the action of hormones from the pituitary gland, the adrenal cortex, and the gonads. During puberty, in both males and females, the hypothalamus produces gonadotropin-releasing hormone (GnRH), which stimulates the production and release of follicle stimulating hormone (FSH) and luteinizing hormone (LH) from the anterior pituitary gland. These hormones regulate the gonads (testes in males and ovaries in females); they are called gonadotropins. In both males and females, FSH stimulates gamete production and LH stimulates production of hormones by the gonads. An increase in gonad hormone levels inhibits GnRH production through a negative feedback loop.

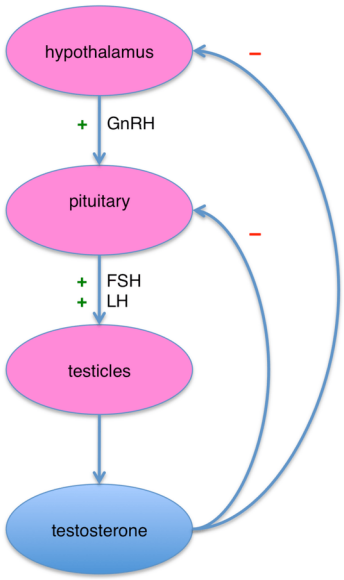


Figure 37.7.1: The negative feedback loop of the male reproductive system: GnRH, secreted by the hypothalamus, stimulates the production of FSH and LH from the pituitary gland. These hormones encourage the development of sperm cells within the testicles, which then produce inhibin and inhibit the production of GnRH, FSH and LH in a negative feedback loop.

Regulation of the Male Reproductive System

At the pituitary, GnRH stimulates the synthesis and secretion of the gonadotropins, FSH and LH. These processes are controlled by the size and frequency of GnRH pulses, as well as by feedback from androgens and estrogens. Low-frequency GnRH pulses lead to FSH release, whereas high-frequency GnRH pulses stimulate LH release. In males, FSH stimulates primary spermatocytes to undergo the first division of meiosis, to form secondary spermatocytes, leading to the maturation of sperm cells. FSH also enhances the production of androgen-binding protein by the Sertoli cells of the testes by binding to FSH receptors on their basolateral membranes. FSH production is inhibited by the hormone inhibin, which is released by the testes.

LH stimulates production of the sex hormones (androgens) by the Leydig cells of the testes. It is also called interstitial-cell-stimulating hormone. The most widely-known androgen in males is testosterone, which promotes the production of sperm and masculine characteristics. The adrenal cortex also produces small amounts of testosterone precursor, although the role of this additional hormone production is not fully understood.

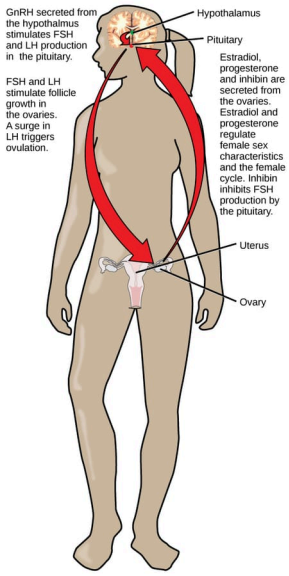


Figure 37.7.1: Regulation of the female reproductive system: Hormonal regulation of the female reproductive system involves hormones from the hypothalamus, pituitary, and ovaries. GnRH secreted by the hypothalamus stimulates the release of FSH, which stimulates the growth of egg cells, and LH, which signals for the the ovulation of an egg from its follicle. The ovaries, in turn, secrete hormones that play a role in female sexual characteristics.

Regulation of the Female Reproductive System

In females, FSH stimulates development of egg cells (or ova) in structures called follicles. Follicle cells produce the hormone inhibin, which inhibits FSH production in the female reproductive system. LH also plays a role in the development of ova, induction of ovulation, and stimulation of estradiol and progesterone production by the ovaries. Estradiol and progesterone are steroid hormones that prepare the body for pregnancy. Estradiol produces secondary sex characteristics in females, while both estradiol and progesterone regulate the menstrual cycle.

In addition to producing FSH and LH, the anterior portion of the pituitary gland also produces the hormone prolactin (PRL) in females. Prolactin stimulates the production of milk by the mammary glands, following childbirth. Prolactin levels are regulated by the hypothalamic hormones, prolactin-releasing hormone (PRH) and prolactin-inhibiting hormone (PIH) (which is now known to be dopamine). PRH stimulates the release of prolactin, while PIH inhibits it.

The posterior pituitary releases the hormone oxytocin, which stimulates uterine contractions during childbirth. The uterine smooth muscles are not very sensitive to oxytocin until late in pregnancy, when the number of oxytocin receptors in the uterus peaks. Stretching of tissues in the uterus and cervix stimulates oxytocin release during childbirth. Contractions increase in intensity as blood levels of oxytocin rise via a positive feedback mechanism until the birth is complete. Oxytocin also stimulates the contraction of myoepithelial cells around the milk-producing mammary glands. As these cells contract, milk is forced from the secretory alveoli into milk ducts and is ejected from the breasts in a milk ejection (“let-down”) reflex. Oxytocin release is stimulated by the suckling of an infant, which triggers the synthesis of oxytocin in the hypothalamus and its release into circulation at the posterior pituitary.

Key Points

- In males, FSH stimulates the production of sperm cells by signaling them to undergo meiosis, while in females, FSH stimulates the growth of the ovum inside the follicle of the ovary.
- In males, LH stimulates the Leydig cells within the testes to produce testosterone, which encourages sperm production and leads to secondary sexual characteristics.
- In females, LH plays a crucial role in signaling ovulation, as well as stimulating the production of other hormones that will prepare the body for pregnancy.
- Other hormones involved in the female reproductive system are oxytocin, which signals the uterus to contract during childbirth, and prolactin, which stimulates milk production.

Key Terms

- **gonadotropin-releasing hormone**: a trophicpeptide responsible for the release of follicle stimulating hormone and lutenizing hormone from the anterior pituitary, synthesized and released from the hypothalamus
- **follicle stimulating hormone**: a gonadotropic glycoprotein hormone, secreted in the anterior pituitary, that stimulates the growth of ovarian follicles in female mammals, and induces spermatogenesis in male mammals
- **luteinizing hormone**: a hormone, produced by part of the pituitary gland, that stimulates ovulation and the development of the corpus luteum in female mammals, and the production of androgens by male mammals
- **gonad**: a sex organ that produces gametes; specifically, a testicle or ovary
- **inhibin**: a peptide hormone, secreted by the gonads, which inhibits the secretion of follicle-stimulating hormone
- **prolactin**: a peptide gonadotrophic hormone secreted by the pituitary gland; it stimulates growth of the mammary glands and lactation in females
- **androgen**: the generic term for any natural or synthetic compound, usually a steroid hormone, that stimulates or controls the development and maintenance of masculine characteristics in vertebrates

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37.8: Regulation of Body Processes - Hormonal Regulation of Metabolism

Learning Objectives

- Explain how the hormones glucagon and insulin regulate blood glucose

Blood glucose levels vary widely over the course of a day as periods of food consumption alternate with periods of fasting. Insulin and glucagon are the two hormones primarily responsible for maintaining homeostasis of blood glucose levels. Additional regulation is mediated by the thyroid hormones.

Regulation of Blood Glucose Levels: Insulin and Glucagon

Cells of the body require nutrients in order to function. These nutrients are obtained through feeding. In order to manage nutrient intake, storing excess intake, and utilizing reserves when necessary, the body uses hormones to moderate energy stores. Insulin is produced by the beta cells of the pancreas, which are stimulated to release insulin as blood glucose levels rise (for example, after a meal is consumed). Insulin lowers blood glucose levels by enhancing the rate of glucose uptake and utilization by target cells, which use glucose for ATP production. It also stimulates the liver to convert glucose to glycogen, which is then stored by cells for later use. As insulin binds to its target cell via insulin receptors and signal transduction, it triggers the cell to incorporate glucose transport proteins into its membrane. This allows glucose to enter the cell, where it can be used as an energy source. These actions mediated by insulin cause blood glucose concentrations to fall, called a hypoglycemic, or “low sugar” effect, which inhibits further insulin release from beta cells through a negative feedback loop.

Impaired insulin function can lead to a condition called diabetes mellitus, which has many effects on the body. It can be caused by low levels of insulin production by the beta cells of the pancreas, or by reduced sensitivity of tissue cells to insulin. This prevents glucose from being absorbed by cells, causing high levels of blood glucose, or hyperglycemia (high sugar). High blood glucose levels make it difficult for the kidneys to recover all the glucose from nascent urine, resulting in glucose being lost in urine. High glucose levels also result in less water being reabsorbed by the kidneys, causing high amounts of urine to be produced; this may result in dehydration. Over time, high blood glucose levels can cause nerve damage to the eyes and peripheral body tissues, as well as damage to the kidneys and cardiovascular system. Oversecretion of insulin can cause hypoglycemia, low blood glucose levels. This causes insufficient glucose availability to cells, often leading to muscle weakness. It can sometimes cause unconsciousness or death if left untreated.

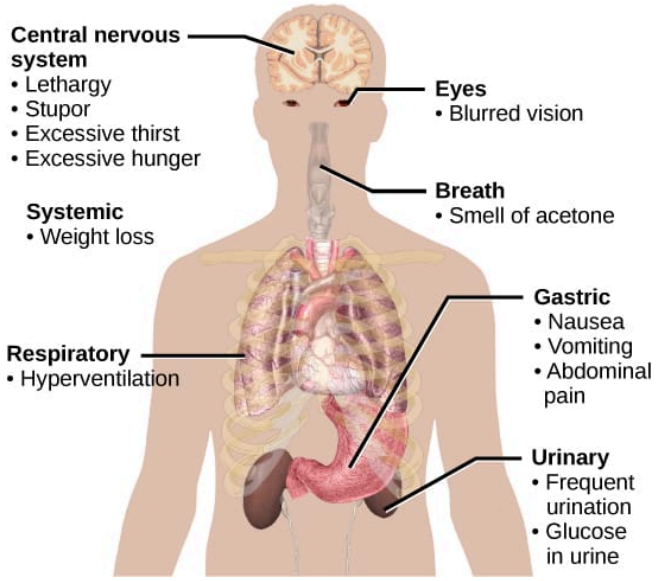


Figure 37.8.1: Diabetes mellitus: Diabetes mellitus can cause a wide range of symptoms, including nausea, vomiting, blurred vision, lethargy, a frequency in urination, and high levels of glucose in the urine.

When blood glucose levels decline below normal levels, for example between meals or when glucose is utilized during exercise, the hormone glucagon is released from the pancreas. Glucagon raises blood glucose levels, eliciting what is called a hyperglycemic effect, by stimulating the breakdown of glycogen to glucose in skeletal muscle cells and liver cells in a process called glycogenolysis. Glucose can then be utilized as energy by muscle cells and released into circulation by the liver cells. Glucagon also stimulates absorption of amino acids from the blood by the liver, which then converts them to glucose. This process of glucose synthesis is called gluconeogenesis. Rising blood glucose levels inhibit further glucagon release by the pancreas via a negative feedback mechanism. In this way, insulin and glucagon work together to maintain homeostatic glucose levels.

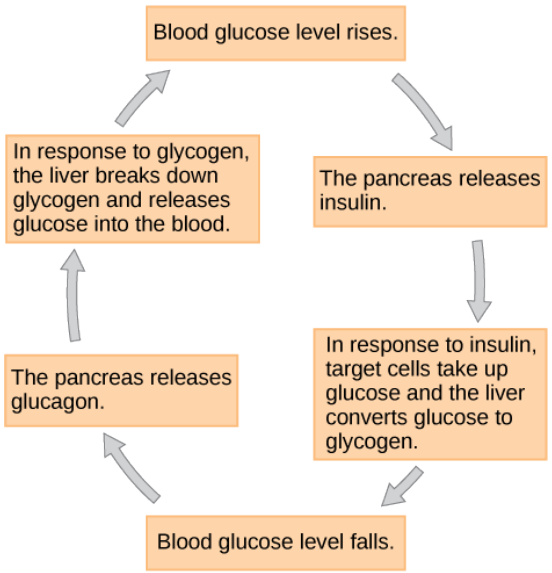


Figure 37.8.1: The regulation of blood glucose levels by insulin and glucagon: As the levels of glucose in the blood rise, insulin stimulates the cells to take up more glucose and signals the liver to convert the excess glucose to glycogen, a form in which it can be stored for later use. When the levels of glucose in the blood fall, glucagon responds by stimulating the breakdown of glycogen into glucose and signals the production of additional glucose from amino acids.

Regulation of Blood Glucose Levels: Thyroid Hormones

The basal metabolic rate, which is the amount of calories required by the body at rest, is determined by two hormones produced by the thyroid gland: thyroxine, also known as tetraiodothyronine or T4, and triiodothyronine, also known as T3. T3 and T4

release from the thyroid gland are stimulated by thyroid-stimulating hormone (TSH), which is produced by the anterior pituitary. These hormones affect nearly every cell in the body except for the adult brain, uterus, testes, blood cells, and spleen. They are transported across the plasma membrane of target cells where they bind to receptors on the mitochondria, resulting in increased ATP production. In the nucleus, T3and T4activate genes involved in energy production and glucose oxidation. This results in increased rates of metabolism and body heat production. This is known as the hormone's calorigenic effect.

Disorders can arise from both the underproduction and overproduction of thyroid hormones. Hypothyroidism, underproduction of the thyroid hormones, can cause a low metabolic rate leading to weight gain, sensitivity to cold, and reduced mental activity, among other symptoms. In children, hypothyroidism can cause cretinism, which can lead to mental retardation and growth defects. Hyperthyroidism, the overproduction of thyroid hormones, can lead to an increased metabolic rate, which may cause weight loss, excess heat production, sweating, and an increased heart rate.

Key Points

- When blood glucose levels rise, insulin is secreted by the pancreas, lowering blood glucose by increasing its uptake in cells and stimulating the liver to convert glucose to glycogen, in which form it can be stored.
- If insulin secretion is impaired, it can result in diabetes mellitus: a disease in which blood glucose levels remain high, leading to excess glucose in the urine, increased urine output, and dehydration, among other symptoms.
- When blood glucose levels fall, glucagon is secreted by the pancreas, which increases blood glucose levels by stimulating the breakdown of glycogen into glucose and the creation of glucose from amino acids.
- The basal metabolic rate of the body is controlled by the hormones T3 and T4, produced by the thyroid gland in response to the thyroid stimulating hormone (TSH), produced by the anterior pituitary.
- T3 and T4 bind to receptors on the mitochondria, causing an increase in the production of ATP, as well as increase in the transcription of genes that help utilize glucose and produce ATP, resulting in higher metabolism of the cell.

Key Terms

- **insulin**: a polypeptide hormone that regulates carbohydrate metabolism
- **glucagon**: a hormone, produced by the pancreas, that opposes the action of insulin by stimulating the production of sugar
- **glycogen**: a polysaccharide that is the main form of carbohydrate storage in animals; converted to glucose as needed
- **hypoglycemia**: a condition in which blood glucose levels are too low
- **glycogenolysis**: the production of glucose-1-phosphate by splitting a glucose monomer from glycogen using inorganic phosphate
- **gluconeogenesis**: the metabolic process in which glucose is formed, mostly in the liver, from non-carbohydrate precursors
- **thyroxine**: a hormone (an iodine derivative of tyrosine), produced by the thyroid gland, that regulates cell metabolism and growth
- **triiodothyronine**: the most powerful thyroid hormone, affecting almost every process in the body, including body temperature, growth, and heart rate
- **hypothyroidism**: the disease state caused by insufficient production of thyroid hormone by the thyroid gland
- **hyperthyroidism**: the excessive production of hormones by the thyroid

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37.9: Regulation of Body Processes - Hormonal Control of Blood Calcium Levels

Learning Objectives

- Explain how blood calcium levels are regulated by parathyroid hormone

Regulation of blood calcium concentrations is important for generation of muscle contractions and nerve impulses, which are electrically stimulated. If calcium levels get too high, membrane permeability to sodium decreases and membranes become less responsive. If calcium levels get too low, membrane permeability to sodium increases and convulsions or muscle spasms may result.

Blood calcium levels are regulated by parathyroid hormone (PTH), which is produced by the parathyroid glands. PTH is released in response to low blood calcium levels. It increases calcium levels by targeting the skeleton, the kidneys, and the intestine. In the skeleton, PTH stimulates osteoclasts, which are cells that cause bone to be reabsorbed, releasing calcium from bone into the blood. PTH also inhibits osteoblasts, cells which deposit bone, reducing calcium deposition in bone. In the intestines, PTH increases dietary calcium absorption and in the kidneys, PTH stimulates re-absorption of the calcium. While PTH acts directly on the kidneys to increase calcium re-absorption, its effects on the intestine are indirect. PTH triggers the formation of calcitriol, an active form of vitamin D, which acts on the intestines to increase absorption of dietary calcium. PTH release is inhibited by rising blood calcium levels.

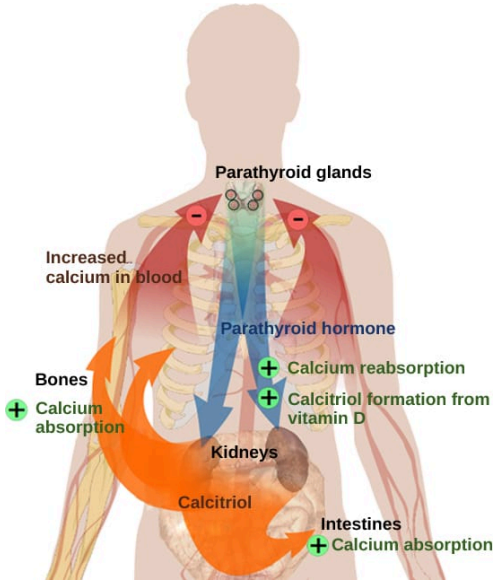


Figure 37.9.1: Regulation of blood calcium levels: Parathyroid hormone (PTH) is released in response to low blood calcium levels. It increases blood calcium levels by stimulating the resorption of bones, increasing calcium resorption in the kidneys, and indirectly increasing calcium absorption in the intestines.

Hyperparathyroidism results from an overproduction of PTH, which leads to excessive amounts of calcium being removed from bones and introduced into blood circulation. This may produce structural weakness of the bones, which can lead to deformation and fractures, plus nervous system impairment due to high blood calcium levels. Hypoparathyroidism, the underproduction of PTH, results in extremely low levels of blood calcium, which causes impaired muscle function and may result in tetany (severe sustained muscle contraction).

The hormone calcitonin, which is produced by the parafollicular (or C) cells of the thyroid, has the opposite effect on blood calcium levels as PTH. Calcitonin decreases blood calcium levels by inhibiting osteoclasts, stimulating osteoblasts, and stimulating calcium excretion by the kidneys. This results in calcium being added to the bones to promote structural integrity. Calcitonin is most important in children (when it stimulates bone growth), during pregnancy (when it reduces maternal bone loss), and during

prolonged starvation (because it reduces bone mass loss). In healthy, nonpregnant, unstarved adults, the role of calcitonin is unclear.

Key Points

- The parathyroid hormone (PTH), secreted by the parathyroid glands, is responsible for regulating blood calcium levels; it is released whenever blood calcium levels are low.
- PTH increases blood calcium levels by stimulating osteoclasts, which break down bone to release calcium into the blood stream.
- PTH increases blood calcium levels by increasing the amount of calcium resorbed by the kidneys before it can be excreted in the urine.
- PTH increases blood calcium levels by triggering the formation of calcitriol, which increases absorption of dietary calcium through the intestines.
- Calcitonin, a hormone produced by the thyroid, acts in opposition to PTH by inhibiting osteoclasts, stimulating osteoblasts, and increasing excretion of calcium into the urine by the kidneys.

Key Terms

- **osteoblast**: a mononucleate cell from which bone develops
- **parathyroid hormone**: a polypeptide hormone that is released by the chief cells of the parathyroid glands and is involved in raising the levels of calcium ions in the blood
- **calcitonin**: a hormone, secreted by parenchymal cells, that regulates calcium and phosphate metabolism
- **hypoparathyroidism**: deficiency of parathyroid hormone
- **hyperparathyroidism**: an abnormal increase in parathyroid gland activity
- **calcitriol**: the active metabolite 1,25-dihydroxycholecalciferol of vitamin D3 that is involved in the absorption of calcium
- **osteoclast**: a large multinuclear cell associated with the resorption of bone

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37.10: Regulation of Body Processes - Hormonal Regulation of Growth

Learning Objectives

- Describe the hormonal regulation of growth

Hormonal regulation is required for the growth and replication of most cells in the body. Growth hormone (GH), produced by the anterior portion of the pituitary gland, accelerates the rate of protein synthesis, particularly in skeletal muscle and bones. Effects of growth hormone on the tissues of the body can generally be described as anabolic (building up). Like most other protein hormones, GH acts by interacting with a specific receptor on the surface of cells. Increased height during childhood is the most widely-known effect of GH. Height appears to be stimulated by at least two mechanisms: Because polypeptide hormones are not fat-soluble, they cannot penetrate cell membranes. Thus, GH exerts some of its effects by binding to receptors on target cells, where it activates a pathway that directly stimulates division and multiplication of chondrocytes of cartilage.

GH also stimulates, through another pathway, the production of insulin-like growth factor 1 (IGF-1), a hormone homologous to proinsulin. The liver, a major target organ of GH for this process, is the principal site of IGF-1 production. IGF-1 has growth-stimulating effects on a wide variety of tissues. IGFs stimulate the uptake of amino acids from the blood, allowing the formation of new proteins, particularly in skeletal muscle cells, cartilage cells, and other target cells. This is especially important after a meal, when glucose and amino acid concentration levels are high in the blood. GH levels are regulated by two hormones produced by the hypothalamus. GH release is stimulated by growth hormone-releasing hormone (GHRH) and is inhibited by growth hormone-inhibiting hormone (GHIH), also called somatostatin. IGF-1 also has stimulatory effects on osteoblast and chondrocyte activity to promote bone growth.

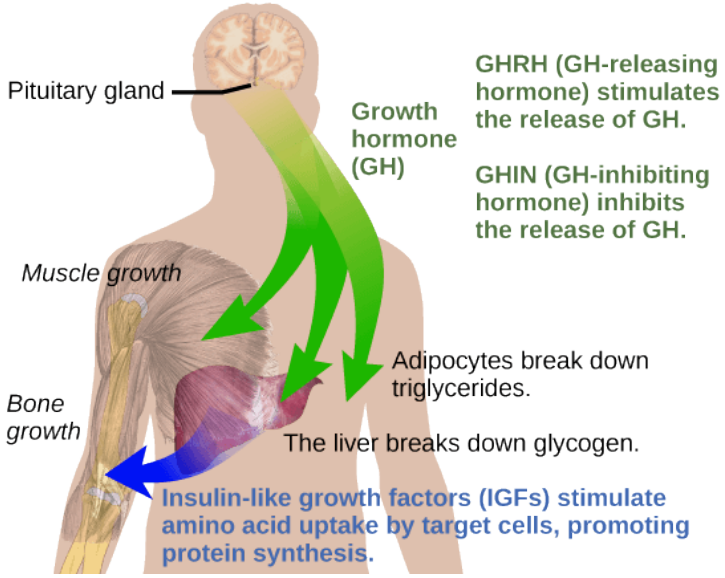


Figure 37.10.1: Effects of growth hormone: Growth hormone directly accelerates the rate of protein synthesis in skeletal muscle and bones. Insulin-like growth factor 1 (IGF-1) is activated by growth hormone and also allows formation of new proteins in muscle cells and bone.

A balanced production of growth hormone is critical for proper development. Underproduction of GH in adults does not appear to cause any abnormalities, but in children it can result in pituitary dwarfism, in which growth is reduced. Pituitary dwarfism is characterized by symmetric body formation. In some cases, individuals are under 30 inches in height. Oversecretion of growth hormone can lead to gigantism in children, causing excessive growth. In some documented cases, individuals can reach heights of over eight feet. In adults, excessive GH can lead to acromegaly, a condition in which there is enlargement of bones in the face, hands, and feet that are still capable of growth.

Key Points

- Growth hormone binds to receptors on target cells, causing mature cartilage cells to divide, creating new cartilage tissue.
- Growth hormone stimulates the production of IGF-1, a hormone that increases the uptake of amino acids when they are at high levels in the blood, so that they can be formed into new proteins.
- Growth hormone-releasing hormone stimulates the production of GH by the anterior pituitary, while growth hormone-inhibiting hormone inhibits its production.
- When growth hormone production is abnormally low in children, it can result in pituitary dwarfism, in which individuals can be less than 30 inches tall; when growth hormone production is high in children, it can result in gigantism, in which individuals can be over 8 feet tall.

Key Terms

- **growth hormone**: any polypeptide hormone secreted by the pituitary gland that promotes growth and regulates the metabolism of carbohydrates, proteins, and lipids
- **somatostatin**: a polypeptide hormone, secreted by the pancreas, that inhibits the production of certain other hormones
- **gigantism**: a condition caused by an over-production of growth hormone, resulting in excessive bone growth

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37.11: Regulation of Body Processes - Hormonal Regulation of Stress

Learning Objectives

- Describe the role of the adrenal glands in the “fight-or-flight” response and the body’s reaction to stress

When a threat or danger is perceived, the body responds by releasing hormones that will ready it for the “fight-or-flight” response. The effects of this response are familiar to anyone who has been in a stressful situation: increased heart rate, dry mouth, and hair standing erect.

The sympathetic nervous system regulates the stress response via the hypothalamus. Stressful stimuli cause the hypothalamus to signal the adrenal medulla (which mediates short-term stress responses) via nerve impulses, and the adrenal cortex, which mediates long-term stress responses via the hormone adrenocorticotropic hormone (ACTH), which is produced by the anterior pituitary.

Short-term Stress Response

Interactions of the endocrine hormones have evolved to ensure the body’s internal environment remains stable. Stressors are stimuli that disrupt homeostasis. The sympathetic division of the vertebrate autonomic nervous system has evolved the fight-or-flight response to counter stress-induced disruptions of homeostasis. In the initial alarm phase, the sympathetic nervous system stimulates an increase in energy levels through increased blood glucose levels. This prepares the body for physical activity that may be required to respond to stress: to either fight for survival or to flee from danger.



Figure 37.11.1: Fight-or-flight response: When an animal feels threatened, epinephrine and norepinephrine released by the adrenal medulla prepare the body to fight a threat or flee from it by breaking down stores of glycogen, which provides an immediate boost of energy.

When presented with a stressful situation, the body responds by calling for the release of hormones that provide a burst of energy. The hormones epinephrine (also known as adrenaline) and norepinephrine (also known as noradrenaline) are released by the adrenal medulla. Epinephrine and norepinephrine increase blood glucose levels by stimulating the liver and skeletal muscles to break down glycogen and by stimulating glucose release by liver cells. Additionally, these hormones increase oxygen availability to cells by increasing the heart rate and dilating the bronchioles. The hormones also prioritize body function by increasing blood supply to essential organs, such as the heart, brain, and skeletal muscles, while restricting blood flow to organs not in immediate need, such as the skin, digestive system, and kidneys. Epinephrine and norepinephrine are collectively called catecholamines.

Long-term Stress Response

Some stresses, such as illness or injury, can last for a long time. Glycogen reserves, which provide energy in the short-term response to stress, are exhausted after several hours and cannot meet long-term energy needs. If glycogen reserves were the only energy source available, neural functioning could not be maintained once the reserves became depleted due to the nervous system's high requirement for glucose. In this situation, the body has evolved a response to counter long-term stress through the actions of the glucocorticoids, which ensure that long-term energy requirements can be met. The glucocorticoids mobilize lipid and protein reserves, stimulate gluconeogenesis, conserve glucose for use by neural tissue, and stimulate the conservation of salts and water.

Long-term stress response differs from short-term stress response. The body cannot sustain the bursts of energy mediated by epinephrine and norepinephrine for long times. Instead, other hormones come into play. In a long-term stress response, the hypothalamus triggers the release of ACTH from the anterior pituitary gland. The adrenal cortex is stimulated by ACTH to release steroid hormones called corticosteroids. Corticosteroids turn on transcription of certain genes in the nuclei of target cells. They change enzyme concentrations in the cytoplasm and affect cellular metabolism.

There are two main corticosteroids: glucocorticoids, such as cortisol, and mineralocorticoids, such as aldosterone. These hormones target the breakdown of fat into fatty acids in the adipose tissue. The fatty acids are released into the bloodstream for other tissues to use for ATP production. The glucocorticoids primarily affect glucose metabolism by stimulating glucose synthesis. Glucocorticoids also have anti-inflammatory properties through inhibition of the immune system. For example, cortisone is used as an anti-inflammatory medication; however, it cannot be used long term as it increases susceptibility to disease due to its immune-suppressing effects. Mineralocorticoids function to regulate ion and water balance of the body. The hormone aldosterone stimulates the reabsorption of water and sodium ions in the kidney, which results in increased blood pressure and volume.

Hypersecretion of glucocorticoids can cause a condition known as Cushing's disease, characterized by a shifting of fat storage areas of the body. This can cause the accumulation of adipose tissue in the face and neck, and excessive glucose in the blood. Hyposecretion of the corticosteroids can cause Addison's disease, which may result in bronzing of the skin, hypoglycemia, and low electrolyte levels in the blood.

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Key Points

- When the body senses stress, the hypothalamus signals the adrenal medulla to release epinephrine or norepinephrine, or the anterior pituitary to release ACTH.
- In short-term stressful situations, such as when a threat is perceived, epinephrine (adrenaline) and norepinephrine (noradrenaline) are released to prepare the body for a “fight-or-flight” response.
- Epinephrine and norepinephrine act to provide a burst of energy to the body by stimulating the breakdown of glycogen into glucose, increasing the heart rate, and dilating the bronchioles.
- In long-term stress situations, such as when the body must deal with injury or illness, ACTH is released, stimulating the production of corticosteroids, which include glucocorticoids and mineralocorticoids.
- Glucocorticoids stimulate the synthesis of glucose and inhibit the immune system.
- Mineralocorticoids regulate ion and water balance of the body by stimulating the kidneys to excrete less water and sodium ions in the urine.

Key Terms

- **epinephrine**: (adrenaline) an amino acid-derived hormone secreted by the adrenal gland in response to stress
- **norepinephrine**: a neurotransmitter found in the locus coeruleus which is synthesized from dopamine
- **corticosteroid**: any of a group of steroid hormones, secreted by the adrenal cortex, that are involved in a large range of physiological systems
- **mineralocorticoid**: any of a group of steroid hormones, characterised by their similarity to aldosterone and their influence on salt and water metabolism
- **catecholamine**: any of a class of aromatic amines derived from pyrocatechol that are hormones produced by the adrenal gland
- **glucocorticoid**: any of a group of steroid hormones, produced by the adrenal cortex, that are involved in metabolism and have anti-inflammatory properties
- **adrenocorticotropic hormone**: a peptide hormone, secreted by the pituitary gland, that stimulates the secretion of other hormones

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38: THE MUSCULOSKELETAL SYSTEM

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38.1: Types of Skeletal Systems - Functions of the Musculoskeletal System

Learning Objectives

- Summarize the structure and role of the musculoskeletal system

The Musculoskeletal System

The musculoskeletal system provides support to the body and gives humans (and many animal species) the ability to move. The body's bones (the skeletal system), muscles (muscular system), cartilage, tendons, ligaments, joints, and other connective tissue that supports and binds tissues and organs together comprise the musculoskeletal system.

Most importantly, the system provides form, support, stability, and movement to the body. For example, the bones of the skeletal system protect the body's internal organs and support the weight of the body. The skeletal portion of the system serves as the main storage depot for calcium and phosphorus. It also contains critical components of the hematopoietic system (blood cell production). The muscles of the muscular system keep bones in place; they also play a role in movement of the bones by contracting and pulling on the bones, allowing for movements as diverse as standing, walking, running, and grasping items. To allow motion, different bones are connected by joints. Within these joints, bones are connected to other bones and muscle fibers via connective tissue such as tendons and ligaments. Cartilage prevents the bone ends from rubbing directly on each other. Muscles contract (bunch up) to move the bone attached at the joint.

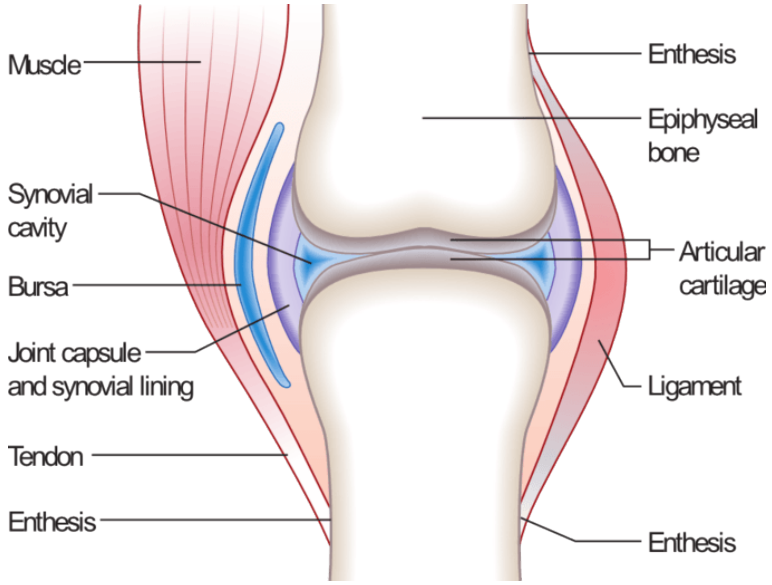


Figure 38.1.1: Joints, tendons, and ligaments: To allow motion, different bones are connected by joints. Within these joints, bones are connected to other bones and muscle fibers via connective tissue such as tendons and ligaments.

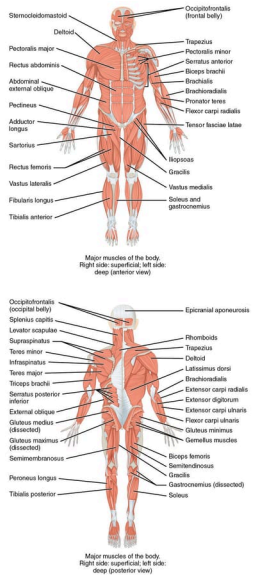


Figure 38.1.1: Human muscular system: The muscles of the muscular system keep bones in place while assisting with movement by contracting and pulling on the bones.

Unfortunately, diseases and disorders that may adversely affect the function and overall effectiveness of the system exist and can be detrimental to the body. These potentially debilitating diseases can be difficult to diagnose due to the close relation of the musculoskeletal system to other internal systems. In humans, the most common musculoskeletal diseases worldwide are caused by malnutrition. Ailments that affect the joints, such as arthritis, are also widespread. These can make movement difficult; in advanced cases, they completely impair mobility. In severe cases in which the joint has suffered extensive damage, joint replacement surgery may be needed.

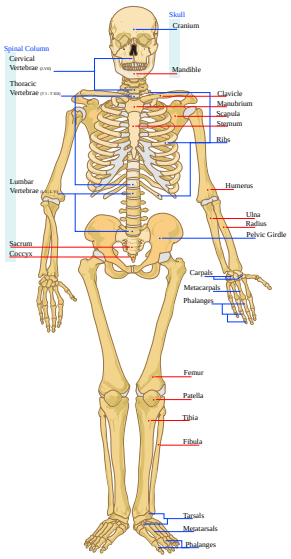


Figure 38.1.1: Human skeletal system: The bones of the skeletal system protect the body's internal organs, support the weight of the body, and serve as the main storage system for calcium and phosphorus.

Progress in the science of prosthesis design has resulted in the development of artificial joints, with joint replacement surgery in the hips and knees being the most common. Replacement joints for shoulders, elbows, and fingers are also available. Even with this progress, there is still room for improvement in the design of prostheses. The state-of-the-art prostheses have limited durability, wearing out quickly, particularly in young or active individuals. Current research is focused on the use of new materials, such as carbon fiber, that may make prostheses more durable.



Figure 38.1.1: Prostheses: Improvements in the design of prostheses, artificial replacements for body parts such as joints, elbows, legs, and fingers, have allowed for a wider range of activities in impaired recipients.

Key Points

- The skeleton, muscles, cartilage, tendons, ligaments, joints, and other connective tissues are all part of the musculoskeletal system, which work together to provide the body with support, protection, and movement.
- The bones of the skeletal system protect the body's internal organs, support the weight of the body, and serve as the main storage system for calcium and phosphorus.
- The muscles of the muscular system keep bones in place; they assist with movement by contracting and pulling on the bones.
- To allow motion, different bones are connected by joints which are connected to other bones and muscle fibers via connective tissues such as tendons and ligaments.
- Cartilage prevents the bone ends from rubbing directly on each other.
- Malnutrition and arthritis are examples of disorders and diseases in the body that can severely impair the function of the musculoskeletal system.

Key Terms

- **prosthesis**: an artificial replacement for a body part, either internal or external
- **arthritis**: inflammation of a joint or joints causing pain and/or disability, swelling, and stiffness due to various causes, such as infection, trauma, degenerative changes, or metabolic disorders
- **musculoskeletal system**: an organ system made up of the muscular and skeletal systems; the system provides form, support, stability, and movement to the body

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38.2: Types of Skeletal Systems - Types of Skeletal Systems

Learning Objectives

- Differentiate among skeletal types: hydrostatic skeleton, exoskeleton, and endoskeleton

Types of Skeletal Designs

A skeletal system is necessary to support the body, protect internal organs, and allow for the movement of an organism. There are three different skeleton designs that provide organisms these functions: hydrostatic skeleton, exoskeleton, and endoskeleton.

Hydrostatic Skeleton

A hydrostatic skeleton is one formed by a fluid-filled compartment within the body: the coelom. The organs of the coelom are supported by the aqueous fluid, which also resists external compression. This compartment is under hydrostatic pressure because of the fluid and supports the other organs of the organism. This type of skeletal system is found in soft-bodied animals such as sea anemones, earthworms, Cnidaria, and other invertebrates.



Figure 38.2.1: Hydrostatic skeleton: The skeleton of the red-knobbed sea star (Protoreaster linckii) is an example of a hydrostatic skeleton.

Movement in a hydrostatic skeleton is provided by muscles that surround the coelom. The muscles in a hydrostatic skeleton contract to change the shape of the coelom; the pressure of the fluid in the coelom produces movement. For example, earthworms move by waves of muscular contractions (peristalsis) of the skeletal muscle of the body wall hydrostatic skeleton, which alternately shorten and lengthen the body. Lengthening the body extends the anterior end of the organism. Most organisms have a mechanism to fix themselves in the substrate. Shortening the muscles then draws the posterior portion of the body forward. Although a hydrostatic skeleton is well-suited to invertebrate organisms such as earthworms and some aquatic organisms, it is not an efficient skeleton for terrestrial animals.

Exoskeleton

An exoskeleton is an external, hard, encasement on the surface of an organism. For example, the shells of crabs and insects are exoskeletons. This skeleton type provides defense against predators, supports the body, and allows for movement through the contraction of attached muscles. As with vertebrates, muscles must cross a joint inside the exoskeleton. Shortening of the muscle

changes the relationship of the two segments of the exoskeleton. Arthropods, such as crabs and lobsters, have exoskeletons that consist of 30–50 percent chitin, a polysaccharide derivative of glucose that is a strong-but-flexible material. Chitin is secreted by the epidermal cells. The exoskeleton is further strengthened by the addition of calcium carbonate in organisms such as the lobster. Because the exoskeleton is acellular and does not grow as the organism grows, arthropods must periodically shed their exoskeletons.



Figure 38.2.1: Exoskeletons: Muscles attached to the exoskeleton of the Halloween crab (Gecarcinus quadratus) allow it to move.

Endoskeleton

An endoskeleton consists of hard, mineralized structures located within the soft tissue of organisms. An example of a primitive endoskeletal structure is the spicule of sponges. The bones of vertebrates are composed of tissues, whereas sponges have no true tissues. Endoskeletons provide support for the body, protect internal organs, and allow for movement through contraction of muscles attached to the skeleton.



Figure 38.2.1: Endoskeletons: The skeletons of humans and horses are examples of endoskeletons. They provide bodies with support, protection of organs, and aid in movement.

The human skeleton is an endoskeleton that consists of 206 bones in the adult. It has five main functions: providing support to the body, storing minerals and lipids, producing blood cells, protecting internal organs, and allowing for movement. The skeletal

system in vertebrates is divided into the axial skeleton (which consists of the skull, vertebral column, and rib cage), and the appendicular skeleton (which consists of the shoulders, limb bones, the pectoral girdle, and the pelvic girdle).

Key Points

- In organisms with hydrostatic skeletons, the muscles contract to change the shape of the coelom, which then produces movement due to the pressure of the fluid inside the fluid-filled cavity.
- Exoskeletons are external skeletal systems that are made up of chitin and calcium carbonate.
- Organisms with an endoskeleton are supported by a hard, mineralized skeletal system that resides inside the body.
- In vertebrates, the endoskeleton system is further divided into the axial skeleton and appendicular skeleton.

Key Terms

- **coelom**: a fluid-filled cavity within the body of an animal; the digestive system is suspended within the cavity, which is lined by a tissue called the peritoneum
- **peristalsis**: the rhythmic, wave-like contraction and relaxation of muscles which propagates in a wave down a muscular tube
- **endoskeleton**: the internal skeleton of an animal, which in vertebrates is comprised of bone and cartilage
- **exoskeleton**: a hard outer structure that provides both structure and protection to creatures such as insects, Crustacea, and Nematoda

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38.3: Types of Skeletal Systems - Human Axial Skeleton

Learning Objectives

- Describe the bones and function of the human axial skeleton

Human Axial Skeleton

The axial skeleton forms the central axis of the human body and includes the bones of the skull, the ossicles of the middle ear, the hyoid bone of the throat, the vertebral column, and the thoracic cage (ribcage). The function of the axial skeleton is to provide support and protection for the brain, spinal cord, and organs in the ventral body cavity. It also provides a surface for the attachment of muscles that move the head, neck, and trunk; performs respiratory movements; and stabilizes parts of the appendicular skeleton, which will be discussed later.

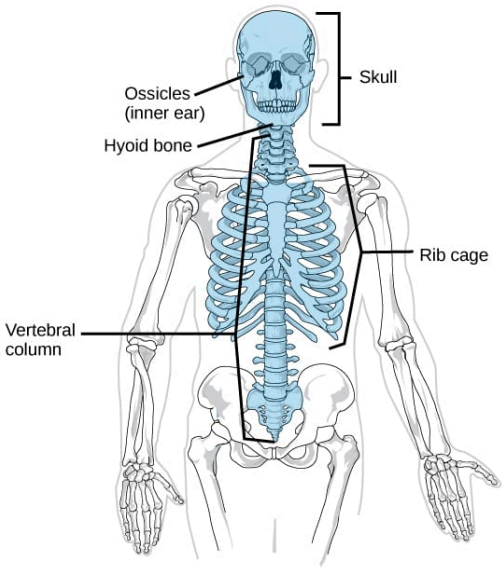


Figure 38.3.1: Axial skeleton: The axial skeleton consists of the bones of the skull, ossicles of the middle ear, hyoid bone, vertebral column, and rib cage.

The Skull

The bones of the skull support the structures of the face and protect the brain. The skull consists of 22 bones, which are divided into two categories: cranial bones and facial bones. The cranial bones are eight bones that form the cranial cavity, which encloses the brain and serves as an attachment site for the muscles of the head and neck. The eight cranial bones include the frontal bone, two parietal bones, two temporal bones, the occipital bone, the sphenoid bone, and the ethmoid bone.

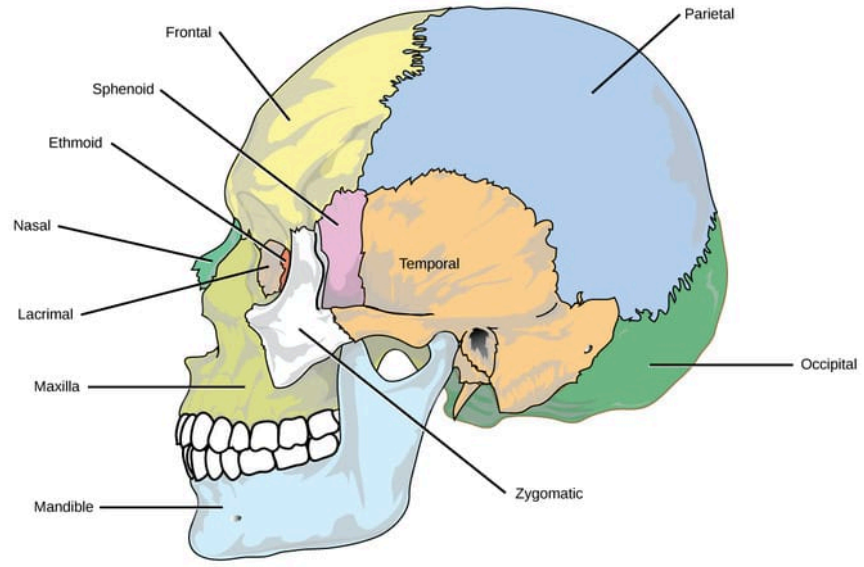


Figure 38.3.1: Skull: The bones of the skull support the structures of the face and protect the brain.

Fourteen facial bones form the face, provide cavities for the sense organs (eyes, mouth, and nose), protect the entrances to the digestive and respiratory tracts, and serve as attachment points for facial muscles. The 14 facial bones are the nasal bones, maxillary bones, zygomatic bones, palatine, vomer, lacrimal bones, inferior nasal conchae, and mandible.

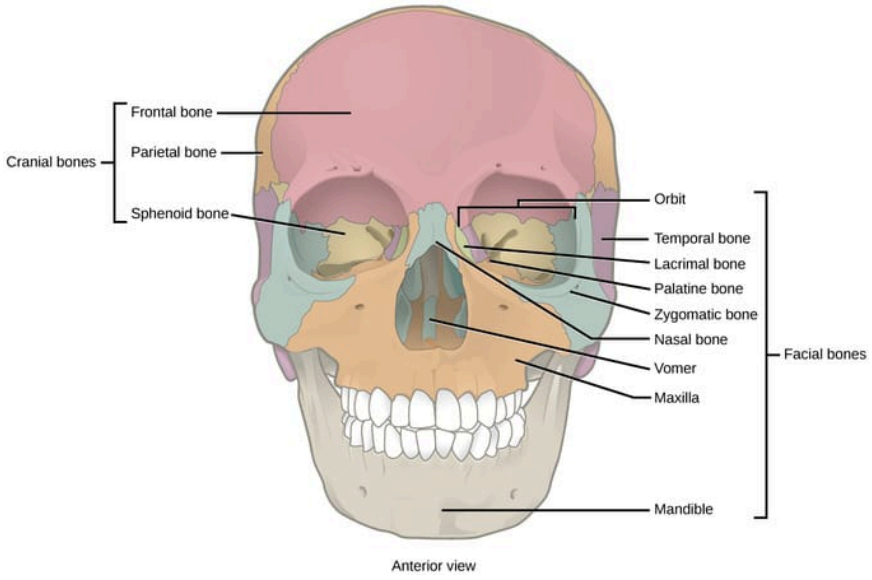


Figure 38.3.1: Cranial and facial bones: The facial bones of the skull form the face and provide cavities for the eyes, nose, and mouth. The cranial bones, including the frontal, parietal, temporal, occipital, ethmoid, and sphenoid bones.

The auditory ossicles of the middle ear transmit sounds from the air as vibrations to the fluid-filled cochlea. The auditory ossicles consist of six bones: two malleus bones, two incus bones, and two stapes, one of each on each side. These bones are unique to mammals.

The hyoid bone lies below the mandible in the front of the neck. It acts as a movable base for the tongue and is connected to muscles of the jaw, larynx, and tongue. The mandible articulates with the base of the skull, controling the opening to the airway and gut. In animals with teeth, the mandible brings the surfaces of the teeth in contact with the maxillary teeth.

The Vertebral Column

The vertebral column, or spinal column, surrounds and protects the spinal cord, supports the head, and acts as an attachment

point for the ribs and muscles of the back and neck. The adult vertebral column is comprised of 26 bones: the 24 vertebrae, the sacrum, and the coccyx bones. In the adult, the sacrum is typically composed of five vertebrae that fuse into one. We begin life with approximately 33 vertebrae, but as we grow, several vertebrae fuse together. The adult vertebrae are further divided into the 7 cervical vertebrae, 12 thoracic vertebrae, and 5 lumbar vertebrae.

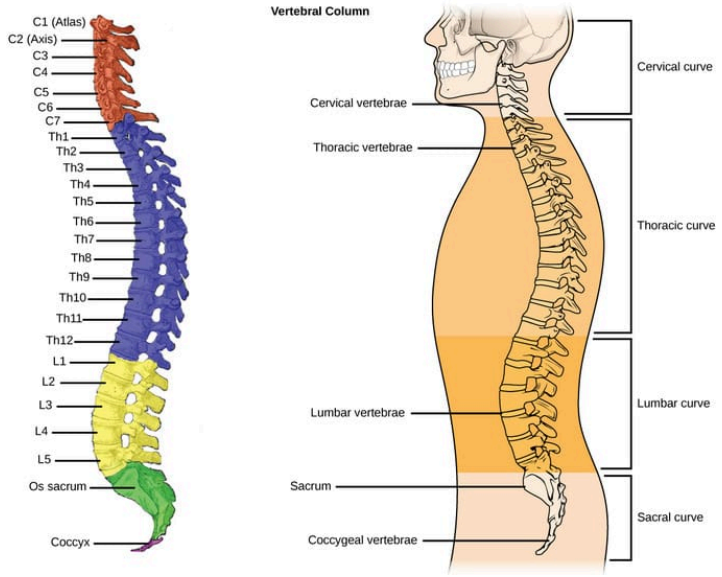


Figure 38.3.1: Vertebral column: (a) The vertebral column consists of seven cervical vertebrae (C1–7), twelve thoracic vertebrae (Th1–12), five lumbar vertebrae (L1–5), the sacrum, and the coccyx. (b) Spinal curves increase the strength and flexibility of the spine.

Each vertebral body has a large hole in the center through which the nerves of the spinal cord pass. There is also a notch on each side through which the spinal nerves, which serve the body at that level, can exit from the spinal cord. The names of the spinal curves correspond to the region of the spine in which they occur. The thoracic and sacral curves are concave, while the cervical and lumbar curves are convex. The arched curvature of the vertebral column increases its strength and flexibility, allowing it to absorb shocks like a spring.

Intervertebral discs composed of fibrous cartilage lie between adjacent vertebral bodies from the second cervical vertebra to the sacrum. Each disc is part of a joint that allows for some movement of the spine, acting as a cushion to absorb shocks from movements, such as walking and running. Intervertebral discs also act as ligaments to bind vertebrae together. The inner part of discs, the nucleus pulposus, hardens as people age, becoming less elastic. This loss of elasticity diminishes its ability to absorb shocks.

The Thoracic Cage

The thoracic cage, also known as the ribcage, is the skeleton of the chest. It consists of the ribs, sternum, thoracic vertebrae, and costal cartilages. The thoracic cage encloses and protects the organs of the thoracic cavity, including the heart and lungs. It also provides support for the shoulder girdles and upper limbs, and serves as the attachment point for the diaphragm, muscles of the back, chest, neck, and shoulders. Changes in the volume of the thorax enable breathing.

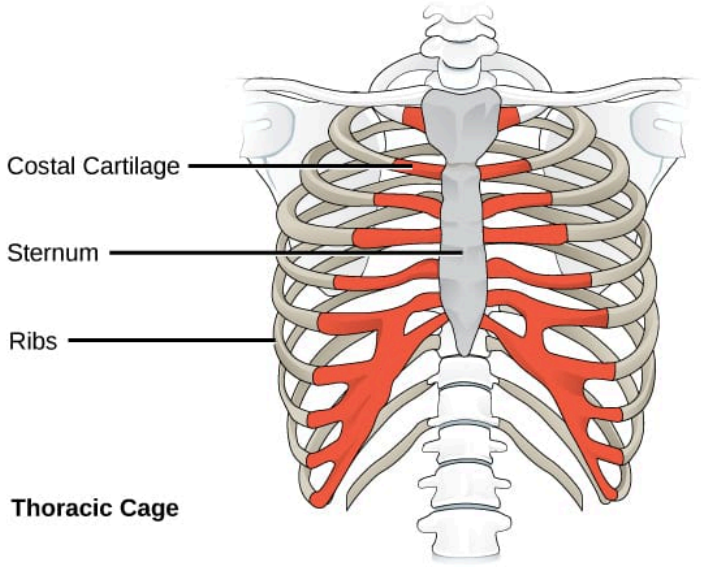


Figure 38.3.1: Thoracic cage: The thoracic cage, or rib cage, protects the heart and the lungs.

The sternum, or breastbone, is a long, flat bone located at the anterior of the chest. It is formed from three bones that fuse in the adult. The ribs are 12 pairs of long, curved bones that attach to the thoracic vertebrae and curve toward the front of the body, forming the ribcage. Costal cartilages connect the anterior ends of the ribs to the sternum, with the exception of rib pairs 11 and 12, which are free-floating ribs.

Key Points

- The axial skeleton provides support and protection for the brain, spinal cord, and the organs in the ventral body cavity; it also provides a surface for the attachment of muscles, directs respiratory movements, and stabilizes portions of the appendicular skeleton.
- The bones of the skull are divided into cranial bones and facial bones; their main roles consist of supporting the structures of the face and protecting the brain.
- The vertebral column protects the spinal cord, supports the head, and acts as an attachment point for the ribs and muscles of the back and neck.
- The thoracic cage's most notable role is in breathing; however, it also protects the organs of the thoracic cavity, provides support for the shoulder girdles and upper limbs, and functions as the attachment point for the diaphragm, muscles of the back, chest, neck, and shoulders.

Key Terms

- **intervertebral disc**: a disc between the vertebra in the spine
- **ossicle**: a small bone (or bony structure), especially one of the three of the middle ear
- **convex**: curved or bowed outward like the outside of a bowl, sphere or circle
- **vertebral column**: the series of vertebrae that protect the spinal cord; the spinal column
- **concave**: curved or bowed inward like the inner surface of a sphere or bowl

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38.4: Types of Skeletal Systems - Human Appendicular Skeleton

Learning Objectives

- Describe the bones and functions of the human appendicular skeleton

Human Appendicular Skeleton

The human appendicular skeleton is composed of the bones of the upper limbs (which function to grasp and manipulate objects) and the lower limbs (which permit locomotion). It also includes the pectoral (or shoulder) girdle and the pelvic girdle, which attach the upper and lower limbs to the body, respectively.

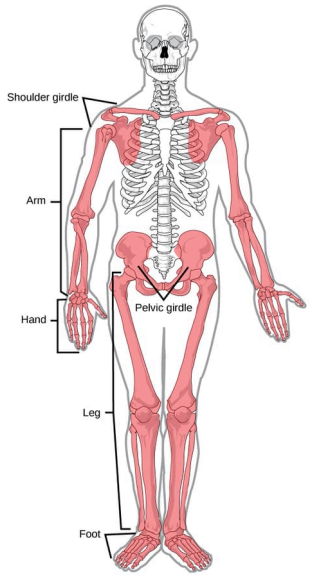


Figure 38.4.1: Appendicular skeleton: The appendicular skeleton is composed of the bones of the pectoral limbs (arm, forearm, hand), the pelvic limbs (thigh, leg, foot), the pectoral girdle, and the pelvic girdle.

The Pectoral Girdle

The pectoral girdle bones, providing the points of attachment of the upper limbs to the axial skeleton, consists of the clavicle (or collarbone) in the anterior, as well as the scapula (or shoulder blades) in the posterior. The clavicles, S-shaped bones that position the arms on the body, lie horizontally across the front of the thorax (chest) just above the first rib.

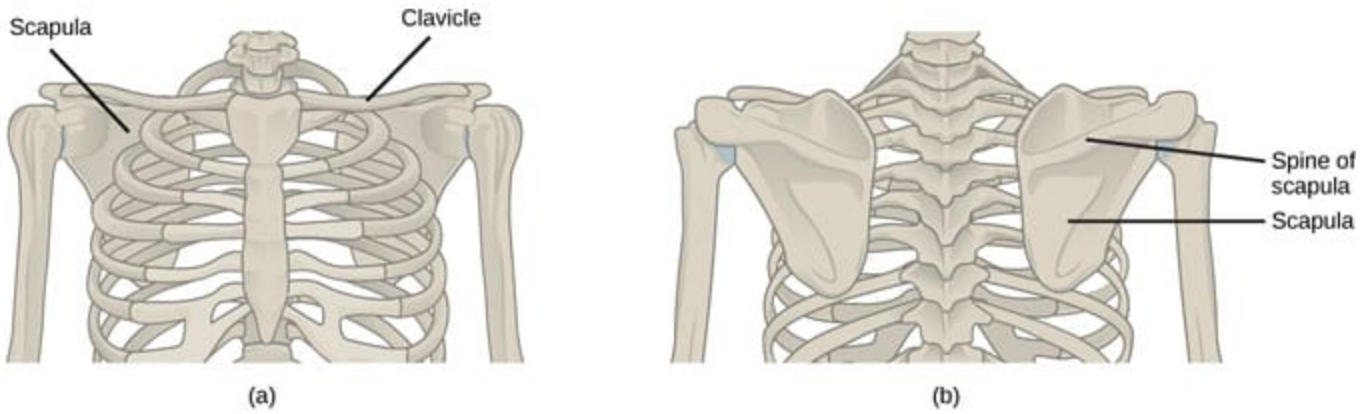


Figure 38.4.1: Pectoral girdle: (a) The pectoral girdle in primates consists of the clavicles and scapulae. (b) The posterior view reveals the spine of the scapula to which muscle attaches.

The scapulae are flat, triangular bones that are located at the back of the pectoral girdle. They support the muscles crossing the shoulder joint. The spine runs across the back of the scapula; it is a good example of a bony protrusion that facilitates a broad area of attachment for muscles to bone.

The Upper Limbs

The upper limbs contain 30 bones in three regions: the arm (shoulder to elbow), the forearm (ulna and radius), and the wrist and hand. The humerus is the largest and longest bone of the upper limb and the only bone of the arm. It articulates (joins) with the scapula at the shoulder and with the forearm at the elbow. The forearm, extending from the elbow to the wrist, consists of two bones: the ulna and the radius. The radius, located along the lateral (thumb) side of the forearm, articulates with the humerus at the elbow. The ulna, located on the medial aspect (pinky-finger side) of the forearm, is longer than the radius. It articulates with the humerus at the elbow. The radius and ulna also articulate with the carpal bones and with each other, which in vertebrates enables a variable degree of rotation of the carpus with respect to the long axis of the limb. The hand includes the eight bones of the carpus (wrist), the five bones of the metacarpus (palm), and the 14 bones of the phalanges (digits). Each digit consists of three phalanges, except for the thumb, which, when present, has only two.

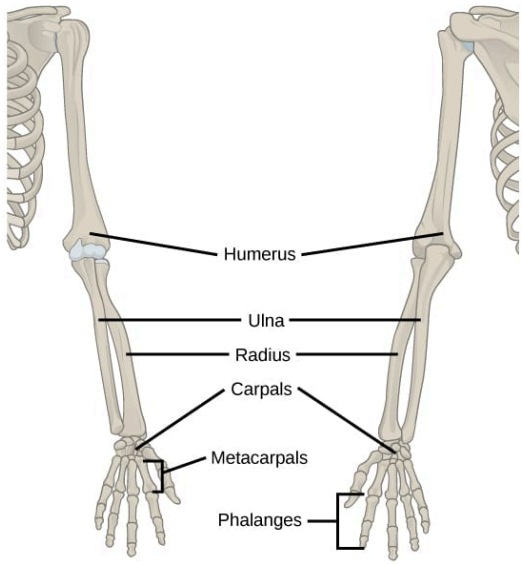


Figure 38.4.1: Upper limb: The upper limb consists of the humerus of the upper arm, the radius and ulna of the forearm, eight bones of the carpus, five bones of the metacarpus, and 14 bones of the phalanges.

The Pelvic Girdle

The pelvic girdle attaches to the lower limbs of the axial skeleton and is responsible for bearing the weight of the body and for

locomotion. It is securely attached to the axial skeleton by strong ligaments. It also has deep sockets with robust ligaments to securely attach the femur to the body. The pelvic girdle is further strengthened by two large hip bones. In adults, the hip bones are formed by the fusion of three pairs of bones: the ilium, ischium, and pubis. The pelvis joins together in the anterior of the body the pubic symphysis joint and with the bones of the sacrum at the posterior of the body.

The Lower Limbs

The lower limbs consists of the thigh, the leg, and the foot. The bones of the lower limb are the femur (thigh bone), patella (kneecap), tibia and fibula (bones of the leg), tarsals (bones of the ankle), and metatarsals and phalanges (bones of the foot). The bones of the lower limbs are thicker and stronger than the bones of the upper limbs because of the need to support the entire weight of the body along with the resulting forces from locomotion.

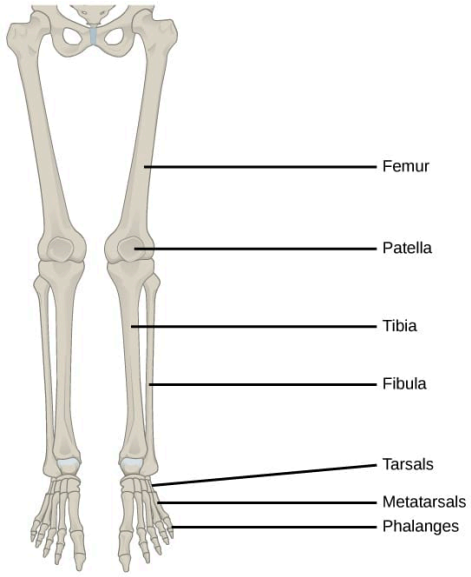


Figure 38.4.1: Lower limb: The lower limb consists of the thigh (femur), kneecap (patella), leg (tibia and fibula), ankle (tarsals), and foot (metatarsals and phalanges) bones.

The femur, or thighbone, is the longest, heaviest, and strongest bone in the body. The femur and pelvis form the hip joint at the proximal end. At the distal end, the femur, tibia, and patella form the knee joint. The patella, or kneecap, is a triangular bone that lies anterior to the knee joint; it is embedded in the tendon of the femoral extensors (quadriceps). It improves knee extension by reducing friction. The tibia, or shinbone, is a large bone of the leg that is located directly below the knee. The tibia articulates with the femur at its proximal end, with the fibula and the tarsal bones at its distal end. As the second largest bone in the human body it is responsible for transmitting the weight of the body from the femur to the foot. The fibula, or calf bone, parallels and articulates with the tibia. It is not weight-bearing, but acts as a site for muscle attachment while forming the lateral part of the ankle joint.

The tarsals are the seven bones of the ankle, which transmits the weight of the body from the tibia and the fibula to the foot. The metatarsals are the five bones of the foot, while the phalanges are the 14 bones of the toes.

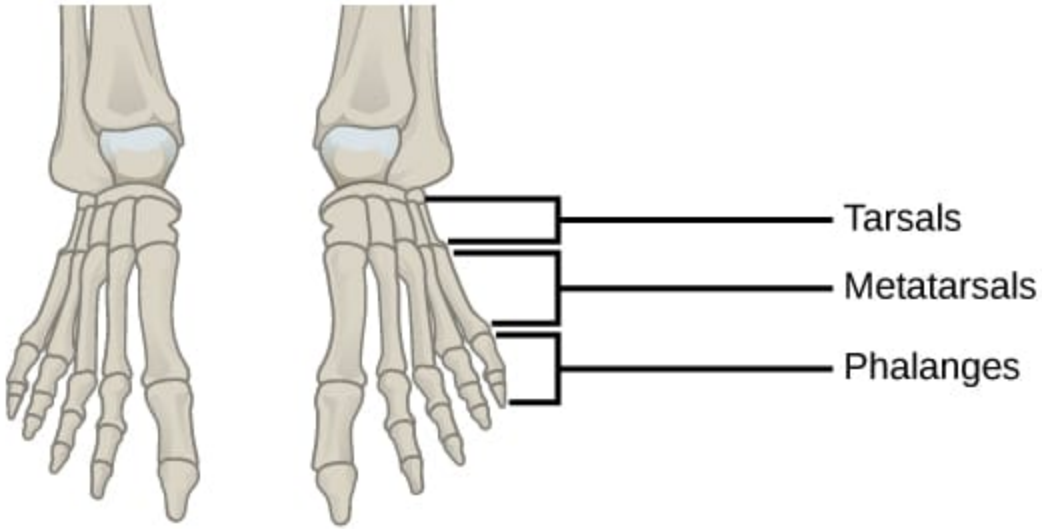


Figure 38.4.1: Foot and ankle: This drawing shows the bones of the human foot and ankle, including the metatarsals and the phalanges.

Contributions and Attributions

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Key Points

- The human appendicular skeleton is composed of the bones of the upper limbs, the lower limbs, the pectoral girdle, and the pelvic girdle.
- The pectoral girdle acts as the point of attachment of the upper limbs to the body.
- The upper limb consists of the arm, the forearm, and the wrist and hand.
- The pelvic girdle is responsible for bearing the weight of the body and is responsible for locomotion; it is also responsible for attaching the lower limbs to the body.
- The lower limbs, including the thighs, legs, and feet, support the entire weight of the body and absorb the resulting forces from locomotion.

Key Terms

- **axial skeleton**: the bones of the head and trunk of an organism
- **appendicular**: of or pertaining to a limb or appendage
- **clavicle**: the collar bone; the prominent bone at the top of the chest between the shoulder and the neck
- **scapula**: either of the two large, flat, bones forming the back of the shoulder
- **articulate**: to form a joint or connect by joints

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38.5: Bone - Introduction

Learning Objectives

- Distinguish between compact and spongy bone tissues

Bone Tissue

Bones are considered organs because they contain various types of tissue, such as blood, connective tissue, nerves, and bone tissue. Osteocytes, the living cells of bone tissue, form the mineral matrix of bones. There are two types of bone tissue: compact and spongy.

Compact Bone Tissue

Compact bone (or cortical bone), forming the hard external layer of all bones, surrounds the medullary cavity (innermost part or bone marrow). It provides protection and strength to bones. Compact bone tissue consists of units called osteons or Haversian systems. Osteons are cylindrical structures that contain a mineral matrix and living osteocytes connected by canaliculi which transport blood. They are aligned parallel to the long axis of the bone. Each osteon consists of lamellae, layers of compact matrix that surround a central canal (the Haversian or osteonic canal), which contains the bone's blood vessels and nerve fibers. Osteons in compact bone tissue are aligned in the same direction along lines of stress, helping the bone resist bending or fracturing. Therefore, compact bone tissue is prominent in areas of bone at which stresses are applied in only a few directions.

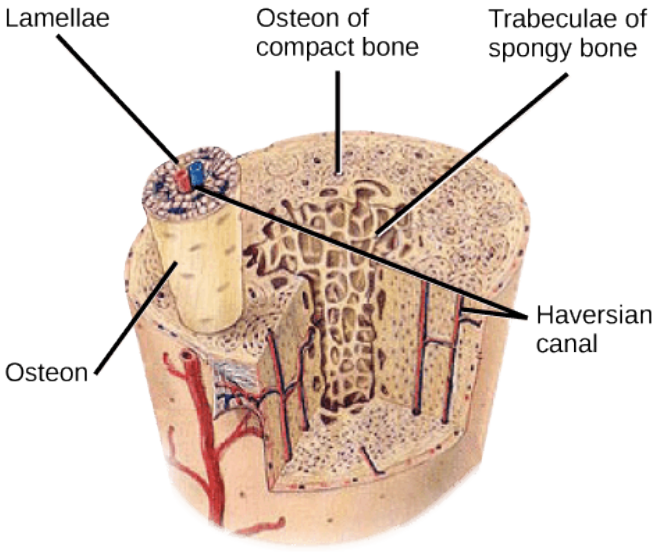


Figure 38.5.1: Components of compact bone tissue: Compact bone tissue consists of osteons that are aligned parallel to the long axis of the bone and the Haversian canal that contains the bone's blood vessels and nerve fibers. The inner layer of bones consists of spongy bone tissue. The small dark ovals in the osteon represent the living osteocytes.

Spongy Bone Tissue

Compact bone tissue forms the outer layer of all bones while spongy or cancellous bone forms the inner layer of all bones. Spongy bone tissue does not contain osteons. Instead, it consists of trabeculae, which are lamellae that are arranged as rods or plates. Red bone marrow is found between the trabuculae. Blood vessels within this tissue deliver nutrients to osteocytes and remove waste. The red bone marrow of the femur and the interior of other large bones, such as the ileum, forms blood cells.

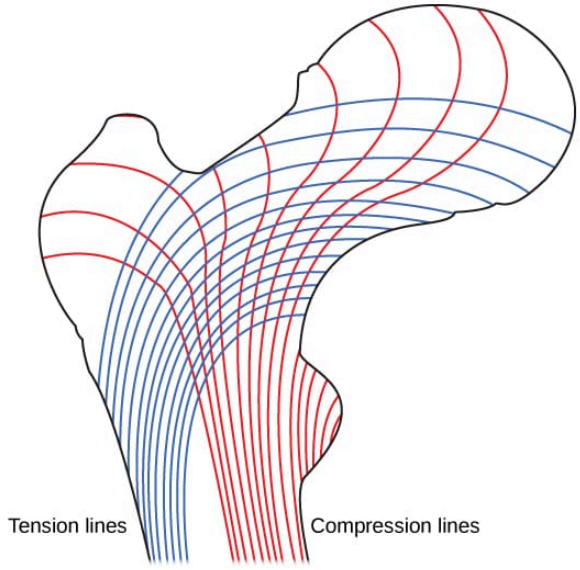


Figure 38.5.1: Arrangement of trabeculae in spongy bone: Trabeculae in spongy bone are arranged such that one side of the bone bears tension and the other withstands compression.

Spongy bone reduces the density of bone, allowing the ends of long bones to compress as the result of stresses applied to the bone. Spongy bone is prominent in areas of bones that are not heavily stressed or where stresses arrive from many directions. The epiphysis of a bone, such as the neck of the femur, is subject to stress from many directions. Imagine laying a heavy-framed picture flat on the floor. You could hold up one side of the picture with a toothpick if the toothpick were perpendicular to the floor and the picture. Now, drill a hole and stick the toothpick into the wall to hang up the picture. In this case, the function of the toothpick is to transmit the downward pressure of the picture to the wall. The force on the picture is straight down to the floor, but the force on the toothpick is both the picture wire pulling down and the bottom of the hole in the wall pushing up. The toothpick will break off right at the wall.

The neck of the femur is horizontal like the toothpick in the wall. The weight of the body pushes it down near the joint, but the vertical diaphysis of the femur pushes it up at the other end. The neck of the femur must be strong enough to transfer the downward force of the body weight horizontally to the vertical shaft of the femur.

Key Points

- Compact bone is the hard external layer of all bones that protects, strengthens, and surrounds the medullary cavity filled with marrow.
- Cylindrical structures, called osteons, are aligned along lines of the greatest stress to the bone in order to resist bending or fracturing.
- Spongy or cancellous bone tissue consists of trabeculae that are arranged as rods or plates with red bone marrow in between.
- Spongy bone is prominent in regions where the bone is less dense and at the ends of long bones where the bone has to be more compressible due to stresses that arrive from many directions.

Key Terms

- **trabecula**: a small mineralized spicule that forms a network in spongy bone
- **epiphysis**: the rounded end of any long bone
- **osteocyte**: a mature bone cell involved with the maintenance of bone
- **osteon**: any of the central canals and surrounding bony layers found in compact bone

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38.6: Bone - Cell Types in Bones

Learning Objectives

- Distinguish among the four cell types in bone

Bone consists of four types of cells: osteoblasts, osteoclasts, osteocytes, and osteoprogenitor (or osteogenic) cells. Each cell type has a unique function and is found in different locations in bones. The osteoblast, the bone cell responsible for forming new bone, is found in the growing portions of bone, including the periosteum and endosteum. Osteoblasts, which do not divide, synthesize and secrete the collagen matrix and calcium salts. As the secreted matrix surrounding the osteoblast calcifies, the osteoblast becomes trapped within it. As a result, it changes in structure, becoming an osteocyte, the primary cell of mature bone and the most common type of bone cell. Each osteocyte is located in a space (lacuna) surrounded by bone tissue. Osteocytes maintain the mineral concentration of the matrix via the secretion of enzymes. As is the case with osteoblasts, osteocytes lack mitotic activity. They are able to communicate with each other and receive nutrients via long cytoplasmic processes that extend through canaliculi (singular = canaliculus), channels within the bone matrix.

Bone Cells		
Cell type	**Function**	**Location**
Osteogenic cells	Develop into osteoblasts	Deep layers of the periosteum and the marrow
Osteoblasts	Bone formation	Growing portions of bone, including periosteum and endosteum
Osteocytes	Maintain mineral concentration of matrix	Entrapped in matrix
Osteoclasts	Bone resorption	Bone surfaces and at sites of old, injured, or unneeded bone

Figure 38.6.1: Bone cell types: Table listing the function and location of the four types of bone cells.

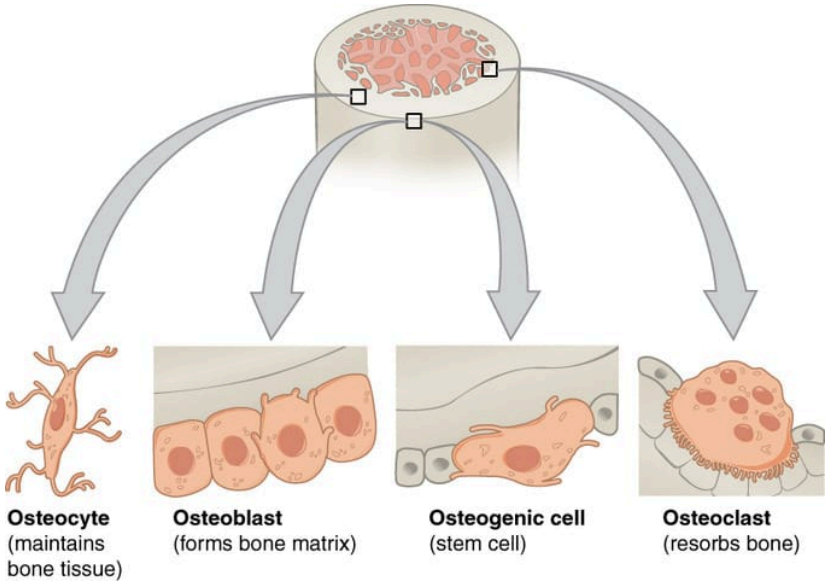


Figure 38.6.1: Four types of bone cells: Four types of cells are found within bone tissue. Osteogenic cells are undifferentiated and develop into osteoblasts. When osteoblasts get trapped within the calcified matrix, their structure and function changes; they become osteocytes. Osteoclasts develop from monocytes and macrophages and differ in appearance from other bone cells.

If osteoblasts and osteocytes are incapable of mitosis, then how are they replenished when old ones die? The answer lies in the properties of a third category of bone cells: the osteogenic cell. These osteogenic cells are undifferentiated with high mitotic

activity; they are the only bone cells that divide. Immature osteogenic cells are found in the deep layers of the periosteum and the marrow. When they differentiate, they develop into osteoblasts. The dynamic nature of bone means that new tissue is constantly formed, while old, injured, or unnecessary bone is dissolved for repair or for calcium release. The cell responsible for bone resorption, or breakdown, is the osteoclast, which is found on bone surfaces, is multinucleated, and originates from monocytes and macrophages (two types of white blood cells) rather than from osteogenic cells. Osteoclasts continually break down old bone while osteoblasts continually form new bone. The ongoing balance between osteoblasts and osteoclasts is responsible for the constant, but subtle, reshaping of bone.

Key Points

- Osteogenic cells are the only bone cells that divide.
- Osteogenic cells differentiate and develop into osteoblasts which, in turn, are responsible for forming new bones.
- Osteoblasts synthesize and secrete a collagen matrix and calcium salts.
- When the area surrounding an osteoblast calcifies, the osteoblast becomes trapped and transforms into an osteocyte, the most common and mature type of bone cell.
- Osteoclasts, the cells that break down and reabsorb bone, stem from monocytes and macrophages rather than osteogenic cells..
- There is a continual balance between osteoblasts generating new bone and osteoclasts breaking down bone.

Key Terms

- **osteoclast**: a large multinuclear cell associated with the resorption of bone
- **osteocyte**: a mature bone cell involved with the maintenance of bone
- **osteoprogenitor**: a stem cell that is the precursor of an osteoblast
- **canaliculus**: any of many small canals or ducts in bone or in some plants
- **periosteum**: a membrane surrounding a bone
- **endosteum**: a membranous vascular layer of cells which line the medullary cavity of a bone
- **lacuna**: a small opening; a small pit or depression; a small blank space; a gap or vacancy; a hiatus
- **osteoblast**: a mononucleate cell from which bone develops

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38.7: Bone - Bone Development

LEARNING OBJECTIVEs

- Distinguish between intramembranous and endochondral ossification

Ossification, or osteogenesis, is the process of bone formation by osteoblasts. Ossification is distinct from the process of calcification; whereas calcification takes place during the ossification of bones, it can also occur in other tissues. Ossification begins approximately six weeks after fertilization in an embryo. Before this time, the embryonic skeleton consists entirely of fibrous membranes and hyaline cartilage. The development of bone from fibrous membranes is called intramembranous ossification; development from hyaline cartilage is called endochondral ossification. Bone growth continues until approximately age 25. Bones can grow in thickness throughout life, but after age 25, ossification functions primarily in bone remodeling and repair.

Intramembranous Ossification

Intramembranous ossification is the process of bone development from fibrous membranes. It is involved in the formation of the flat bones of the skull, the mandible, and the clavicles. Ossification begins as mesenchymal cells form a template of the future bone. They then differentiate into osteoblasts at the ossification center. Osteoblasts secrete the extracellular matrix and deposit calcium, which hardens the matrix. The non-mineralized portion of the bone or osteoid continues to form around blood vessels, forming spongy bone. Connective tissue in the matrix differentiates into red bone marrow in the fetus. The spongy bone is remodeled into a thin layer of compact bone on the surface of the spongy bone.

Endochondral Ossification

Endochondral ossification is the process of bone development from hyaline cartilage. All of the bones of the body, except for the flat bones of the skull, mandible, and clavicles, are formed through endochondral ossification.

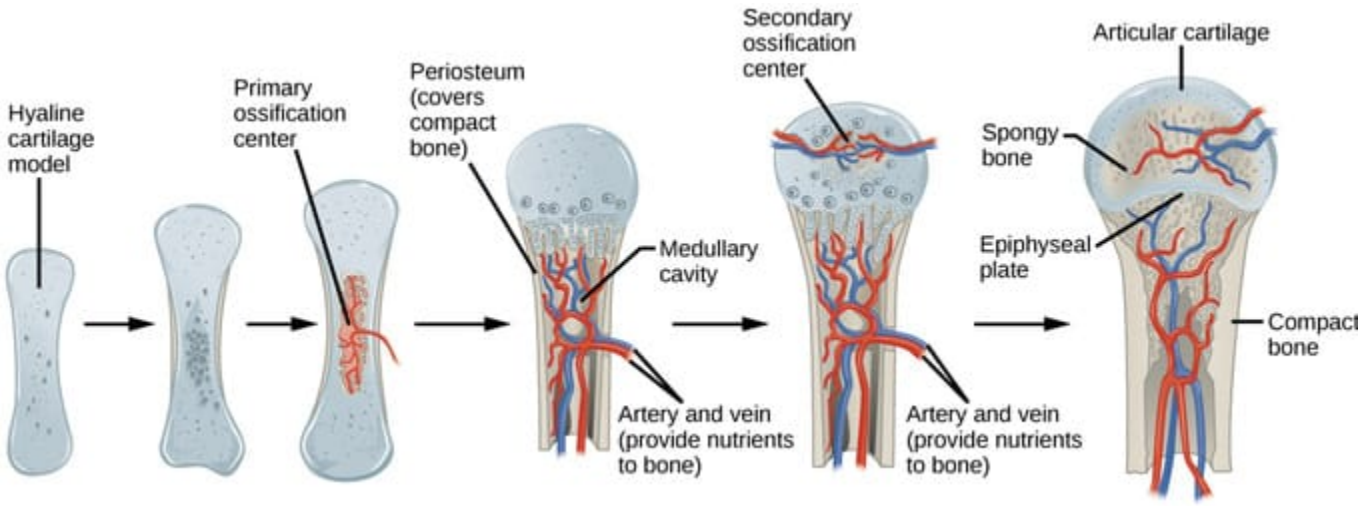


Figure 38.7.1: Process of endochondral ossification: Endochondral ossification is the process of bone development from hyaline cartilage. The periosteum is the connective tissue on the outside of bone that acts as the interface between bone, blood vessels, tendons, and ligaments.

In long bones, chondrocytes form a template of the hyaline cartilage diaphysis. Responding to complex developmental signals, the matrix begins to calcify. This calcification prevents diffusion of nutrients into the matrix, resulting in chondrocytes dying and the opening up of cavities in the diaphysis cartilage. Blood vessels invade the cavities, while osteoblasts and osteoclasts modify the calcified cartilage matrix into spongy bone. Osteoclasts then break down some of the spongy bone to create a marrow, or medullary cavity, in the center of the diaphysis. Dense, irregular connective tissue forms a sheath (periosteum) around the bones.

The periosteum assists in attaching the bone to surrounding tissues, tendons, and ligaments. The bone continues to grow and elongate as the cartilage cells at the epiphyses divide.

In the last stage of prenatal bone development, the centers of the epiphyses begin to calcify. Secondary ossification centers form in the epiphyses as blood vessels and osteoblasts enter these areas and convert hyaline cartilage into spongy bone. Until adolescence, hyaline cartilage persists at the epiphyseal plate (growth plate), which is the region between the diaphysis and epiphysis that is responsible for the lengthwise growth of long bones.

Key Points

- The ossification of the flat bones of the skull, the mandible, and the clavicles begins with mesenchymal cells, which then differentiate into calcium-secreting and bone matrix-secreting osteoblasts.
- Osteoids form spongy bone around blood vessels, which is later remodeled into a thin layer of compact bone.
- During enchondral ossification, the cartilage template in long bones is calcified; dying chondrocytes provide space for the development of spongy bone and the bone marrow cavity in the interior of the long bones.
- The periosteum, an irregular connective tissue around bones, aids in the attachment of tissues, tendons, and ligaments to the bone.
- Until adolescence, lengthwise long bone growth occurs in secondary ossification centers at the epiphyseal plates (growth plates) near the ends of the bones.

Key Terms

- **osteoid**: an organic matrix of protein and polysaccharides, secreted by osteoblasts, that becomes bone after mineralization
- **endochondral**: within cartilage
- **chondrocyte**: a cell that makes up the tissue of cartilage
- **diaphysis**: the central shaft of any long bone

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38.8: Bone - Growth of Bone

Learning Objectives

- Describe the processes of post-fetal bone growth and bone thickening

Growth of Bone

Long bones continue to lengthen (potentially throughout adolescence) through the addition of bone tissue at the epiphyseal plate. They also increase in width through appositional growth.

Lengthening of Long Bones

The epiphyseal plate is the area of growth in a long bone. It is a layer of hyaline cartilage where ossification occurs in immature bones. On the epiphyseal side of the epiphyseal plate, cartilage is formed. On the diaphyseal side, cartilage is ossified, allowing the diaphysis to grow in length. The metaphysis is the wide portion of a long bone between the epiphysis and the narrow diaphysis. It is considered a part of the growth plate: the part of the bone that grows during childhood, which, as it grows, ossifies near the diaphysis and the epiphyses.

The epiphyseal plate is composed of four zones of cells and activity.

1. The reserve zone, the region closest to the epiphyseal end of the plate, contains small chondrocytes within the matrix. These chondrocytes do not participate in bone growth; instead, they secure the epiphyseal plate to the osseous tissue of the epiphysis.
2. The proliferative zone, the next layer toward the diaphysis, contains stacks of slightly-larger chondrocytes. It continually makes new chondrocytes via mitosis.
3. The zone of maturation and hypertrophy contains chondrocytes that are older and larger than those in the proliferative zone. The more mature cells are situated closer to the diaphyseal end of the plate. In this zone, lipids, glycogen, and alkaline phosphatase accumulate, causing the cartilaginous matrix to calcify. The longitudinal growth of bone is a result of cellular division in the proliferative zone along with the maturation of cells in the zone of maturation and hypertrophy.
4. The zone of calcified matrix, the zone closest to the diaphysis, contains chondrocytes that are dead because the matrix around them has calcified. Capillaries and osteoblasts from the diaphysis penetrate this zone. The osteoblasts secrete bone tissue on the remaining calcified cartilage. Thus, the zone of calcified matrix connects the epiphyseal plate to the diaphysis. A bone grows in length when osseous tissue is added to the diaphysis.

After the zone of calcified matrix, there is the zone of ossification, which is actually part of the metaphysis. Arteries from the metaphysis branch through the newly-formed trabeculae in this zone. The newly-deposited bone tissue at the top of the zone of ossification is called the primary spongiosa. The older bone at the bottom of the zone of ossification is called the secondary spongiosa.

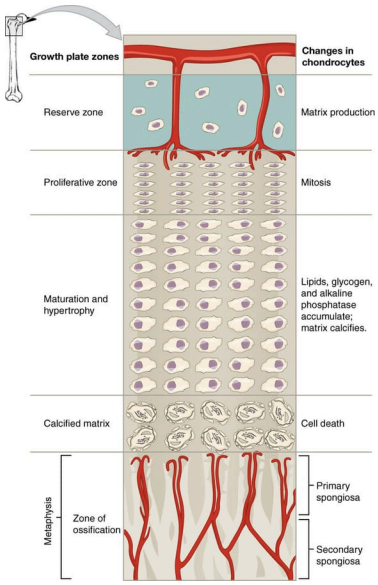


Figure 38.8.1: Longitudinal bone growth: The epiphyseal plate is responsible for longitudinal bone growth. This illustration shows the zones bordering the epiphyseal plate of the epiphysis. The topmost layer of the epiphysis is the reserve zone. The second zone, the proliferative zone, is where chondrocytes are continually undergoing mitosis. The next zone is the zone of maturation and hypertrophy where lipids, glycogen, and alkaline phosphatase accumulate, causing the cartilaginous matrix to calcify. The following zone is the calcified matrix where the chondrocytes have hardened and die as the matrix around them has calcified. The bottom-most row is the zone of ossification which is part of the metaphysis. The newly-deposited bone tissue at the top of the zone of ossification is called the primary spongiosa, while the older bone is labeled the secondary spongiosa.

Bones continue to grow in length until early adulthood with the rate of growth controlled by hormones. When the chondrocytes in the epiphyseal plate cease their proliferation and bone replaces the cartilage, longitudinal growth stops. All that remains of the epiphyseal plate is the epiphyseal line.

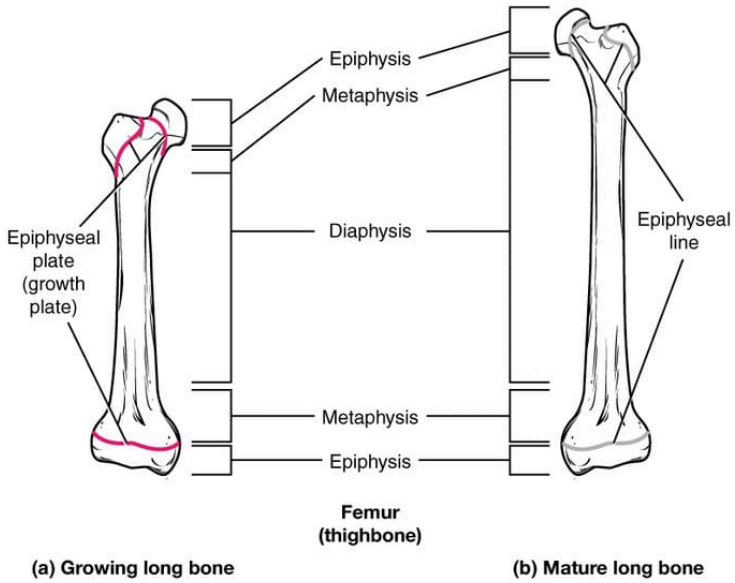


Figure 38.8.1: From epiphyseal plate to epiphyseal line: As a bone matures, the epiphyseal plate progresses to an epiphyseal line. (a) Epiphyseal plates are visible in a growing bone. (b) Epiphyseal lines are the remnants of epiphyseal plates in a mature bone.

Thickening of Long Bones

While bones are increasing in length, they are also increasing in diameter; growth in diameter can continue even after longitudinal growth ceases. This is called appositional growth. Osteoclasts, cells that work to break down bone, resorb old bone that lines the medullary cavity. At the same time, osteoblasts via intramembranous ossification, produce new bone tissue beneath the

periosteum. The erosion of old bone along the medullary cavity and the deposition of new bone beneath the periosteum not only increase the diameter of the diaphysis, but also increase the diameter of the medullary cavity. This process is called modeling.

Key Points

- The epiphyseal plate, the area of growth composed of four zones, is where cartilage is formed on the epiphyseal side while cartilage is ossified on the diaphyseal side, thereby lengthening the bone.
- Each of the four zones has a role in the proliferation, maturation, and calcification of bone cells that are added to the diaphysis.
- The longitudinal growth of long bones continues until early adulthood at which time the chondrocytes in the epiphyseal plate stop proliferating and the epiphyseal plate transforms into the epiphyseal line as bone replaces the cartilage.
- Bones can increase in diameter even after longitudinal growth has stopped.
- Appositional growth is the process by which old bone that lines the medullary cavity is reabsorbed and new bone tissue is grown beneath the periosteum, increasing bone diameter.

Key Terms

- **metaphysis**: the part of a long bone that grows during development
- **periosteum**: a membrane surrounding a bone
- **ossification**: the normal process by which bone is formed
- **chondrocyte**: a cell that makes up the tissue of cartilage
- **hypertrophy**: to increase in size
- **diaphysis**: the central shaft of any long bone
- **epiphysis**: the rounded end of any long bone
- **medullary**: pertaining to, consisting of, or resembling, marrow or medulla

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38.9: Bone - Bone Remodeling and Repair

Learning Objectives

- Outline the process of bone remodeling and repair

Bone Remodeling and Repair

Bone renewal continues after birth into adulthood. Bone remodeling is the replacement of old bone tissue by new bone tissue. It involves the processes of bone deposition or bone production done by osteoblasts and bone resorption done by osteoclasts, which break down old bone. Normal bone growth requires vitamins D, C, and A, plus minerals such as calcium, phosphorous, and magnesium. Hormones such as parathyroid hormone, growth hormone, and calcitonin are also required for proper bone growth and maintenance.

Bone turnover rates, the rates at which old bone is replaced by new bone, are quite high, with five to seven percent of bone mass being recycled every week. Differences in turnover rates exist in different areas of the skeleton and in different areas of a bone. For example, the bone in the head of the femur may be fully replaced every six months, whereas the bone along the shaft is altered much more slowly.

Bone remodeling allows bones to adapt to stresses by becoming thicker and stronger when subjected to stress. Bones that are not subject to normal everyday stress (for example, when a limb is in a cast) will begin to lose mass.

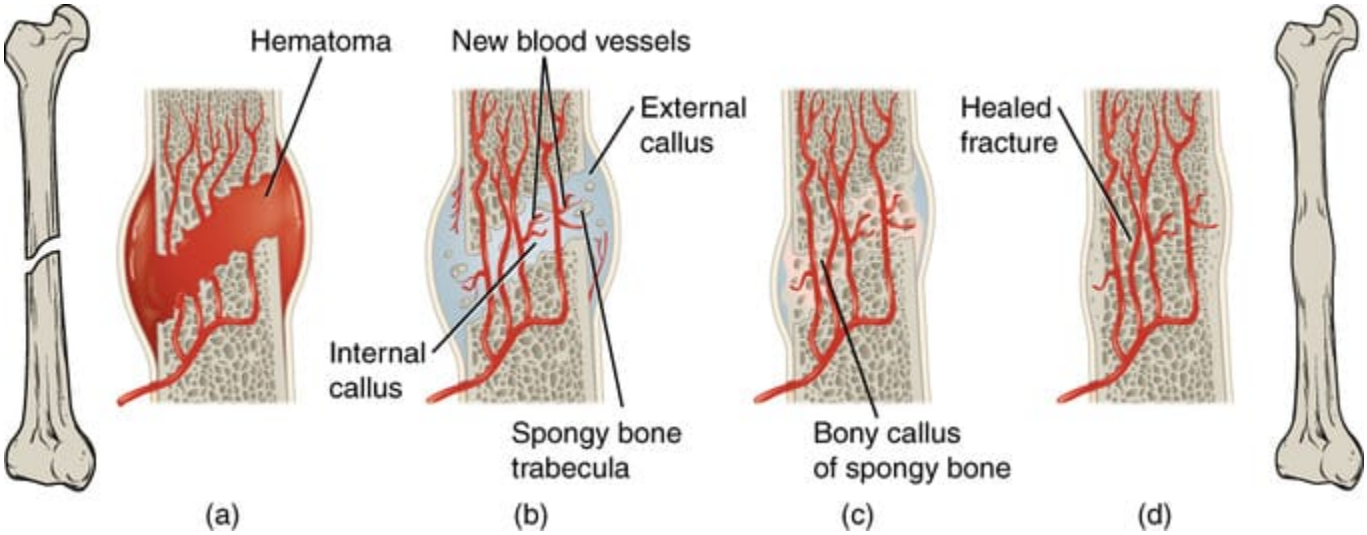


Figure 38.9.1: Stages of fracture repair: The healing of a bone fracture follows a series of progressive steps: (a) A fracture hematoma forms. (b) Internal and external calli form. (c) Cartilage of the calli is replaced by trabecular bone. (d) Remodeling occurs.

A fractured or broken bone undergoes repair through four stages:

1. Hematoma formation: Blood vessels in the broken bone tear and hemorrhage, resulting in the formation of clotted blood, or a hematoma, at the site of the break. The severed blood vessels at the broken ends of the bone are sealed by the clotting process. Bone cells deprived of nutrients begin to die.
2. Bone generation: Within days of the fracture, capillaries grow into the hematoma, while phagocytic cells begin to clear away the dead cells. Though fragments of the blood clot may remain, fibroblasts and osteoblasts enter the area and begin to reform bone. Fibroblasts produce collagen fibers that connect the broken bone ends, while osteoblasts start to form spongy bone. The repair tissue between the broken bone ends, the fibrocartilaginous callus, is composed of both hyaline and fibrocartilage. Some bone spicules may also appear at this point.
3. Bony callous formation: The fibrocartilaginous callus is converted into a bony callus of spongy bone. It takes about two months for the broken bone ends to be firmly joined together after the fracture. This is similar to the endochondral formation

of bone when cartilage becomes ossified; osteoblasts, osteoclasts, and bone matrix are present.

4. Bone remodeling: The bony callus is then remodelled by osteoclasts and osteoblasts, with excess material on the exterior of the bone and within the medullary cavity being removed. Compact bone is added to create bone tissue that is similar to the original, unbroken bone. This remodeling can take many months; the bone may remain uneven for years.

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Key Points

- Bone replacement involves the osteoclasts which break down bone and the osteoblasts which make new bone.
- Bone turnover rates differ depending on the bone and the area within the bone.
- There are four stages in the repair of a broken bone: 1) the formation of hematoma at the break, 2) the formation of a fibrocartilaginous callus, 3) the formation of a bony callus, and 4) remodeling and addition of compact bone.
- Proper bone growth and maintenance requires many vitamins (D, C, and A), minerals (calcium, phosphorous, and magnesium), and hormones (parathyroid hormone, growth hormone, and calcitonin).

Key Terms

- **callus**: the material of repair in fractures of bone which is at first soft or cartilaginous in consistency, but is ultimately converted into true bone and unites the fragments into a single piece
- **spicule**: a sharp, needle-like piece
- **fibroblast**: a cell found in connective tissue that produces fibers, such as collagen

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38.10: Joints and Skeletal Movement - Classification of Joints on the Basis of Structure and Function

Learning Objectives

- Differentiate among the types of skeletal joints based on structure and function

Classification of Joints on the Basis of Structure and Function

The point at which two or more bones meet is called a joint or articulation. Joints are responsible for movement (e.g., the movement of limbs) and stability (e.g.,the stability found in the bones of the skull). There are two ways to classify joints: on the basis of their structure or on the basis of their function.

The structural classification divides joints into fibrous, cartilaginous, and synovial joints depending on the material composing the joint and the presence or absence of a cavity in the joint. The functional classification divides joints into three categories: synarthroses, amphiarthroses, and diarthroses.

Fibrous Joints

The bones of fibrous joints are held together by fibrous connective tissue. There is no cavity, or space, present between the bones, so most fibrous joints do not move at all. There are three types of fibrous joints: sutures, syndesmoses, and gomphoses. Sutures are found only in the skull and possess short fibers of connective tissue that hold the skull bones tightly in place.

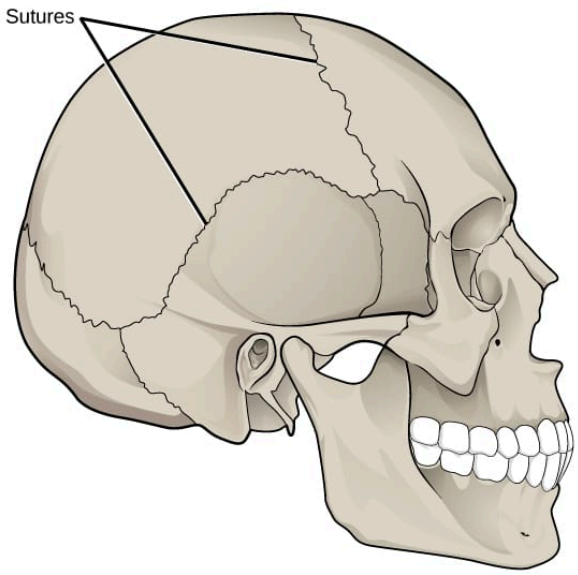


Figure 38.10.1: Sutures: Sutures are fibrous joints found only in the skull.

Syndesmoses are joints in which the bones are connected by a band of connective tissue, allowing for more movement than in a suture. An example of a syndesmosis is the joint of the tibia and fibula in the ankle. The amount of movement in these types of joints is determined by the length of the connective tissue fibers. Gomphoses occur between teeth and their sockets; the term refers to the way the tooth fits into the socket like a peg. The tooth is connected to the socket by a connective tissue called the periodontal ligament. Fibrous joints classified as synarthroses, or immovable, include: sutures, gomphoses, and synchondroses

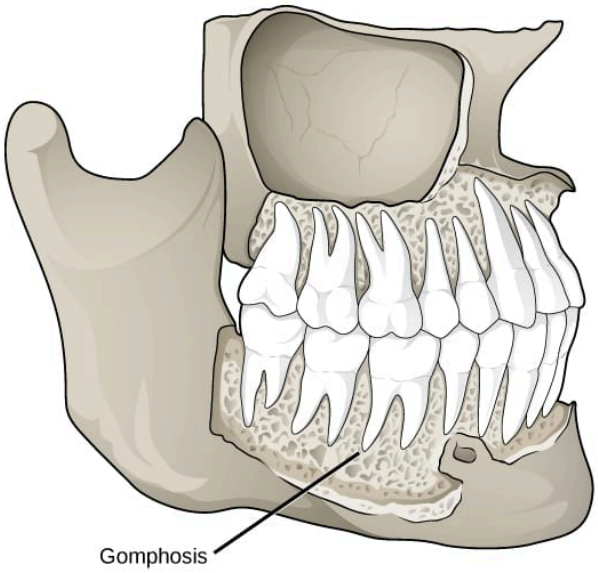


Figure 38.10.1: Gomphoses: Gomphoses are fibrous joints between the teeth and their sockets.

Cartilaginous Joints

Cartilaginous joints are those in which the bones are connected by cartilage. There are two types of cartilaginous joints: synchondroses and symphyses. In a synchondrosis, the bones are joined by hyaline cartilage. Synchondroses are found in the epiphyseal plates of growing bones in children. In symphyses, hyaline cartilage covers the end of the bone, but the connection between bones occurs through fibrocartilage. Symphyses are found at the joints between vertebrae and between the pubic bones. Amphiarthroses allow only slight movement; therefore, either type of cartilaginous joint is an amphiarthrosis.

Synovial Joints

Synovial joints are the only joints that have a space between the adjoining bones. This space, referred to as the synovial (or joint) cavity, is filled with synovial fluid. Synovial fluid lubricates the joint, reducing friction between the bones and allowing for greater movement. The ends of the bones are covered with articular cartilage, a hyaline cartilage. The entire joint is surrounded by an articular capsule composed of connective tissue. This allows movement of the joint as well as resistance to dislocation. Articular capsules may also possess ligaments that hold the bones together. Synovial joints are capable of the greatest movement of the three structural joint types; however, the more mobile a joint, the weaker the joint. Knees, elbows, and shoulders are examples of synovial joints. Since they allow for free movement, synovial joints are classified as diarthroses.

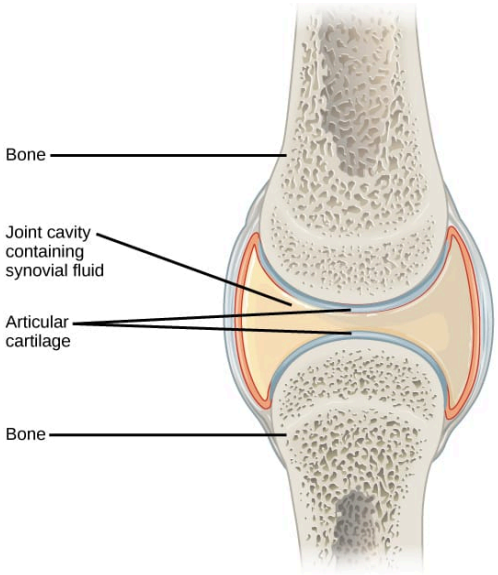


Figure 38.10.1: Synovial Joints: Synovial joints are the only joints that have a space or “synovial cavity” in the joint.

Key Points

- Fibrous joints contain fibrous connective tissue and cannot move; fibrous joints include sutures, syndesmoses, and gomphoses.
- Cartilaginous joints contain cartilage and allow very little movement; there are two types of cartilaginous joints: synchondroses and symphyses.
- Synovial joints are the only joints that have a space (a synovial cavity filled with fluid) between the adjoining bones.
- The presence of synovial fluid and an articular capsule give synovial joints the greatest range of movement among the three joint types; however they are the weakest of the joint types.
- Based on function, joints can be divided into synarthroses, amphiarthroses, and diarthroses.
- Synarthrosis joints include fibrous joints; amphiarthrosis joints include cartilaginous joints; diarthrosis joints include synovial joints.

Key Terms

- **synovial fluid**: a viscous, fluid found in the cavities of synovial joints whose main purpose is to reduce friction between the articular cartilage of synovial joints during movement
- **diarthrosis**: a joint that can move freely in various planes
- **synarthrosis**: immovable joint in which two bones are connected rigidly by fibrous tissue
- **amphiarthrosis**: slightly movable joint in which the surfaces of bones are connected by ligaments or cartilage

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38.11: Joints and Skeletal Movement - Movement at Synovial Joints

Learning Objectives

- Differentiate among the types of movements possible at synovial joints

Movement at Synovial Joints

The range of movement allowed by synovial joints is fairly wide. These movements can be classified as: gliding, angular, rotational, or special movement.

Gliding Movement

Gliding movements occur as relatively flat bone surfaces move past each other. They produce very little rotation or angular movement of the bones. The joints of the carpal and tarsal bones are examples of joints that produce gliding movements.

Angular Movement

Angular movements are produced by changing the angle between the bones of a joint. There are several different types of angular movements, including flexion, extension, hyperextension, abduction, adduction, and circumduction. Flexion, or bending, occurs when the angle between the bones decreases. Moving the forearm upward at the elbow or moving the wrist to move the hand toward the forearm are examples of flexion. In extension, the opposite of flexion, the angle between the bones of a joint increases. Straightening a limb after flexion is an example of extension. Extension past the normal anatomical position is referred to as hyperextension. This includes moving the neck back to look upward or bending the wrist so that the hand moves away from the forearm.

Abduction occurs when a bone moves away from the midline of the body. Examples of abduction include moving the arms or legs laterally to lift them straight out to the side. Adduction is the movement of a bone toward the midline of the body. Movement of the limbs inward after abduction is an example of adduction. Circumduction is the movement of a limb in a circular motion, as in swinging an arm around.

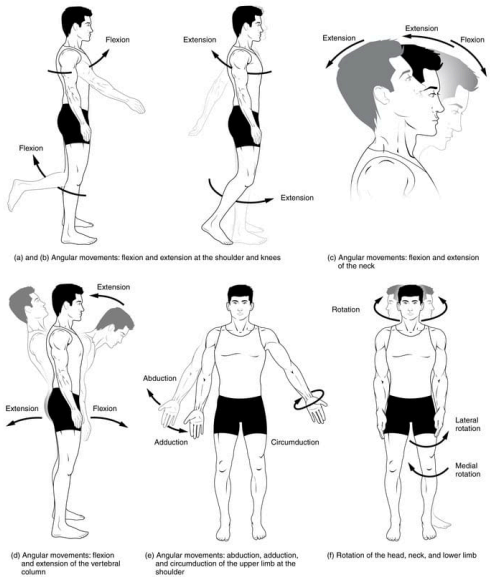


Figure 38.11.1: Angular and rotational movements: Synovial joints give the body many ways in which to move. (a)–(b) Flexion and extension motions are in the sagittal (anterior–posterior) plane of motion. These movements take place at the shoulder, hip, elbow, knee, wrist, metacarpophalangeal, metatarsophalangeal, and interphalangeal joints. (c)–(d) Anterior bending of the head or vertebral column is flexion, while any posterior movement of the head is extension. (e) Abduction and adduction are motions of the limbs, hand, fingers, or toes in the coronal (medial–lateral) plane of movement. Moving the limb or hand laterally away from the body, or spreading the fingers or toes, is abduction. Adduction brings the limb or hand toward or across the midline of the body or brings the fingers or toes together. Circumduction is the movement of the limb, hand, or fingers in a circular pattern, using the sequential combination of flexion, adduction, extension, and abduction motions. Adduction/abduction and circumduction take place at the shoulder, hip, wrist, metacarpophalangeal, and metatarsophalangeal joints. (f) Turning of the head side to side or twisting of the body is rotation. Medial and lateral rotation of the upper limb at the shoulder or lower limb at the hip involves turning the anterior surface of the limb toward the midline of the body (medial or internal rotation) or away from the midline (lateral or external rotation).

Rotational Movement

Rotational movement is the movement of a bone as it rotates around its longitudinal axis. Rotation can be toward the midline of the body, which is referred to as medial rotation, or away from the midline of the body, which is referred to as lateral rotation. Movement of the head from side to side is an example of rotation.

Special Movements

Some movements that cannot be classified as gliding, angular, or rotational are called special movements. Inversion involves moving the soles of the feet inward, toward the midline of the body. Eversion, the opposite of inversion, involves moving of the sole of the foot outward, away from the midline of the body. Protraction is the anterior movement of a bone in the horizontal plane. Retraction occurs as a joint moves back into position after protraction. Protraction and retraction can be seen in the movement of the mandible as the jaw is thrust outwards and then back inwards. Elevation is the movement of a bone upward, such as shrugging the shoulders, lifting the scapulae. Depression is the opposite of elevation and involves moving the bone downward, such as after the shoulders are shrugged and the scapulae return to their normal position from an elevated position. Dorsiflexion is a bending at the ankle such that the toes are lifted toward the knee. Plantarflexion is a bending at the ankle when the heel is lifted, such as when standing on the toes. Supination is the movement of the radius and ulna bones of the forearm so that the palm faces forward or up. Pronation is the opposite movement, in which the palm faces backward or down. Opposition is the movement of the thumb toward the fingers of the same hand, making it possible to grasp and hold objects.

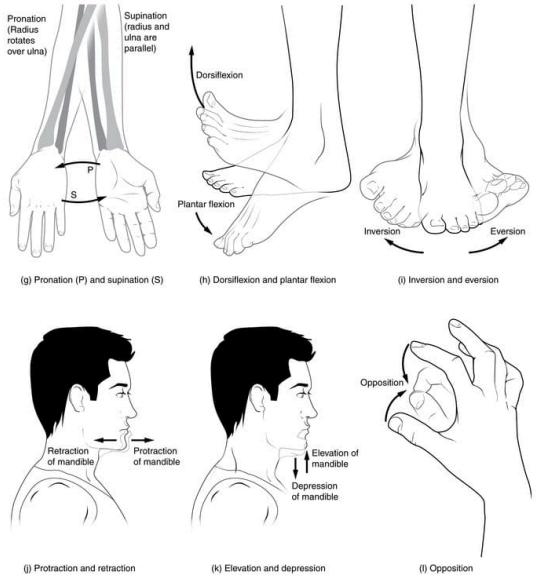


Figure 38.11.1: Special movements: (g) Supination of the forearm turns the palm upward in which the radius and ulna are parallel, while forearm pronation turns the palm downward in which the radius crosses over the ulna to form an "X." (h) Dorsiflexion of the foot at the ankle joint moves the top of the foot toward the leg, while plantar flexion lifts the heel and points the toes. (i) Eversion of the foot moves the bottom (sole) of the foot away from the midline of the body, while foot inversion faces the sole toward the midline. (j) Protraction of the mandible pushes the chin forward, while retraction pulls the chin back. (k) Depression of the mandible opens the mouth, while elevation closes it. (l) Opposition of the thumb brings the tip of the thumb into contact with the tip of the fingers of the same hand.

Key Points

- Gliding movements occur as relatively flat bone surfaces move past each other, but they produce very little movement of the bones.
- Angular movements are produced when the angle between the bones of a joint changes; they include flexion, extension, hyperextension, abduction, adduction, and circumduction.
- Rotational movement involves moving the bone around its longitudinal axis; this can be movement toward the midline of the body (medial rotation) or away from the midline of the body (lateral rotation).
- Special movements are all the other movements that cannot be classified as gliding, angular, or rotational; these movements include inversion, eversion, protraction, and retraction.
- Other special movements include elevation, depression, supination, and pronation.

Key Terms

- **adduction**: the movement of a bone toward the midline of the body
- **abduction**: moving a bone away from the midline of the body
- **supination**: the action of rotating the forearm so that the palm of the hand is turned up or forward
- **pronation**: the action of rotating the forearm so that the palm of the hand is turned down or back

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38.12: Joints and Skeletal Movement - Types of Synovial Joints

Learning Objectives

- Differentiate among the six categories of joints based on shape and structure

Types of Synovial Joints

Synovial joints are further classified into six different categories on the basis of the shape and structure of the joint. The shape of the joint affects the type of movement permitted by the joint. These joints can be described as planar, hinge, pivot, condyloid, saddle, or ball-and-socket joints.

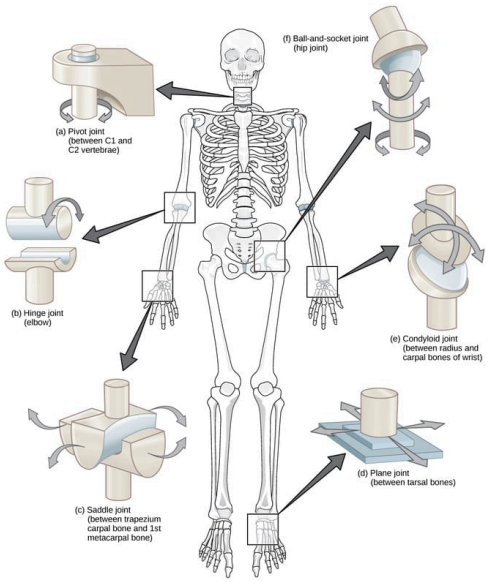


Figure 38.12.1: Types of synovial joints: The six types of synovial joints allow the body to move in a variety of ways. (a) Pivot joints allow for rotation around an axis, such as between the first and second cervical vertebrae, which allows for side-to-side rotation of the head. (b) The hinge joint of the elbow works like a door hinge. (c) The articulation between the trapezium carpal bone and the first metacarpal bone at the base of the thumb is a saddle joint. (d) Planar (or plane) joints, such as those between the tarsal bones of the foot, allow for limited gliding movements between bones. (e) The radiocarpal joint of the wrist is a condyloid joint. (f) The hip and shoulder joints are the only ball-and-socket joints of the body.

Planar Joints

Planar joints have bones with articulating surfaces that are flat or slightly curved. These joints allow for gliding movements; therefore, the joints are sometimes referred to as gliding joints. The range of motion is limited and does not involve rotation. Planar joints are found in the carpal bones in the hand and the tarsal bones of the foot, as well as between vertebrae.

Hinge Joints

In hinge joints, the slightly-rounded end of one bone fits into the slightly-hollow end of the other bone. In this way, one bone moves while the other remains stationary, similar to the hinge of a door. The elbow is an example of a hinge joint. The knee is sometimes classified as a modified hinge joint.

Pivot Joints

Pivot joints consist of the rounded end of one bone fitting into a ring formed by the other bone. This structure allows rotational movement, as the rounded bone moves around its own axis. An example of a pivot joint is the joint of the first and second vertebrae of the neck that allows the head to move back and forth. The joint of the wrist that allows the palm of the hand to be turned up and down is also a pivot joint.

Condyloid Joints

Condyloid joints consist of an oval-shaped end of one bone fitting into a similarly oval-shaped hollow of another bone. This is also sometimes called an ellipsoidal joint. This type of joint allows angular movement along two axes, as seen in the joints of the wrist and fingers, which can move both side to side and up and down.

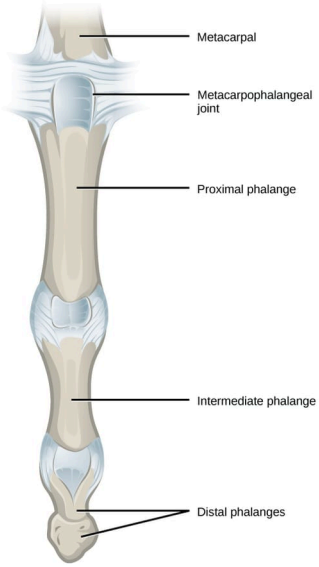


Figure 38.12.1: Condyloid: The metacarpophalangeal joints in the finger are examples of condyloid joints.

Saddle Joints

Each bone in a saddle joint resembles a saddle, with concave and convex portions that fit together. Saddle joints allow angular movements similar to condyloid joints, but with a greater range of motion. An example of a saddle joint is the thumb joint, which can move back and forth and up and down; it can move more freely than the wrist or fingers.

Ball-and-Socket Joints

Ball-and-socket joints possess a rounded, ball-like end of one bone fitting into a cup-like socket of another bone. This organization allows the greatest range of motion, as all movement types are possible in all directions. Examples of ball-and-socket joints are the shoulder and hip joints.

The Role of Rheumatologists

Rheumatologists are medical doctors who specialize in the diagnosis and treatment of disorders of the joints, muscles, and bones. They diagnose and treat diseases such as arthritis, musculoskeletal disorders, osteoporosis, and autoimmune diseases such as ankylosing spondylitis and rheumatoid arthritis.

Rheumatoid arthritis (RA) is an inflammatory disorder that primarily affects the synovial joints of the hands, feet, and cervical spine. Affected joints become swollen, stiff, and painful. Although it is known that RA is an autoimmune disease in which the body's immune system mistakenly attacks healthy tissue, the cause of RA remains unknown. Immune cells from the blood enter

joints and the synovium, causing cartilage breakdown, swelling, and inflammation of the joint lining. Breakdown of cartilage results in bones rubbing against each other, causing pain. RA is more common in women than men; the age of onset is usually 40–50 years of age.

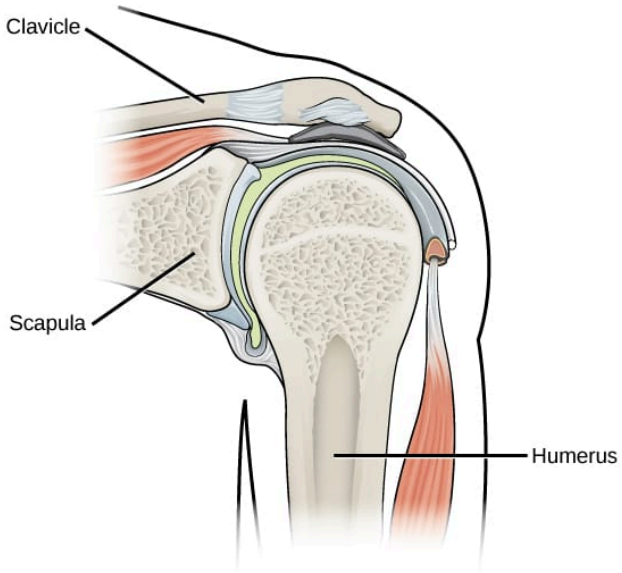


Figure 38.12.1: Ball-and-socket: The shoulder joint is an example of a ball-and-socket joint.

Rheumatologists diagnose RA on the basis of symptoms (joint inflammation and pain), X-ray and MRI imaging, and blood tests. Arthrography, a type of medical imaging of joints, uses a contrast agent, such as a dye, that is opaque to X-rays. This allows the soft tissue structures of joints, such as cartilage, tendons, and ligaments, to be visualized. An arthrogram differs from a regular X-ray by showing the surface of soft tissues lining the joint in addition to joint bones. An arthrogram allows early degenerative changes in joint cartilage to be detected before bones become affected.

There is currently no cure for RA; however, rheumatologists have a number of treatment options available. Early stages can be treated by resting the affected joints, using a cane or joint splints, to minimize inflammation. When inflammation has decreased, exercise can be used to strengthen the muscles that surround the joint in order to maintain joint flexibility. If joint damage is more extensive, medications can be used to relieve pain and decrease inflammation. Anti-inflammatory drugs such as aspirin, topical pain relievers, and corticosteroid injections may be used. Surgery may be required in cases in which joint damage is severe.

Key Points

- Planar joints have bones with articulating surfaces that are flat or slightly curved, allowing for limited movement; pivot joints consist of the rounded end of one bone fitting into a ring formed by the other bone to allow rotational movement.
- Hinge joints act like the hinge of a door; the slightly-rounded end of one bone fits into the slightly-hollow end of the other bone; one bone remains stationary.
- Condyloid joints consist of an oval-shaped end of one bone fitting into a similarly oval-shaped hollow of another bone to allow angular movement along two axes.
- Saddle joints include concave and convex portions that fit together and allow angular movement; ball-and-socket joints include a rounded, ball-like end of one bone fitting into a cup-like socket of another bone which allows the greatest range of motion.
- Rheumatologists diagnose and treat joint disorders, which include rheumatoid arthritis and osteoporosis.
- Immune cells enter joints and the synovium, causing cartilage breakdown, swelling, and inflammation of the joint lining, which breaks down cartilage, resulting in bones rubbing against each other, causing pain.

Key Terms

- **condyloid joint**: consists of an oval-shaped end of one bone fitting into a similarly oval-shaped hollow of another bone
- **ball-and-socket joint**: consists of a rounded, ball-like end of one bone fitting into a cup-like socket of another bone, allowing the first segment to move around an indefinite number of axes which have one common center

- **rheumatoid arthritis**: chronic, progressive disease in which the immune system attacks the joints; characterized by pain, inflammation and swelling of the joints, stiffness, weakness, loss of mobility, and deformity

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38.13: Joints and Skeletal Movement - Bone and Joint Disorders

Learning Objectives

- Describe the causes and treatments for gout, rheumatoid arthritis, and osteoarthritis

Synovial joints are the most common type of joint in the body. A key structural characteristic for a synovial joint that is not seen at fibrous or cartilaginous joints is the presence of a joint cavity.

Arthritis is a common disorder of synovial joints that involves inflammation of the joint. This often results in significant joint pain, along with swelling, stiffness, and reduced joint mobility. There are more than 100 different forms of arthritis. Arthritis may arise from aging, damage to the articular cartilage, autoimmune diseases, bacterial or viral infections, or unknown (probably genetic) causes.
Arthritis is the most common cause of disability in the USA. More than 20 million individuals with arthritis have severe limitations in function on a daily basis.

Osteoarthritis

The most common type of arthritis is osteoarthritis, which is associated with aging and “wear and tear” of the articular cartilage. Risk factors that may lead to osteoarthritis later in life include injury to a joint; jobs that involve physical labor; sports with running, twisting, or throwing actions; and being overweight.



Osteoarthritis of the Finger Joints

The formation of hard nobs at the middle finger joints (known as Bouchard’s nodes) and at the farther away finger joint (known as Heberden’s node) are a common feature of Osteoarthritis in the hands.

Osteoarthritis begins in the cartilage and eventually causes the two opposing bones to erode into each other. Osteoarthritis typically affects the weight-bearing joints, such as the back, knee and hip. There is no cure for osteoarthritis, but several treatments (surgery, lifestyle changes, medications) can help alleviate the pain.

Gout

Gout is a form of arthritis that results from the deposit of uric acid crystals within a body joint. Usually only one or a few joints are affected, such as the big toe, knee, or ankle. The attack may only last a few days, but could return to the same or another joint. Gout occurs when the body makes too much uric acid or the kidneys do not properly excrete it. A diet with excessive fructose has been implicated in raising the chances of a susceptible individual developing gout.

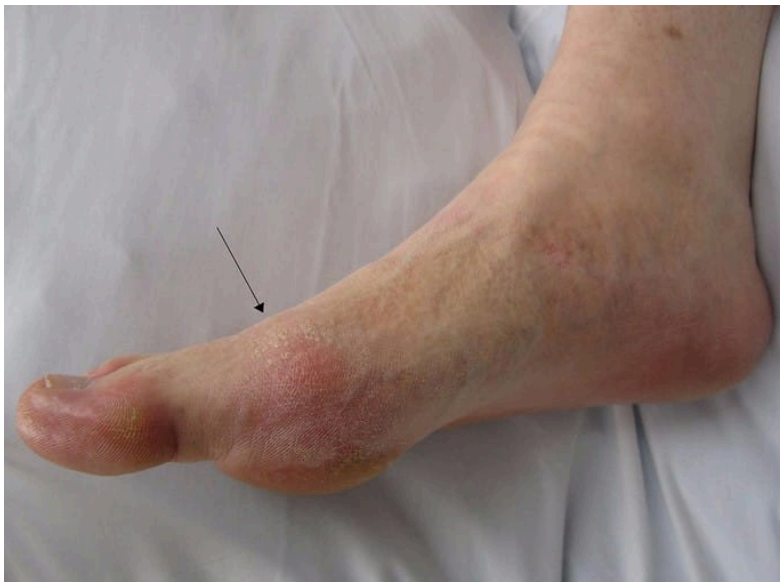


Figure 38.13.1: Gout: Gout presenting in the metatarsal-phalangeal joint of the big toe: Note the slight redness of the skin overlying the joint.

Rheumatoid Arthritis

Other forms of arthritis are associated with various autoimmune diseases, bacterial infections of the joint, or unknown genetic causes. Autoimmune diseases like rheumatoid arthritis produce arthritis because the immune system of the body attacks the body joints.

In rheumatoid arthritis, the joint capsule and synovial membrane become inflamed. As the disease progresses, the articular cartilage is severely damaged or destroyed, resulting in joint deformation, loss of movement, and severe disability. The most commonly involved joints are the hands, feet, and cervical spine, with corresponding joints on both sides of the body usually affected, though not always to the same extent.



Figure 38.13.1: Rheumatoid Arthritis: A untreated hand affected by rheumatoid arthritis.

Rheumatoid Arthritis: A untreated hand affected by rheumatoid arthritis.

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Key Points

- Arthritis is a common disorder of synovial joints that involves inflammation of the joint; there are a few major subtypes of this disorder.
- The most common type of arthritis is osteoarthritis, which is associated with “wear and tear” of cartilage.
- Gout is a form of arthritis resulting from the deposit of uric acid crystals within a body joint.
- Rheumatoid arthritis is an autoimmune disease in which the joint capsule and synovial membrane become inflamed.

Key Terms

- **synovial joints**: The most common type of joint in the body, which includes a joint cavity.
- **arthritis**: A joint disorder that involves inflammation in one or more joints.

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38.14: Muscle Contraction and Locomotion - Structure and Function of the Muscular System

Learning Objectives

- Describe the three types of muscle tissue

The Musculoskeletal System

The muscular system is made up of muscle tissue and is responsible for functions such as maintenance of posture, locomotion and control of various circulatory systems. This includes the beating of the heart and the movement of food through the digestive system. The muscular system is closely associated with the skeletal system in facilitating movement. Both voluntary and involuntary muscular system functions are controlled by the nervous system.



Figure 38.14.1: The muscular system: Skeletal muscle of the muscular system is closely associated with the skeletal system and acts to maintain posture and control voluntary movement.

Muscle is a highly-specialized soft tissue that produces tension which results in the generation of force. Muscle cells, or myocytes, contain myofibrils comprised of actin and myosin myofilaments which slide past each other producing tension that changes the shape of the myocyte. Numerous myocytes make up muscle tissue and the controlled production of tension in these cells can generate significant force.

Muscle tissue can be classified functionally as voluntary or involuntary and morphologically as striated or non-striated. Voluntary refers to whether the muscle is under conscious control, while striation refers to the presence of visible banding within myocytes caused by the organization of myofibrils to produce constant tension.

Types of Muscle

The above classifications describe three forms of muscle tissue that perform a wide range of diverse functions.

Skeletal Muscle

Skeletal muscle mainly attaches to the skeletal system via tendons to maintain posture and control movement. For example, contraction of the biceps muscle, attached to the scapula and radius, will raise the forearm. Some skeletal muscle can attach directly to other muscles or to the skin, as seen in
the face where numerous muscles control facial expression.

Skeletal muscle is under voluntary control, although this can be subconscious when maintaining posture or balance. Morphologically skeletal myocytes are elongated and tubular and appear striated with multiple peripheral nuclei.

Cardiac Muscle Tissue

Cardiac muscle tissue is found only in the heart, where cardiac contractions pump blood throughout the body and maintain blood pressure.

As with skeletal muscle, cardiac muscle is striated; however it is not consciously controlled and so is classified as involuntary. Cardiac muscle can be further differentiated from skeletal muscle by the presence of intercalated discs that control the synchronized contraction of cardiac tissues. Cardiac myocytes are shorter than skeletal equivalents and contain only one or two centrally located nuclei.

Smooth Muscle Tissue

Smooth muscle tissue is associated with numerous organs and tissue systems, such as the digestive system and respiratory system. It plays an important role in the regulation of flow in such systems, such as aiding the movement of food through the digestive system via peristalsis.

Smooth muscle is non-striated and involuntary. Smooth muscle myocytes are spindle shaped with a single centrally located nucleus.

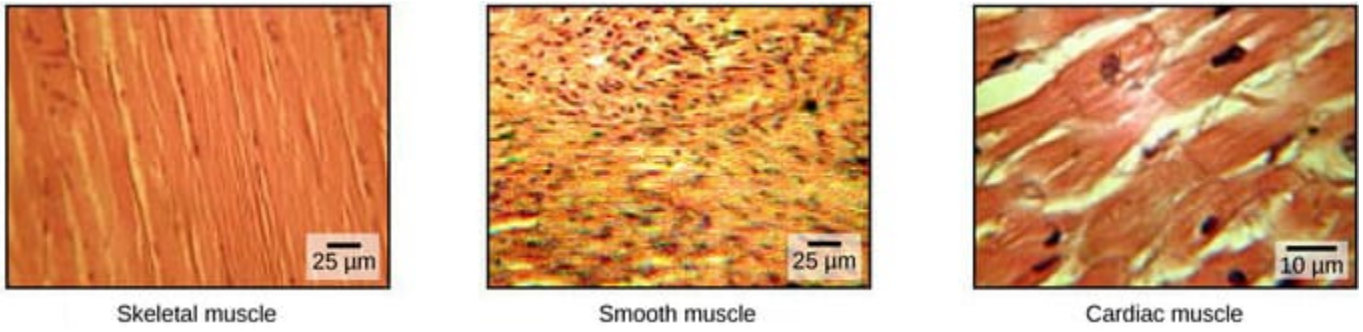


Figure 38.14.1: Types of muscle: The body contains three types of muscle tissue: skeletal muscle, smooth muscle, and cardiac muscle, visualized here using light microscopy. Visible striations in skeletal and cardiac muscle are visible, differentiating them from the more randomised appearance of smooth muscle.

Key Points

- The muscular system is responsible for functions such as maintenance of posture, locomotion, and control of various circulatory systems.
- Muscle tissue can be divided functionally (voluntarily or involuntarily controlled) and morphologically (striated or non-striated).
- These classifications describe three distinct muscle types: skeletal, cardiac and smooth. Skeletal muscle is voluntary and striated, cardiac muscle is involuntary and striated, and smooth muscle is involuntary and non-striated.

Key Terms

- **myofibril**: A fiber made up of several myofilaments that facilitates the generation of tension in a myocyte.
- **myofilament**: A filament composed of either multiple myosin or actin proteins that slide over each other to generate tension.
- **myosin**: A motor protein which forms myofilaments that interact with actin filaments to generate tension.
- **actin**: A protein which forms myofilaments that interact with myosin filaments to generate tension.
- **striated**: The striped appearance of certain muscle types in which myofibrils are aligned to produce a constant directional tension.
- **voluntary**: A muscle movement under conscious control (e.g. deciding to move the forearm).
- **involuntary**: A muscle movement not under conscious control (e.g. the beating of the heart).
- **myocyte**: A muscle cell.

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38.15: Muscle Contraction and Locomotion - Skeletal Muscle Fibers

Learning Objectives

- Outline the structure of a skeletal muscle fiber

Skeletal Muscle Fiber Structure

Myocytes, sometimes called muscle fibers, form the bulk of muscle tissue. They are bound together by perimysium, a sheath of connective tissue, into bundles called fascicles, which are in turn bundled together to form muscle tissue. Myocytes contain numerous specialized cellular structures which facilitate their contraction and therefore that of the muscle as a whole.

The highly specialized structure of myocytes has led to the creation of terminology which differentiates them from generic animal cells.

Generic cell > Myocyte

Cytoplasm > Sarcoplasm

Cell membrane > Sarcolemma

Smooth endoplasmic reticulum > Sarcoplasmic reticulum

Myocyte Structure

Myocytes can be incredibly large, with diameters of up to 100 micrometers and lengths of up to 30 centimeters. The sarcoplasm is rich with glycogen and myoglobin, which store the glucose and oxygen required for energy generation, and is almost completely filled with myofibrils, the long fibers composed of
myofilaments that facilitate muscle contraction.

The sarcolemma of myocytes contains numerous invaginations (pits) called transverse tubules which are usually perpendicular to the length of the myocyte. Transverse tubules play an important role in supplying the myocyte with Ca^{+} ions, which are key for muscle contraction.

Each myocyte contains multiple nuclei due to their derivation from multiple myoblasts, progenitor cells that give rise to myocytes. These myoblasts asre located to the periphery of the myocyte and flattened so
as not to impact myocyte contraction.

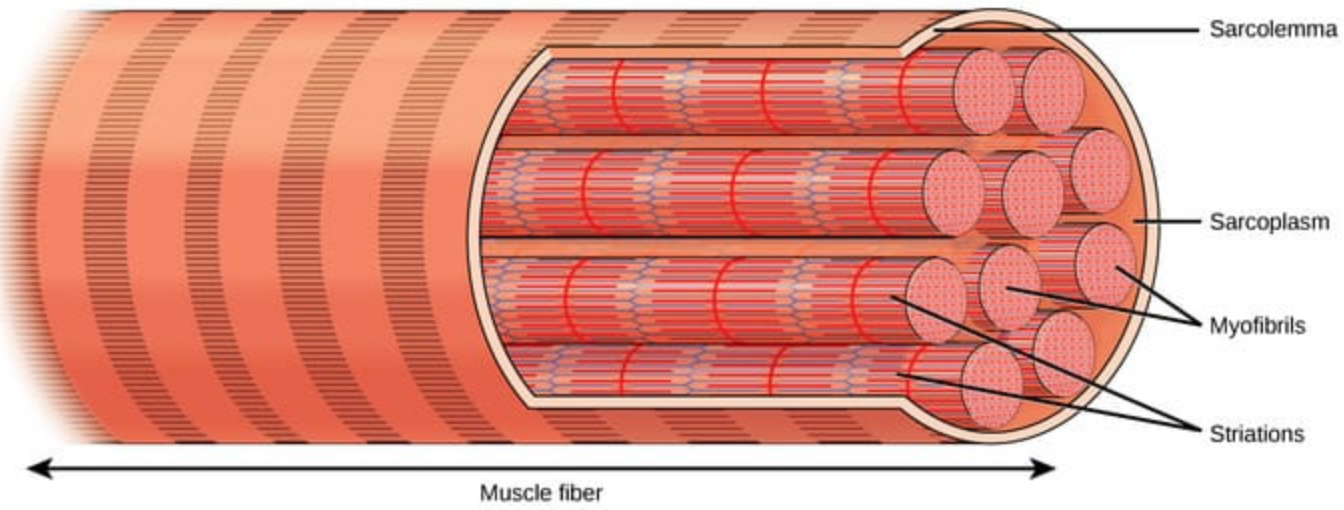


Figure 38.15.1: Myocyte: Skeletal muscle cell: A skeletal muscle cell is surrounded by a plasma membrane called the sarcolemma with a cytoplasm called the sarcoplasm. A muscle fiber is composed of many myofibrils, packaged into orderly units.

Myofibril Structure

Each myocyte can contain many thousands of myofibrils. Myofibrils run parallel to the myocyte and typically run for its entire length, attaching to the sarcolemma at either end. Each myofibril is surrounded by the sarcoplasmic reticulum, which is closely associated with the transverse tubules. The sarcoplasmic reticulum acts as a sink of Ca^{+} ions, which are released upon signalling from the transverse tubules.

Sarcomeres

Myofibrils are composed of long myofilaments of actin, myosin, and other associated proteins. These proteins are organized into regions termed sarcomeres, the functional contractile region of the myocyte. Within the sarcomere actin and myosin, myofilaments are interlaced with each other and slide over each other via the sliding filament model of contraction. The regular organization of these sarcomeres gives skeletal and cardiac muscle their distinctive striated appearance.

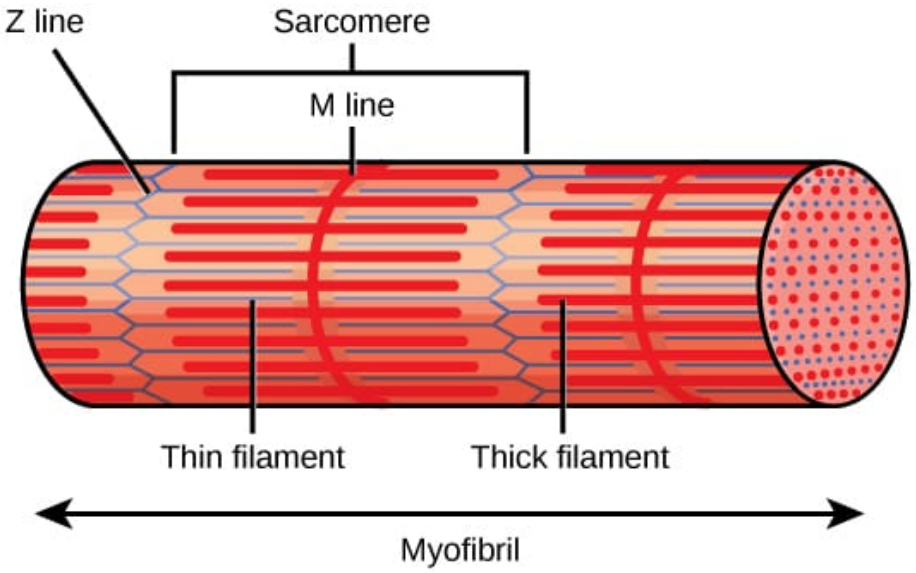


Figure 38.15.1:

Sarcomere: The sarcomere is the functional contractile region of the myocyte, and defines the region of interaction between a

set of thick and thin filaments.

Myofilaments (Thick and Thin Filaments)

Myofibrils are composed of smaller structures called myofilaments. There are two main types of myofilaments: thick filaments and thin filaments. Thick filaments are composed primarily of myosin proteins, the tails of which bind together leaving the heads exposed to the interlaced thin filaments. Thin filaments are composed of actin, tropomyosin, and troponin. The molecular model of contraction which describes the interaction between actin and myosin myofilaments is called the cross-bridge cycle.

Key Points

- Muscles are composed of long bundles of myocytes or muscle fibers.
- Myocytes contain thousands of myofibrils.
- Each myofibril is composed of numerous sarcomeres, the functional contracile region of a striated muscle. Sarcomeres are composed of myofilaments of myosin and actin, which interact using the sliding filament model and cross-bridge cycle to contract.

Key Terms

- **sarcoplasm**: The cytoplasm of a myocyte.
- **sarcoplasmic reticulum**: The equivalent of the smooth endoplasmic reticulum in a myocyte.
- **sarcolemma**: The cell membrane of a myocyte.
- **sarcomere**: The functional contractile unit of the myofibril of a striated muscle.

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38.16: Muscle Contraction and Locomotion - Sliding Filament Model of Contraction

Learning Objectives

- Describe the sliding filament model of muscle contraction

Movement often requires the contraction of a skeletal muscle, as can be observed when the bicep muscle in the arm contracts, drawing the forearm up towards the trunk. The sliding filament model describes the process used by muscles to contract. It is a cycle of repetitive events that causes actin and myosin myofilaments to slide over each other, contracting the sarcomere and generating tension in the muscle.

Sarcomere Structure

To understand the sliding filament model requires an understanding of sarcomere structure. A sarcomere is defined as the segment between two neighbouring, parallel Z-lines. Z lines are composed of a mixture of actin myofilaments and molecules of the highly elastic protein titin crosslinked by alpha-actinin. Actin myofilaments attach directly to the Z-lines, whereas myosin myofilaments attach via titin
molecules.

Surrounding the Z-line is the I-band, the region where actin myofilaments are not superimposed by myosin myofilaments. The I-band is spanned by the titin molecule connecting the Z-line with a myosin filament.

The region between two neighboring, parallel I-bands is known as the A-band and contains the entire length of single myosin myofilaments. Within the A-band is a region known as the H-band, which is the region not superimposed by actin myofilaments. Within the H-band is the M-line, which is composed of myosin myofilaments and titin molecules crosslinked by myomesin.

Titin molecules connect the Z-line with the M-line and provide a scaffold for myosin myofilaments. Their elasticity provides the underpinning of muscle contraction. Titin molecules are thought to play a key role as a molecular ruler maintaining parallel alignment within the sarcomere. Another protein, nebulin, is thought to perform a similar role for actin myofilaments.

Model of Contraction

The molecular mechanism whereby myosin and acting myofilaments slide over each other is termed the cross-bridge cycle. During muscle contraction, the heads of myosin myofilaments quickly bind and release in a ratcheting fashion, pulling themselves along the actin myofilament.

At the level of the sliding filament model, expansion and contraction only occurs within the I and H-bands. The myofilaments themselves do not contract or expand and so the A-band remains constant.

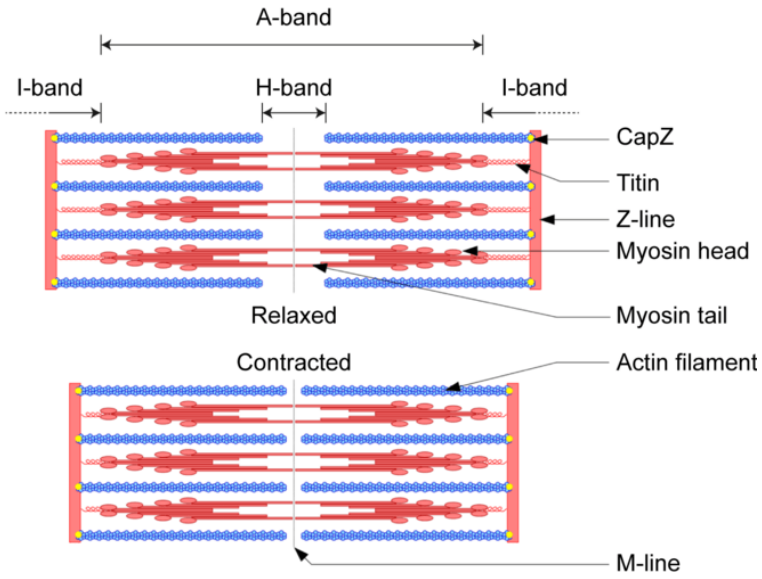


Figure 38.16.1: The sarcomere and the sliding filament model of contraction: During contraction myosin ratchets along actin myofilaments compressing the I and H bands. During stretching this tension is release and the I and H bands expand. The A-band remains constant throughout as the length of the myosin myofilaments does not change.

The amount of force and movement generated generated by an individual sarcomere is small. However, when multiplied by the number of sarcomeres in a myofibril, myofibrils in a myocyte and myocytes in a muscle, the amount of force and movement generated is significant.

Key Points

- The sarcomere is the region in which sliding filament contraction occurs.
- During contraction, myosin myofilaments ratchet over actin myofilaments contracting the sarcomere.
- Within the sarcomere, key regions known as the I and H band compress and expand to facilitate this movement.
- The myofilaments themselves do not expand or contract.

Key Terms

- **I-band**: The area adjacent to the Z-line, where actin myofilaments are not superimposed by myosin myofilaments.
- **A-band**: The length of a myosin myofilament within a sarcomere.
- **M-line**: The line at the center of a sarcomere to which myosin myofilaments bind.
- **Z-line**: Neighbouring, parallel lines that define a sarcomere.
- **H-band**: The area adjacent to the M-line, where myosin myofilaments are not superimposed by actin myofilaments.

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38.17: Muscle Contraction and Locomotion - ATP and Muscle Contraction

Learning Objectives

- Discuss how energy is consumed during movement

ATP and Muscle Contraction

Muscles contract in a repeated pattern of binding and releasing between the two thin and thick strands of the sarcomere. ATP is critical to prepare myosin for binding and to "recharge" the myosin.

The Cross-Bridge Muscle Contraction Cycle

ATP first binds to myosin, moving it to a high-energy state. The ATP is hydrolyzed into ADP and inorganic phosphate (P_i) by the enzyme ATPase. The energy released during ATP hydrolysis changes the angle of the myosin head into a "cocked" position, ready to bind to actin if the sites are available. ADP and Pi remain attached; myosin is in its high energy configuration.

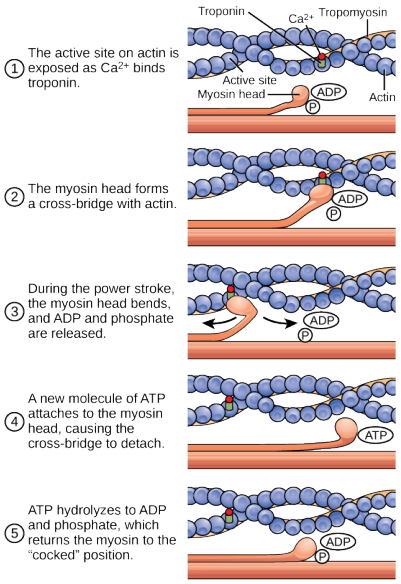


Figure 38.17.1: Cross-bridge muscle contraction cycle: The cross-bridge muscle contraction cycle, which is triggered by Ca2+ binding to the actin active site, is shown. With each contraction cycle, actin moves relative to myosin.

The muscle contraction cycle is triggered by calcium ions binding to the protein complex troponin, exposing the active-binding sites on the actin. As soon as the actin-binding sites are uncovered, the high-energy myosin head bridges the gap, forming a cross-bridge. Once myosin binds to the actin, the P_i is released, and the myosin undergoes a conformational change to a lower energy state. As myosin expends the energy, it moves through the "power stroke," pulling the actin filament toward the M-line. When the actin is pulled approximately 10 nm toward the M-line, the sarcomere shortens and the muscle contracts. At the end of the power stroke, the myosin is in a low-energy position.

After the power stroke, ADP is released, but the cross-bridge formed is still in place. ATP then binds to myosin, moving the myosin to its high-energy state, releasing the myosin head from the actin active site. ATP can then attach to myosin, which allows the cross-bridge cycle to start again; further muscle contraction can occur. Therefore, without ATP, muscles would remain in their contracted state, rather than their relaxed state.

Key Points

- ATP prepares myosin for binding with actin by moving it to a higher- energy state and a “cocked” position.
- Once the myosin forms a cross-bridge with actin, the Pi disassociates and the myosin undergoes the power stroke, reaching a lower energy state when the sarcomere shortens.
- ATP must bind to myosin to break the cross-bridge and enable the myosin to rebind to actin at the next muscle contraction.

Key Terms

- **M-line**: the disc in the middle of the sarcomere, inside the H-zone
- **troponin**: a complex of three regulatory proteins that is integral to muscle contraction in skeletal and cardiac muscle, or any member of this complex
- **ATPase**: a class of enzymes that catalyze the decomposition of ATP into ADP and a free phosphate ion, releasing energy that is often harnessed to drive other chemical reactions

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38.18: Muscle Contraction and Locomotion - Regulatory Proteins

Learning Objectives

- Describe how calcium, tropomyosin, and the troponin complex regulate the binding of actin by myosin

Regulatory Proteins

The binding of the myosin heads to the muscle actin is a highly-regulated process. When a muscle is in a resting state, actin and myosin are separated. To keep actin from binding to the active site on myosin, regulatory proteins block the molecular binding sites. Tropomyosin blocks myosin binding sites on actin molecules, preventing cross-bridge formation, which prevents contraction in a muscle without nervous input. The protein complex troponin binds to tropomyosin, helping to position it on the actin molecule.

Regulation of Troponin and Tropomyosin

To enable muscle contraction, tropomyosin must change conformation and uncover the myosin-binding site on an actin molecule, thereby allowing cross-bridge formation. Troponin, which regulates the tropomyosin, is activated by calcium, which is kept at extremely low concentrations in the sarcoplasm. If present, calcium ions bind to troponin, causing conformational changes in troponin that allow tropomyosin to move away from the myosin-binding sites on actin. Once the tropomyosin is removed, a cross-bridge can form between actin and myosin, triggering contraction. Cross-bridge cycling continues until Ca^{2+} ions and ATP are no longer available; tropomyosin again covers the binding sites on actin.

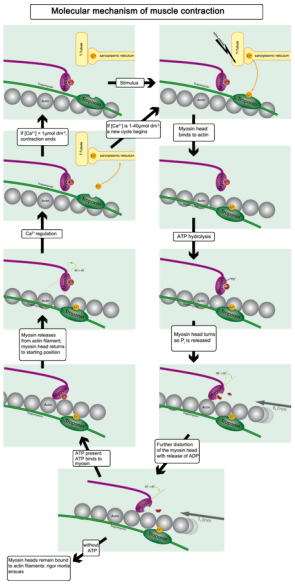


Figure 38.18.1: Muscle contraction: Calcium remains in the sarcoplasmic reticulum until released by a stimulus. Calcium then binds to troponin, causing the troponin to change shape and remove the tropomyosin from the binding sites. Cross-bridge cling continues until the calcium ions and ATP are no longer available.

Calcium-Induced Calcium Release

The concentration of calcium within muscle cells is controlled by the sarcoplasmic reticulum, a unique form of endoplasmic reticulum in the sarcoplasm. Muscle contraction ends when calcium ions are pumped back into the sarcoplasmic reticulum,

allowing the muscle cell to relax. During stimulation of the muscle cell, the motor neuron releases the neurotransmitter acetylcholine, which then binds to a post-synaptic nicotinic acetylcholine receptor.

A change in the receptor conformation causes an action potential, activating voltage-gated L-type calcium channels, which are present in the plasma membrane. The inward flow of calcium from the L-type calcium channels activates ryanodine receptors to release calcium ions from the sarcoplasmic reticulum. This mechanism is called calcium-induced calcium release (CICR). It is not understood whether the physical opening of the L-type calcium channels or the presence of calcium causes the ryanodine receptors to open. The outflow of calcium allows the myosin heads access to the actin cross-bridge binding sites, permitting muscle contraction.

Key Points

- Tropomyosin covers the actin binding sites, preventing myosin from forming cross-bridges while in a resting state.
- When calcium binds to troponin, the troponin changes shape, removing tropomyosin from the binding sites.
- The sarcoplasmic reticulum stores calcium ions, which it releases when a muscle cell is stimulated; the calcium ions then enable the cross-bridge muscle contraction cycle.

Key Terms

- **tropomyosin**: any of a family of muscle proteins that regulate the interaction of actin and myosin
- **acetylcholine**: a neurotransmitter in humans and other animals, which is an ester of acetic acid and choline
- **sarcoplasmic reticulum**: s smooth endoplasmic reticulum found in smooth and striated muscle; it contains large stores of calcium, which it sequesters and then releases when the muscle cell is stimulated

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38.19: Muscle Contraction and Locomotion - Excitation–Contraction Coupling

Learning Objectives

- Explain the process of excitation-contraction coupling and the role of neurotransmitters

Excitation–Contraction Coupling

Excitation–contraction coupling is the physiological process of converting an electrical stimulus to a mechanical response. It is the link (transduction) between the action potential generated in the sarcolemma and the start of a muscle contraction.

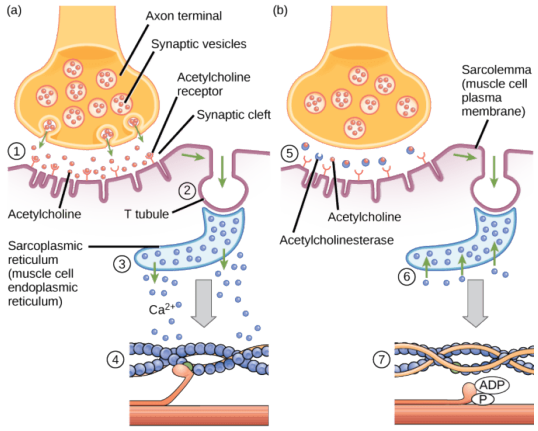


Figure 38.19.1: Excitation-contraction coupling: This diagram shows excitation-contraction coupling in a skeletal muscle contraction. The sarcoplasmic reticulum is a specialized endoplasmic reticulum found in muscle cells.

Communication between Nerves and Muscles

A neural signal is the electrical trigger for calcium release from the sarcoplasmic reticulum into the sarcoplasm. Each skeletal muscle fiber is controlled by a motor neuron, which conducts signals from the brain or spinal cord to the muscle. Electrical signals called action potentials travel along the neuron's axon, which branches through the muscle, connecting to individual muscle fibers at a neuromuscular junction. The area of the sarcolemma on the muscle fiber that interacts with the neuron is called the motor-end plate. The end of the neuron's axon is called the synaptic terminal; it does not actually contact the motor-end plate. A small space called the synaptic cleft separates the synaptic terminal from the motor-end plate.

Because neuron axons do not directly contact the motor-end plate, communication occurs between nerves and muscles through neurotransmitters. Neuron action potentials cause the release of neurotransmitters from the synaptic terminal into the synaptic cleft, where they can then diffuse across the synaptic cleft and bind to a receptor molecule on the motor end plate. The motor end plate possesses junctional folds: folds in the sarcolemma that create a large surface area for the neurotransmitter to bind to receptors. The receptors are sodium channels that open to allow the passage of Na^+ into the cell when they receive neurotransmitter signal.

Depolarization in the Sarcolemma

Acetylcholine (ACh) is a neurotransmitter released by motor neurons that binds to receptors in the motor end plate. Neurotransmitter release occurs when an action potential travels down the motor neuron's axon, resulting in altered permeability of the synaptic terminal membrane and an influx of calcium. The Ca^{2+} ions allow synaptic vesicles to move to and bind with the presynaptic membrane (on the neuron) and release neurotransmitter from the vesicles into the synaptic cleft. Once released by the synaptic terminal, ACh diffuses across the synaptic cleft to the motor end plate, where it binds with ACh receptors.

As a neurotransmitter binds, these ion channels open, and Na^{+} ions cross the membrane into the muscle cell. This reduces the voltage difference between the inside and outside of the cell, which is called depolarization. As ACh binds at the motor end plate, this depolarization is called an end-plate potential. The depolarization then spreads along the sarcolemma and down the T tubules, creating an action potential. The action potential triggers the sarcoplasmic reticulum to release of Ca^{2+}, which activate troponin and stimulate muscle contraction.

ACh is broken down by the enzyme acetylcholinesterase (AChE) into acetyl and choline. AChE resides in the synaptic cleft, breaking down ACh so that it does not remain bound to ACh receptors, which would cause unwanted extended muscle contraction.

Key Points

- A motor neuron connects to a muscle at the neuromuscular junction, where a synaptic terminal forms a synaptic cleft with a motor-end plate.
- The neurotransmitter acetylcholine diffuses across the synaptic cleft, causing the depolarization of the sarcolemma.
- The depolarization of the sarcolemma stimulates the sarcoplasmic reticulum to release Ca^{2+}, which causes the muscle to contract.

Key Terms

- **motor-end plate**: postjunctional folds which increase the surface area of the membrane (and acetylcholine receptors) exposed to the synaptic cleft
- **sarcolemma**: a thin cell membrane that surrounds a striated muscle fiber
- **acetylcholinesterase**: an enzyme that catalyzes the hydrolysis of the neurotransmitter acetylcholine into choline and acetic acid

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38.20: Muscle Contraction and Locomotion - Control of Muscle Tension

Learning Objectives

- Describe the factors that control muscle tension

Control of Muscle Tension

Neural control initiates the formation of actin – myosin cross-bridges, leading to the sarcomere shortening involved in muscle contraction. These contractions extend from the muscle fiber through connective tissue to pull on bones, causing skeletal movement. The pull exerted by a muscle is called tension. The amount of force created by this tension can vary, which enables the same muscles to move very light objects and very heavy objects. In individual muscle fibers, the amount of tension produced depends primarily on the amount of cross-bridges formed, which is influenced by the cross-sectional area of the muscle fiber and the frequency of neural stimulation.

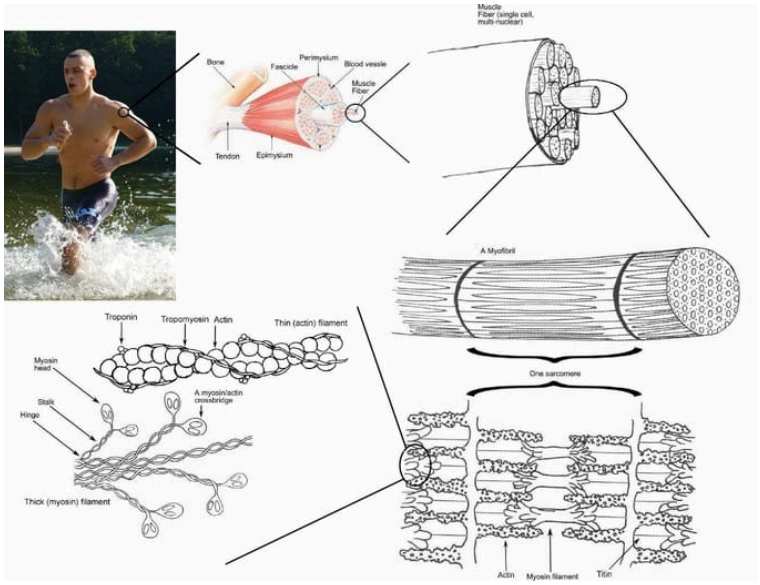


Figure 38.20.1: Muscle tension: Muscle tension is produced when the maximum amount of cross-bridges are formed, either within a muscle with a large diameter or when the maximum number of muscle fibers are stimulated. Muscle tone is residual muscle tension that resists passive stretching during the resting phase.

Cross-bridges and Tension

The number of cross-bridges formed between actin and myosin determine the amount of tension that a muscle fiber can produce. Cross-bridges can only form where thick and thin filaments overlap, allowing myosin to bind to actin. If more cross-bridges are formed, more myosin will pull on actin and more tension will be produced.

Maximal tension occurs when thick and thin filaments overlap to the greatest degree within a sarcomere. If a sarcomere at rest is stretched past an ideal resting length, thick and thin filaments do not overlap to the greatest degree so fewer cross-bridges can form. This results in fewer myosin heads pulling on actin and less muscle tension. As a sarcomere shortens, the zone of overlap reduces as the thin filaments reach the H zone, which is composed of myosin tails. Because myosin heads form cross-bridges, actin will not bind to myosin in this zone, reducing the tension produced by the myofiber. If the sarcomere is shortened even more, thin filaments begin to overlap with each other, reducing cross-bridge formation even further, and producing even less tension. Conversely, if the sarcomere is stretched to the point at which thick and thin filaments do not overlap at all, no cross-

bridges are formed and no tension is produced. This amount of stretching does not usually occur because accessory proteins, internal sensory nerves, and connective tissue oppose extreme stretching.

The primary variable determining force production is the number of myofibers (long muscle cells) within the muscle that receive an action potential from the neuron that controls that fiber. When using the biceps to pick up a pencil, for example, the motor cortex of the brain only signals a few neurons of the biceps so only a few myofibers respond. In vertebrates, each myofiber responds fully if stimulated. On the other hand, when picking up a piano, the motor cortex signals all of the neurons in the biceps so that every myofiber participates. This is close to the maximum force the muscle can produce. As mentioned above, increasing the frequency of action potentials (the number of signals per second) can increase the force a bit more because the tropomyosin is flooded with calcium.

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Key Points

- The more cross-bridges that are formed, the more tension in the muscle.
- The amount of tension produced depends on the cross-sectional area of the muscle fiber and the frequency of neural stimulation.
- Maximal tension occurs when thick and thin filaments overlap to the greatest degree within a sarcomere; less tension is produced when the sarcomere is stretched.
- If more motor neurons are stimulated, more myofibers contract, and there is greater tension in the muscle.

Key Terms

- **tension**: condition of being held in a state between two or more forces, which are acting in opposition to each other

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39: THE RESPIRATORY SYSTEM

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39.1: Systems of Gas Exchange - The Respiratory System and Direct Diffusion

Learning Objectives

- Review an overview of the functions of the respiratory system

Introduction

Breathing is an involuntary event. How often a breath is taken and how much air is inhaled or exhaled are tightly regulated by the respiratory center in the brain. Under normal breathing conditions, humans will breathe approximately 15 times per minute on average. A respiratory cycle consists of an inhalation and an exhalation: with every normal inhalation, oxygenated air fills the lungs, while with every exhalation, deoxygenated air rushes back out. The oxygenated air crosses the lung tissue, enters the bloodstream, and travels to organs and tissues. Oxygen (O_2) enters the cells where it is used for metabolic reactions that produce ATP, a high-energy compound. At the same time, these reactions release carbon dioxide (CO_2) as a by-product. CO_2 is toxic and must be eliminated; thus, CO_2 exits the cells, enters the bloodstream, travels back to the lungs, and is expired out of the body during exhalation.

The primary function of the respiratory system is to deliver oxygen to the cells of the body's tissues and remove carbon dioxide. The main structures of the human respiratory system are the nasal cavity, the trachea, and the lungs. All aerobic organisms require oxygen to carry out their metabolic functions.

Along the evolutionary tree, different organisms have devised different means of obtaining oxygen from the surrounding atmosphere. The environment in which the animal lives greatly determines how an animal respires. The complexity of the respiratory system correlates with the size of the organism. As animal size increases, diffusion distances increase and the ratio of surface area to volume drops. In unicellular (single-celled) organisms, diffusion across the cell membrane is sufficient for supplying oxygen to the cell. Diffusion is a slow, passive transport process. In order to be a feasible means of providing oxygen to the cell, the rate of oxygen uptake must match the rate of diffusion across the membrane. In other words, if the cell were very large or thick, diffusion would not be able to provide oxygen quickly enough to the inside of the cell. Therefore, dependence on diffusion as a means of obtaining oxygen and removing carbon dioxide remains feasible only for small organisms or those with highly-flattened bodies, such as flatworms (platyhelminthes). Larger organisms have had to evolve specialized respiratory tissues, such as gills, lungs, and respiratory passages, accompanied by a complex circulatory system to transport oxygen throughout their entire body.



Figure 39.1.1: Direct diffusion: This flatworm's process of respiration works by diffusion across the outer membrane.

Direct Diffusion

For small multicellular organisms, diffusion across the outer membrane is sufficient to meet their oxygen needs. Gas exchange by direct diffusion across surface membranes is efficient for organisms less than 1 mm in diameter. In simple organisms, such as cnidarians and flatworms, every cell in the body is close to the external environment. Their cells are kept moist so that gases diffuse quickly via direct diffusion. Flatworms are small, literally flat worms, which 'breathe' through diffusion across the outer membrane. The flat shape of these organisms increases the surface area for diffusion, ensuring that each cell within the body is close to the outer membrane surface and has access to oxygen. If the flatworm had a cylindrical body, then the cells in the center would not be able to get oxygen.

Key Points

- Respiration ensures that cells, tissues, and major organs of the body receive an adequate supply of oxygen and that the carbon dioxide, a waste product, is efficiently removed; the exchange of oxygen and carbon dioxide occurs via diffusion across cell membranes.
- The mechanisms, processes, and structures used for respiration are dictated by the type, size, and complexity of the organism.
- Direct diffusion of gases through the outer membranes can be used by organisms such as flatworms as a means of respiration due to their small size and simplicity.

Key Terms

- **deoxygenated**: having removed the oxygen atoms from a molecule
- **diffusion**: The passive movement of a solute across a permeable membrane
- **aerobic**: living or occurring only in the presence of oxygen

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39.2: Systems of Gas Exchange - Skin, Gills, and Tracheal Systems

Learning Objectives

- Describe how the skin, gills, and tracheal system are used in the process of respiration

Skin and Gills

There are various methods of gas exchange used by animals. As seen in mammals, air is taken in from the external environment to the lungs. Other animals, such as earthworms and amphibians, use their skin (integument) as a respiratory organ. A dense network of capillaries lies just below the skin, facilitating gas exchange between the external environment and the circulatory system. The respiratory surface must be kept moist in order for the gases to dissolve and diffuse across cell membranes.

Organisms that live in water also need a way to obtain oxygen. Oxygen dissolves in water, but at a lower concentration in comparison to the atmosphere, which has roughly 21 percent oxygen. Fish and many other aquatic organisms have evolved gills to take up the dissolved oxygen from water. Gills are thin tissue filaments that are highly branched and folded. When water passes over the gills, the dissolved oxygen in the water rapidly diffuses across the gills into the bloodstream. The circulatory system can then carry the oxygenated blood to the other parts of the body. In animals that contain coelomic fluid instead of blood, oxygen diffuses across the gill surfaces into the coelomic fluid. Gills are found in mollusks, annelids, and crustaceans.



Figure 39.2.1: Common carp: This common carp, like many other aquatic organisms, has gills that allow it to obtain oxygen from water.

The folded surfaces of the gills provide a large surface area to ensure that fish obtain sufficient oxygen. Diffusion is a process in which material travels from regions of high concentration to low concentration until equilibrium is reached. In this case, blood with a low concentration of oxygen molecules circulates through the gills. The concentration of oxygen molecules in water is higher than the concentration of oxygen molecules in gills. As a result, oxygen molecules diffuse from water (high concentration) to blood (low concentration). Similarly, carbon dioxide molecules diffuse from the blood (high concentration) to water (low concentration).

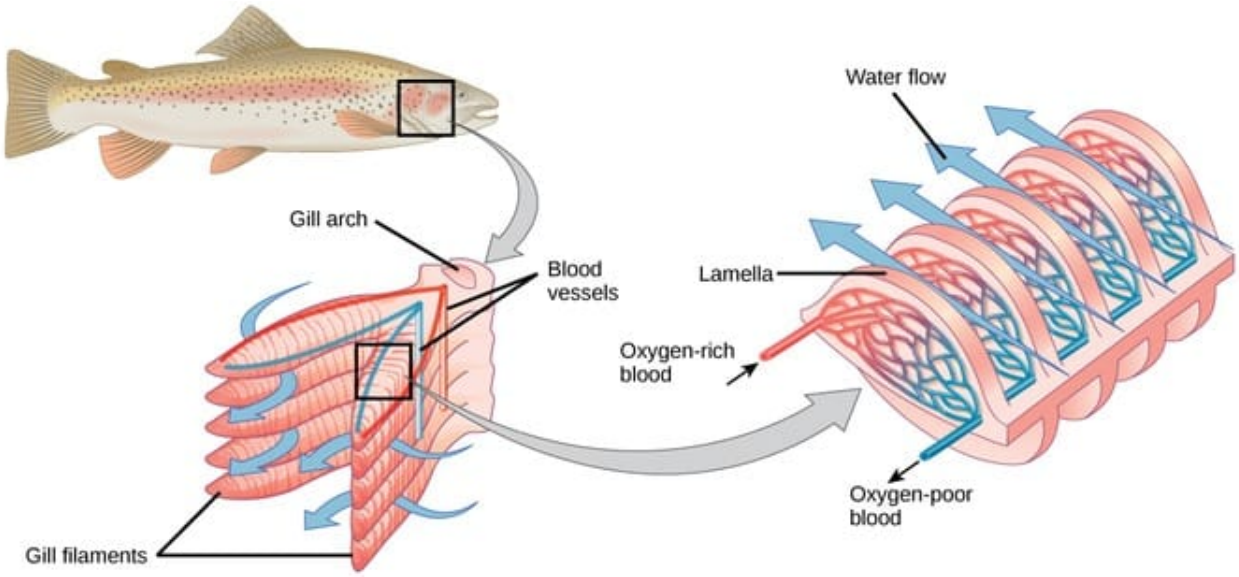


Figure 39.2.1: Oxygen transport and gills: As water flows over the gills, oxygen is transferred to blood via the veins.

Tracheal Systems

Insect respiration is independent of its circulatory system; therefore, the blood does not play a direct role in oxygen transport. Insects have a highly-specialized type of respiratory system called the tracheal system, which consists of a network of small tubes that carries oxygen to the entire body. The tracheal system, the most direct and efficient respiratory system in active animals, has tubes made of a polymeric material called chitin.

Insect bodies have openings, called spiracles, along the thorax and abdomen. These openings connect to the tubular network, allowing oxygen to pass into the body, regulating the diffusion of CO_2 and water vapor. Air enters and leaves the tracheal system through the spiracles. Some insects can ventilate the tracheal system with body movements.

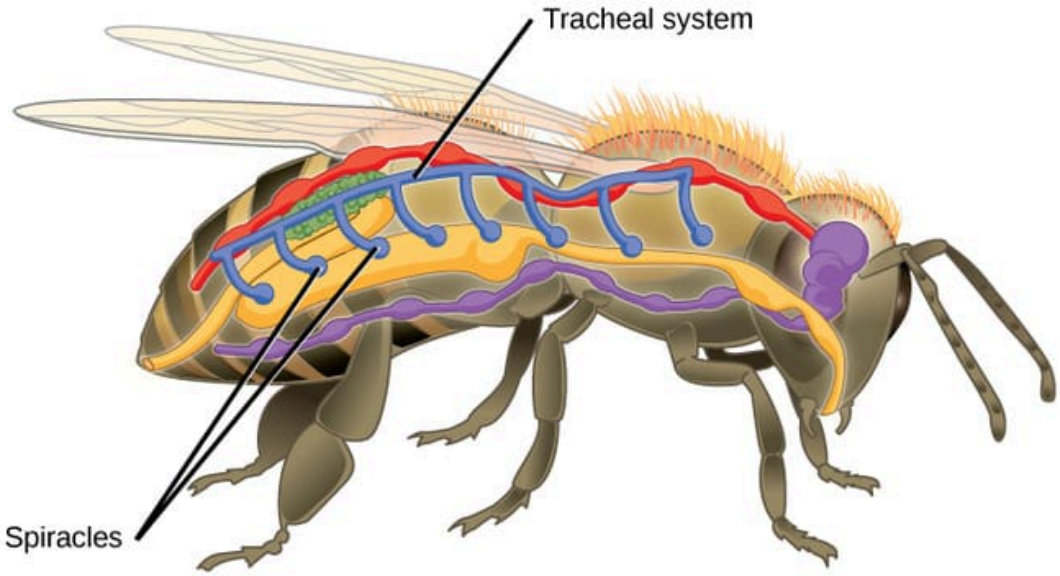


Figure 39.2.1: Insect respiration: Insects perform respiration via a tracheal system, in which openings called spiracles allow oxygen to pass into the body.

Key Points

- Some animals, such as amphibians and earthworms, can use their skin (integument) to exchange gases between the external

environment and the circulatory system due to the network of capillaries that lie below the skin.
- Fish and other aquatic organisms use gills to take up oxygen dissolved in the water and diffuse carbon dioxide out of the bloodstream.
- Some insects utilize a tracheal system that transports oxygen from the external environment through openings called spiracles.

Key Terms

- **coelom**: a fluid-filled cavity within the body of an animal; the digestive system is suspended within the cavity, which is lined by a tissue called the peritoneum
- **gill**: a breathing organ of fish and other aquatic animals
- **spiracle**: a pore or opening used (especially by spiders and some fish) for breathing

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39.3: Systems of Gas Exchange - Amphibian and Bird Respiratory Systems

Learning Objectives

- Differentiate among the types of breathing in amphibians and birds

Amphibian Respiration

Amphibians have evolved multiple ways of breathing. Young amphibians, like tadpoles, use gills to breathe, and they do not leave the water. As the tadpole grows, the gills disappear and lungs grow (though some amphibians retain gills for life). These lungs are primitive and are not as evolved as mammalian lungs. Adult amphibians are lacking or have a reduced diaphragm, so breathing through the lungs is forced. The other means of breathing for amphibians is diffusion across the skin. To aid this diffusion, amphibian skin must remain moist. It has vascular tissues to make this gaseous exchange possible. This moist skin interface can be a detriment on land, but works well under water.

Avian Respiration

Birds are different from other vertebrates, with birds having relatively small lungs and nine air sacs that play an important role in respiration. The lungs of birds also do not have the capacity to inflate as birds lack a diaphragm and a pleural cavity. Gas exchange in birds occurs between air capillaries and blood capillaries, rather than in alveoli.

Flight poses a unique challenge with respect to breathing. Flying consumes a great amount of energy; therefore, birds require a lot of oxygen to aid their metabolic processes. Birds have evolved a respiratory system that supplies them with the oxygen needed to sustain flight. Similar to mammals, birds have lungs, which are organs specialized for gas exchange. Oxygenated air, taken in during inhalation, diffuses across the surface of the lungs into the bloodstream, and carbon dioxide diffuses from the blood into the lungs, and is then expelled during exhalation. The details of breathing between birds and mammals differ substantially.

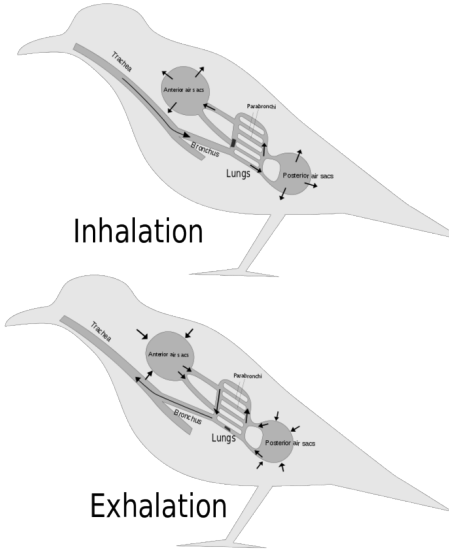


Figure 39.3.1: Bird Respiration: The process of inhalation and exhalation in birds. Three distinct sets of organs perform respiration — the anterior air sacs, the lungs, and the posterior air sacs.

In addition to lungs, birds have air sacs inside their body. Air flows in one direction from the posterior air sacs to the lungs and out of the anterior air sacs. The flow of air is in the opposite direction from blood flow, and gas exchange takes place much

more efficiently. This type of breathing enables birds to obtain the requisite oxygen, even at higher altitudes where the oxygen concentration is low. This directionality of airflow requires two cycles of air intake and exhalation to completely get the air out of the lungs.

Key Points

- Amphibians utilize gills for breathing early in life, and develop primitive lungs in their adult life; additionally, they are able to breathe through their skin.
- Birds have evolved a directional respiratory system that allows them to obtain oxygen at high altitudes: air flows in one direction while blood flows in another, allowing efficient gas exchange.

Key Terms

- **gills**: A breathing organ of fish, amphibians, and other aquatic animals.

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39.4: Systems of Gas Exchange - Mammalian Systems and Protective Mechanisms

Learning Objectives

- Explain how air passes from the outside environment to the lungs, protecting them from particulate matter

Mammalian Respiratory System

In mammals, pulmonary ventilation occurs via inhalation when air enters the body through the nasal cavity. Air passes through the nasal cavity and is warmed to body temperature and humidified. The respiratory tract is coated with mucus that is high in water to seal the tissues from direct contact with air. As air crosses the surfaces of the mucous membranes, it picks up water. This equilibrates the air to the body, reducing damage that cold, dry air can cause. Particulates in the air are also removed in the nasal passages. These processes are all protective mechanisms that prevent damage to the trachea and lungs.

From the nasal cavity, air passes through the pharynx and the larynx to the trachea. The function of the trachea is to funnel the inhaled air to the lungs and the exhaled air out of the body. The human trachea, a cylinder about 10-12cm long, 2cm in diameter found in front of the esophagus, extends from the larynx into the chest cavity. It is made of incomplete rings of hyaline cartilage and smooth muscle that divides into the two primary bronchi at the midthorax. The trachea is lined with mucus-producing goblet cells and ciliated epithelia that propel foreign particles trapped in the mucus toward the pharynx. The cartilage provides strength and support to the trachea to keep the passage open. The smooth muscle can contract, causing a decrease in the trachea's diameter, which propels expired air upwards from the lungs at a great force. The forced exhalation helps expel mucus when we cough.

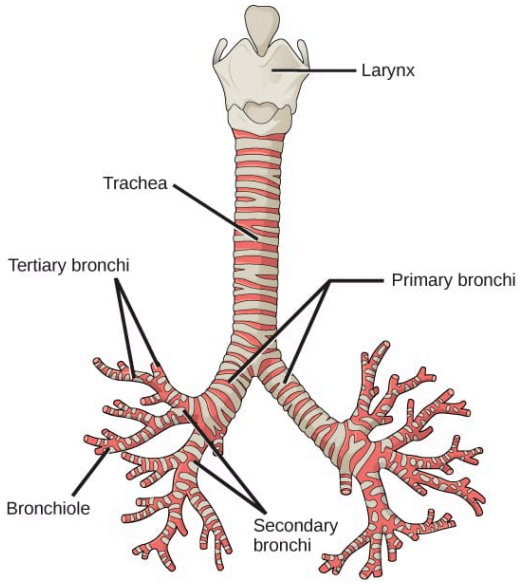


Figure 39.4.1: Trachea and bronchi structure: The trachea and bronchi are made of incomplete rings of cartilage.

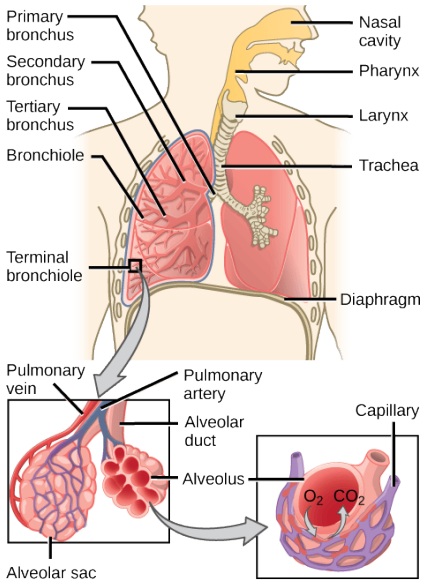


Figure 39.4.1: Route of inhalation: Air enters the respiratory system through the nasal cavity and pharynx. It then passes through the trachea and into the bronchi, which bring air into the lungs.

Lungs: Bronchi and Alveoli

The end of the trachea bifurcates to the right and left lungs, which are not identical. The larger right lung has three lobes, while the smaller left lung has two lobes. The muscular diaphragm, which facilitates breathing, is inferior to the lungs, marking the end of the thoracic cavity.

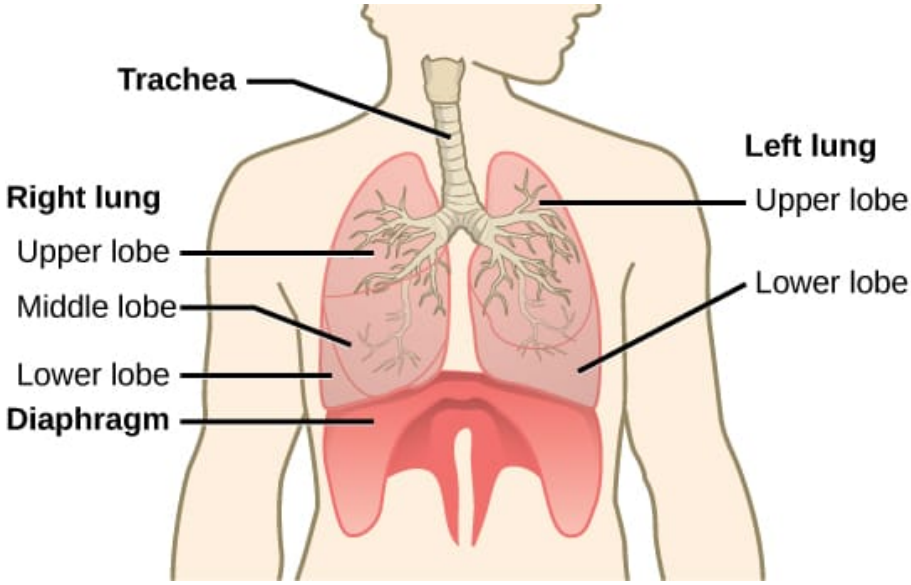


Figure 39.4.1: Lung structure: The trachea bifurcates into the right and left bronchi in the lungs. The larger right lung is made of three lobes. To accommodate the heart, the left lung is smaller, having only two lobes.

As air enters the lungs, it is diverted through bronchi beginning with the two primary bronchi. Each bronchus divides into secondary, then into tertiary bronchi, which further divide to create smaller diameter bronchioles that split and spread through the lung. The bronchi are made of cartilage and smooth muscle; at the bronchioles, the cartilage is replaced with elastic fibers. Bronchi are innervated by nerves of both the parasympathetic and sympathetic nervous systems that control muscle contraction or relaxation, respectively. In humans, bronchioles with a diameter smaller than 0.5 mm are the respiratory bronchioles. Since they lack cartilage, they rely on inhaled air to support their shape. As the passageways decrease in diameter, the relative amount of smooth muscle increases.

The terminal bronchioles then subdivide into respiratory bronchioles which subdivide into alveolar ducts. Numerous alveoli (sing. alveolus) and alveolar sacs surround the alveolar ducts. The alveolar ducts are attached to the end of each bronchiole; each duct ends in approximately 100 alveolar sacs. Each sac contains 20-30 alveoli that are 200-300 microns in diameter. Alveoli are made of thin-walled, parenchymal cells that are in direct contact with capillaries of the circulatory system. This ensures that oxygen will diffuse from alveoli into the blood and that carbon dioxide produced by cells as a waste product will diffuse from the blood into alveoli to be exhaled. The anatomical arrangement of capillaries and alveoli emphasizes the relationship of the respiratory and circulatory systems. As there are so many alveoli (around 300 million per lung) within each alveolar sac and so many sacs at the end of each alveolar duct, the lungs have a sponge-like consistency. This organization produces a very large surface area that is available for gas exchange.

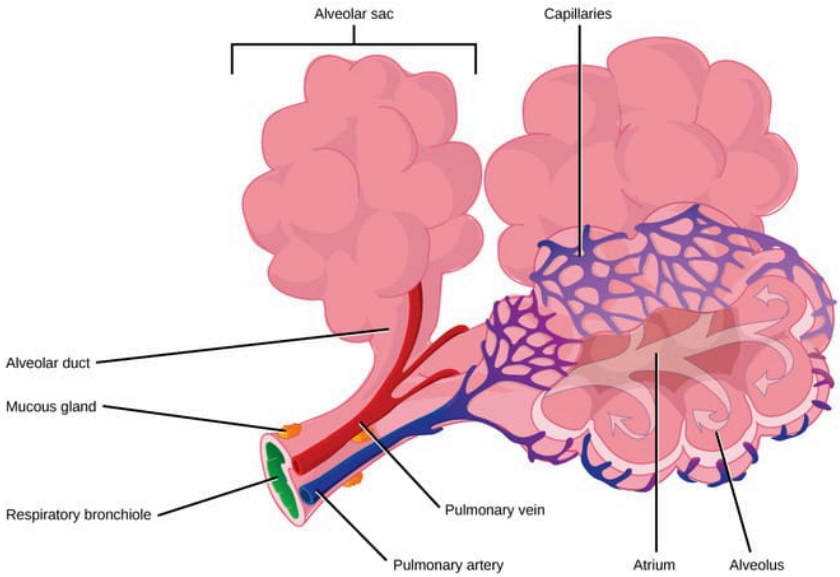


Figure 39.4.1: Alveolar structure: Terminal bronchioles are connected by respiratory bronchioles to alveolar ducts and alveolar sacs. Each alveolar sac contains 20 to 30 spherical alveoli and has the appearance of a bunch of grapes. Air flows into the atrium of the alveolar sac, then circulates into alveoli where gas exchange occurs with the capillaries. Mucus glands secrete mucus into the airways, keeping them moist and flexible.

Protective Mechanisms

The air that organisms breathe contains particulate matter such as dust, dirt, viral particles, and bacteria that can damage the lungs. The respiratory system has protective mechanisms to avoid damage. In the nasal cavity, hairs and mucus trap small particles, viruses, bacteria, dust, and dirt to prevent entry. If particulates make it beyond the nose or enter via the mouth, the bronchi and bronchioles contain several protective devices. The lungs produce mucus that traps particulates. The bronchi and bronchioles contain cilia, small hair-like projections that line the walls of the bronchi and bronchioles. These cilia move mucus and particles out of the bronchi and bronchioles back up to the throat where it is swallowed and eliminated via the esophagus.

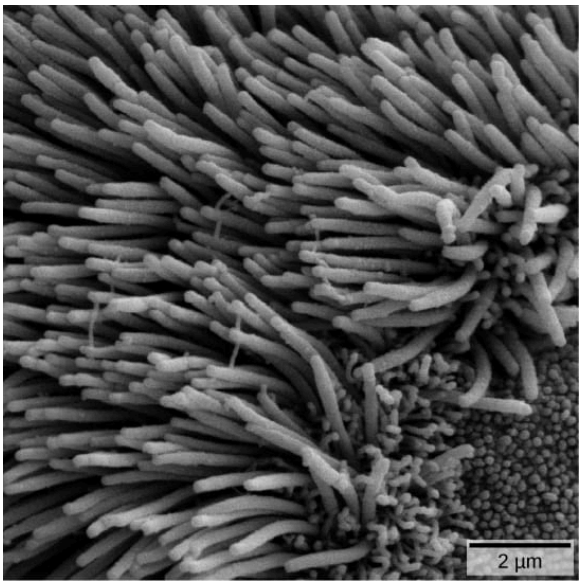


Figure 39.4.1: Electron microscope image of cilia: The bronchi and bronchioles contain cilia that help move mucus and other particles out of the lungs.

In humans, tar and other substances in cigarette smoke destroy or paralyze the cilia, making the removal of particles more difficult. In addition, smoking causes the lungs to produce more mucus, which the damaged cilia are unable to move. This causes a persistent cough, as the lungs try to rid themselves of particulate matter, making smokers more susceptible to respiratory ailments.

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Key Points

- The air that moves from the external environment into the body must pass through the nasal cavity where it is warmed, humidified, and surveyed for particulates.
- As air moves out of the nasal cavity, it moves into the pharynx, larynx, trachea, the primary bronchi (right and left lung), secondary and tertiary bronchi, bronchioles, terminal then respiratory bronchioles, alveolar ducts then alveolar sacs where gas exchange occurs with the capillaries.
- Components in the respiratory system allow for protection from foreign material; these include mucus production in the lungs and cilia in the bronchi and bronchioles to move matter out of the system.

- Components in the respiratory system that allow for protection from foreign material and include mucus production in the lungs and cilia in the bronchi and bronchioles.

Key Terms

- **alveolus**: a small air sac in the lungs, where oxygen and carbon dioxide are exchanged with the blood
- **bifurcate**: to divide or fork into two channels or branches
- **bronchus**: either of two airways, which are primary branches of the trachea, leading directly into the lungs

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39.5: Gas Exchange across Respiratory Surfaces - Gas Pressure and Respiration

Learning Objectives

- Describe how gas pressure influences the flow of gases during respiration

Gas Pressure and Respiration

The respiratory process can be better understood by examining the properties of gases. Gases move freely with their movement resulting in the constant hitting of particles against vessel walls. This collision between gas particles and vessel walls produces gas pressure.

Air is a mixture of gases: primarily nitrogen (N_2; 78.6 percent), oxygen (O_2; 20.9 percent), water vapor (H_2O; 0.5 percent), and carbon dioxide (CO_2; 0.04 percent). Each gas component of that mixture exerts a pressure. The pressure for an individual gas in the mixture is the partial pressure of that gas. Approximately 21 percent of atmospheric gas is oxygen. Carbon dioxide, however, is found in relatively small amounts (0.04 percent); therefore, the partial pressure for oxygen is much greater than that of carbon dioxide. The partial pressure of any gas can be calculated by: P = (Patm) (percent content in mixture).

P_{atm}, the atmospheric pressure, is the sum of all of the partial pressures of the atmospheric gases added together: Patm = PN2 + PO_2 + PH_2O + PCO_2= 760 mm Hg. The pressure of the atmosphere at sea level is 760 mm Hg. Therefore, the partial pressure of oxygen is: PO_2 = (760 mm Hg) (0.21) = 160 mm Hg, while for carbon dioxide: PCO_2 = (760 mm Hg) (0.0004) = 0.3 mm Hg. At high altitudes, P_{atm}decreases, but concentration does not change; the partial pressure decrease is due to the reduction in P_{atm} .

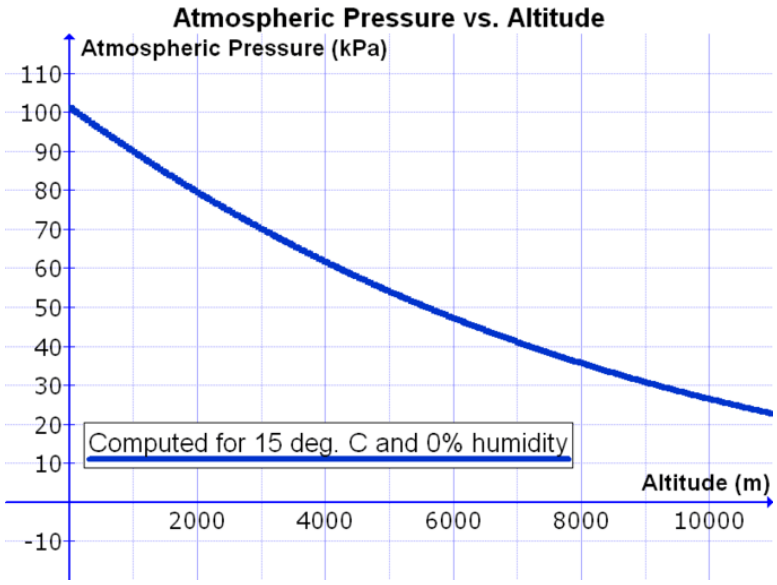


Figure 39.5.1: Atmospheric pressure vs altitude: At high altitudes, there is a decrease in Patm, causing the partial pressures to decrease as well.

When the air mixture reaches the lung, it has been warmed and humidified within the nasal cavity upon inhalation. The pressure of the water vapor in the lung does not change the pressure of the air, but it must be included in the partial pressure equation. For this calculation, the water pressure (47 mm Hg) is subtracted from the atmospheric pressure: 760 mm Hg 47 mm Hg = 713 mm Hg, and the partial pressure of oxygen is: (760 mm Hg 47 mm Hg) 0.21 = 150 mm Hg.

These pressures determine the gas exchange, or the flow of gas, in the system. Oxygen and carbon dioxide will flow according to

their pressure gradient from high to low. Therefore, understanding the partial pressure of each gas will aid in understanding how gases move in the respiratory system.

Key Points

- Atmospheric pressure is the sum of all the partial pressures of the gases in the atmosphere, including oxygen, carbon dioxide, nitrogen, and water vapor.
- In the atmosphere, the partial pressure of oxygen is much greater than the partial pressure of carbon dioxide.
- The partial pressure of oxygen in the atmosphere is much greater in comparison to the lungs, creating a pressure gradient; this allows oxygen to flow from the atmosphere into the lungs during inhalation.

Key Terms

- **atmospheric pressure**: the pressure caused by the weight of the atmosphere above an area
- **partial pressure**: the pressure one component of a mixture of gases would contribute to the total pressure

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39.6: Gas Exchange across Respiratory Surfaces - Basic Principles of Gas Exchange

Learning Objectives

- Discuss how gas pressures influence the exchange of gases into and out of the body

The purpose of the respiratory system is to perform gas exchange. Pulmonary ventilation provides air to the alveoli for this gas exchange process. At the respiratory membrane, where the alveolar and capillary walls meet, gases move across the membranes, with oxygen entering the bloodstream and carbon dioxide exiting. It is through this mechanism that blood is oxygenated and carbon dioxide, the waste product of cellular respiration, is removed from the body.

In order to understand the mechanisms of gas exchange in the lung, it is important to understand the underlying principles of gases and their behavior. In addition to Boyle's law, several other gas laws help to describe the behavior of gases.

Gas Laws and Air Composition

Gas molecules exert force on the surfaces with which they are in contact; this force is called pressure. In natural systems, gases are normally present as a mixture of different types of molecules. For example, the atmosphere consists of oxygen, nitrogen, carbon dioxide, and other gaseous molecules, and this gaseous mixture exerts a certain pressure referred to as atmospheric pressure (Table 2). Partial pressure (Px) is the pressure of a single type of gas in a mixture of gases. For example, in the atmosphere, oxygen exerts a partial pressure, and nitrogen exerts another partial pressure, independent of the partial pressure of oxygen (Figure 1). Total pressure is the sum of all the partial pressures of a gaseous mixture. Dalton's law describes the behavior of nonreactive gases in a gaseous mixture and states that a specific gas type in a mixture exerts its own pressure; thus, the total pressure exerted by a mixture of gases is the sum of the partial pressures of the gases in the mixture.



Figure 39.6.1: Partial and total pressure of a gas: Partial pressure is the force exerted by a gas. The sum of the partial pressures of all the gases in a mixture equals the total pressure.

Partial pressure is extremely important in predicting the movement of gases. Recall that gases tend to equalize their pressure in two regions that are connected. A gas will move from an area where its partial pressure is higher to an area where its partial pressure is lower. In addition, the greater the partial pressure difference between the two areas, the more rapid is the movement of gases.

Solubility of Gases in Liquids

Henry's law describes the behavior of gases when they come into contact with a liquid, such as blood. Henry's law states that the concentration of gas in a liquid is directly proportional to the solubility and partial pressure of that gas. The greater the partial pressure of the gas, the greater the number of gas molecules that will dissolve in the liquid. The concentration of the gas in a liquid is also dependent on the solubility of the gas in the liquid. For example, although nitrogen is present in the atmosphere, very little nitrogen dissolves into the blood, because the solubility of nitrogen in blood is very low. The exception to this occurs in scuba divers; the composition of the compressed air that divers breathe causes nitrogen to have a higher partial pressure than normal, causing it to dissolve in the blood in greater amounts than normal. Too much nitrogen in the bloodstream results in a serious condition that can be fatal if not corrected. Gas molecules establish an equilibrium between those molecules dissolved in liquid and those in air.

The composition of air in the atmosphere and in the alveoli differs. In both cases, the relative concentration of gases is nitrogen > oxygen > water vapor > carbon dioxide. The amount of water vapor present in alveolar air is greater than that in atmospheric air (Table 3). Recall that the respiratory system works to humidify incoming air, thereby causing the air present in the alveoli to have a greater amount of water vapor than atmospheric air. In addition, alveolar air contains a greater amount of carbon dioxide and less oxygen than atmospheric air. This is no surprise, as gas exchange removes oxygen from and adds carbon dioxide to alveolar air. Both deep and forced breathing cause the alveolar air composition to be changed more rapidly than during quiet breathing. As a result, the partial pressures of oxygen and carbon dioxide change, affecting the diffusion process that moves these materials across the membrane. This will cause oxygen to enter and carbon dioxide to leave the blood more quickly.

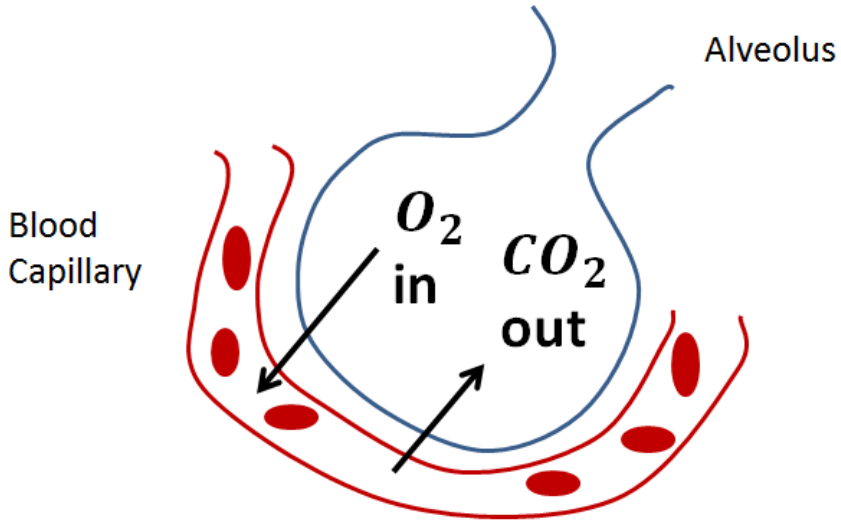


Figure 39.6.1: Gas exchange: This illustrates the exchange of gas in humans between a capillary and an alveolus.

Ventilation and Perfusion

Two important aspects of gas exchange in the lung are ventilation and perfusion. Ventilation is the movement of air into and out of the lungs, and perfusion is the flow of blood in the pulmonary capillaries. For gas exchange to be efficient, the volumes involved in ventilation and perfusion should be compatible. However, factors such as regional gravity effects on blood, blocked alveolar ducts, or disease can cause ventilation and perfusion to be imbalanced.

Key Points

- The purpose of the respiratory system is to perform gas exchange.
- Gases tend to equalize their pressure in two regions that are connected; in such a situation, the respective pressure of each gas is known as that gas's " partial pressure."
- A gas will move from an area where its partial pressure is higher to an area where its partial pressure is lower, and the greater the difference in pressure, the more rapidly the gases will move.

- Ventilation is the movement of air into and out of the lungs, and perfusion is the flow of blood in the pulmonary capillaries. For gas exchange to be efficient, the volumes involved in ventilation and perfusion should be compatible.

Key Terms

- **oxyhaemoglobin**: the form of hemoglobin, loosely combined with oxygen, present in arterial and capillary blood
- **hemoglobin**: iron-containing substance in red blood cells that transports oxygen from the lungs to the rest of the body; it consists of a protein (globulin) and heme (a porphyrin ring with iron at its center)
- **partial pressure**: the pressure one component of a mixture of gases would contribute to the total pressure

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39.7: Gas Exchange across Respiratory Surfaces - Lung Volumes and Capacities

Learning Objectives

- Distinguish between lung volume and lung capacity

Lung Volumes and Capacities

Different animals exhibit different lung capacities based on their activities. For example, cheetahs have evolved a much higher lung capacity than humans in order to provide oxygen to all the muscles in the body, allowing them to run very fast. Elephants also have a high lung capacity due to their large body and their need to take up oxygen in accordance with their body size.

Human lung size is determined by genetics, gender, and height. At maximal capacity, an average lung can hold almost six liters of air; however, lungs do not usually operate at maximal capacity. Air in the lungs is measured in terms of lung volumes and lung capacities. Volume measures the amount of air for one function (such as inhalation or exhalation) and capacity is any two or more volumes (for example, how much can be inhaled from the end of a maximal exhalation).

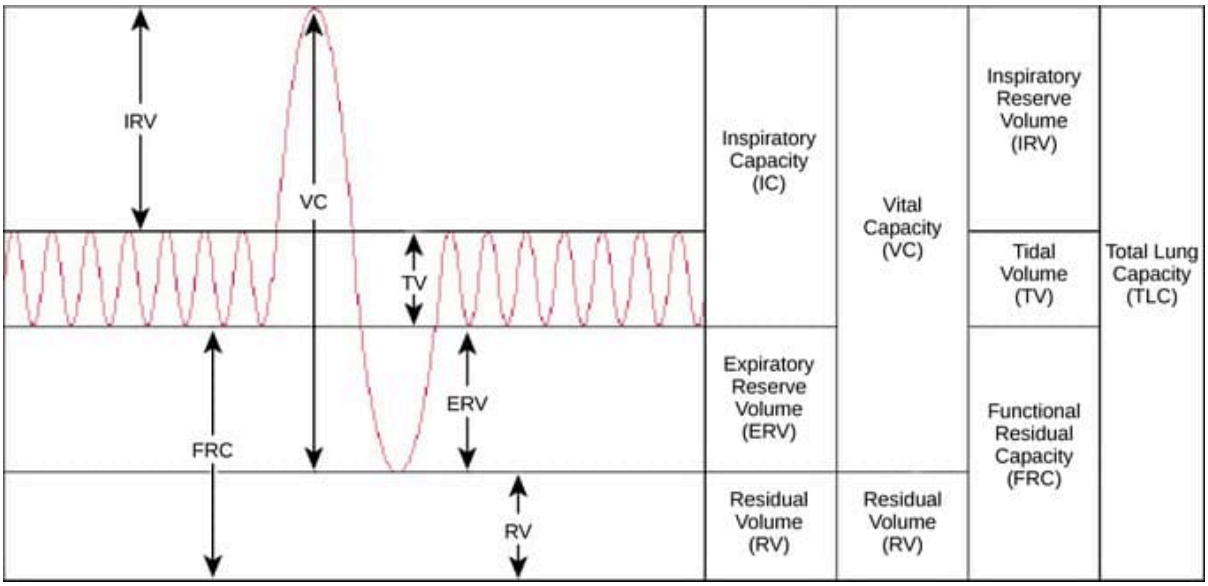


Figure 39.7.1: Human lung volumes and capacities: The total lung capacity of the adult male is six liters. Tidal volume is the volume of air inhaled in a single, normal breath. Inspiratory capacity is the amount of air taken in during a deep breath, while residual volume is the amount of air left in the lungs after forceful respiration.

Lung Volumes

The volume in the lung can be divided into four units: tidal volume, expiratory reserve volume, inspiratory reserve volume, and residual volume. Tidal volume (TV) measures the amount of air that is inspired and expired during a normal breath. On average, this volume is around one-half liter, which is a little less than the capacity of a 20-ounce drink bottle. The expiratory reserve volume (ERV) is the additional amount of air that can be exhaled after a normal exhalation. It is the reserve amount that can be exhaled beyond what is normal. Conversely, the inspiratory reserve volume (IRV) is the additional amount of air that can be inhaled after a normal inhalation. The residual volume (RV) is the amount of air that is left after expiratory reserve volume is exhaled. The lungs are never completely empty; there is always some air left in the lungs after a maximal exhalation. If this residual volume did not exist and the lungs emptied completely, the lung tissues would stick together. The energy necessary to re-inflate the lung could be too great to overcome. Therefore, there is always some air remaining in the lungs. Residual volume

is also important for preventing large fluctuations in respiratory gases (O_2 and CO_2). The residual volume is the only lung volume that cannot be measured directly because it is impossible to completely empty the lung of air. This volume can only be calculated rather than measured..

Lung volumes are measured by a technique called spirometry. An important measurement taken during spirometry is the forced expiratory volume (FEV), which measures how much air can be forced out of the lung over a specific period, usually one second (FEV1). In addition, the forced vital capacity (FVC), which is the total amount of air that can be forcibly exhaled, is measured. The ratio of these values (FEV1/FVC ratio) is used to diagnose lung diseases including asthma, emphysema, and fibrosis. If the FEV1/FVC ratio is high, the lungs are not compliant (meaning they are stiff and unable to bend properly); the patient probably has lung fibrosis. Patients exhale most of the lung volume very quickly. Conversely, when the FEV1/FVC ratio is low, there is resistance in the lung that is characteristic of asthma. In this instance, it is difficult for the patient to get the air out of his or her lungs. It takes a long time to reach the maximal exhalation volume. In either case, breathing is difficult and complications arise.

Lung Capacities

The lung capacities are measurements of two or more volumes. The vital capacity (VC) measures the maximum amount of air that can be inhaled or exhaled during a respiratory cycle. It is the sum of the expiratory reserve volume, tidal volume, and inspiratory reserve volume. The inspiratory capacity (IC) is the amount of air that can be inhaled after the end of a normal expiration. It is, therefore, the sum of the tidal volume and inspiratory reserve volume. The functional residual capacity (FRC) includes the expiratory reserve volume and the residual volume. The FRC measures the amount of additional air that can be exhaled after a normal exhalation. The total lung capacity (TLC) is a measurement of the total amount of air that the lung can hold. It is the sum of the residual volume, expiratory reserve volume, tidal volume, and inspiratory reserve volume..

Key Points

- The lung volumes that can be measured using a spirometer include tidal volume (TV), expiratory reserve volume (ERV), and inspiratory reserve volume (IRV).
- Residual volume (RV) is a lung volume representing the amount of air left in the lungs after a forced exhalation; this volume cannot be measured, only calculated.
- The lung capacities that can be calculated include vital capacity (ERV+TV+IRV), inspiratory capacity (TV+IRV), functional residual capacity (ERV+RV), and total lung capacity (RV+ERV+TV+IRV).

Key Terms

- **tidal volume**: the amount of air breathed in or out during normal respiration
- **residual volume**: the volume of unexpended air that remains in the lungs following maximum expiration
- **spirometry**: the measurement of the volume of air that a person can move into and out of the lungs

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39.8: Gas Exchange across Respiratory Surfaces - Gas Exchange across the Alveoli

Learning Objectives

- Explain the process of gas exchange across the alveoli

Gas Exchange across the Alveoli

In the human body, oxygen is used by cells of the body's tissues to produce ATP, while carbon dioxide is produced as a waste product. The ratio of carbon dioxide production to oxygen consumption is referred to as the respiratory quotient (RQ), which typically varies between 0.7 and 1.0. If glucose alone were used to fuel the body, the RQ would equal one, as one mole of carbon dioxide would be produced for every mole of oxygen consumed. Glucose, however, is not the only fuel for the body; both proteins and fats are used as well. Since glucose, proteins, and fats are used as fuel sources, less carbon dioxide is produced than oxygen is consumed; the RQ is, on average, about 0.7 for fat and about 0.8 for protein.

The RQ is a key factor because it is used to calculate the partial pressure of oxygen in the alveolar spaces within the lung: the alveolar PO_2 ($P_{ALV}O_2$). The lungs never fully deflate with an exhalation; therefore, the inspired air mixes with this residual air, lowering the partial pressure of oxygen within the alveoli. This results in a lower concentration of oxygen in the lungs than is found in the air outside the body. When the RQ is known, the partial pressure of oxygen in the alveoli can be calculated: alveolar PO_2 = inspired PO_2–((alveolar PO_2)/RQ)

In the lungs, oxygen diffuses out of the alveoli and into the capillaries surrounding the alveoli. Oxygen (about 98 percent) binds reversibly to the respiratory pigment hemoglobin found in red blood cells. These red blood cells carry oxygen to the tissues where oxygen dissociates from the hemoglobin, diffusing into the cells of the tissues. More specifically, alveolar PO_2 is higher in the alveoli ($P_{ALV}O_2$=100mmHg) than blood PO_2 in the capillaries (40mmHg). Since this pressure gradient exists, oxygen can diffuse down its pressure gradient, moving out of the alveoli and entering the blood of the capillaries where O_2 binds to hemoglobin. At the same time, alveolar PCO_2 is lower (P_{ALV} CO_2=40mmHg) than blood PCO_2 (45mmHg). Due to this gradient, CO_2 diffuses down its pressure gradient, moving out of the capillaries and entering the alveoli.

Oxygen and carbon dioxide move independently of each other; they diffuse down their own pressure gradients. As blood leaves the lungs through the pulmonary veins, the venous PO_2=100mmHg, whereas the venous PCO_2=40mmHg. As blood enters the systemic capillaries, the blood will lose oxygen and gain carbon dioxide because of the pressure difference between the tissues and blood. In systemic capillaries, PO_2=100mmHg, but in the tissue cells, PO_2=40mmHg. This pressure gradient drives the diffusion of oxygen out of the capillaries and into the tissue cells. At the same time, blood PCO_2=40mmHg and systemic tissue PCO_2=45mmHg. The pressure gradient drives CO_2 out of tissue cells and into the capillaries. The blood returning to the lungs through the pulmonary arteries has a venous PO_2=40mmHg and a PCO_2=45mmHg. The blood enters the lung capillaries where the process of exchanging gases between the capillaries and alveoli begins again.

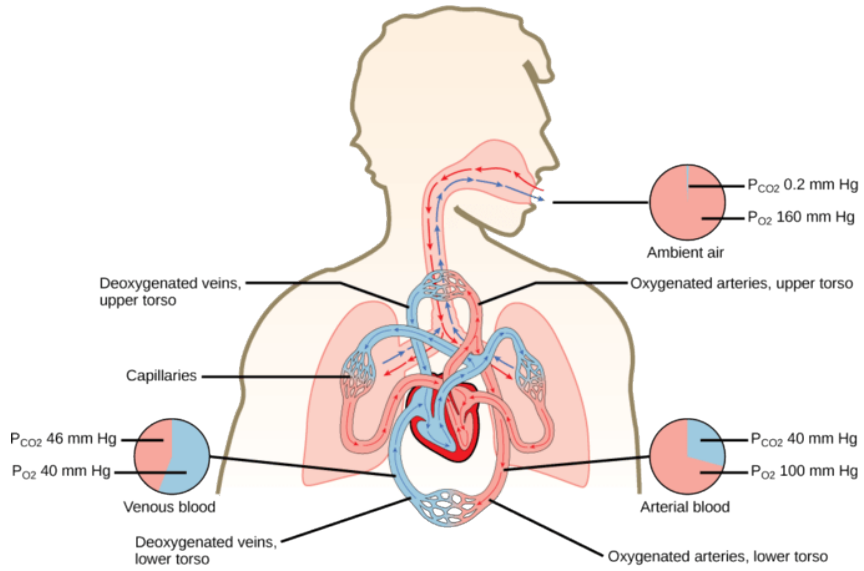


Figure 39.8.1: Partial pressures: The partial pressures of oxygen and carbon dioxide change as blood moves through the body.

In short, the change in partial pressure from the alveoli to the capillaries drives the oxygen into the tissues and the carbon dioxide into the blood from the tissues. The blood is then transported to the lungs where differences in pressure in the alveoli result in the movement of carbon dioxide out of the blood into the lungs and oxygen into the blood.

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Key Points

- The change in partial pressure from the alveoli (high concentration) to the capillaries (low concentration) drives the oxygen into the tissue and the carbon dioxide into the blood (high concentration) from the tissues (low concentration), which is then returned to the lungs and exhaled.
- Once in the blood of the capillaries, the O_2 binds to the hemoglobin in red blood cells which carry it to the tissues where it dissociates to enter the cells of the tissues.
- The lungs never fully deflate, so air that is inhaled mixes with the residual air left from the previous respiration, resulting in a lower partial pressure of oxygen within the alveoli.

Key Terms

- **hemoglobin**: iron-containing substance in red blood cells that transports oxygen from the lungs to the rest of the body; it consists of a protein (globulin) and heme (a porphyrin ring with iron at its center)
- **mole**: in the International System of Units, the base unit of amount of substance

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39.9: Breathing - The Mechanics of Human Breathing

Learning Objectives

- Describe how the structures of the lungs and thoracic cavity control the mechanics of breathing

The Mechanics of Human Breathing

The relationship between gas pressure and volume helps to explain the mechanics of breathing. Boyle's Law is the gas law which states that in a closed space, pressure and volume are inversely related. As volume decreases, pressure increases and vice versa. When discussing the detailed mechanics of breathing, it is important to keep this inverse relationship in mind.

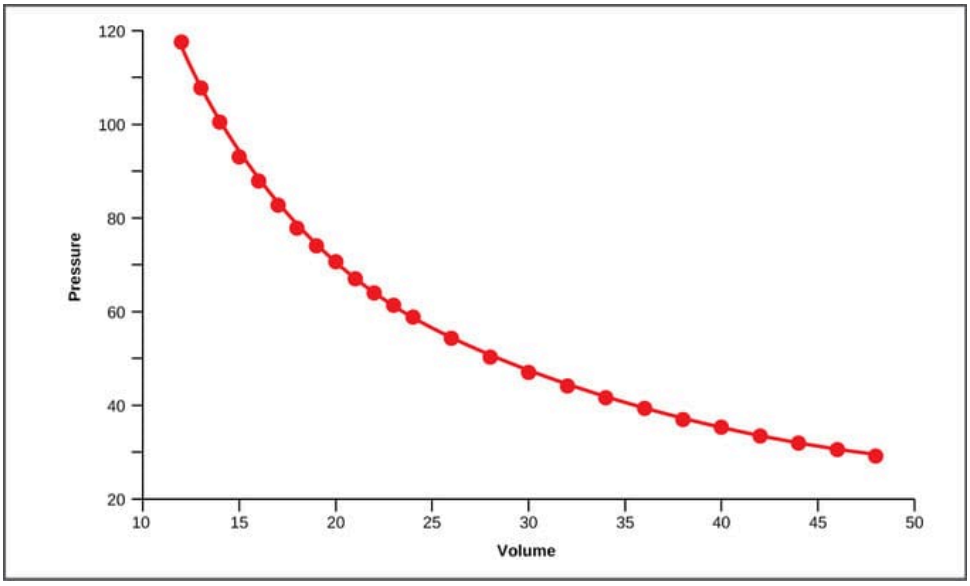


Figure 39.9.1: Boyles law: This graph of data from Boyle's original 1662 experiment shows that pressure and volume are inversely related. No units are given as Boyle used arbitrary units in his experiments.

Inhalation and Exhalation

The thoracic cavity, or chest cavity, always has a slight, negative pressure which aids in keeping the airways of the lungs open. During the process of inhalation, the lung volume expands as a result of the contraction of the diaphragm and intercostal muscles (the muscles that are connected to the rib cage), thus expanding the thoracic cavity. Due to this increase in volume, the pressure is decreased, based on the principles of Boyle's Law. This decrease of pressure in the thoracic cavity relative to the environment makes the cavity pressure less than the atmospheric pressure. This pressure gradient between the atmosphere and the thoracic cavity allows air to rush into the lungs; inhalation occurs. The resulting increase in volume is largely attributed to an increase in alveolar space because the bronchioles and bronchi are stiff structures that do not change in size.

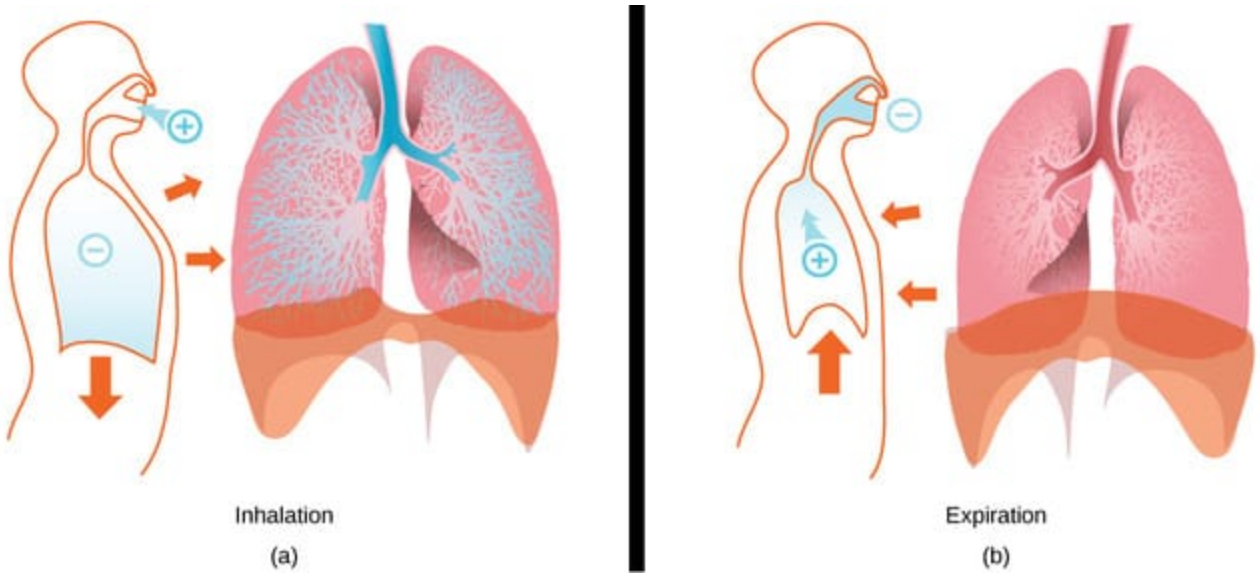


Figure 39.9.1: Inhalation and exhalation: The lungs, chest wall, and diaphragm are all involved in respiration, both (a) inhalation and (b) expiration.

During this process, the chest wall expands out and away from the lungs. The lungs are elastic; therefore, when air fills the lungs, the elastic recoil within the tissues of the lung exerts pressure back toward the interior of the lungs. These outward and inward forces compete to inflate and deflate the lung with every breath. Upon exhalation, the lungs recoil to force the air out of the lungs. The intercostal muscles relax, returning the chest wall to its original position. During exhalation, the diaphragm also relaxes, moving higher into the thoracic cavity. This increases the pressure within the thoracic cavity relative to the environment. Air rushes out of the lungs due to the pressure gradient between the thoracic cavity and the atmosphere. This movement of air out of the lungs is classified as a passive event since there are no muscles contracting to expel the air.

Protection of the Lung

Each lung is surrounded by an invaginated sac. The layer of tissue that covers the lung and dips into spaces is called the visceral pleura. A second layer of parietal pleura lines the interior of the thorax. The space between these layers, the intrapleural space, contains a small amount of fluid that protects the tissue by reducing the friction generated from rubbing the tissue layers together as the lungs contract and relax. If these layers of tissues become inflamed, this is categorized as pleurisy: a painful inflammation that increases the pressure within the thoracic cavity, reducing the volume of the lung.

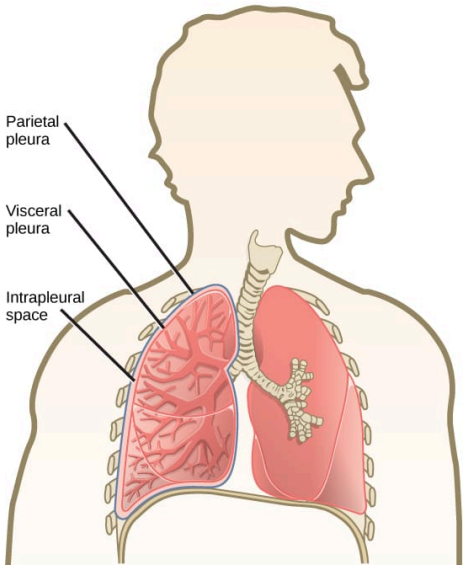


Figure 39.9.1: Visceral pleura: A tissue layer called pleura surrounds the lung and interior of the thoracic cavity.

Key Points

- The mechanics of breathing follow Boyle's Law which states that pressure and volume have an inverse relationship.
- The process of inhalation occurs due to an increase in the lung volume (diaphragm contraction and chest wall expansion) which results in a decrease in lung pressure in comparison to the atmosphere; thus, air rushes in the airway.
- The process of exhalation occurs due to an elastic recoil of the lung tissue which causes a decrease in volume, resulting in increased pressure in comparison to the atmosphere; thus, air rushes out of the airway.
- There is no contraction of muscles during exhalation; it is considered a passive process.
- The lung is protected by layers of tissue referred to as the visceral pleura and parietal pleura; the intrapleural space contains a small amount of fluid that protects the tissue by reducing friction.

Key Terms

- **visceral pleura**: the portion of protective tissue that is attached directly to the lungs
- **parietal pleura**: the portion of the protective tissue that lines the inner surface of the chest wall and covers the diaphragm

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39.10: Breathing - Types of Breathing

Learning Objectives

- Differentiate among the types of breathing in humans, amphibians, and birds

Types of Breathing

There are different types, or modes, of breathing that require a slightly different process to allow inspiration and expiration. All mammals have lungs that are the main organs for breathing. Lung capacity has evolved to support the animal's activities. During inhalation, the lungs expand with air and oxygen diffuses across the lung's surface, entering the bloodstream. During exhalation, the lungs expel air and lung volume decreases. The various types of breathing, specifically in humans, include:

1) Eupnea: a mode of breathing that occurs at rest and does not require the cognitive thought of the individual. During eupnea, also referred to as quiet breathing, the diaphragm and external intercostals must contract.

2) Diaphragmatic breathing: a mode of breathing that requires the diaphragm to contract. As the diaphragm relaxes, air passively leaves the lungs. This type of breathing is also known as deep breathing.

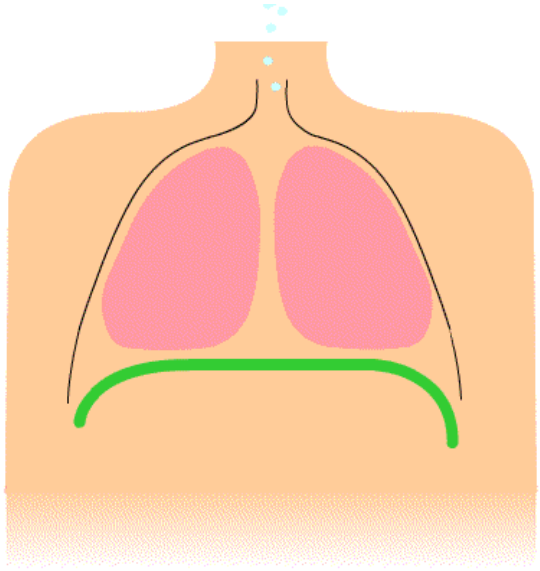


Figure 39.10.1: Diaphragmatic breathing: Animation of a diaphragm exhaling and inhaling, demonstrating diaphragmatic breathing. During inhalation, the diaphragm is contracted which increases the volume of the lung cavity. During exhalation, the diaphragm is relaxed which decreases the volume of the lung cavity.

3) Costal breathing: a mode of breathing that requires contraction of the intercostal muscles. As the intercostal muscles relax, air passively leaves the lungs. This type of breathing is also known as shallow breathing.

4) Hyperpnea: a mode of breathing that can occur during exercise or actions that require the active manipulation of breathing, such as singing. During hyperpnea, also known as forced breathing, inspiration and expiration both occur due to muscle contractions. In addition to the contraction of the diaphragm and intercostal muscles, other accessory muscles must also contract. During forced inspiration, muscles of the neck, including the scalenes, contract and lift the thoracic wall, increasing lung volume. During forced expiration, accessory muscles of the abdomen, including the obliques, contract, forcing abdominal organs upward against the diaphragm. This helps to push the diaphragm further into the thorax, pushing more air out. In addition, accessory muscles (primarily the internal intercostals) help to compress the rib cage, which also reduces the volume of the thoracic cavity.

Types of Breathing in Amphibians and Birds

In animals such as amphibians, there have been multiple ways of breathing that have evolved. In young amphibians, such as tadpoles that do not leave the water, gills are used to breathe. There are some amphibians that retain gills for life. As the tadpole grows, the gills disappear and lungs grow. These lungs are primitive and not as evolved as mammalian lungs. Adult amphibians are lacking or have a reduced diaphragm, so breathing via lungs is forced. The other means of breathing for amphibians is diffusion across the skin. To aid this diffusion, amphibian skin must remain moist.

Other animals, such as birds, must face a unique challenge with respect to breathing, which is that they fly. Flying consumes a large amount of energy; therefore, birds require a lot of oxygen to aid their metabolic processes. They have evolved a respiratory system that supplies them with the oxygen needed to enable flying. Similar to mammals, birds have lungs, which are organs specialized for gas exchange. Oxygenated air, taken in during inhalation, diffuses across the surface of the lungs into the bloodstream, while carbon dioxide diffuses from the blood into the lungs and is expelled during exhalation. However, the details of breathing between birds and mammals differ substantially.

In addition to lungs, birds have air sacs inside their body that are attached to the lungs. Air flows in one direction from the posterior air sacs to the lungs and out of the anterior air sacs. The flow of air is in the opposite direction from blood flow, which allows efficient gas exchange. This type of breathing enables birds to obtain the requisite oxygen, even at higher altitudes where the oxygen concentration is low. This directionality of airflow requires two cycles of air intake and exhalation to completely remove the air from the lungs.

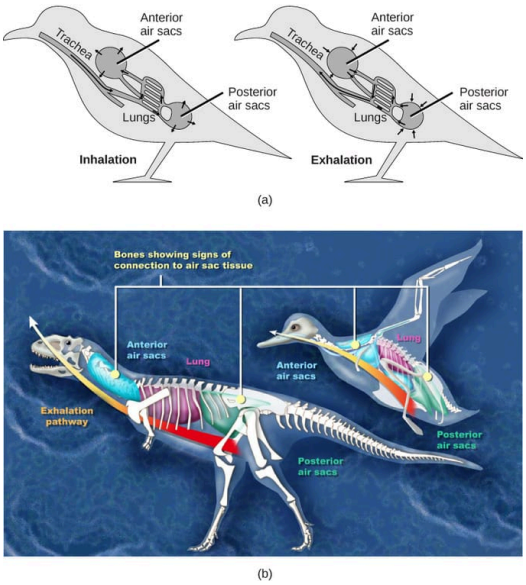


Figure 39.10.1: Avian respiratory system: (a) Birds have a flow-through respiratory system in which air flows unidirectionally from the posterior sacs into the lungs, then into the anterior air sacs. The air sacs connect to openings in hollow bones. (b) Dinosaurs, from which birds descended, have similar hollow bones and are believed to have had a similar respiratory system.

Key Points

- Eupnea is normal quiet breathing that requires contraction of the diaphragm and external intercostal muscles.
- Diaphragmatic breathing requires contraction of the diaphragm and is also called deep breathing.
- Costal breathing requires contraction of the intercostal muscles and is also called shallow breathing.
- Hyperpnea is forced breathing and requires muscle contractions during both inspiration and expiration such as contraction of the diaphragm, intercostal muscles, and accessory muscles.
- Amphibians utilize gills for breathing early in life and later develop primitive lungs in their adult life; additionally, they are able to breathe through their skin.
- Birds have evolved a directional respiratory system that allows them to obtain oxygen at high altitudes: air flows in one direction while blood flows in another, allowing efficient gas exchange.

Key Terms

- **eupnea**: normal, relaxed breathing; healthy condition of inhalation and exhalation
- **hyperpnea**: deep and rapid respiration that occurs normally after exercise or abnormally with fever or various disorders
- **intercostal**: between the ribs of an animal or person

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39.11: Breathing - The Work of Breathing

Learning Objectives

- Explain the roles played by surfactant, flow-resistive and elastic work, and lung resistance and compliance in breathing

The Work of Breathing

The number of breaths per minute is the respiratory rate; under non-exertion conditions, the human respiratory rate averages around 12–15 breaths/minute. The respiratory rate contributes to the alveolar ventilation, or how much air moves into and out of the alveoli, which prevents carbon dioxide buildup in the alveoli. There are two ways to keep the alveolar ventilation constant: increase the respiratory rate while decreasing the tidal volume of air per breath (shallow breathing), or decrease the respiratory rate while increasing the tidal volume per breath. In either case, the ventilation remains the same, but the work done and type of work needed are quite different. Both tidal volume and respiratory rate are closely regulated when oxygen demand increases.

There are two types of work conducted during respiration: flow-resistive and elastic work. Flow-resistive work refers to the work of the alveoli and tissues in the lung, whereas elastic work refers to the work of the intercostal muscles, chest wall, and diaphragm. When the respiratory rate is increased, the flow-resistive work of the airways is increased and the elastic work of the muscles is decreased. When the respiratory rate is decreased, the flow-resistive work is decreased and the elastic work is increased.

Surfactant

The air-tissue/water interface of the alveoli has a high surface tension, which is similar to the surface tension of water at the liquid-air interface of a water droplet that results in the bonding of the water molecules together. Surfactant is a complex mixture of phospholipids and lipoproteins that works to reduce the surface tension that exists between the alveoli tissue and the air found within the alveoli. By lowering the surface tension of the alveolar fluid, it reduces the tendency of alveoli to collapse.

Surfactant works like a detergent to reduce the surface tension, allowing for easier inflation of the airways. When a balloon is first inflated, it takes a large amount of effort to stretch the plastic and start to inflate the balloon. If a little bit of detergent were applied to the interior of the balloon, then the amount of effort or work needed to begin to inflate the balloon would decrease; it would become much easier. This same principle applies to the airways. A small amount of surfactant on the airway tissues reduces the effort or work needed to inflate those airways and is also important for preventing collapse of small alveoli relative to large alveoli. Sometimes, in babies that are born prematurely, there is lack of surfactant production; as a result, they suffer from respiratory distress syndrome and require more effort to inflate the lungs.

Lung Resistance and Compliance

In pulmonary diseases, the rate of gas exchange into and out of the lungs is reduced. Two main causes of decreased gas exchange are compliance (how elastic the lung is) and resistance (how much obstruction exists in the airways). A change in either can dramatically alter breathing and the ability to take in oxygen and release carbon dioxide.

Examples of restrictive diseases are respiratory distress syndrome and pulmonary fibrosis. In both diseases, the airways are less compliant and stiff or fibrotic, resulting in a decrease in compliance because the lung tissue cannot bend and move. In these types of restrictive diseases, the intrapleural pressure is more positive and the airways collapse upon exhalation, which traps air in the lungs. Forced or functional vital capacity (FVC), which is the amount of air that can be forcibly exhaled after taking the deepest breath possible, is much lower than in normal patients; the time it takes to exhale most of the air is greatly prolonged. A patient suffering from these diseases cannot exhale the normal amount of air.

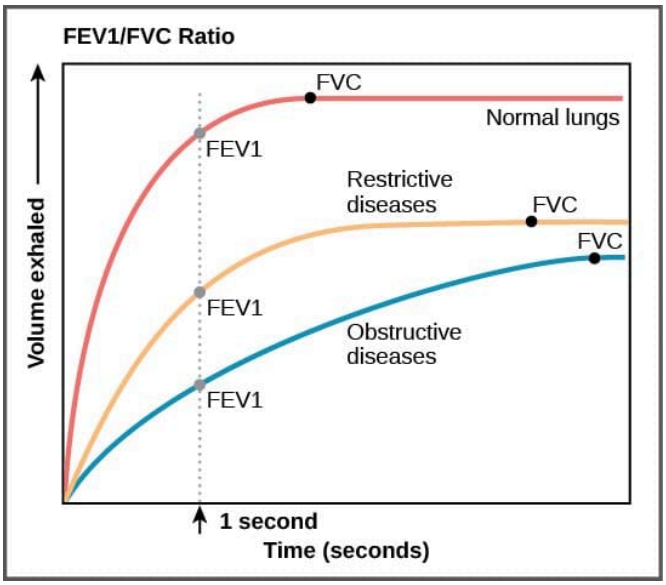


Figure 39.11.1: FEV1/FVC ratio: The ratio of FEV1 (the amount of air that can be forcibly exhaled in one second after taking a deep breath) to FVC (the total amount of air that can be forcibly exhaled) can be used to diagnose whether a person has restrictive or obstructive lung disease.

Obstructive diseases and conditions include emphysema, asthma, and pulmonary edema. In emphysema, which mostly arises from smoking tobacco, the walls of the alveoli are destroyed, decreasing the surface area for gas exchange. The overall compliance of the lungs is increased, because as the alveolar walls are damaged, lung elastic recoil decreases due to a loss of elastic fibers; more air is trapped in the lungs at the end of exhalation. Asthma is a disease in which inflammation is triggered by environmental factors, obstructing the airways. The obstruction may be due to edema, smooth muscle spasms in the walls of the bronchioles, increased mucus secretion, damage to the epithelia of the airways, or a combination of these events. Those with asthma or edema experience increased occlusion from increased inflammation of the airways. This tends to block the airways, preventing the proper movement of gases. Those with obstructive diseases have large volumes of air trapped after exhalation. They breathe at a very high lung volume to compensate for the lack of airway recruitment.

Key Points

- Both flow-resistive and elastic work are conducted during the act of respiration; flow-resistive work involves the alveoli and tissues, while elastic work involves the intercostal muscles, chest wall, and diaphragm.
- These types of work function in an inverse relationship; for example, increasing the rate of respiration results in an increase in the flow-resistive work and a decrease in the elastic work.
- Surfactant is a phospholipid and lipoprotein substance produced in the lungs that functions similarly to a detergent: it reduces the surface tension between alveoli tissue and air within the alveoli, thereby reducing the work needed for airway inflation.
- Lung resistance plays a key role in the ability to efficiently exchange gases; if there is obstruction (resistance) within the airways, the result will be decreased gas exchange.
- Lung compliance plays a key role in the ability to efficiently exchange gases; if there is too much of an increase or decrease in elasticity of the lung, the result will be disruption of gas exchange, which will cause obstructive or restrictive diseases.

Key Terms

- **surfactant**: a lipoprotein in the tissues of the lung that reduces surface tension and permits more efficient gas transport
- **tidal volume**: the amount of air breathed in or out during normal respiration

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39.12: Breathing - Dead Space- V/Q Mismatch

Learning Objectives

- Compare and contrast anatomical and physiological dead space and their role in V/Q mismatch

Dead Space: V/Q Mismatch

The pulmonary circulation pressure is very low compared to that of the systemic circulation; it is also independent of cardiac output. Recruitment is the process of opening airways that normally remain closed when cardiac output increases. As cardiac output increases, the number of capillaries and arteries that are perfused (filled with blood) increases. These capillaries and arteries are not always in use, but are ready if needed. However, at times, there is a mismatch between the amount of air (ventilation, V) and the amount of blood (perfusion, Q) in the lungs. This is referred to as ventilation/perfusion (V/Q) mismatch.

There are two types of V/Q mismatch that produce dead space. Dead space is characterized by regions of broken down or blocked lung tissue. Dead spaces can severely impact breathing due to the reduction in surface area available for gas diffusion. As a result, the amount of oxygen in the blood decreases, whereas the carbon dioxide level increases. Dead space is created when no ventilation and/or perfusion takes place. Anatomical dead space, or anatomical shunt, arises from an anatomical failure, while physiological dead space, or physiological shunt, arises from a functional impairment of the lung or arteries.

An example of an anatomical shunt is the effect of gravity on the lungs. The lung is particularly susceptible to changes in the magnitude and direction of gravitational forces. When someone is standing or sitting upright, the pleural pressure gradient leads to increased ventilation further down in the lung. As a result, the intrapleural pressure is more negative at the base of the lung than at the top; more air fills the bottom of the lung than the top. Likewise, it takes less energy to pump blood to the bottom of the lung than to the top when in a prone position (lying down). Perfusion of the lung is not uniform while standing or sitting. This is a result of hydrostatic forces combined with the effect of airway pressure. An anatomical shunt develops because the ventilation of the airways does not match the perfusion of the arteries surrounding those airways. As a result, the rate of gas exchange is reduced. Note that this does not occur when lying down because in this position, gravity does not preferentially pull the bottom of the lung down. When a healthy individual stands up quickly after lying down for a while, both ventilation and perfusion increase.

A physiological shunt can develop if there is infection or edema in the lung that obstructs an area. This will decrease ventilation but not affect perfusion; therefore, the V/Q ratio changes and gas exchange is affected.

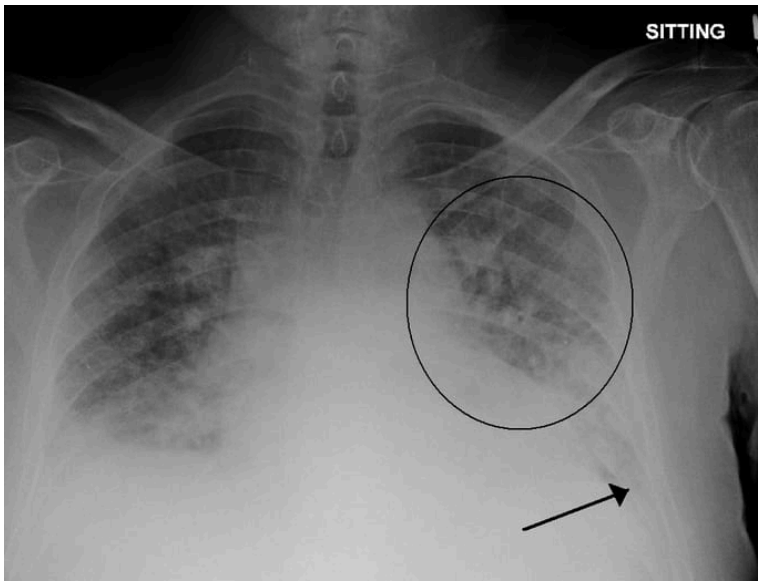


Figure 39.12.1: Pulmonary edema: A physiological shunt can develop if there is infection or edema in the lung which decreases ventilation, but does not affect perfusion; thus, the ventilation/perfusion ratio is affected. Pulmonary edema with small pleural effusions on both sides (as shown) can cause changes in the V/Q ratio.

The lung has the capability to compensate for mismatches in ventilation and perfusion. If ventilation is greater than perfusion, the arterioles dilate and the bronchioles constrict, increasing perfusion while reducing ventilation. Likewise, if ventilation is less than perfusion, the arterioles constrict while the bronchioles dilate to correct the imbalance.

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Key Points

- At times, there is a mismatch between the amount of air (ventilation, V) and the amount of blood (perfusion, Q) in the lungs, referred to as ventilation/perfusion (V/Q) mismatch.
- The two major types of V/Q mismatch that result in dead space include: anatomical dead space (caused by an anatomical issue) and physiological dead space (caused by a functional issue with the lung or arteries).
- Anatomical dead space can occur due to changes in gravity (i.e. posture positions: sitting, standing, lying); it will affect both ventilation (V) and perfusion (Q).
- Physiological dead space can occur due to changes in function, such as in cases of infection of the lung; it will typically affect

ventilation if the infection is in the lung and will affect perfusion if the functional impairment is in the arteries.
- In a normal, healthy individual, changes in either ventilation or perfusion will result in correction of the other factor to ensure an appropriate V/Q ratio.

Key Terms

- **perfuse**: to force a fluid to flow over or through something, especially through an organ of the body
- **dead space**: air that is inhaled by the body in breathing, but does not partake in gas exchange
- **hydrostatic**: of or relating to fluids, especially to the pressure that they exert or transmit
- **pulmonary circulation**: the part of blood circulation which carries oxygen-depleted blood away from the heart, to the lungs, and returns oxygenated blood back to the heart
- **systemic circulation**: the part of blood circulation which carries oxygenated blood away from the heart, to the body, and returns deoxygenated blood back to the heart

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39.13: Transport of Gases in Human Bodily Fluids - Transport of Oxygen in the Blood

Learning Objectives

- Describe how oxygen is bound to hemoglobin and transported to body tissues

Transport of Oxygen in the Blood

Although oxygen dissolves in blood, only a small amount of oxygen is transported this way. Only 1.5 percent of oxygen in the blood is dissolved directly into the blood itself. Most oxygen, 98.5 percent, is bound to a protein called hemoglobin and carried to the tissues.

Hemoglobin

Hemoglobin, or Hb, is a protein molecule found in red blood cells (erythrocytes) made of four subunits: two alpha subunits and two beta subunits. Each subunit surrounds a central heme group that contains iron and binds one oxygen molecule, allowing each hemoglobin molecule to bind four oxygen molecules. Molecules with more oxygen bound to the heme groups are brighter red. As a result, oxygenated arterial blood where the Hb is carrying four oxygen molecules is bright red, while venous blood that is deoxygenated is darker red.

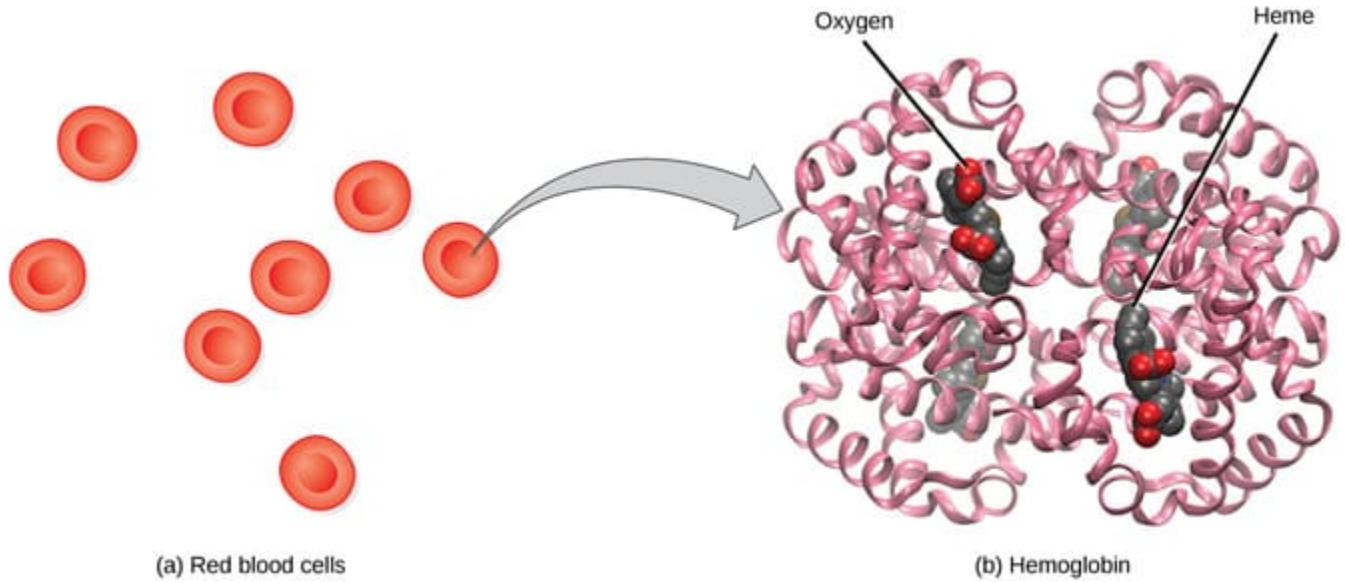


Figure 39.13.1: Hemoglobin: The protein inside red blood cells (a) that carries oxygen to cells and carbon dioxide to the lungs is hemoglobin (b). Hemoglobin is made up of four symmetrical subunits and four heme groups. Iron associated with the heme binds oxygen. It is the iron in hemoglobin that gives blood its red color.

It is easier to bind a second and third oxygen molecule to Hb than the first molecule. This is because the hemoglobin molecule changes its shape, or conformation, as oxygen binds. The fourth oxygen is then more difficult to bind. The binding of oxygen to hemoglobin can be plotted as a function of the partial pressure of oxygen in the blood (x-axis) versus the relative Hb-oxygen saturation (y-axis). The resulting graph, an oxygen dissociation curve, is sigmoidal, or S-shaped. As the partial pressure of oxygen increases, the hemoglobin becomes increasingly saturated with oxygen.

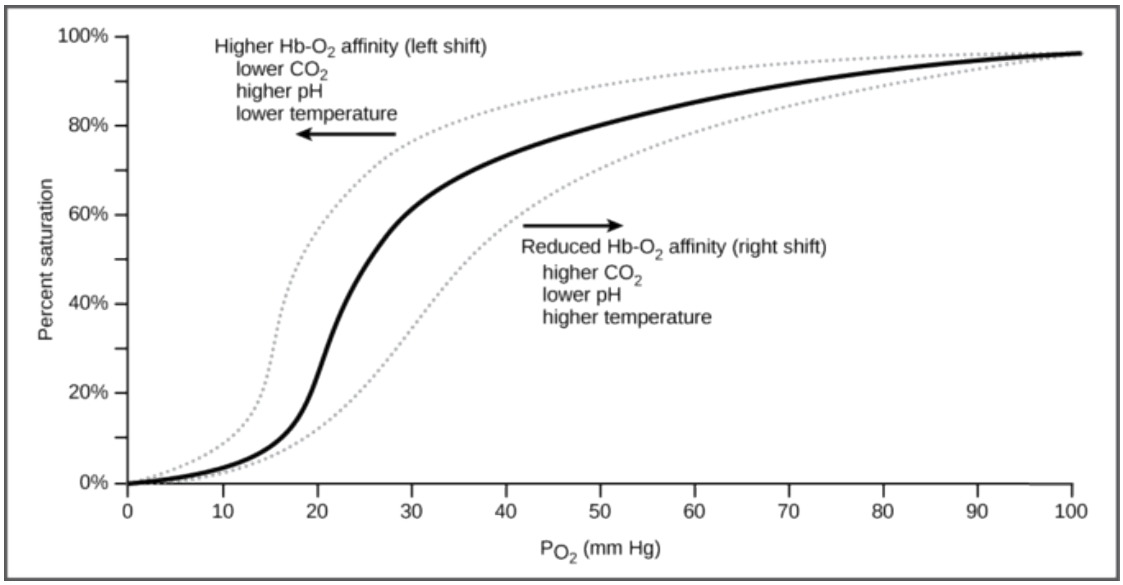


Figure 39.13.1: Oxygen dissociation curve: The oxygen dissociation curve demonstrates that as the partial pressure of oxygen increases, more oxygen binds hemoglobin. However, the affinity of hemoglobin for oxygen may shift to the left or the right depending on environmental conditions.

Factors That Affect Oxygen Binding

The oxygen-carrying capacity of hemoglobin determines how much oxygen is carried in the blood. In addition, other environmental factors and diseases can also affect oxygen-carrying capacity and delivery; the same is true for carbon dioxide levels, blood pH, and body temperature. When carbon dioxide is in the blood, it reacts with water to form bicarbonate (HCO_3^-) and hydrogen ions (H^+). As the level of carbon dioxide in the blood increases, more H^+ is produced and the pH decreases. The increase in carbon dioxide and subsequent decrease in pH reduce the affinity of hemoglobin for oxygen. The oxygen dissociates from the Hb molecule, shifting the oxygen dissociation curve to the right. Therefore, more oxygen is needed to reach the same hemoglobin saturation level as when the pH was higher. A similar shift in the curve also results from an increase in body temperature. Increased temperature, such as from increased activity of skeletal muscle, causes the affinity of hemoglobin for oxygen to be reduced.

Diseases such as sickle cell anemia and thalassemia decrease the blood's ability to deliver oxygen to tissues and its oxygen-carrying capacity. In sickle cell anemia, the shape of the red blood cell is crescent-shaped, elongated, and stiffened, reducing its ability to deliver oxygen. In this form, red blood cells cannot pass through the capillaries. This is painful when it occurs. Thalassemia is a rare genetic disease caused by a defect in either the alpha or the beta subunit of Hb. Patients with thalassemia produce a high number of red blood cells, but these cells have lower-than-normal levels of hemoglobin. Therefore, the oxygen-carrying capacity is diminished.

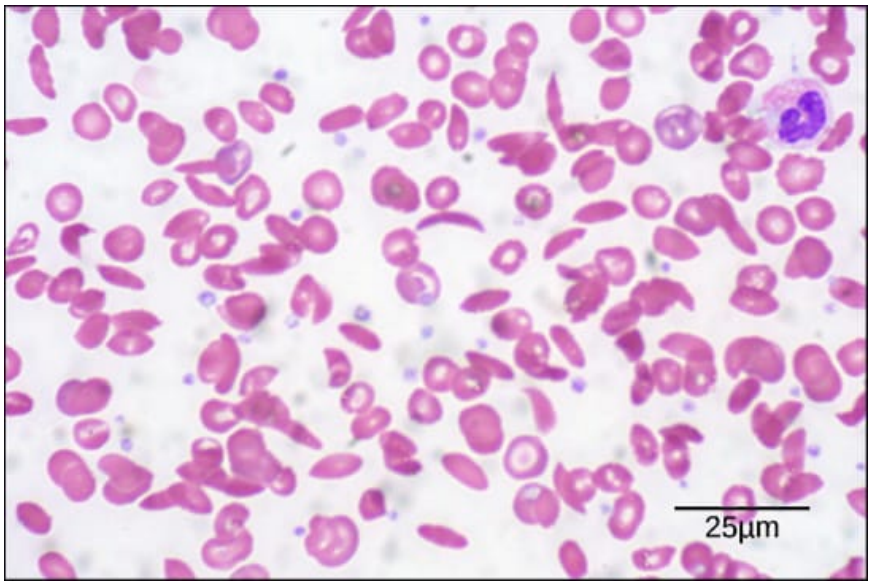


Figure 39.13.1: Sickle cell anemia: Individuals with sickle cell anemia have crescent-shaped red blood cells. Diseases such as this one cause a decreased ability in oxygen delivery throughout the body.

Key Points

- Hemoglobin is made up of four subunits and can bind up to four oxygen molecules.
- Carbon dioxide levels, blood pH, body temperature, environmental factors, and diseases can all affect oxygen's carrying capacity and delivery.
- A decrease in the oxygen-carrying ability of hemoglobin is observed with an increase in carbon dioxide and temperature, as well as a decrease in pH within the body.
- Sickle cell anemia and thalassemia are two hereditary diseases that decrease the blood's oxygen-carrying capacity.

Key Terms

- **thalassemia**: an inherited disorder in which the person produces a high number of red blood cells, but the cells have lower levels of hemoglobin
- **sickle cell anemia**: a hereditary blood disorder, characterized by red blood cells that assume an abnormal, rigid, sickle shape
- **heme**: the component of hemoglobin responsible for binding oxygen; consists of an iron ion that binds oxygen and a porphyrin ring that binds the globin molecules; one molecule binds one molecule of oxygen

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39.14: Transport of Gases in Human Bodily Fluids - Transport of Carbon Dioxide in the Blood

Learning Objectives

- Explain how carbon dioxide is transported from body tissues to the lungs

Transport of Carbon Dioxide in the Blood

Carbon dioxide molecules are transported in the blood from body tissues to the lungs by one of three methods:

1. Dissolution directly into the blood
2. Binding to hemoglobin
3. Carried as a bicarbonate ion

Several properties of carbon dioxide in the blood affect its transport. First, carbon dioxide is more soluble in blood than is oxygen. About 5 to 7 percent of all carbon dioxide is dissolved in the plasma. Second, carbon dioxide can bind to plasma proteins or can enter red blood cells and bind to hemoglobin. This form transports about 10 percent of the carbon dioxide. When carbon dioxide binds to hemoglobin, a molecule called carbaminohemoglobin is formed. Binding of carbon dioxide to hemoglobin is reversible. Therefore, when it reaches the lungs, the carbon dioxide can freely dissociate from the hemoglobin and be expelled from the body.

Third, the majority of carbon dioxide molecules (85 percent) are carried as part of the bicarbonate buffer system. In this system, carbon dioxide diffuses into the red blood cells. Carbonic anhydrase (CA) within the red blood cells quickly converts the carbon dioxide into carbonic acid (H_2CO_3). Carbonic acid is an unstable, intermediate molecule that immediately dissociates into bicarbonate ions (HCO_3^-) and hydrogen (H^+) ions. Since carbon dioxide is quickly converted into bicarbonate ions, this reaction allows for the continued uptake of carbon dioxide into the blood, down its concentration gradient. It also results in the production of H^+ ions. If too much H^+ is produced, it can alter blood pH. However, hemoglobin binds to the free H^+ ions, limiting shifts in pH. The newly-synthesized bicarbonate ion is transported out of the red blood cell into the liquid component of the blood in exchange for a chloride ion (Cl-); this is called the chloride shift. When the blood reaches the lungs, the bicarbonate ion is transported back into the red blood cell in exchange for the chloride ion. The H^+ ion dissociates from the hemoglobin and binds to the bicarbonate ion. This produces the carbonic acid intermediate, which is converted back into carbon dioxide through the enzymatic action of CA. The carbon dioxide produced is expelled through the lungs during exhalation.

The benefit of the bicarbonate buffer system is that carbon dioxide is “soaked up” into the blood with little change to the pH of the system. This is important because it takes only a small change in the overall pH of the body for severe injury or death to result. The presence of this bicarbonate buffer system also allows for people to travel and live at high altitudes. When the partial pressure of oxygen and carbon dioxide change at high altitudes, the bicarbonate buffer system adjusts to regulate carbon dioxide while maintaining the correct pH in the body.

Carbon Monoxide Poisoning

While carbon dioxide can readily associate and dissociate from hemoglobin, other molecules, such as carbon monoxide (CO), cannot. Carbon monoxide has a greater affinity for hemoglobin than does oxygen. Therefore, when carbon monoxide is present, it binds to hemoglobin preferentially over oxygen. As a result, oxygen cannot bind to hemoglobin, so very little oxygen is transported throughout the body. Carbon monoxide is a colorless, odorless gas which is difficult to detect. It is produced by gas-powered vehicles and tools. Carbon monoxide can cause headaches, confusion, and nausea; long-term exposure can cause brain damage or death. Administering 100 percent (pure) oxygen is the usual treatment for carbon monoxide poisoning as it speeds up the separation of carbon monoxide from hemoglobin.

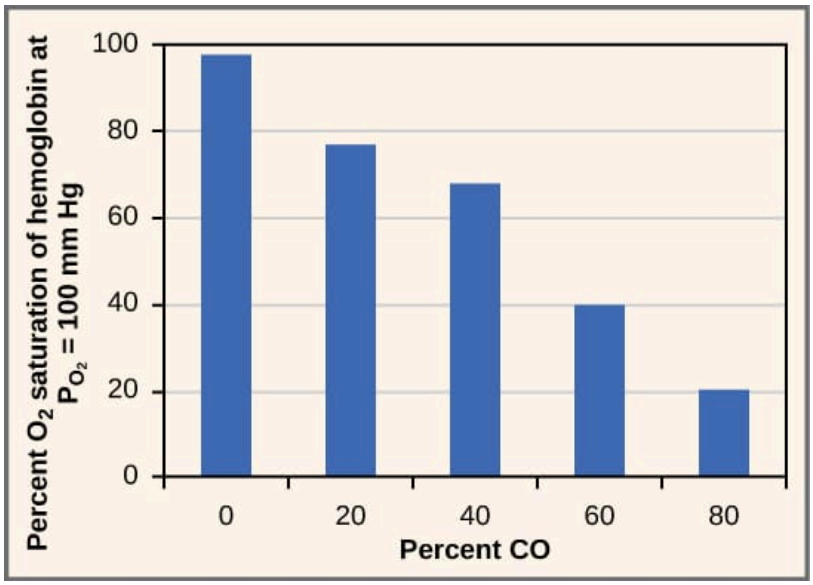


Figure 39.14.1: Carbon monoxide poisoning: When carbon monoxide (CO) in the body increases, the oxygen saturation of hemoglobin decreases since hemoglobin will bind more readily to CO than to oxygen. Therefore, CO exposure leads to death due to a decreased transportation of oxygen in the body.

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Key Points

- Carbon dioxide is more soluble in blood than is oxygen; about 5 to 7 percent of all carbon dioxide is dissolved in the plasma.
- Carbon dioxide has the ability to attach to hemoglobin molecules; it will be removed from the body once they become dissociated from one another.
- In the bicarbonate buffer system, the most common form of carbon dioxide transportation in the blood, carbon dioxide is finally expelled from the body through the lungs during exhalation.
- Importantly, the bicarbonate buffer system allows little change to the pH of the body system; it allows for people to travel and live at high altitudes because the system can adjust itself to regulate carbon dioxide while maintaining the correct pH in the body.

Key Terms

- **carbaminohemoglobin**: a compound made up of hemoglobin and carbon dioxide; one of the forms in which carbon dioxide exists in the blood
- **carbonic anhydrase**: a family of enzymes that catalyze the rapid interconversion of carbon dioxide and water to bicarbonate and protons
- **carbon monoxide**: a colorless, odourless, flammable, highly toxic gas

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40: THE CIRCULATORY SYSTEM

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40.13: Blood Flow and Blood Pressure Regulation - Blood Pressure

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40.1: Overview of the Circulatory System - The Role of the Circulatory System

Learning Objectives

- Describe the basic properties of the circulatory systems

Most animals are complex, multicellular organisms that require a mechanism for transporting nutrients throughout their bodies and for removing waste products. The circulatory system has evolved over time from simple diffusion through cells, in the early evolution of animals, to a complex network of blood vessels that reach all parts of the human body. This extensive network supplies the cells, tissues, and organs with oxygen and nutrients, while removing carbon dioxide and waste, the byproducts of respiration. The circulatory system can be thought of as a highway system that runs throughout the body.



Figure 40.1.1: Circulatory system is analogous to a highway system: Just as highway systems transport people and goods through a complex network, the circulatory system transports nutrients, gases, and wastes throughout the animal body.

At the core of the human circulatory system is the heart. The size of a clenched fist, the human heart is protected beneath the rib cage. Made of specialized and unique cardiac muscle, it pumps blood throughout the body and to the heart itself. Heart contractions are driven by intrinsic electrical impulses that the brain and endocrine hormones help to regulate. Understanding the heart's basic anatomy and function is important to understanding the body's circulatory and respiratory systems.

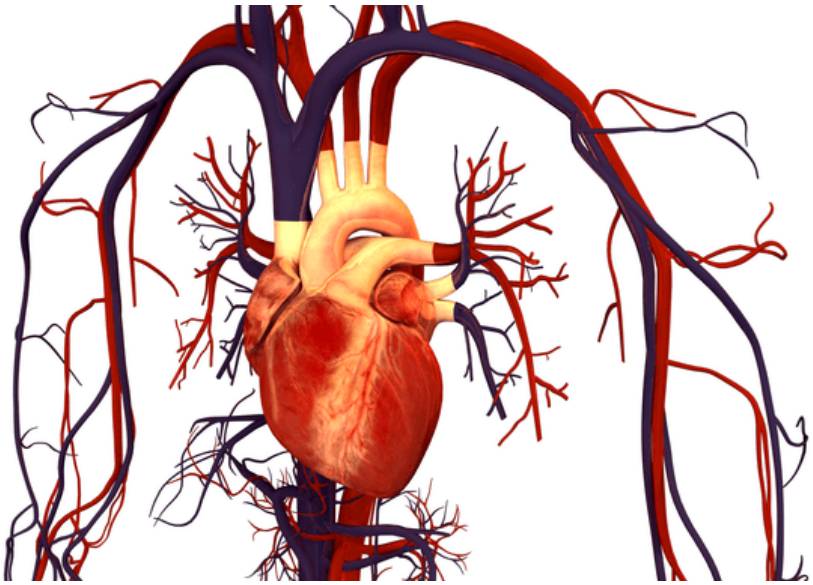


Figure 40.1.1: Human heart: The heart is central to the human circulatory system, as it pumps blood throughout the body.

Gas exchange is one essential function of the circulatory system. A circulatory system is not needed in organisms with no specialized respiratory organs, such as unicellular organisms, because oxygen and carbon dioxide diffuse directly between their body tissues and the external environment. However, in organisms that possess lungs and gills, oxygen must be transported from these specialized respiratory organs to the body tissues via a circulatory system. Therefore, circulatory systems have had to evolve to accommodate the great diversity of body sizes and body types present among animals.

Key Points

- The heart is central to the circulatory system as it is the fist-sized pump that circulates the blood throughout the body.
- As animals became more complex and multicellular, the circulatory system evolved because simple diffusion was insufficient to supply all of the cells with nutrients.
- The coordination of the circulatory system and the respiratory system to ensure proper gas exchange is very important in animals that have lungs and gills.

Key Terms

- **respiration**: the process by which cells obtain chemical energy by the consumption of oxygen and the release of carbon dioxide; the process of inhaling and exhaling; breathing
- **cardiac**: pertaining to the heart

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40.2: Overview of the Circulatory System - Open and Closed Circulatory Systems

Learning Objectives

- Summarize circulatory system architecture

Circulatory System Architecture

The circulatory system is effectively a network of cylindrical vessels (the arteries, veins, and capillaries) that emanate from a pump (the heart). In all vertebrate organisms, as well as some invertebrates, this is a closed-loop system in which the blood is not moving freely in a cavity. In a closed circulatory system, blood is contained inside blood vessels, circulating unidirectionally (in one direction) from the heart around the systemic circulatory route, then returning to the heart again.

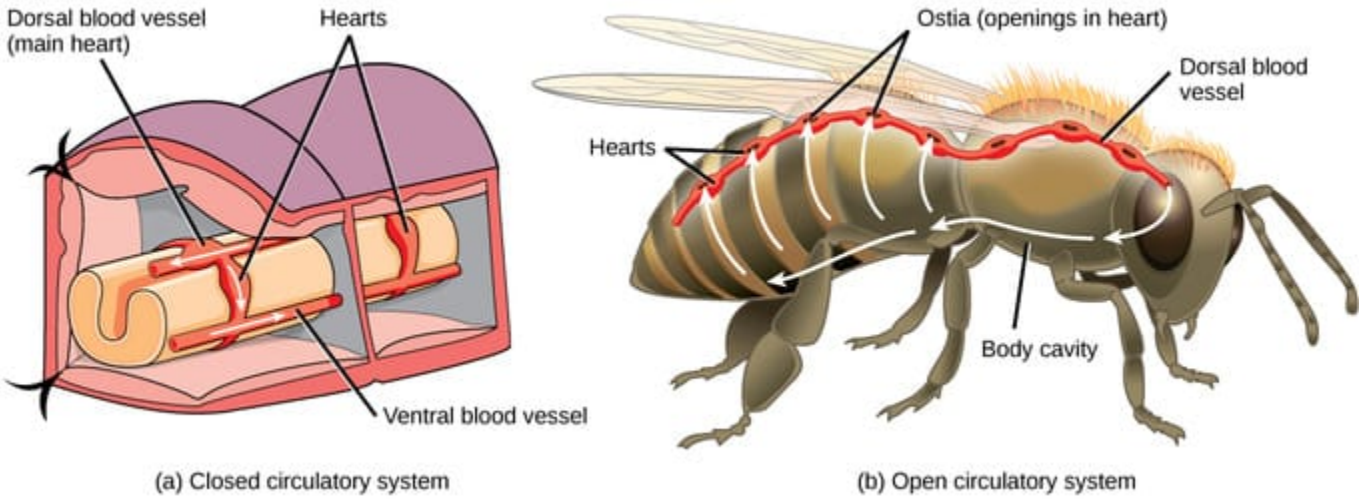


Figure 40.2.1: Closed and open circulatory systems: (a) In closed circulatory systems, the heart pumps blood through vessels that are separate from the interstitial fluid of the body. Most vertebrates and some invertebrates, such as this annelid earthworm, have a closed circulatory system. (b) In open circulatory systems, a fluid called hemolymph is pumped through a blood vessel that empties into the body cavity. Hemolymph returns to the blood vessel through openings called ostia. Arthropods, such as this bee and most mollusks, have open circulatory systems.

In contrast to a closed system, arthropods (including insects, crustaceans, and most mollusks) have an open circulatory system. In an open circulatory system, the blood is not enclosed in the blood vessels, but is pumped into a cavity called a hemocoel. The blood is called hemolymph because it mixes with the interstitial fluid. As the heart beats and the animal moves, the hemolymph circulates around the organs within the body cavity, reentering the heart through openings called ostia (singular: ostium). This movement allows for gas and nutrient exchange. An open circulatory system does not use as much energy to operate and maintain as a closed system; however, there is a trade-off with the amount of blood that can be moved to metabolically-active organs and tissues that require high levels of oxygen. In fact, one reason that insects with wing spans of up to two feet wide (70 cm) are not around today is probably because they were outmatched by the arrival of birds 150 million years ago. Birds, having a closed circulatory system, are thought to have moved more agilely, allowing them to obtain food faster and possibly to prey on the insects.

Key Points

- A closed circulatory system, found in all vertebrates and some invertebrates, circulates blood unidirectionally from the heart, around the body, and back to the heart.
- An open circulatory system, found in arthropods, pumps blood into a cavity called a hemocoel where it surrounds the organs

and then returns to the heart(s) through ostia (openings).
- The blood found in arthropods, a mix of blood and interstitial fluid, is called hemolymph.

Key Terms

- **ostium**: a small opening or orifice, as in a body organ or passage
- **hemolymph**: a circulating fluid in the bodies of some invertebrates that is the equivalent of blood
- **hemocoel**: the system of cavities between the organs of arthropods and mollusks through which the blood circulates

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40.3: Overview of the Circulatory System - Types of Circulatory Systems in Animals

Learning Objectives

- Describe how circulation differs between fish, amphibians, reptiles, birds, and mammals

Simple Circulatory Systems

The circulatory system varies from simple systems in invertebrates to more complex systems in vertebrates. The simplest animals, such as the sponges (Porifera) and rotifers (Rotifera), do not need a circulatory system because diffusion allows adequate exchange of water, nutrients, and waste, as well as dissolved gases (figure a). Organisms that are more complex, but still have only two layers of cells in their body plan, such as jellies (Cnidaria) and comb jellies (Ctenophora), also use diffusion through their epidermis and internally through the gastrovascular compartment. Both their internal and external tissues are bathed in an aqueous environment and exchange fluids by diffusion on both sides (figure b). Exchange of fluids is assisted by the pulsing of the jellyfish body.

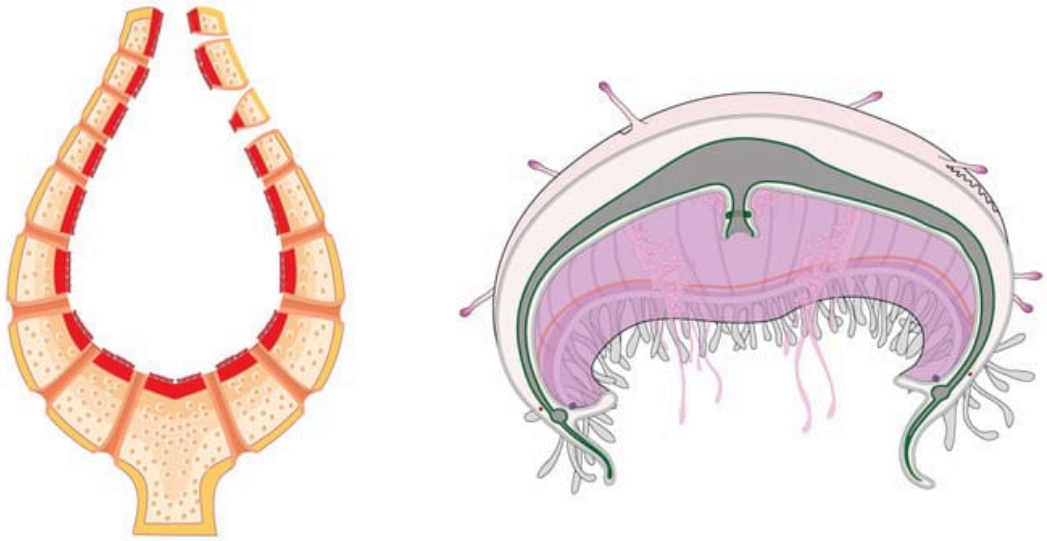


Figure 40.3.1: Animals without circulatory systems: Simple animals consisting of a single cell layer, such as the (a) sponge, or only a few cell layers, such as the (b) jellyfish, do not have a circulatory system. Instead, gases, nutrients, and wastes are exchanged by diffusion.

For more complex organisms, diffusion is not efficient for cycling gases, nutrients, and waste effectively through the body; therefore, more complex circulatory systems evolved. Closed circulatory systems are a characteristic of vertebrates; however, there are significant differences in the structure of the heart and the circulation of blood between the different vertebrate groups due to adaptation during evolution and associated differences in anatomy.

Fish Circulatory Systems

Fish have a single circuit for blood flow and a two-chambered heart that has only a single atrium and a single ventricle (figure a). The atrium collects blood that has returned from the body, while the ventricle pumps the blood to the gills where gas exchange occurs and the blood is re-oxygenated; this is called gill circulation. The blood then continues through the rest of the body before arriving back at the atrium; this is called systemic circulation. This unidirectional flow of blood produces a gradient of oxygenated to deoxygenated blood around the fish's systemic circuit. The result is a limit in the amount of oxygen that can reach some of the organs and tissues of the body, reducing the overall metabolic capacity of fish.

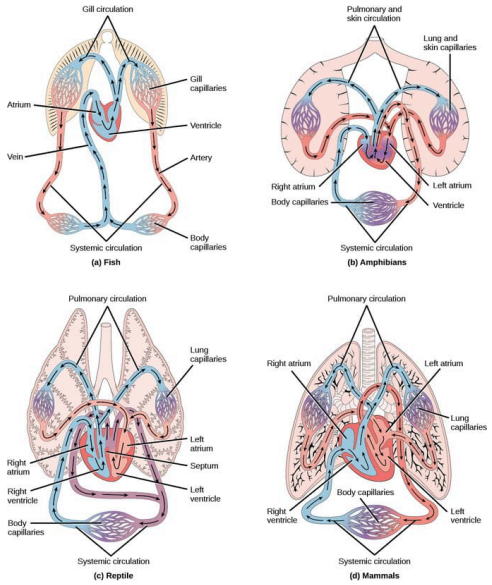


Figure 40.3.1: Examples of animal circulatory systems: (a) Fish have the simplest circulatory systems of the vertebrates: blood flows unidirectionally from the two-chambered heart through the gills and then to the rest of the body. (b) Amphibians have two circulatory routes: one for oxygenation of the blood through the lungs and skin, and the other to take oxygen to the rest of the body. The blood is pumped from a three-chambered heart with two atria and a single ventricle. (c) Reptiles also have two circulatory routes; however, blood is only oxygenated through the lungs. The heart is three chambered, but the ventricles are partially separated so some mixing of oxygenated and deoxygenated blood occurs, except in crocodilians and birds. (d) Mammals and birds have the most efficient heart with four chambers that completely separate the oxygenated and deoxygenated blood; it pumps only oxygenated blood through the body and deoxygenated blood to the lungs.

Amphibian Circulatory Systems

In amphibians, reptiles, birds, and mammals, blood flow is directed in two circuits: one through the lungs and back to the heart (pulmonary circulation) and the other throughout the rest of the body and its organs, including the brain (systemic circulation).

Amphibians have a three-chambered heart that has two atria and one ventricle rather than the two-chambered heart of fish (figure b). The two atria receive blood from the two different circuits (the lungs and the systems). There is some mixing of the blood in the heart's ventricle, which reduces the efficiency of oxygenation. The advantage to this arrangement is that high pressure in the vessels pushes blood to the lungs and body. The mixing is mitigated by a ridge within the ventricle that diverts oxygen-rich blood through the systemic circulatory system and deoxygenated blood to the pulmocutaneous circuit where gas exchange occurs in the lungs and through the skin. For this reason, amphibians are often described as having double circulation.

Reptile Circulatory Systems

Most reptiles also have a three-chambered heart similar to the amphibian heart that directs blood to the pulmonary and systemic circuits (figure c). The ventricle is divided more effectively by a partial septum, which results in less mixing of oxygenated and deoxygenated blood. Some reptiles (alligators and crocodiles) are the most primitive animals to exhibit a four-chambered heart. Crocodilians have a unique circulatory mechanism where the heart shunts blood from the lungs toward the stomach and other organs during long periods of submergence; for instance, while the animal waits for prey or stays underwater waiting for prey to rot. One adaptation includes two main arteries that leave the same part of the heart: one takes blood to the lungs and the other provides an alternate route to the stomach and other parts of the body. Two other adaptations include a hole in the heart between the two ventricles, called the foramen of Panizza, which allows blood to move from one side of the heart to the other, and specialized connective tissue that slows the blood flow to the lungs. Together, these adaptations have made crocodiles and alligators one of the most successfully-evolved animal groups on earth.

Mammal and Bird Circulatory Systems

In mammals and birds, the heart is also divided into four chambers: two atria and two ventricles (figure d). The oxygenated blood is separated from the deoxygenated blood, which improves the efficiency of double circulation and is probably required for the

warm-blooded lifestyle of mammals and birds. The four-chambered heart of birds and mammals evolved independently from a three-chambered heart.

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Key Points

- Fish have a single systemic circuit for blood, where the heart pumps the blood to the gills to be re-oxygenated (gill circulation), after which the blood flows to the rest of the body and back to the heart.
- Other animals, such as amphibians, reptiles, birds, and mammals, have a pulmonary circuit, where blood is pumped from the heart to the lungs and back, and a second, systemic circuit where blood is pumped to the body and back.
- Amphibians are unique in that they have a third circuit that brings deoxygenated blood to the skin in order for gas exchange to occur; this is called pulmocutaneous circulation.
- The number of heart chambers, atria and ventricles, mitigates the amount of mixing of oxygenated and deoxygenated blood in the heart as more chambers usually mean more separation between the systemic and pulmonary circuits.
- Warm-blooded animals require the more-efficient system of four chambers that has the oxygenated blood completely separated from the deoxygenated blood.

Key Terms

- **atrium**: an upper chamber of the heart that receives blood from the veins and forces it into a ventricle
- **ventricle**: a lower chamber of the heart

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40.4: Components of the Blood - The Role of Blood in the Body

Learning Objectives

- Identify the variety of roles played by blood in the body

The Role of Blood in the Body

Blood is a bodily fluid in animals that delivers necessary substances such as nutrients and oxygen to the cells and transports metabolic waste products away from those same cells. The components of blood include plasma (the liquid portion, which contains water, proteins, salts, lipids, and glucose), red blood cells and white blood cells, and cell fragments called platelets.

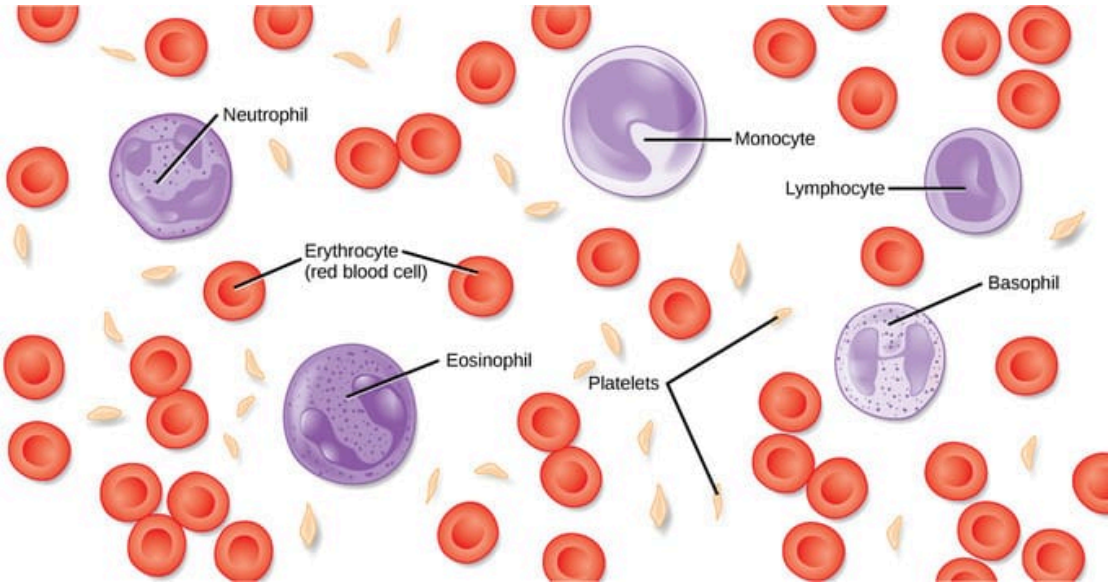


Figure 40.4.1: Components of human blood: The cells and cellular components of human blood are shown. Red blood cells deliver oxygen to the cells and remove carbon dioxide. White blood cells (including neutrophils, monocytes, lymphocytes, eosinophils, and basophils) are involved in the immune response. Platelets form clots that prevent blood loss after injury.

Blood plays an important role in regulating the body's systems and maintaining homeostasis. It performs many functions within the body, including:

- Supplying oxygen to tissues (bound to hemoglobin, which is carried in red cells)
- Supplying nutrients such as glucose, amino acids, and fatty acids either dissolved in the blood or bound to plasma proteins (e.g., blood lipids)
- Removing waste such as carbon dioxide, urea, and lactic acid
- Immunological functions, including circulation of white blood cells and detection of foreign material by antibodies
- Coagulation, which is one part of the body's self-repair mechanism (blood clotting by the platelets after an open wound in order to stop bleeding)
- Messenger functions, including the transport of hormones and the signaling of tissue damage
- Regulating body pH
- Regulating core body temperature
- Hydraulic functions, including the regulation of the colloidal osmotic pressure of blood

Medical terms related to blood often begin with hemo- or hemato- (also spelled haemo- and haemato-), which is from the Greek word α (haima) for "blood". In terms of anatomy and histology, blood is considered a specialized form of connective tissue, given

its origin in the bones.

Key Points

- Blood plays an important role in regulating the body's systems and maintaining homeostasis.
- Other functions include supplying oxygen and nutrients to tissues, removing waste, transporting hormones and other signals throughout the body, and regulating body pH and core body temperature.
- Blood is composed of plasma, red blood cells, white blood cells, and platelets.
- Blood platelets play a role in coagulation (the clotting of blood to stop bleed from an open wound); white blood cells play an important role in the immune system; red blood cells transport oxygen and carbon dioxide.
- Blood is considered a type of connective tissue because it is made in the bones.

Key Terms

- **hydraulic**: pertaining to water
- **coagulation**: the process by which blood forms solid clots
- **homeostasis**: the ability of a system or living organism to adjust its internal environment to maintain a stable equilibrium

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40.5: Components of the Blood - Red Blood Cells

Learning Objectives

- Explain the structure and function of red blood cells

Red Blood Cells

Red blood cells, or erythrocytes (erythro- = “red”; -cyte = “cell”), specialized cells that circulate through the body delivering oxygen to other cells, are formed from stem cells in the bone marrow. In mammals, red blood cells are small, biconcave cells that, at maturity, do not contain a nucleus or mitochondria; they are only 7–8 µm in size. In birds and non-avian reptiles, red blood cells contain a nucleus.

The red coloring of blood comes from the iron-containing protein hemoglobin (see [a] in) The principal job of this protein is to carry oxygen, but it transports carbon dioxide as well. Hemoglobin is packed into red blood cells at a rate of about 250 million molecules of hemoglobin per cell. Each hemoglobin molecule binds four oxygen molecules so that each red blood cell carries one billion molecules of oxygen. There are approximately 25 trillion red blood cells in the five liters of blood in the human body, which could carry up to 25 sextillion (25×10^{21}) molecules of oxygen at any time. In mammals, the lack of organelles in erythrocytes leaves more room for the hemoglobin molecules. The lack of mitochondria also prevents use of the oxygen for metabolic respiration. Only mammals have anucleated red blood cells; however, some mammals (camels, for instance) have nucleated red blood cells. The advantage of nucleated red blood cells is that these cells can undergo mitosis. Anucleated red blood cells metabolize anaerobically (without oxygen), making use of a primitive metabolic pathway to produce ATP and increase the efficiency of oxygen transport.

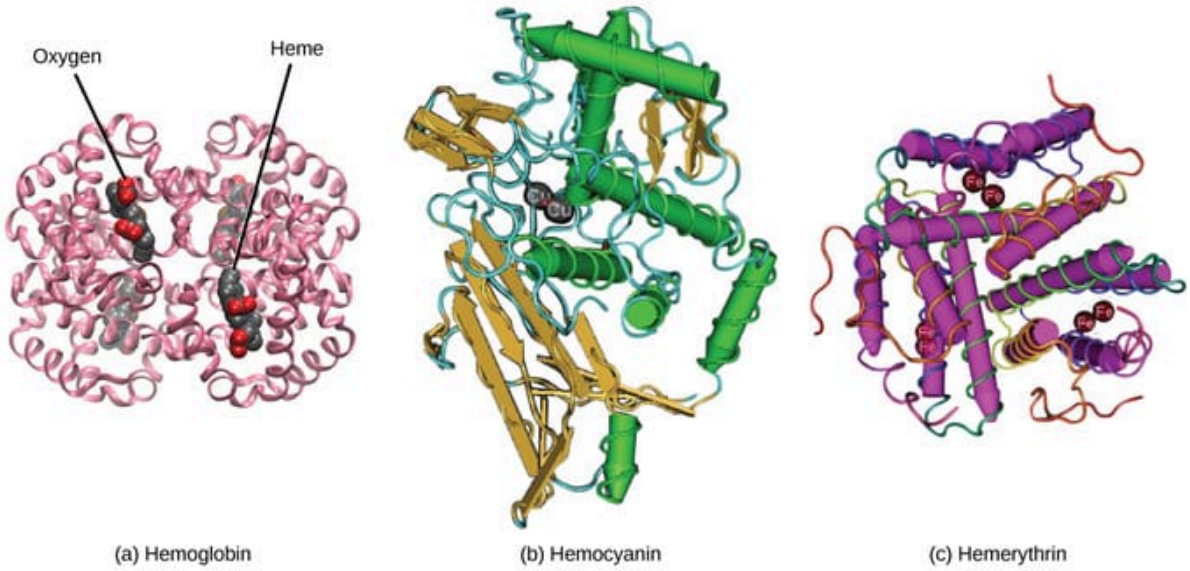


Figure 40.5.1: Different oxygen-carrying proteins: (a) In most vertebrates, hemoglobin delivers oxygen to the body and removes some carbon dioxide. Hemoglobin is composed of four protein subunits, two alpha chains and two beta chains, and a heme group that has iron associated with it. The iron reversibly associates with oxygen; in so doing, it is oxidized from Fe2+ to Fe3+. (b) In most mollusks and some arthropods, hemocyanin delivers oxygen. Unlike hemoglobin, hemolymph is not carried in blood cells, but floats free in the hemolymph. Copper, instead of iron, binds the oxygen, giving the hemolymph a blue-green color. (c) In annelids, such as the earthworm and some other invertebrates, hemerythrin carries oxygen. Like hemoglobin, hemerythrin is carried in blood cells and has iron associated with it, but despite its name, hemerythrin does not contain heme.

Not all organisms use hemoglobin as the method of oxygen transport. Invertebrates that utilize hemolymph rather than blood use different pigments containing copper or iron to bind to the oxygen. Hemocyanin, a blue-green, copper-containing protein is found in mollusks, crustaceans, and some of the arthropods (b). Chlorocruorin, a green-colored, iron-containing pigment, is found

in four families of polychaete tubeworms. Hemerythrin, a red, iron-containing protein, is found in some polychaete worms and annelids (c). Despite the name, hemerythrin does not contain a heme group; its oxygen-carrying capacity is poor compared to hemoglobin.

The small size and large surface area of red blood cells allow for rapid diffusion of oxygen and carbon dioxide across the plasma membrane. In the lungs, carbon dioxide is released while oxygen is taken in by the blood. In the tissues, oxygen is released from the blood while carbon dioxide is bound for transport back to the lungs. Studies have found that hemoglobin also binds nitrous oxide (NO). Nitrous oxide is a vasodilator: an agent that causes dilation of the blood vessels, thereby reducing blood pressure. It relaxes the blood vessels and capillaries which may help with gas exchange and the passage of red blood cells through narrow vessels. Nitroglycerin, a heart medication for angina and heart attacks, is converted to NO to help relax the blood vessels, increasiing oxygen flow throughout the body.

A characteristic of red blood cells is their glycolipid and glycoprotein coating; these are lipids and proteins that have carbohydrate molecules attached. In humans, the surface glycoproteins and glycolipids on red blood cells vary between individuals, producing the different blood types, such as A, B, and O. Red blood cells have an average life span of 120 days, at which time they are broken down and recycled in the liver and spleen by phagocytic macrophages, a type of white blood cell.

Key Points

- Red blood cells, or erythrocytes, get their color from the iron-containing protein hemoglobin that carries oxygen from the lungs to the body and carbon dioxide back to the lungs.
- In most mammals, erythrocytes do not have any organelles (e.g. nucleus, mitochondria); this frees up room for the hemoglobin molecules and prevents the cell from using the oxygen it is carrying.
- Invertebrates use different pigments, such as hemocyanin (a blue-green, copper-containing protein), chlorocruorin (a green-colored, iron-containing pigment), and hemerythrin (a red, iron-containing protein), to bind and carry oxygen.
- Red blood cells have a variety of surface glycoproteins and glycolipids that result in the different blood types A, B, and O.
- The average life span of a red blood cell is 120 days, at which time the liver and spleen break them down for recycling.

Key Terms

- **hemoglobin**: iron-containing substance in red blood cells that transports oxygen from the lungs to the rest of the body; it consists of a protein (globulin) and heme (a porphyrin ring with iron at its center)
- **hemolymph**: a circulating fluid in the bodies of some invertebrates that is the equivalent of blood
- **anucleate**: of a cell which does not have a nucleus
- **erythrocyte**: an anucleate cell in the blood involved with the transport of oxygen called a red blood cell because of the red coloring of hemoglobin

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40.6: Components of the Blood - White Blood Cells

Learning Objectives

- Explain the structure and function of white blood cells

White Blood Cells

White blood cells, also called leukocytes (leuko = white), make up approximately one percent, by volume, of the cells in blood. The role of white blood cells is very different from that of red blood cells. They are primarily involved in the immune response to identify and target pathogens, such as invading bacteria, viruses, and other foreign organisms. White blood cells are formed continually; some live only for hours or days, while some live for years.

The morphology of white blood cells differs significantly from red blood cells. They have nuclei and do not contain hemoglobin. The different types of white blood cells are identified by their microscopic appearance after histologic staining. Each has a different, specialized function. One of the two main groups are the granulocytes, which contain granules in their cytoplasm, and include the neutrophils, eosinophils, and basophils (a). The second main group is the agranulocytes, which lack granules in their cytoplasm, and include the monocytes and lymphocytes (b).



Figure 40.6.1: Types of white blood cells: (a) Granulocytes (neutrophils, eosinophils and basophils) are characterized by a lobed nucleus and granular inclusions in the cytoplasm. Granulocytes are typically first-responders during injury or infection. (b) Agranulocytes include lymphocytes and monocytes. Lymphocytes, including B and T cells, are responsible for adaptive immune response. Monocytes differentiate into macrophages and dendritic cells, which in turn respond to infection or injury.

Some white blood cells become macrophages that either stay at the same site or move through the blood stream and gather at sites of infection or inflammation where they are attracted by chemical signals from foreign particles and damaged cells. Lymphocytes are the primary cells of the immune system. They include B cells, T cells, and natural killer cells. B cells destroy bacteria and inactivate their toxins; they also produce antibodies. T cells attack viruses, fungi, some bacteria, transplanted cells, and cancer cells. Natural killer cells attack a variety of infectious microbes and certain tumor cells.

One reason that HIV poses significant management challenges is because the virus directly targets T cells by gaining entry through a receptor. Once inside the cell, HIV then multiplies using the T cell's own genetic machinery. After the HIV virus replicates, it is transmitted directly from the infected T cell to macrophages. The presence of HIV can remain unrecognized for an extensive period of time before full disease symptoms develop.

Key Points

- White blood cells contain nuclei; they can be divided into granulocytes (e.g. neutrophils, eosinophils, and basophils) and agranulocytes (e.g. monocytes and lymphocytes).
- White blood cells can become macrophages at sites of infection or inflammation or they can circulate in the bloodstream

searching for damaged tissue or foreign particles.
- Lymphocytes make up the majority of the cells in the immune system; they include B cells, T cells, and natural killer cells, all of which attack foreign particles or cells such as viruses, fungi, bacteria, transplanted cells, and cancer cells.

Key Terms

- **macrophage**: a white blood cell that phagocytizes necrotic cell debris and foreign material, including viruses, bacteria, and tattoo ink; part of the innate immune system
- **pathogen**: any organism or substance, especially a microorganism, capable of causing disease, such as bacteria, viruses, protozoa, or fungi
- **leukocyte**: a white blood cell
- **granule**: a small structure in a cell

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40.7: Components of the Blood - Platelets and Coagulation Factors

Learning Objectives

- Describe the roles played by platelets and coagulation factors

Blood must form clots to heal wounds and prevent excess blood loss. Small cell fragments called platelets (thrombocytes) are formed from the disintegration of larger cells called megakaryocytes (a). For each megakaryocyte, 2000–3000 platelets are formed with 150,000 to 400,000 platelets present in each cubic millimeter of blood. Each platelet is disc shaped and 2–4 μm in diameter. They contain many small vesicles, but do not contain a nucleus.

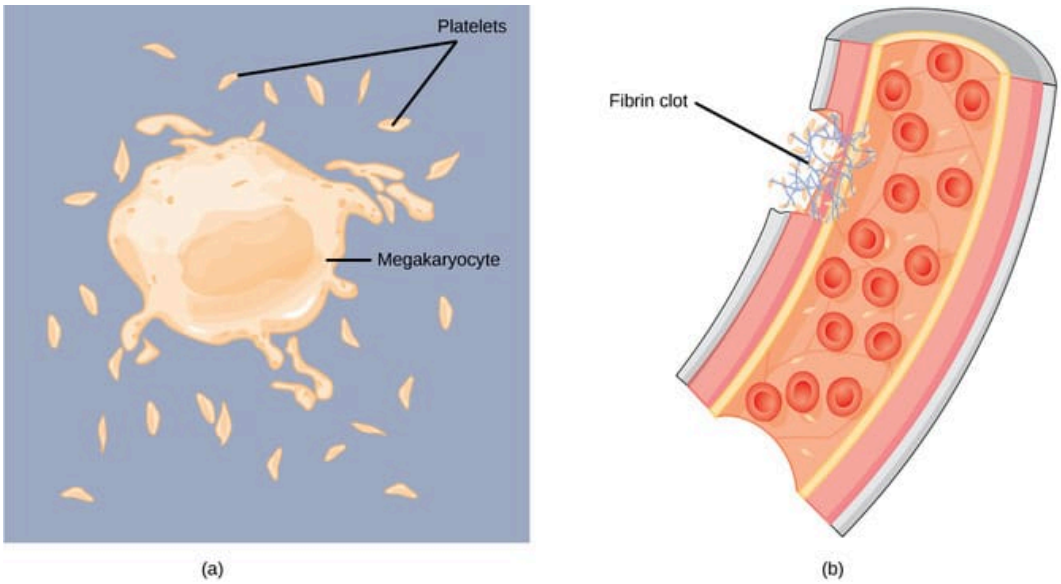


Figure 40.7.1: How platelets are made and how they work: (a) Platelets are formed from large cells called megakaryocytes. The megakaryocyte breaks up into thousands of fragments that become platelets. (b) Platelets are required for clotting of the blood. The platelets collect at a wound site in conjunction with other clotting factors, such as fibrinogen, to form a fibrin clot that prevents blood loss and allows the wound to heal.

The inner surface of blood vessels is lined with a thin layer of cells (endothelial cells) that under normal situations produce chemical messengers that inhibit platelet activation. When the endothelial layer is injured, collagen is exposed, releasing other factors to the bloodstream which attracts platelets to the wound site. When the platelets are activated, they clump together to form a platelet plug (fibrin clot) (b), releasing their contents. The released contents of the platelets activate other platelets and also interact with other coagulation factors. Coagulation factors (clotting factors) are proteins in the blood plasma that respond in a complex cascade to convert fibrinogen, a water-soluble protein present in blood serum, into fibrin, a non-water soluble protein, which strengthens the platelet plug. Many of the clotting factors require vitamin K to function. Vitamin K deficiency can lead to problems with blood clotting. The plug or clot lasts for a number of days, stopping the loss of blood.

Outside of the body, platelets can also be activated by a negatively-charged surface, such as glass. Non-physiological flow conditions (especially high values of shear stress) caused by arterial stenosis or artificial devices (e.g. mechanical heart valves or blood pumps) can also lead to platelet activation.

Key Points

- Platelets (thrombocytes) are small, anucleated cell fragments that result from the disintegration of megakaryocytes.
- Under normal conditions, blood vessel walls produce chemical messengers that inhibit platelet activation, but, when injured,

they expose collagen, releasing factors that attract platelets to the wound site.
- Activated platelets stick together to form a platelet plug, which activates coagulation factor proteins found in the blood to further enhance the response to injury by strengthening the plug with fibrin.
- Vitamin K is necessary for the proper function of many coagulation factors; a deficiency is detrimental to blood clotting.
- Platelets can become activated and form clots in situations with non-physiological flow caused by disease or artificial devices.

Key Terms

- **collagen**: Any of more than 28 types of glycoprotein that forms elongated fibers, usually found in the extracellular matrix of connective tissue.
- **clot**: a solidified mass of blood
- **stenosis**: an abnormal narrowing or stricture in a blood vessel or other tubular organ

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40.8: Components of the Blood - Plasma and Serum

Learning Objectives

- Explain the structure and function of plasma and serum

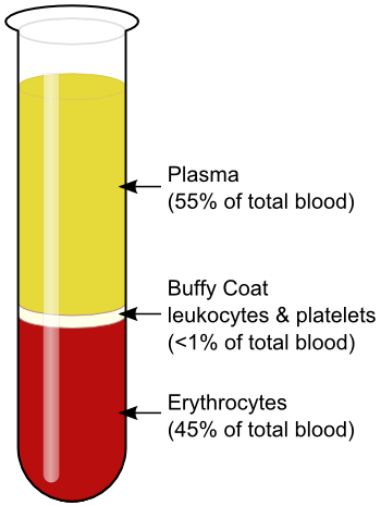


Figure 40.8.1: Blood sample after centrifugation: The liquid components of blood called plasma (yellow section) can be separated from the erythrocytes (red section) and platelets (white section) by using a centrifuging or spinning the blood.

Plasma and Serum

Plasma, the liquid component of blood, comprises 55 percent of the total blood volume. It can separated by artificially spinning or centrifuging the blood at high rotations of 3000 rpm or higher. The blood cells and platelets that make up about 45 percent of the blood are separated by centrifugal forces to the bottom of a specimen tube, leaving the plasma as the upper layer. Plasma consists of 90 percent water along with various substances required for maintaining the body's pH, osmotic load, and for protecting the body. The plasma also contains the coagulation factors and antibodies.

Serum, the plasma component of blood which lacks coagulation factors, is similar to interstitial fluid in which the correct composition of key ions acting as electrolytes is essential for normal functioning of muscles and nerves. Other components in the serum include proteins, which assist with maintaining pH and osmotic balance while giving viscosity to the blood; antibodies, or specialized proteins that are important for defense against viruses and bacteria; lipids, including cholesterol, which are transported in the serum; and various other substances including nutrients, hormones, metabolic waste, and external substances, such as drugs, viruses, and bacteria.

Human serum albumin, the most abundant protein in human blood plasma, is synthesized in the liver. Albumin, which constitutes about one-half of the blood serum protein, transports hormones and fatty acids, buffers pH, and maintains osmotic pressures. Immunoglobin, a protein antibody produced in the mucosal lining, plays an important role in antibody mediated immunity.

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Key Points

- Plasma, the liquid component of blood, comprises 55 percent of the total blood volume.
- Plasma is composed of 90 percent water with antibodies, coagulation factors, and other substances such as electrolytes, lipids, and proteins required for maintaining the body.
- The removal of coagulation factors from plasma leaves a fluid similar to interstitial fluid, known as serum.
- Albumin, a protein produced in the liver, comprises about one-half of the blood serum proteins; it functions to maintain osmotic pressures and to transport hormones and fatty acids.
- Immunoglobin is a protein antibody produced in the mucosal lining; it plays an important role in antibody mediated immunity.

Key Terms

- **interstitial fluid**: a solution found in tissue spaces that inundates and moistens cells in multicellular animals
- **electrolyte**: any of the various ions (such as sodium or chloride) that regulate the electric charge on cells and the flow of water across their membranes
- **viscosity**: a quantity expressing the magnitude of internal friction in a fluid, as measured by the force per unit area resisting uniform flow

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40.9: Mammalian Heart and Blood Vessels - Structures of the Heart

Learning Objectives

- Diagram the anatomical structure of the heart

Structure of the Heart

The heart is a complex muscle that pumps blood through the three divisions of the circulatory system: the coronary (vessels that serve the heart), pulmonary (heart and lungs), and systemic (systems of the body). Coronary circulation intrinsic to the heart takes blood directly from the main artery (aorta) coming from the heart. For pulmonary and systemic circulation, the heart has to pump blood to the lungs or the rest of the body, respectively.

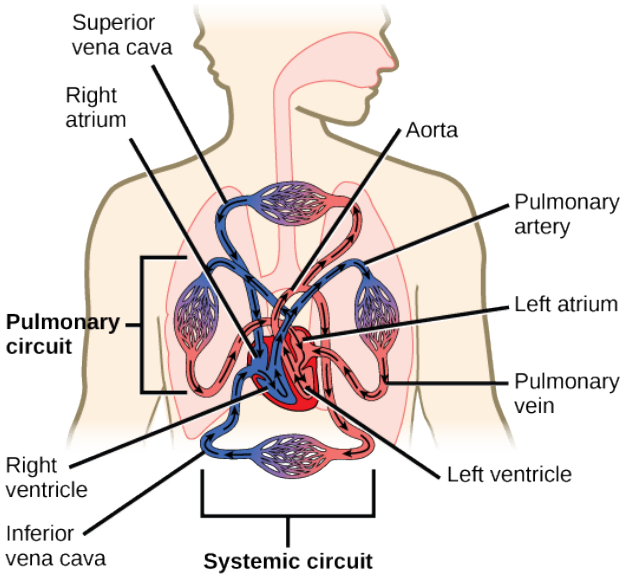


Figure 40.9.1: Circulatory System: The mammalian circulatory system is divided into three circuits: the systemic circuit, the pulmonary circuit, and the coronary circuit. Blood is pumped from veins of the systemic circuit into the right atrium of the heart, then into the right ventricle. Blood then enters the pulmonary circuit and is oxygenated by the lungs. From the pulmonary circuit, blood re-enters the heart through the left atrium. From the left ventricle, blood re-enters the systemic circuit through the aorta and is distributed to the rest of the body. The coronary circuit, which provides blood to the heart, is not shown.

The heart muscle is asymmetrical as a result of the distance blood must travel in the pulmonary and systemic circuits. Since the right side of the heart sends blood to the pulmonary circuit, it is smaller than the left side, which must send blood out to the whole body in the systemic circuit.

In humans, the heart is about the size of a clenched fist. It is divided into four chambers: two atria and two ventricles. There are one atrium and one ventricle on the right side and one atrium and one ventricle on the left side. The atria are the chambers that receive blood while the ventricles are the chambers that pump blood. The right atrium receives deoxygenated blood from the superior vena cava, which drains blood from the veins of the upper organs and arms. The right atrium also receives blood from the inferior vena cava, which drains blood from the veins of the lower organs and legs. In addition, the right atrium receives blood from the coronary sinus, which drains deoxygenated blood from the heart itself. This deoxygenated blood then passes to the right ventricle through the right atrioventricular valve (tricuspid valve), a flap of connective tissue that opens in only one direction to prevent the backflow of blood. After it is filled, the right ventricle pumps the blood through the pulmonary arteries to the lungs for re-oxygenation. After blood passes through the pulmonary arteries, the right semilunar valves close, preventing the blood from flowing backwards into the right ventricle. The left atrium then receives the oxygen-rich blood from the lungs via the pulmonary

veins. The valve separating the chambers on the left side of the heart is called the biscuspid or mitral valve (left atrioventricular valve).The blood passes through the bicuspid valve to the left ventricle where it is pumped out through the aorta, the major artery of the body, taking oxygenated blood to the organs and muscles of the body. Once blood is pumped out of the left ventricle and into the aorta, the aortic semilunar valve (or aortic valve) closes, preventing blood from flowing backward into the left ventricle. This pattern of pumping is referred to as double circulation and is found in all mammals.

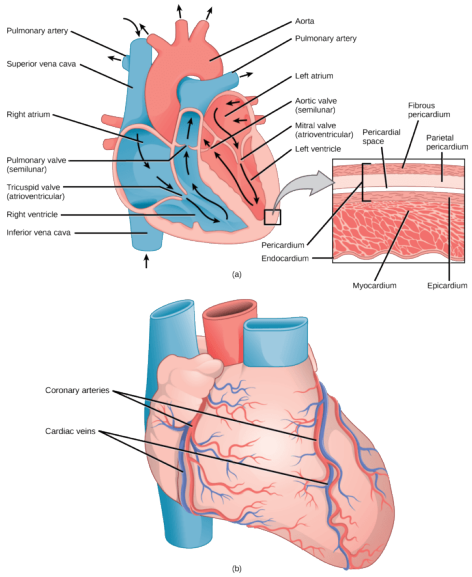


Figure 40.9.1: Human Heart: (a) The heart is primarily made of a thick muscle layer, called the myocardium, surrounded by membranes. One-way valves separate the four chambers. (b) Blood vessels of the coronary system, including the coronary arteries and veins, keep the heart muscles oxygenated.

Layers of the Heart

The heart is composed of three layers: the epicardium, the myocardium, and the endocardium. The inner wall of the heart is lined by the endocardium. The myocardium consists of the heart muscle cells that make up the middle layer and the bulk of the heart wall. The outer layer of cells is called the epicardium, the second layer of which is a membranous layered structure (the pericardium) that surrounds and protects the heart; it allows enough room for vigorous pumping, but also keeps the heart in place, reducing friction between the heart and other structures.

Blood Vessels

The heart has its own blood vessels that supply the heart muscle with blood. The coronary arteries branch from the aorta, surrounding the outer surface of the heart like a crown. They diverge into capillaries where the heart muscle is supplied with oxygen before converging again into the coronary veins to take the deoxygenated blood back to the right atrium, where the blood will be re-oxygenated through the pulmonary circuit.

Atherosclerosis is the blockage of an artery by the buildup of fatty plaques. The heart muscle will die without a steady supply of blood; because of the narrow size of the coronary arteries and their function in serving the heart itself, atherosclerosis can be deadly in these arteries. The slowing of blood flow and subsequent oxygen deprivation can cause severe pain, known as angina. Complete blockage of the arteries will cause myocardial infarction—death of cardiac muscle tissue—which is commonly known as a heart attack.

Key Points

- The heart is divided into four chambers consisting of two atria and two ventricles; the atria receive blood, while the ventricles pump blood.
- The right atrium receives blood from the superior and inferior vena cavas and the coronary sinus; blood then moves to the right ventricle where it is pumped to the lungs.

- The lungs re-oxygenate the blood and send it to the left atrium.
- Blood moves from the left atrium to the left ventricle via the bicuspid valve; blood is pumped out of the left ventricle to the aorta, which sends blood to the organs and muscles of the body.
- The heart is composed of three layers: the epicardium (outer layer), the myocardium (middle layer), and the endocardium (inner layer).

Key Terms

- **aorta**: the largest artery in the human body which carries the blood from the heart to all parts of the body except the lungs
- **inferior vena cava**: large vein that carries deoxygenated blood from the lower half of the body to the right atrium of the heart
- **superior vena cava**: large vein that carries deoxygenated blood from the upper half of the body to the right atrium of the heart

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40.10: Mammalian Heart and Blood Vessels - Arteries, Veins, and Capillaries

Learning Objectives

- Explain the structure of arteries, veins, and capillaries and how blood flows through the body

Arteries, Veins, and Capillaries

The blood from the heart is carried through the body by a complex network of blood vessels. Arteries take blood away from the heart. The main artery is the aorta that branches into other major arteries, which take blood to different limbs and organs. These major arteries include the carotid artery, which takes blood to the brain; the brachial arteries, which take blood to the arms; and the thoracic artery, which takes blood to the thorax and then into the hepatic, renal, and gastric arteries for the liver, kidneys, and stomach, respectively. The iliac artery takes blood to the lower limbs. The major arteries diverge into minor arteries, and then into smaller vessels called arterioles, to reach more deeply into the muscles and organs of the body.

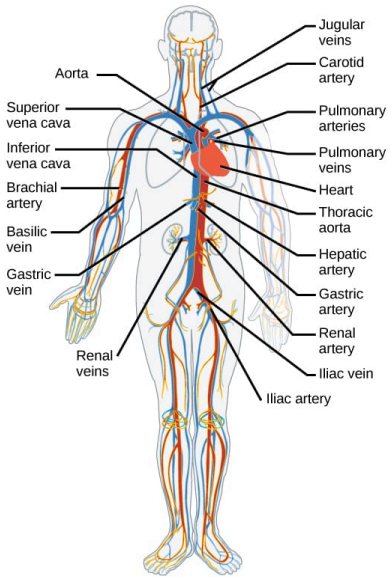


Figure 40.10.1: Major arteries and veins: The blood from the heart is carried through the body by a complex network of blood vessels. This diagram illustrates the major human arteries and veins of the human body.

Arterioles diverge into capillary beds. Capillary beds contain a large number (10 to 100) of capillaries that branch among the cells and tissues of the body. Capillaries are narrow-diameter tubes that can fit red blood cells in single-file lines and are the sites for the exchange of nutrients, waste, and oxygen with tissues at the cellular level. Fluid also crosses into the interstitial space from the capillaries. The capillaries converge again into venules that connect to minor veins, which connect to major veins that take blood high in carbon dioxide back to the heart. The major veins drain blood from the same organs and limbs that the major arteries supply. Fluid is also brought back to the heart via the lymphatic system.

The structure of the different types of blood vessels reflects their function or layers. There are three distinct layers, or tunics, that form the walls of blood vessels. The inner, tunica intima is a smooth, inner lining of endothelial cells that are in contact with the red blood cells. This tunic is continuous with the endocardium of the heart. Unlike veins and arteries, capillaries have only one tunic; this single layer of cells is the location of diffusion of oxygen and carbon dioxide between the endothelial cells and red blood cells, as well as the exchange site via endocytosis and exocytosis. The movement of materials at the site of capillaries is regulated by vasoconstriction, narrowing of the blood vessels, and vasodilation, widening of the blood vessels; this is important in the overall regulation of blood pressure.

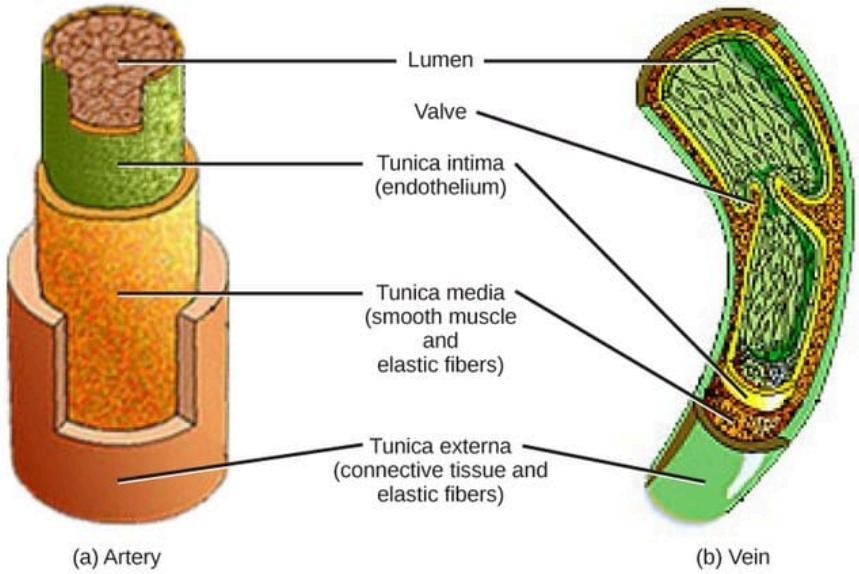


Figure 40.10.1: Blood vessel layers: Arteries and veins consist of three layers: an outer tunica externa, a middle tunica media, and an inner tunica intima. Capillaries consist of a single layer of epithelial cells, the endothelium tunic (tunica intima).

Veins and arteries both have two further tunics that surround the endothelium: the middle, tunica media is composed of smooth muscle, while the outer tunica externa is connective tissue (collagen and elastic fibers). The elastic, connective tissue stretches and supports the blood vessels, while the smooth muscle layer helps regulate blood flow by altering vascular resistance through vasoconstriction and vasodilation. The arteries have thicker smooth muscle and connective tissue than the veins to accommodate the higher pressure and speed of freshly-pumped blood. The veins are thinner walled as the pressure and rate of flow are much lower. In addition, veins are structurally different from arteries in that veins have valves to prevent the backflow of blood. Because veins have to work against gravity to get blood back to the heart, contraction of skeletal muscle assists with the flow of blood back to the heart.

Key Points

- Arteries carry blood away from the heart; the main artery is the aorta.
- Smaller arteries called arterioles diverge into capillary beds, which contain 10-100 capillaries that branch among the cells and tissues of the body.
- Capillaries carry blood away from the body and exchange nutrients, waste, and oxygen with tissues at the cellular level.
- Veins are blood vessels that bring blood back to the heart and drain blood from organs and limbs.
- Capillaries have one layer of cells (the endothelial tunic or tunica intima) where diffusion and exchange of materials takes place.
- Veins and arteries have two more tunics that surround the endothelium: the middle tunica media is composed of smooth muscle that regulates blood flow, while the outer tunica externa is connective tissue that supports blood vessels.

Key Terms

- **vasodilation**: dilation of the blood vessels
- **vasoconstriction**: constriction of a blood vessel
- **venule**: small vein, especially one that connects capillaries to a larger vein

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40.11: Mammalian Heart and Blood Vessels - The Cardiac Cycle

Learning Objectives

- Summarize the caridac cycle and explain the role of the SA node and the AV node in regulating the its rhythm

The Cardiac Cycle

The main purpose of the heart is to pump blood through the body; it does so in a repeating sequence called the cardiac cycle. The cardiac cycle is the coordination of the filling and emptying of blood by electrical signals that cause the heart muscles to contract and relax. The human heart beats over 100,000 times per day. In each cardiac cycle, the heart contracts (systole), pushing out the blood and pumping it through the body. This is followed by a relaxation phase (diastole), where the heart fills with blood. The atria contract at the same time, forcing blood through the atrioventricular valves into the ventricles. Closing of the atrioventricular valves produces a monosyllabic “lup” sound. Following a brief delay, the ventricles contract at the same time forcing blood through the semilunar valves into the aorta and the pulmonary artery (which transports blood to the lungs). Closing of the semilunar valves produces a monosyllabic “dup” sound.

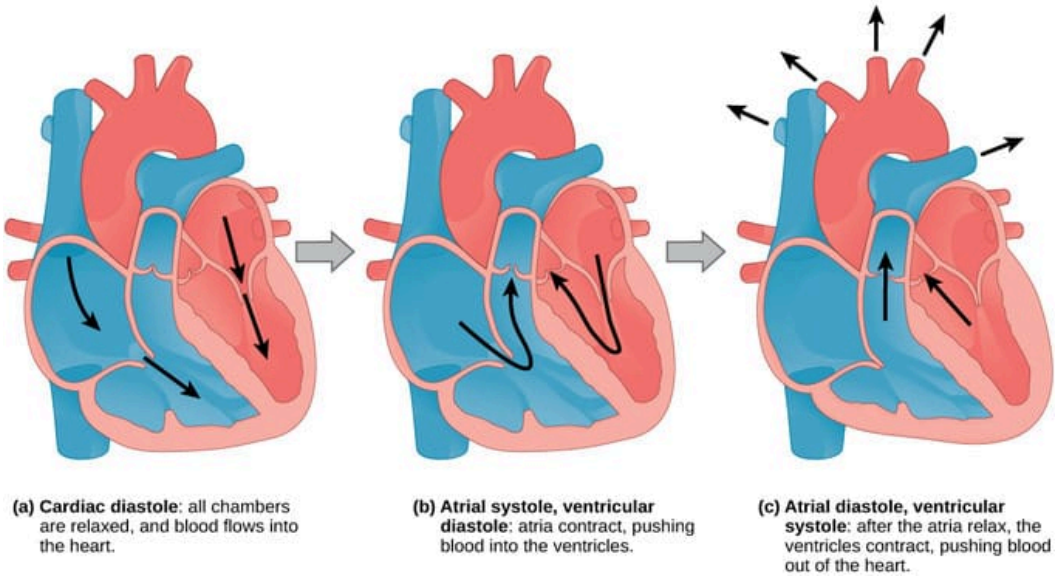


Figure 40.11.1: Diastole and systole: (a) During cardiac diastole, the heart muscle is relaxed and blood flows into the heart. (b) During atrial systole, the atria contract, pushing blood into the ventricles. (c) During atrial diastole, the ventricles contract, forcing blood out of the heart.

The pumping of the heart is a function of the cardiac muscle cells, or cardiomyocytes, that comprise the heart muscle. Cardiomyocytes are distinctive muscle cells that are striated like skeletal muscle, but pump rhythmically and involuntarily like smooth muscle; they are connected by intercalated disks exclusive to cardiac muscle. Cardiomyocytes are self-stimulated for a period of time; isolated cardiomyocytes will beat if given the correct balance of nutrients and electrolytes.

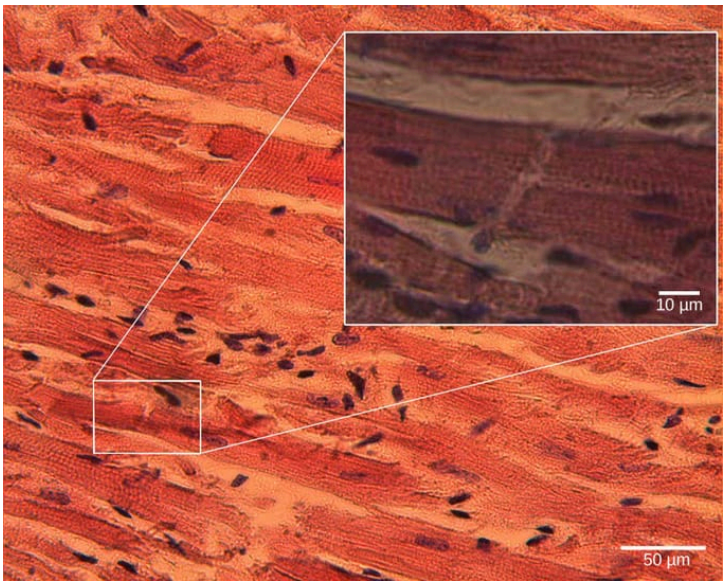


Figure 40.11.1: Cardiomyocytes: Cardiomyocytes are striated muscle cells found in cardiac tissue.

The autonomous beating of cardiac muscle cells is regulated by the heart's internal pacemaker that uses electrical signals to time the beating of the heart. The electrical signals and mechanical actions are intimately intertwined. The internal pacemaker starts at the sinoatrial (SA) node, which is located near the wall of the right atrium. Electrical charges spontaneously pulse from the SA node, causing the two atria to contract in unison. The pulse reaches a second node, the atrioventricular (AV) node, between the right atrium and right ventricle, where it pauses for approximately 0.1 seconds before spreading to the walls of the ventricles. This pause allows the blood in the atria to empty completely into the ventricles before the ventricles pump out the blood. From the AV node, the electrical impulse enters the bundle of His, then to the left and right bundle branches extending through the interventricular septum. Finally, the Purkinje fibers conduct the impulse from the apex of the heart up the ventricular myocardium, causing the ventricles to contract. The electrical impulses in the heart produce electrical currents that flow through the body and can be measured on the skin using electrodes. This information can be observed as an electrocardiogram (ECG): a recording of the electrical impulses of the cardiac muscle.

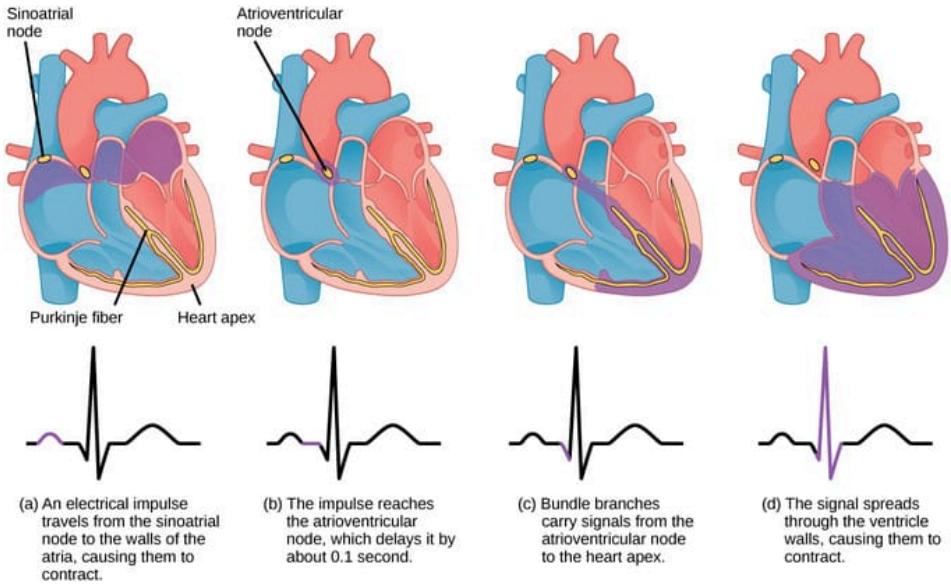


Figure 40.11.1: Electrical signals: The beating of the heart is regulated by an electrical impulse that causes the characteristic reading of an ECG. The signal is initiated at the sinoatrial valve. The signal then (a) spreads to the atria, causing them to contract. The signal is (b) delayed at the atrioventricular node before it is passed on to the (c) heart apex. The delay allows the atria to relax before the (d) ventricles contract. The final part of the ECG cycle prepares the heart for the next beat.

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Key Points

- During the cardiac cycle, the heart contracts via systole, pushing blood out of the heart, and relaxes via diastole, filling the heart with blood.
- Cardiomyocytes, or cardiac cells, are striated and are responsible for the pumping of the heart; they are the only muscle cells with intercalated disks.
- The heart's internal pacemaker regulates and times the beating of the heart via electrical signals.
- Electrical signals start at the SA node, causing atria contraction, and then move on to AV node, delaying electrical impulses to allow blood from the atrium to fill the ventricles.
- Signals move from the AV node to the bundle of His and then to the Prukinje fibers, which then allows the ventricles to contract.

Key Terms

- **bundle of His**: specialized heart muscle cells that transmit electrical impulses from the AV node in the heart to the muscle cells of the heart wall, which contract in response producing the heart beat
- **sinoatrial (SA) node**: impulse-generating (pacemaker) tissue located in the right atrium of the heart, and thus the generator of normal sinus rhythm
- **diastole**: relaxation and dilation of the heart chambers, between contractions, during which they fill with blood
- **systole**: rhythmic contraction of the heart, by which blood is driven through the arteries
- **atrioventricular (AV) node**: part of the electrical control system of the heart that coordinates the top of the heart; electrically connects atrial and ventricular chambers

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40.12: Blood Flow and Blood Pressure Regulation - Blood Flow Through the Body

Learning Objectives

- Explain the blood flow through the body

How Blood Flows Through the Body

As the heart pumps, blood is pushed through the body through the entire circulatory system. Oxygenated blood is pumped away from the heart to the rest of the body, while deoxygenated blood is pumped to the lungs where it is reoxygenated before returning to the heart.

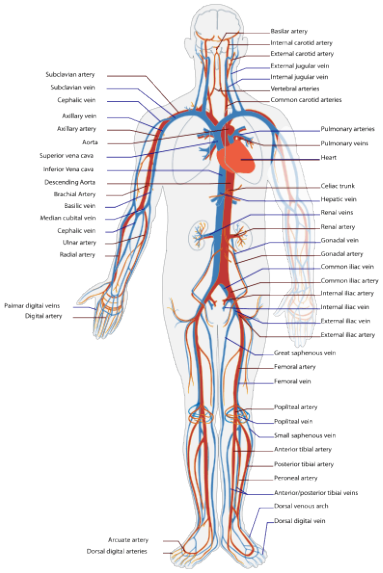


Figure 40.12.1: Circulatory system: This illustration of the circulatory system shows where blood flows in the body. Red indicates oxygenated blood, while blue indicates deoxygenated blood.

Blood Flow Away from the Heart

With each rhythmic pump of the heart, blood is pushed under high pressure and velocity away from the heart, initially along the main artery, the aorta. In the aorta, the blood travels at 30 cm/sec. From the aorta, blood flows into the arteries and arterioles and, ultimately, to the capillary beds. As it reaches the capillary beds, the rate of flow is dramatically (one-thousand times) slower than the rate of flow in the aorta. While the diameter of each individual arteriole and capillary is far narrower than the diameter of the aorta, the rate is actually slower due to the overall diameter of all the combined capillaries being far greater than the diameter of the individual aorta.

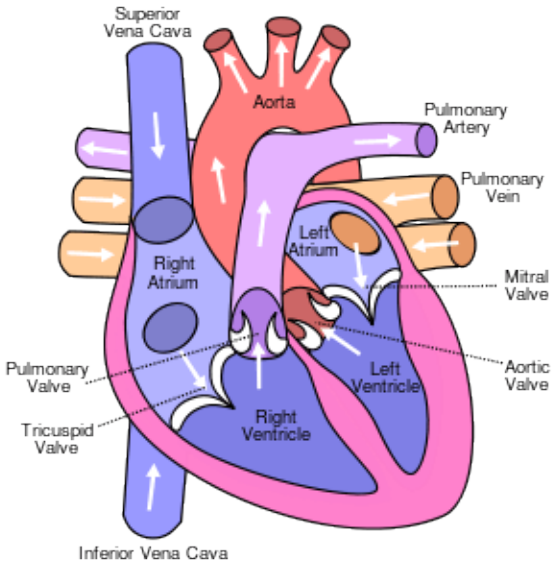


Figure 40.12.1: View of the heart: This front view of the heart shows the direction of blood flow to and from the heart. Blood leaves the heart through the pulmonary artery and aorta, while blood enters the heart through the two venae cavae and pulmonary veins.

The slow rate of travel through the capillary beds, which reach almost every cell in the body, assists with gas (especially oxygen and carbon dioxide) and nutrient exchange. Blood flow through the capillary beds is regulated depending on the body's needs and is directed by nerve and hormone signals. For example, after a large meal, most of the blood is diverted to the stomach by vasodilation (widening) of vessels of the digestive system and vasoconstriction (narrowing) of other vessels. During exercise, blood is diverted to the skeletal muscles through vasodilation, while blood to the digestive system would be lessened through vasoconstriction. The blood entering some capillary beds is controlled by small muscles called precapillary sphincters. A sphincter is a ringlike band of muscle that surrounds a bodily opening, constricting and relaxing as required for normal physiological functioning. If the precapillary sphincters are open, the blood will flow into the associated branches of the capillary bed. If all of the sphincters are closed, then the blood will flow directly from the arteriole to the venule through the thoroughfare channel. These muscles allow the body to precisely control when capillary beds receive blood flow. At any given moment, only about 5-10 percent of our capillary beds actually have blood flowing through them.

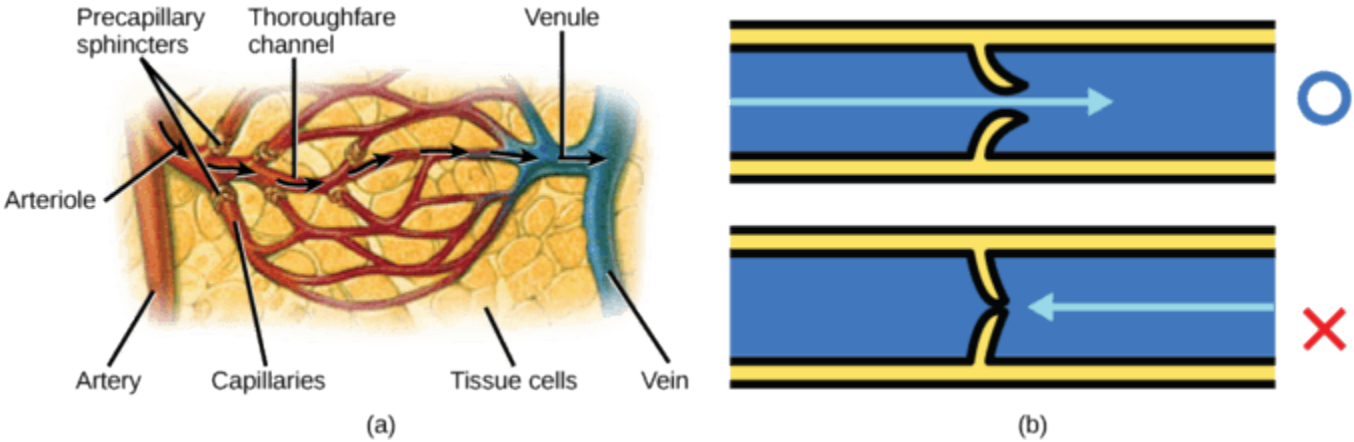


Figure 40.12.1: Precapillary sphincters: (a) Precapillary sphincters are rings of smooth muscle that regulate the flow of blood through capillaries; they help control the blood flow to where it is needed. (b) Valves in the veins prevent blood from moving backward.

Blood Flow to the Heart

After the blood has passed through the capillary beds, it enters the venules, veins, and finally the two main venae cavae (singular, vena cava) that take blood back to the heart. The flow rate increases again, but is still much slower than the initial rate in the aorta. Blood primarily moves in the veins by the rhythmic movement of smooth muscle in the vessel wall and by the action of the skeletal muscle as the body moves. Because most veins must move blood against the pull of gravity, blood is prevented from flowing

backward in the veins by one-way valves. Thus, because skeletal muscle contraction aids in venous blood flow, it is important to get up and move frequently after long periods of sitting so that blood will not pool in the extremities.

Key Points

- As blood is pumped away from the heart, it travels through the aorta to arteries, aterioles, and the capillary beds.
- Blood flow through the capillary beds reaches almost every cell in the body and is controlled to divert blood according to the body's needs.
- After oxygen is removed from the blood, the deoxygenated blood flows to the lungs, where it is reoxygenated and sent through the veins back to the heart.

Key Terms

- **arteriole**: one of the small branches of an artery, especially one that connects with capillaries
- **vein**: a blood vessel that transports blood from the capillaries back to the heart
- **artery**: an efferent blood vessel from the heart, conveying blood away from the heart regardless of oxygenation status
- **vena cava**: either of the two large veins that take oxygen depleted blood from the upper body and lower body and return it to the right atrium of the heart

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40.13: Blood Flow and Blood Pressure Regulation - Blood Pressure

Learning Objectives

- Describe the process of blood pressure regulation

Blood Pressure

Blood pressure is the pressure of the fluid (blood) against the walls of the blood vessels. Fluid will move from areas of high to low hydrostatic pressures. In the arteries, the hydrostatic pressure near the heart is very high. Blood flows to the arterioles (smaller arteries) where the rate of flow is slowed by the narrow openings of the arterioles. The systolic pressure is defined as the peak pressure in the arteries during the cardiac cycle; the diastolic pressure is the lowest pressure at the resting phase of the cardiac cycle. During systole, when new blood is entering the arteries, the artery walls stretch to accommodate the increase of pressure of the extra blood. During diastole, the walls return to normal because of their elastic properties.

Blood pressure values are universally stated in millimeters of mercury (mm Hg). The blood pressure of the systole phase and the diastole phase gives the two readings for blood pressure. For example, the typical value for a resting, healthy adult is 120/80, which indicates a reading of 120 mm Hg during the systole and 80 mm Hg during diastole.

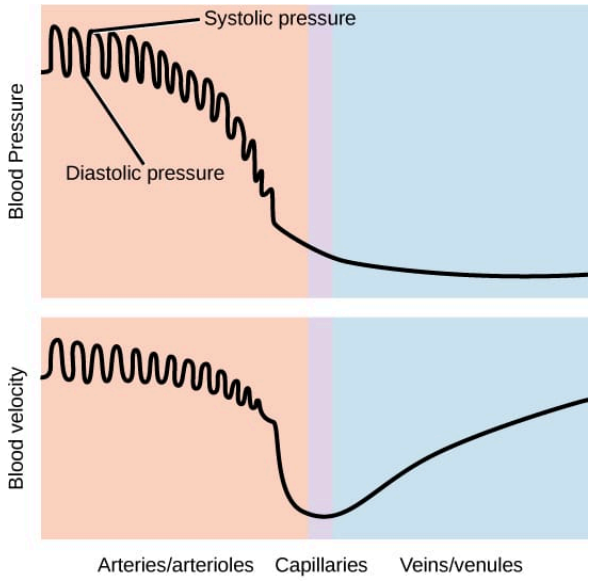


Figure 40.13.1: Relationship between blood pressure and velocity: Blood pressure is related to the blood velocity in the arteries and arterioles. In the capillaries and veins, the blood pressure continues to decease, but velocity increases.

Blood Pressure Regulation

Throughout the cardiac cycle, the blood continues to empty into the arterioles at a relatively even rate. However, these measures of blood pressure are not static; they undergo natural variations from one heartbeat to another and throughout the day. The measures of blood pressure also change in response to stress, nutritional factors, drugs, or disease. The body regulates blood pressure by changes in response to the cardiac output and stroke volume.

Cardiac output is the volume of blood pumped by the heart in one minute. It is calculated by multiplying the number of heart contractions that occur per minute (heart rate) times the stroke volume (the volume of blood pumped into the aorta per contraction of the left ventricle). Therefore, cardiac output can be increased by increasing heart rate, as when exercising. However,

cardiac output can also be increased by increasing stroke volume, such as if the heart were to contract with greater strength. Stroke volume can also be increased by speeding blood circulation through the body so that more blood enters the heart between contractions. During heavy exertion, the blood vessels relax and increase in diameter, offsetting the increased heart rate and ensuring adequate oxygenated blood gets to the muscles. Stress triggers a decrease in the diameter of the blood vessels, consequently increasing blood pressure. These changes can also be caused by nerve signals or hormones; even standing up or lying down can have a great effect on blood pressure.

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Key Points

- Normal blood pressure for a healthy adult is 120 mm Hg during systole (peak pressure in the arteries) and 80 mm Hg during diastole (the resting phase).
- Blood pressure is regulated in the body by changes to the diameters of blood vessels in response to changes in the cardiac output and stroke volume.
- Factors such as stress, nutrition, drugs, exercise, or disease can invoke changes in the diameters of the blood vessels, altering blood pressure.

Key Terms

- **cardiac output**: the volume of blood being pumped by the heart, in particular by a left or right ventricle in the time interval of one minute
- **hydrostatic**: of or relating to fluids, especially to the pressure that they exert or transmit
- **stroke volume**: the volume of blood pumped from one ventricle of the heart with each beat

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41.1: Osmoregulation and Osmotic Balance - Introduction

Learning Objectives

- Describe the process and purpose of osmoregulation

What is osmoregulation?

Doctors typically recommend drinking eight to ten glasses of water a day. This amount is necessary for the proper balance of electrolytes in the human body. The intake is balanced by more or less equal excretion of fluids by urination, defecation, sweating, and, to a lesser extent, respiration. The body's organs and tissues are immersed in fluid at a constant temperature, pH, and solute concentration, each of which contributes to maintaining the body's homeostasis. The solutes in body fluids are mainly mineral salts and sugars. Osmotic regulation, or osmoregulation, keeps these solutes at the ideal concentrations. Osmotic homeostasis is maintained despite the influence of external factors such as temperature, diet, and weather conditions.

Osmosis is the diffusion of water across a membrane in response to osmotic pressure caused by an imbalance of molecules on either side of the membrane. Osmoregulation is the process of maintenance of salt and water balance (osmotic balance) across membranes within the body's fluids, which are composed of water plus electrolytes and non-electrolytes. An electrolyte is a solute that dissociates into ions when dissolved in water. A non-electrolyte, in contrast, does not dissociate into ions during water dissolution. Both electrolytes and non-electrolytes contribute to the osmotic balance. The body's fluids include blood plasma, the cytosol within cells, and interstitial fluid, the fluid that exists in the spaces between cells and tissues of the body. The membranes of the body (such as the pleural, serous, and cell membranes) are semi-permeable: they allow passage of certain types of solutes and water, but not others. Solutions on two sides of a semi-permeable membrane tend to equalize in solute concentration by movement of solutes and/or water across the membrane.

A cell immersed in plain water tends to swell as water diffuses in from the hypotonic or "low salt" solution. In contrast, a cell shrivels when placed in a solution of high salt concentration. The cell loses water, which moves outside to the hypertonic or "high salt" environment. Isotonic cells have an equal concentration of solutes inside and outside the cell; this equalizes the osmotic pressure on either side of the semi-permeable membrane.

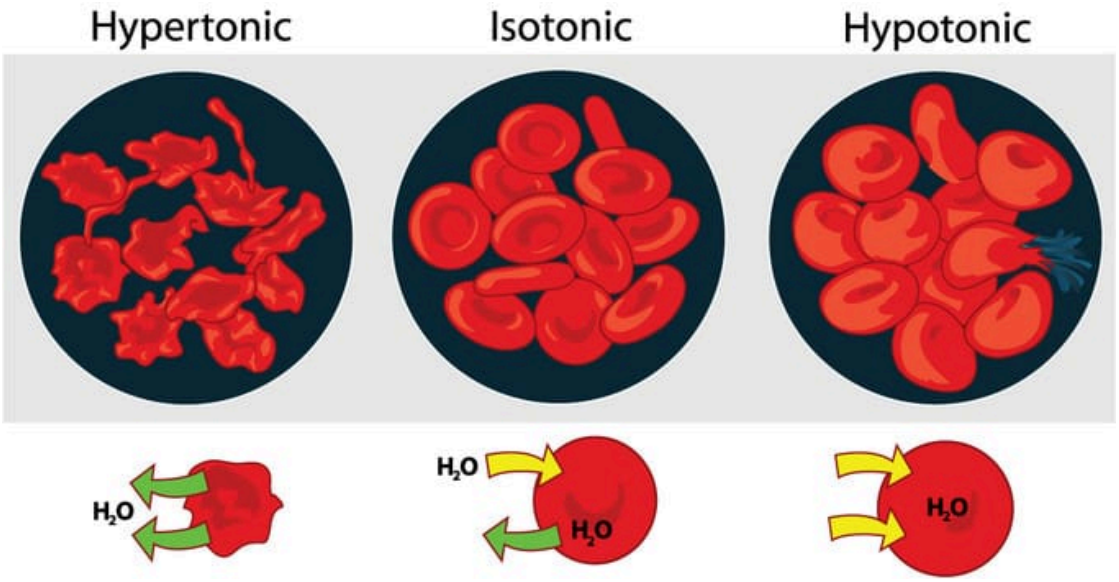


Figure 41.1.1: Response of red blood cells in hypertonic, hypotonic, and isotonic solutions: Cells placed in a hypertonic environment tend to shrink due to loss of water. In a hypotonic environment, cells tend to swell due to intake of water. The blood maintains an isotonic environment so that cells neither shrink nor swell.

Osmoconformers are marine animals which, in contrast to osmoregulators, maintain the osmolarity of their body fluids such that

it is always equal to the surrounding seawater. Osmoconformers decrease the net flux of water into or out of their bodies from diffusion. They maintain internal solute concentrations within their bodies at a level equal to the osmolarity of the surrounding medium.

The body is subject to a continual intake and loss of water and electrolytes. Excess electrolytes and wastes that result from osmoregulation are transported to the kidneys and excreted. The process of excretion helps the body maintain osmotic balance.

Need for Osmoregulation

Complex multicellular animals exchange water and nutrients with the environment by consuming food and water, and by excreting sweat, urine, and feces. When disease or injury damage the mechanisms that regulate osmotic pressure, toxic waste or water may accumulate, with potentially dire consequences.

Mammalian systems have evolved to regulate osmotic pressure by managing concentrations of electrolytes found in the three major fluids: blood plasma, extracellular fluid, and intracellular fluid. Water movement due to osmotic pressure across membranes may change the volume of these fluid compartments. Because blood plasma is one of the fluid components, osmotic pressure can directly influence blood pressure and other medical indicators.

Key Points

- Osmoregulation maintains the proper balance of electrolytes in the human body, despite external factors such as temperature, diet, and weather conditions.
- By diffusion of water or solutes, osmotic balance ensures that optimal concentrations of electrolytes and non-electrolytes are maintained in cells, body tissues, and in interstitial fluid.
- Solutes or water move across a semi-permeable membrane, causing solutions on either side of it to equalize in concentration.
- Cells in hypotonic solutions swell as water moves across the membrane into the cell, whereas cells in hypertonic solutions shrivel as water moves out of the cell.
- Water movement due to osmotic pressure across membranes may change the volume of the body's fluid compartments; therefore, it can directly influence medical indicators, such as blood pressure.

Key Terms

- **electrolyte**: any of the various ions (such as sodium or chloride) that regulate the electric charge on cells and the flow of water across their membranes
- **osmosis**: The net movement of solvent molecules from a region of high solvent potential to a region of lower solvent potential through a partially permeable membrane
- **osmotic pressure**: the hydrostatic pressure exerted by a solution across a semipermeable membrane from a pure solvent

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41.2: Osmoregulation and Osmotic Balance - Transport of Electrolytes across Cell Membranes

Learning Objectives

- Explain the relationship between osmotic pressure and the transport of electrolytes across cell membranes

Transport of Electrolytes across Cell Membranes

A teaspoon of table salt readily dissolves in water. The solubility of sodium chloride results from its capacity to ionize in water. Salt and other compounds that dissociate into their component ions are called electrolytes. In water, sodium chloride (NaCl) dissociates into the sodium ion (Na^+) and the chloride ion (Cl^-). The most important ions, whose concentrations are very closely regulated in body fluids, are the cations sodium (Na+), potassium (K+), calcium (Ca+2),and magnesium (Mg+2); and the anions chloride (Cl-), carbonate (CO3-2), bicarbonate (HCO3-), and phosphate(PO3-). Electrolytes are lost from the body during urination and perspiration. For this reason, athletes are encouraged to replace electrolytes and fluids during periods of increased activity and perspiration.

Osmotic pressure is influenced by the concentration of solutes in a solution. It is directly proportional to the number of solute atoms or molecules and not dependent on the size of the solute molecules. Because electrolytes dissociate into ions, adding relatively more solute molecules to a solution, they exert a greater osmotic pressure per unit mass than non-electrolytes such as glucose.

Water passes through semi-permeable membranes by passive diffusion, moving along a concentration gradient and equalizing the concentration on either side of the membrane. Electrolyte ions may not be able to passively diffuse across a membrane, but may instead require special mechanisms to cross the semi-permeable membrane. The mechanisms that transport ions across membranes are facilitated diffusion and active transport. Facilitated diffusion of solutes occurs through protein-based channels. Active transport requires energy in the form of ATP conversion, carrier proteins, or pumps in order to move ions against the concentration gradient.

Transport across cell membranes: Paul Andersen describes how cells move materials across the cell membrane. All movement can be classified as passive or active. Passive transport, such as diffusion, requires no energy as particles move along their gradient. Active transport requires additional energy as particles move against their gradient. Specific examples, such as GLUT and the Na/K, pump are included.

Key Points

- Important ions cannot pass through membranes by passive diffusion; if they could, maintaining specific concentrations of ions would be impossible.
- Osmotic pressure is directly proportional to the number of solute atoms or molecules; ions exert more pressure per unit mass than do non- electrolytes.
- Electrolyte ions require facilitated diffusion and active transport to cross the semi-permeable membranes.
- Facilitated diffusion occurs through protein -based channels, which allow passage of the solute along a concentration gradient.
- In active transport, energy from ATP changes the shape of membrane proteins that move ions against a concentration gradient.

Key Terms

- **facilitated diffusion**: The spontaneous passage of molecules or ions across a biological membrane passing through specific transmembrane integral proteins.
- **passive diffusion**: movement of water and other molecules across membranes along a concentration gradient

- **active transport**: movement of a substance across a cell membrane against its concentration gradient (from low to high concentration) facilitated by ATP conversion

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41.3: Osmoregulation and Osmotic Balance - Concept of Osmolality and Milliequivalent

Learning Objectives

- Describe osmolality and milliequivalent

Concept of osmolality and milliequivalent

In order to calculate osmotic pressure, it is necessary to understand how solute concentrations are measured. The unit for measuring solutes is the mole. One mole is defined as the molecular weight of the solute in grams. For example, the molecular weight of sodium chloride is 58.44; thus, one mole of sodium chloride weighs 58.44 grams. A solution's molarity is the number of moles of solute per liter of solution. On the other hand, a solution's molality is the number of moles of solute per kilogram of solvent. If the solvent is water, one kilogram of water is equal to one liter of water. Osmolarity is related to osmolality, but is affected by changes in water content, as well as temperature and pressure. In contrast, osmolality is unaffected by temperature and pressure.

Molarity and molality represent solution concentration, but electrolyte concentrations are usually expressed in terms of milliequivalents per liter (mEq/L). The mEq/L is the ion concentration, in millimoles, multiplied by the number of electrical charges on the ion. The milliequivalent unit incorporates both the ion concentration and the charge on the ions.

Thus, for ions that have a charge of one, such as sodium (Na^+), one milliequivalent is equal to one millimole. For ions that have a charge of two, such as calcium (Ca^{2+}), one milliequivalent is equal to 0.5 millimoles. Another unit of electrolyte concentration is the milliosmole (mOsm), which is the number of milliequivalents of solute per kilogram of solvent. Osmoregulation maintains body fluids in a range of 280 to 300 mOsm.

Concentration of solutions; part 2; moles, millimoles & milliequivalents by Professor Fink: Professor Fink reviews the use of moles, millimoles & milliquivalents in expressing concentration and dosage. Example problems are presented explaining how to prepare molar solutions and convert to percent concentration. In addition, Professor Fink explains how to convert from millimoles to milliequivalents, or convert milliequivalents back to millimoles.

Key Points

- Osmotic pressure is calculated from a solution's molarity and the charge on the ions.
- A solution's molarity is the number of moles of solute per liter of solution, while a solution's molality is the number of moles of solute per kilogram of solvent.
- Osmolarity is related to osmolality, but osmolality is unaffected by temperature and pressure.
- Electrolyte concentrations are usually expressed in terms of milliequivalents per liter (mEq/L), which is the ion concentration, in millimoles, multiplied by the number of electrical charges on the ion.

Key Terms

- **osmotic pressure**: the hydrostatic pressure exerted by a solution across a semipermeable membrane from a pure solvent
- **molarity**: the number of moles of solute per liter of solution, giving a solution's molar concentration
- **molality**: the concentration of a substance in solution, expressed as the number of moles of solute per kilogram of solvent
- **mole**: in the International System of Units, the base unit of amount of substance

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41.4: Osmoregulation and Osmotic Balance - Osmoregulators and Osmoconformers

Learning Objectives

- Compare the ability of stenohaline and euryhaline organisms to adapt to external fluctuations in salinity

Persons lost at sea without any fresh water to drink are at risk of severe dehydration because the human body cannot adapt to drinking seawater, which is hypertonic (having higher osmotic pressure) in comparison to body fluids. Stenohaline organisms, such as goldfish, can tolerate only a relatively-narrow range of salinity. About 90 percent of bony fish species can live in either freshwater or seawater, but not both. These fish are incapable of osmotic regulation in the alternate habitat.

However, a few species, known as euryhaline organisms, spend part of their lifecycle in fresh water and part in seawater. These organisms, such as the salmon, are tolerant of a relatively-wide range of salinity. They evolved osmoregulatory mechanisms to survive in a variety of aquatic environments. In relatively hypotonic (low osmotic pressure) fresh water, their skin absorbs water (see [a] in). The fish do not drink much water and balance electrolytes by passing dilute urine while actively taking up salts through the gills. When they move to a hypertonic marine environment, the salmon lose water, excreting the excess salts through their gills and urine (see [b] in).

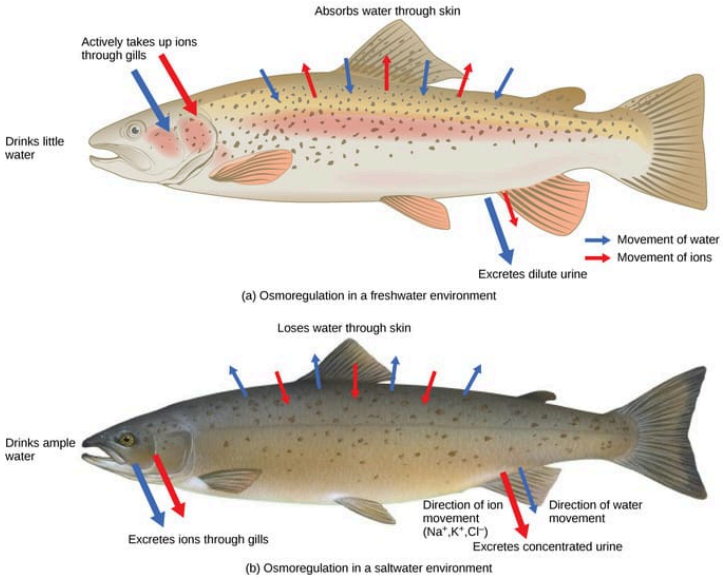


Figure 41.4.1: Salmon physiology responds to freshwater and seawater to maintain osmotic balance: Fish are osmoregulators, but must use different mechanisms to survive in (a) freshwater or (b) saltwater environments.

Most marine invertebrates, on the other hand, may be isotonic with sea water (osmoconformers). Their body fluid concentrations conform to changes in seawater concentration. The blood composition of cartilaginous fishes, such as sharks and rays, is similar to that of bony fishes. However, the blood of sharks contains urea and trimethylamine oxide (TMAO). The shark's blood electrolyte composition is not similar to that of seawater, but maintains isotonicity with seawater by storing urea at high concentrations. Sharks are "ureotelic" animals that secrete urea to maintain osmotic balance. TMAO stabilizes proteins in the presence of high urea levels, preventing the disruption of peptide bonds that would otherwise occur at such high levels of urea.

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Key Points

- Stenohaline organisms can tolerate only a relatively-narrow range of salinity.
- Euryhaline organisms are tolerant of a relatively-wide range of salinity.
- Osmoconformers are organisms that remain isotonic with seawater by conforming their body fluid concentrations to changes in seawater concentration.

Key Terms

- **euryhaline**: able to tolerate various saltwater concentrations
- **osmoconformer**: a marine organism (usually an invertebrate) that maintains its internal salinity such that it is always equal to the surrounding seawater
- **stenohaline**: tolerant of only a narrow range of saltwater concentrations

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41.5: Nitrogenous Wastes - Nitrogenous Waste in Terrestrial Animals- The Urea Cycle

Learning Objectives

- Discuss the urea cycle

Mammals, including humans, are the primary producers of urea. Because they secrete urea as the primary nitrogenous waste product, they are called ureotelic animals. Urea serves an important role in the metabolism of nitrogen-containing compounds by animals. It is the main nitrogen-containing substance in the urine of mammals. Urea is a colorless, odorless solid, highly soluble in water, and practically non-toxic. Dissolved in water, it is neither acidic nor alkaline. The body uses it in many processes, the most notable one being nitrogen excretion. Urea is widely used in fertilizers as a convenient source of nitrogen. It is also an important raw material for the chemical industry.

Apart from mammals, urea is also found in the urine of amphibians, as well as some fish. Interestingly, tadpoles excrete ammonia, but shift to urea production during metamorphosis. In humans, apart from being a carrier of waste nitrogen, urea also plays a role in the countercurrent exchange system of the nephrons, which allows for re-absorption of water and critical ions from the excreted urine. This mechanism, controlled by an anti-diuretic hormone, allows the body to create hyperosmotic urine, which has a higher concentration of dissolved substances than the blood plasma. This mechanism is important to prevent the loss of water, to maintain blood pressure, and to maintain a suitable concentration of sodium ions in the blood plasmas.

The urea cycle is the primary mechanism by which mammals convert ammonia to urea. Urea is made in the liver and excreted in urine. The overall chemical reaction by which ammonia is converted to urea is

$$2\ NH_3\ (\text{ammonia}) + CO_2 + 3\ ATP + H_2O \rightarrow H_2N\text{-}CO\text{-}NH_2\ (\text{urea}) + 2\ ADP + 4\ P_i + AMP.$$

The urea cycle utilizes five intermediate steps, catalyzed by five different enzymes, to convert ammonia to urea. The amino acid L-ornithine is converted into different intermediates before being regenerated at the end of the urea cycle. Hence, the urea cycle is also referred to as the ornithine cycle. The enzyme ornithine transcarbamylase catalyzes a key step in the urea cycle. Its deficiency can lead to accumulation of toxic levels of ammonia in the body. The first two reactions occur in the mitochondria, while the last three reactions occur in the cytosol.

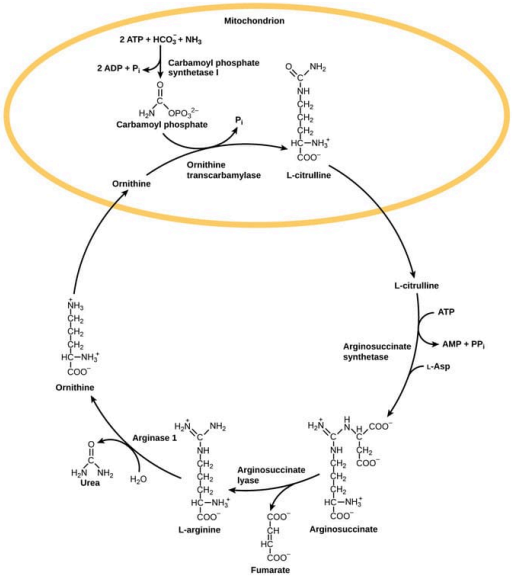


Figure 41.5.1: Urea Cycle: The urea cycle converts ammonia to urea in five steps that include the catalyzation of five different enzymes.

Key Points

- Ureotelic animals, which includes mammals, produce urea as the main nitrogenous waste material.
- 2 NH_3 + CO_2 + 3 ATP + H_2O → H_2N-CO-NH_2 + 2 ADP + 4 Pi + AMP is the chemical reaction by which toxic ammonia is converted to urea.
- The urea cycle involves the multi-step conversion (carried out by five different enzymes) of the amino acid L- ornithine into different intermediates before being regenerated.

Key Terms

- **ureotelic**: animals that secrete urea as the primary nitrogenous waste material
- **ornithine**: an amino acid, which acts as an intermediate in the biosynthesis of urea
- **urea**: a water-soluble organic compound, CO(NH2)2, formed by the metabolism of proteins and excreted in the urine

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41.6: Nitrogenous Wastes - Nitrogenous Waste in Birds and Reptiles- Uric Acid

Learning Objectives

- Compare the major byproduct of ammonia metabolism in mammals to that of birds and reptiles

Of the four major macromolecules in biological systems, both proteins and nucleic acids contain nitrogen. During the catabolism, or breakdown, of nitrogen-containing macromolecules, carbon, hydrogen, and oxygen are extracted and stored in the form of carbohydrates and fats. Excess nitrogen is excreted from the body. Nitrogenous wastes tend to form toxic ammonia, which raises the pH of body fluids. The formation of ammonia itself requires energy in the form of ATP and large quantities of water to dilute it out of a biological system.

While aquatic animals can easily excrete ammonia into their watery surroundings, terrestrial animals have evolved special mechanisms to eliminate the toxic ammonia from their systems. The animals must detoxify ammonia by converting it into a relatively-nontoxic form such as urea or uric acid.

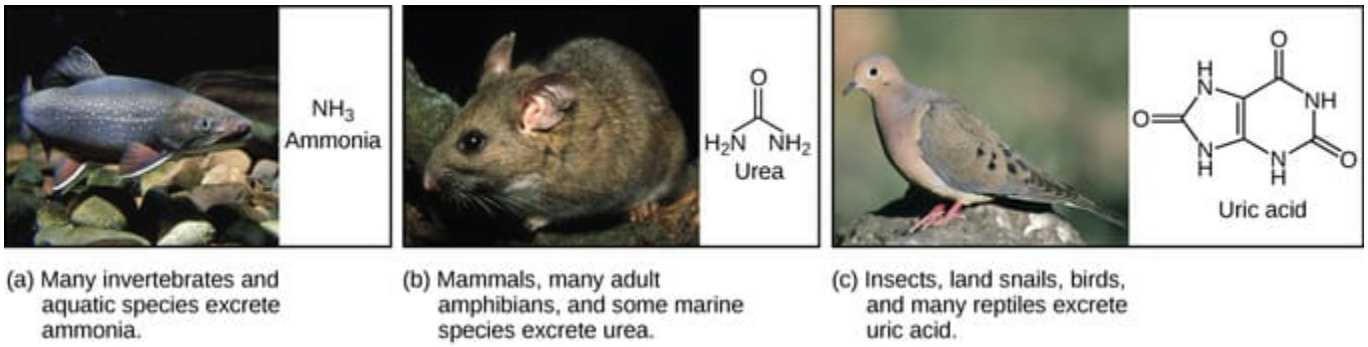


Figure 41.6.1: Nitrogen excretion: Nitrogenous waste is excreted in different forms by different species. These include (a) ammonia, (b) urea, and (c) uric acid.

Birds, reptiles, and most terrestrial arthropods, such as insects, are called uricothelic organisms because they convert toxic ammonia to uric acid or the closely-related compound guanine (guano), rather than urea. In contrast, mammals (including humans) produce urea from ammonia; however, they also form some uric acid during the breakdown of nucleic acids. In this case, uric acid is excreted in urine instead of in feces, as is done in birds and reptiles.

Uric acid is a compound similar to purines found in nucleic acids. It is water insoluble and tends to form a white paste or powder. The production of uric acid involves a complex metabolic pathway that is energetically costly in comparison to processing of other nitrogenous wastes such as urea (from the urea cycle) or ammonia; however, it has the advantages of reducing water loss and, hence, reducing the need for water.

Uric acid is also less toxic than ammonia or urea. It contains four nitrogen atoms; only a small amount of water is needed for its excretion. Out of solute, it precipitates and forms crystals. The enzyme xanthine oxidase makes uric acid from xanthine and hypoxanthine, which in turn are produced from other purines. Xanthine oxidase is a large enzyme whose active site consists of the metal, molybdenum, bound to sulfur and oxygen. Uric acid is released in hypoxic conditions.

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Key Points

- Nitrogenous wastes in the body tend to form toxic ammonia, which must be excreted.
- Mammals such as humans excrete urea, while birds, reptiles, and some terrestrial invertebrates produce uric acid as waste.
- Uricothelic organisms tend to excrete uric acid waste in the form of a white paste or powder.
- Conversion of ammonia into uric acid is more energy intensive than the conversion of ammonia into urea.
- Producing uric acid instead of urea is advantageous because it is less toxic and reduces water loss and the subsequent need for water.

Key Terms

- **urea**: a water-soluble organic compound, CO(NH2)2, formed by the metabolism of proteins and excreted in the urine
- **guano**: the excrement of seabirds, cave-dwelling bats, pinnipeds, or birds more generally
- **purine**: any of a class of organic heterocyclic base containing fused pyrimidine and imidazole rings; they are components of nucleic acids
- **xanthine**: a precursor of uric acid found in many organs of the body
- **hypoxanthine**: an intermediate in the biosynthesis of uric acid
- **uric acid**: a bicyclic heterocyclic phenolic compound, formed in the body by the metabolism of protein and excreted in the urine

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41.7: Excretion Systems - Contractile Vacuoles in Microorganisms

Learning Objectives

- Describe the process of handling wastes in microorganisms

A **contractile vacuole** (CV) is an organelle, or sub-cellular structure, that is involved in osmoregulation and waste removal. Previously, a CV was known as a pulsatile or pulsating vacuole. CVs should not be confused with vacuoles which store food or water. A CV is found predominantly in protists and in unicellular algae. In freshwater environments, the concentration of solutes inside the cell is higher than outside the cell. Under these conditions, water flows from the environment into the cell by osmosis. Thus, the CV acts as a protective mechanism against cellular expansion (and possibly explosion) from too much water; it expels excess water from the cell by contracting. However, not all species that possess a CV are freshwater organisms; some marine and soil microorganisms also have a CV. The CV is predominant in species that do not have a cell wall, but there are exceptions. Through the process of evolution, the CV was mostly eliminated in multicellular organisms; however it still exists in the unicellular stage of several multicellular fungi and in several types of cells in sponges, including amoebocytes, pinacocytes, and choanocytes.

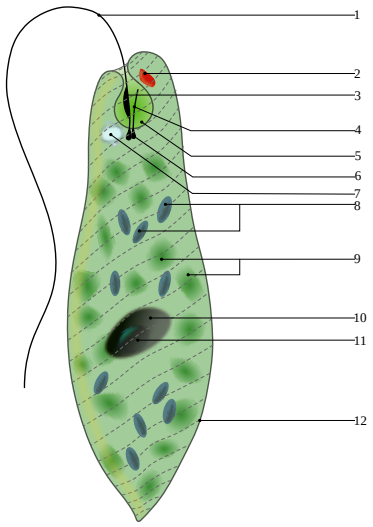


Figure 41.7.1: Contractile vacuole of Euglena: Structure of Euglena: 1 – Flagellum; 2 – Eye spot / Pigment spot / Stigma; 3 – Photoreceptor; 4 – Short second flagellum; 5 – Reservoir; 6 – Basal body; 7 – Contractile vacuole; 8 – Paramylon granule; 9 – Chloroplasts; 10 – Nucleus; 11 – Nucleolus; 12 – Pellicle

The CV's phases of collecting water (expansion) and expelling water (contraction) are periodical. One cycle takes several seconds, depending on the species and the environment's osmolarity. The stage in which water flows into the CV is called diastole. The contraction of the CV and the expulsion of water from the cell is called systole. Water always flows from outside the cell into the cytoplasm; and only then from the cytoplasm into the CV. Species that possess a CV always use it, even in very hypertonic (high concentration of solutes) environments, since the cell tends to adjust its cytoplasm to become even more hyperosmotic (hypertonic) than the environment. The amount of water expelled from the cell and the rate of contraction are related to the osmolarity of the environment. In hyperosmotic environments, less water will be expelled and the contraction cycle will be longer.

The number of CVs per cell varies, depending on the species. Amoeba have one; *Dictyostelium discoideum*, *Paramecium aurelia,* and *Chlamydomonas reinhardtii* have two; and giant amoeba, such as *Chaos carolinensis*, have many. In some unicellular eukaryotic organisms (e.g., amoeba), cellular wastes, such as ammonia and excess water, are excreted by exocytosis as the contractile vacuoles merge with the cell membrane, expelling wastes into the environment. In *Paramecium*, which, presumably, has the most-complex and highly-evolved CV, the vacuole is surrounded by several canals, which absorb water by osmosis from the cytoplasm. After the canals fill with water, it is pumped into the vacuole. When the vacuole is full, it expels the water through

a pore in the cytoplasm that can be opened and closed.

Key Points

- Contractile vacuoles protect a cell from absorbing too much water and potentially exploding by excreting excess water.
- Wastes, such as ammonia, are soluble in water; they are excreted from the cell along with excess water by the contractile vacuoles.
- Contractile vacuoles function in a periodic cycle by expanding while collecting water and contracting to release the water.

Key Terms

- **contractile vacuole**: a vacuole that removes waste or excess water
- **osmoregulation**: the homeostatic regulation of osmotic pressure in the body in order to maintain a constant water content
- **osmolarity**: The osmotic concentration of a solution, normally expressed as osmoles of solute per litre of solution.
- **hypertonic**: having a greater osmotic pressure than another

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41.8: Excretion Systems - Flame Cells of Planaria and Nephridia of Worms

Learning Objectives

- Compare and contrast the way in which planaria and annelids handle waste products

As multi-cellular systems evolved to have organ systems that divided the metabolic needs of the body, individual organs evolved to perform the excretory function. Excretory cells known as flame cells developed in flatworms, while nephridia developed as excretory cells in annelids.

Flame Cells of Planaria

Planaria are flatworms that live in fresh water. Their excretory system consists of two tubules connected to a highly-branched duct system that leads to pores located all along the sides of the body. The filtrate is secreted through these pores. The cells in the tubules are called flame cells (or protonephridia) because they have a cluster of cilia that looks like a flickering flame when viewed under the microscope. Flame cells function like a kidney, removing waste materials through filtration. The cilia propel waste matter down the tubules and out of the body through excretory pores that open on the body surface; cilia also draw water from the interstitial fluid, allowing for filtration. After excretion, any useful metabolites are reabsorbed by the cell. Flame cells are found in freshwater invertebrates, such as flatworms, including parasitic tapeworms and free-living planaria.

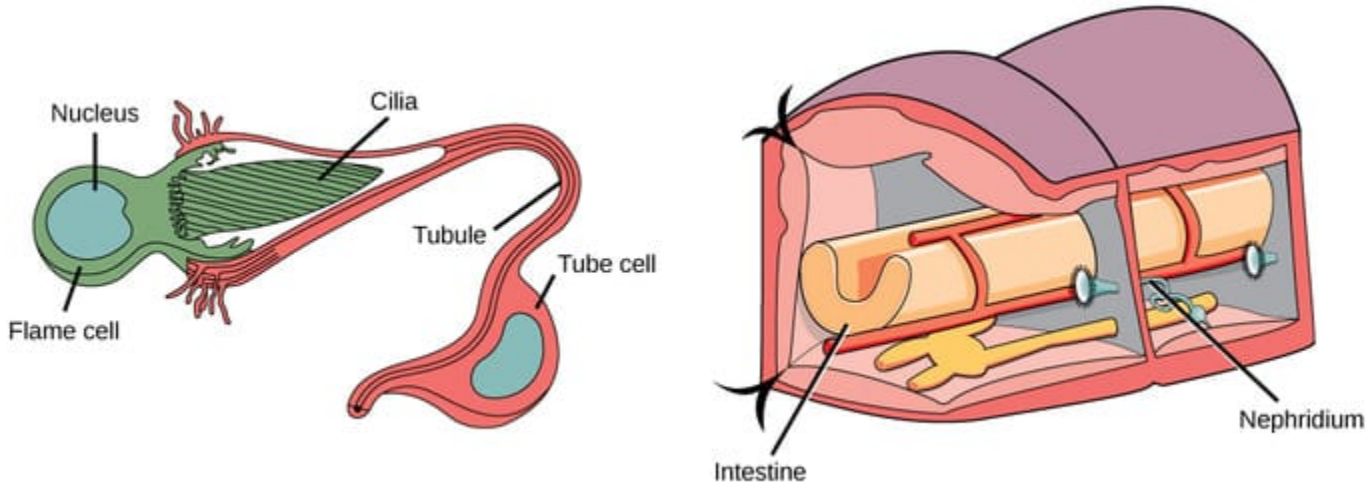


Figure 41.8.1: Flame cells and nephridia: In the excretory system of the (a) planaria, cilia of flame cells propel waste through a tubule formed by a tube cell. In (b) annelids, nephridia filter fluid from the body cavity.

Nephridia of Worms

Earthworms (annelids) and some other invertebrates, such as arthropods and mollusks, have slightly-more-evolved excretory structures called nephridia. A pair of nephridia is present on each segment of the earthworm. They are similar to flame cells in that they have tubules with cilia and function like a kidney to remove wastes, but they often open to the exterior of the organism. The ciliated tubules filter fluid from the body cavity and carry waste, including excess ions, through openings called nephrostomes. From the nephrostomes, excretion occurs through a pore called the nephridiopore. A nephridium is more evolved than a flame cell in that it has a system for reabsorption of some useful waste products, such as metabolites and ions, by a capillary network before excretion (unlike planaria that can only reabsorb useful metabolites after excretion).

Key Points

- Nephridia are more evolved than flame cells because they can reabsorb useful metabolites before excretion of waste.
- Both nephridia and flame cells are ciliated tubules that filter fluids in the cell to remove waste.
- Flame cells are connected to a duct system of pores to expel wastes, while nephridia often are open to the exterior of the organism.

Key Terms

- **flame cell**: a specialized excretory cell found in the simplest freshwater invertebrates
- **nephridium**: a tubular excretory organ in some invertebrates
- **nephridiopore**: the external opening of a nephridium, where waste is excreted from the cell
- **nephrostome**: the funnel-shaped opening of a nephridium into the body cavity

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41.9: Excretion Systems - Malpighian Tubules of Insects

Learning Objectives

- Explain how insects use malpighian tubules to excrete wastes and maintain osmotic balance

Malpighian tubules line the gut of some species of arthropods, such as bees. They are usually found in pairs in the posterior regions of arthropod alimentary canals; the number of tubules varies with the species of insect. The system of malpighian tubules consists of branching tubules, which increase their surface area, near the hemolymph (a mixture of blood and interstitial fluid that is found in insects, other arthropods, and most mollusks) and fat tissues. They are lined with microvilli for reabsorption and maintenance of osmotic balance. They contain actin for support.

Malpighian tubules work cooperatively with specialized glands in the wall of the rectum. Body fluids are not filtered, as in the case of nephridia. Instead, urine is produced by tubular secretion mechanisms by the cells lining the malpighian tubules that are bathed in hemolymph. Metabolic wastes, such as urea and amino acids, freely diffuse into the tubules, while ions are transported through active pump mechanisms. There are exchange pumps lining the tubules which actively transport H^+ ions into the cell and K^+ or Na^+ ions out; water passively follows to form urine. The secretion of ions alters the osmotic pressure, which draws water, electrolytes, and nitrogenous waste (uric acid) into the tubules. Water and electrolytes are reabsorbed when these organisms are faced with low-water environments and uric acid is precipitated and excreted as a thick paste or powder. By not dissolving wastes in water, these organisms are able to conserve water; this is especially important for life in dry environments.

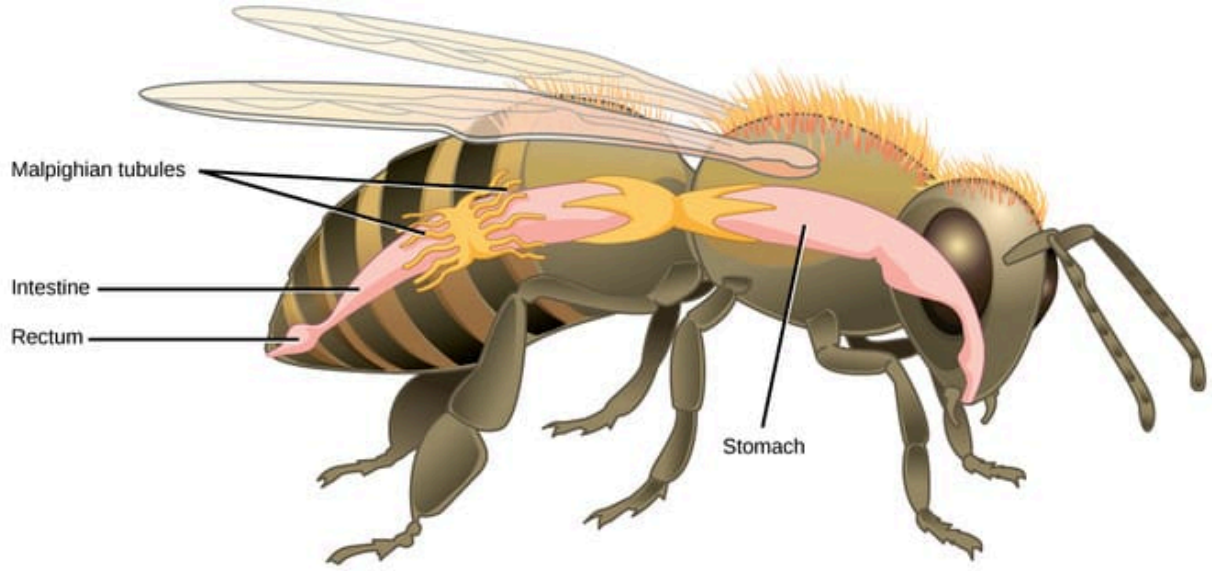


Figure 41.9.1: Malpighian tubules in bees: Malpighian tubules of insects and other terrestrial arthropods remove nitrogenous wastes and other solutes from the hemolymph.

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Key Points

- Malpighian tubules are found in the posterior regions of insects, where they work with glands in the rectum to excrete waste and maintain osmotic balance.
- Ions are transported through active pumps found in the malpighian tubules; as the ions are secreted, water and waste are drawn to the tubules due to the change in osmotic pressure.
- Nitrogenous wastes, such as uric acid, are precipitated as thick pastes or powder to be excreted.

Key Terms

- **malpighian tubule**: a tubule that extends from the alimentary canal to the exterior of the organism, excreting water and

wastes in the form of solid nitrogenous compounds

- **uric acid**: a bicyclic heterocyclic phenolic compound, formed in the body by the metabolism of protein and excreted in the urine
- **hemolymph**: a circulating fluid in the bodies of some invertebrates that is the equivalent of blood

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41.10: Human Osmoregulatory and Excretory Systems - Kidney Structure

Learning Objectives

- Explain how the kidneys serve as the main osmoregulatory organs in mammalian systems, using the functional properties of nephrons

Kidneys: The Main Osmoregulatory Organ

The kidneys are a pair of bean-shaped structures that are located just below and posterior to the liver in the peritoneal cavity. Adrenal glands, also called suprarenal glands, sit on top of each kidney. Kidneys regulate the osmotic pressure of a mammal's blood through extensive filtration and purification in a process known as osmoregulation. All the blood in the human body is filtered many times a day by the kidneys. These organs use almost 25 percent of the oxygen absorbed through the lungs to perform this function. Oxygen allows the kidney cells to efficiently manufacture chemical energy in the form of ATP through aerobic respiration. Kidneys eliminate wastes from the body; urine is the filtrate that exits the kidneys.

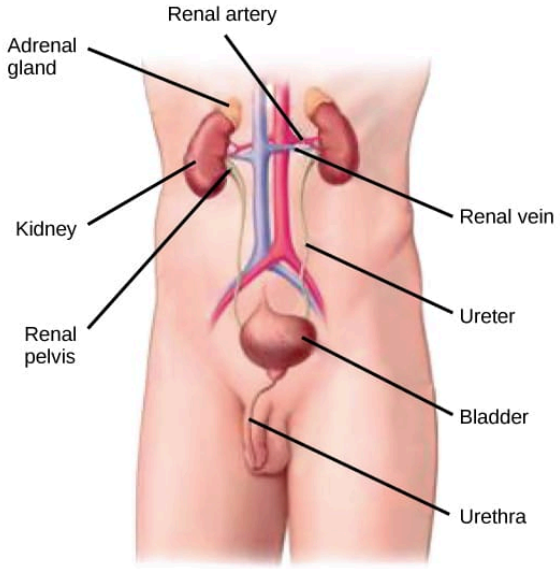


Figure 41.10.1: Kidneys' location and function: Kidneys filter the blood, producing urine that is stored in the bladder prior to elimination through the urethra. They are located in the peritoneal cavity.

Externally, the kidneys are surrounded by three layers. The outermost layer, the renal fascia, is a tough connective tissue layer. The second layer, the perirenal fat capsule, helps anchor the kidneys in place. The third and innermost layer is the renal capsule. Internally, the kidney has three regions: an outer cortex, a medulla in the middle, and the renal pelvis in the region called the hilum of the kidney. The hilum is the concave part of the bean-shape where blood vessels and nerves enter and exit the kidney; it is also the point of exit for the ureters.

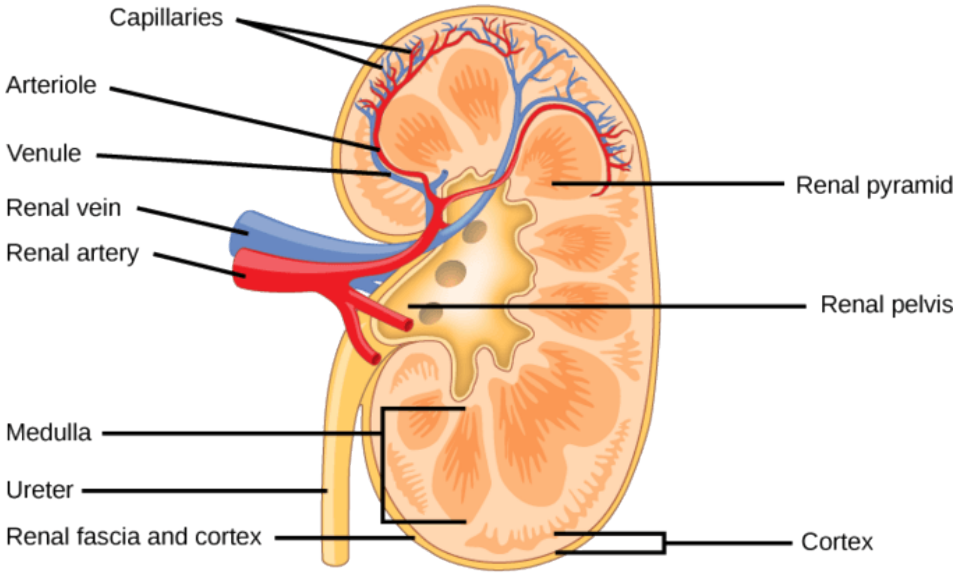


Figure 41.10.1: Structure of the kidney: Externally, the kidney is surrounded by the renal fascia, the perirenal fat capsule, and the renal capsule. Internally, the kidney is most importantly filled with nephrons that filter blood and generate urine.

Because the kidney filters blood, its network of blood vessels is an important component of its structure and function. The arteries, veins, and nerves that supply the kidney enter and exit at the renal hilum. Renal blood supply starts with the branching of the aorta into the renal arteries (which are each named based on the region of the kidney they pass through) and ends with the exiting of the renal veins to join the inferior vena cava. The renal arteries split into several segmental arteries upon entering the kidneys. Each segmental artery splits further into several interlobar arteries that enter the renal columns, which supply the renal lobes. The interlobar arteries split at the junction of the renal cortex and medulla to form the arcuate arteries. The arcuate, “bow shaped” arteries form arcs along the base of the medullary pyramids. Cortical radiate arteries, as the name suggests, radiate out from the arcuate arteries, branch into numerous afferent arterioles, and then enter the capillaries supplying the nephrons.

Key Points

- Kidneys regulate the osmotic pressure of a mammal’s blood through extensive filtration and purification, in a process known as osmoregulation.
- Kidneys filter the blood; urine is the filtrate that eliminates waste from the body via the ureter into the bladder.
- The kidneys are surrounded by three layers: renal fascia, perirenal fat capsule, and the renal capsule.

Key Terms

- **renal**: pertaining to the kidneys

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41.11: Human Osmoregulatory and Excretory Systems - Nephron- The Functional Unit of the Kidney

Learning Objectives

- Explain the role of the nephron as the functional unit of the kidney

The nephron, the functional unit of the kidney, is responsible for removing waste from the body. Each kidney is composed of over one million nephrons that dot the renal cortex, giving it a granular appearance when sectioned sagittally (from front to rear). Eighty-five percent of nephrons are cortical nephrons, deep in the renal cortex; the remaining 15 percent are juxtamedullary nephrons, which lie in the renal cortex close to the renal medulla.

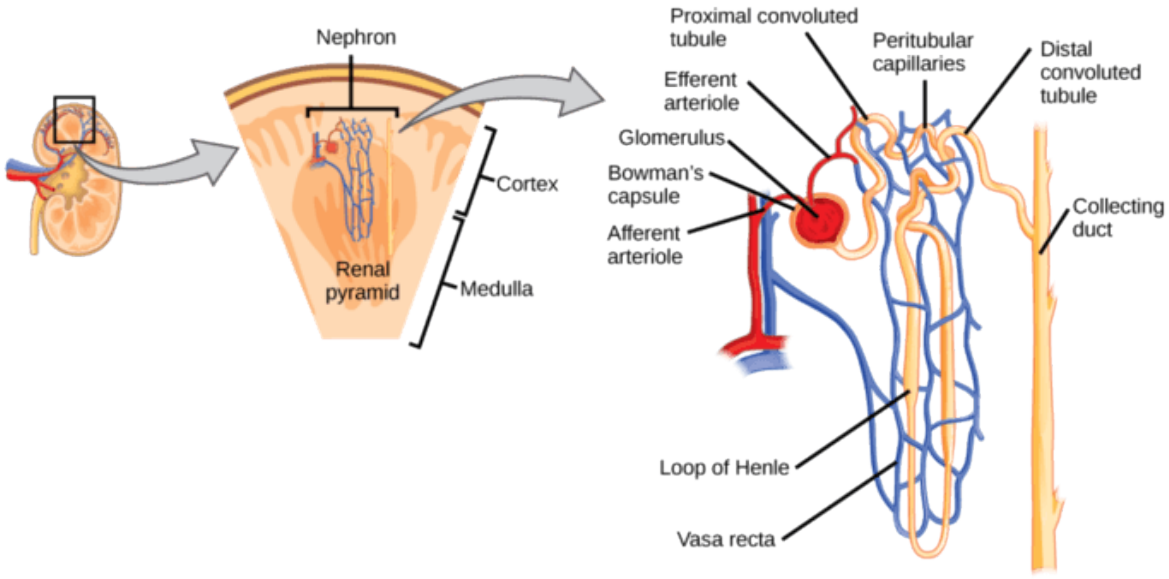


Diagram of a nephron

The nephron is the functional unit of the kidney. The glomerulus and convoluted tubules of the nephron are located in the cortex of the kidney, while the collecting ducts are located in the pyramids of the kidney's medulla.

A nephron consists of three parts: a renal corpuscle, a renal tubule, and the associated capillary network, which originates from the cortical radiate arteries. The renal corpuscle, located in the renal cortex, is composed of a network of capillaries known as the glomerulus, as well as a cup-shaped chamber that surrounds it: the glomerular or Bowman's capsule.

The renal tubule is a long, convoluted structure that emerges from the glomerulus. It can be divided into three parts based on function. The first part is called the proximal convoluted tubule (PCT), due to its proximity to the glomerulus. The second part is called the loop of Henle, or nephritic loop, because it forms a loop (with descending and ascending limbs) that goes through the renal medulla. The third part of the renal tubule is called the distal convoluted tubule (DCT); this part is also restricted to the renal cortex. This last part of the nephron connects with and empties its filtrate into collecting ducts that line the medullary pyramids. The collecting ducts amass contents from multiple nephrons, fusing together as they enter the papillae of the renal medulla.

As urine travels down the collecting duct system, it passes by the medullary interstitium, which has a high sodium concentration as a result of the loop of Henle's countercurrent multiplier system. Urine leaves the medullary collecting ducts through the renal papillae, emptying into the renal calyces, the renal pelvis, and finally into the bladder via the ureter.

Key Points

- Kidneys contain two types of nephrons, each located in different parts of the renal cortex: cortical nephrons and juxtamedullary nephrons.
- A nephron comprises a renal corpuscle, a renal tubule, and the associated capillary network.
- Internally, kidneys are mainly composed of over one million nephrons and an extensive network of blood vessels and capillaries.

Key Terms

- **glomerulus**: A small intertwined group of capillaries within a kidney's nephron that filters the blood to make urine.
- **loop of Henle**: A structure in a kidney's nephron that connects the proximal convoluted tubule to the distal convoluted tubule.

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41.12: Human Osmoregulatory and Excretory Systems - Kidney Function and Physiology

Learning Objectives

- Outline the process by which kidneys filter blood, reabsorb nutrients and water, and produce urine

Blood Filtration and Nutrient and Water Reabsorption

Kidneys filter blood in a three-step process. First, the nephrons filter blood that runs through the capillary network in the glomerulus. Almost all solutes, except for proteins, are filtered out into the glomerulus by a process called glomerular filtration. Second, the renal tubules collect the filtrate. Most of the solutes are reabsorbed in the PCT by a process called tubular reabsorption. In the loop of Henle, the filtrate continues to exchange solutes and water with the renal medulla and the peritubular capillary network.

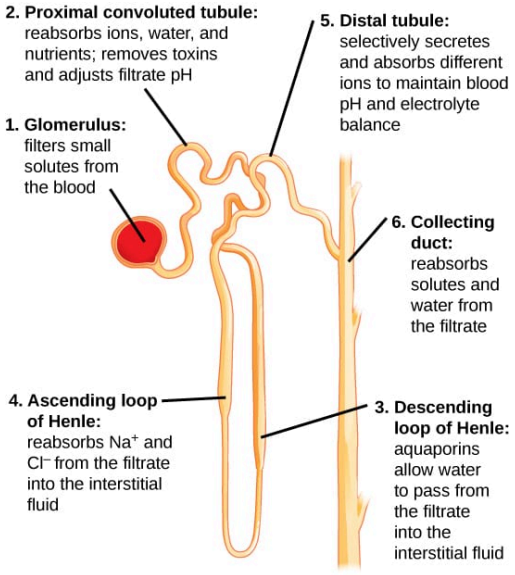


Figure 41.12.1: Nephron structure: Each part of the nephron performs a different function in filtering waste and maintaining homeostatic balance.

Finally, some substances, such as electrolytes and drugs, are removed from blood through the peritubular capillary network into the distal convoluted tubule or collecting duct. Urine is a collection of substances that have not been reabsorbed during glomerular filtration or tubular reabsorbtion.

Glomerular Filtration

The formation of urine occurs through three steps: glomerular filtration, tubular reabsorption, and tubular secretion. The process of glomerular filtration filters out most of the solutes due to the high blood pressure and specialized membranes in the afferent arteriole. The blood pressure in the glomerulus is maintained independent of factors that affect systemic blood pressure. The “leaky” connections between the endothelial cells of the glomerular capillary network allow solutes to pass through easily. All solutes in the glomerular capillaries, including sodium ions and negatively and positively charged ions, pass through by passive diffusion; the only exception is macromolecules such as proteins. There is no energy requirement at this stage of the filtration process. Glomerular filtration rate (GFR) is the volume of glomerular filtrate formed per minute by the kidneys. GFR is regulated by multiple mechanisms and is an important indicator of kidney function.

Tubular Reabsorption and Secretion

Tubular reabsorption occurs in the PCT part of the renal tubule. Almost all nutrients are reabsorbed; this occurs either by passive or active transport. Reabsorption of water and key electrolytes are regulated and influenced by hormones. Sodium (Na^+) is the most abundant ion; most of it is reabsorbed by active transport and then transported to the peritubular capillaries. Because Na^+ is actively transported out of the tubule, water follows to even out the osmotic pressure. Water is also independently reabsorbed into the peritubular capillaries due to the presence of aquaporins, or water channels, in the PCT. This occurs due to the low blood pressure and high osmotic pressure in the peritubular capillaries. Every solute, however, has a transport maximum; the excess solute is not reabsorbed. Kidneys' osmolarity of body fluids is maintained at 300 milliosmole (mOsm).

In the loop of Henle, the permeability of the membrane changes. The descending limb is permeable to water, not solutes; the opposite is true for the ascending limb. Additionally, the loop of Henle invades the renal medulla, which is naturally high in salt concentration. It tends to absorb water from the renal tubule and concentrate the filtrate. The osmotic gradient increases as it moves deeper into the medulla. Because two sides of the loop of Henle perform opposing functions, it acts as a countercurrent multiplier. The vasa recta around the loop of Henle acts as the countercurrent exchanger.

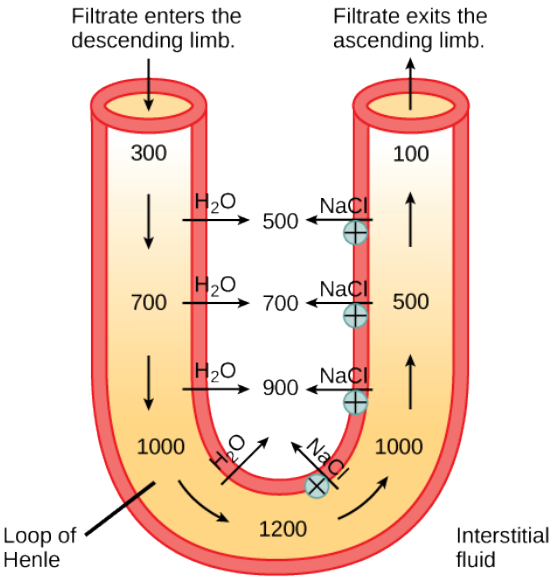


Figure 41.12.1: Loop of Henle: The loop of Henle acts as a countercurrent multiplier that uses energy to create concentration gradients. The descending limb is water permeable. Water flows from the filtrate to the interstitial fluid, so osmolality inside the limb increases as it descends into the renal medulla. At the bottom, the osmolality is higher inside the loop than in the interstitial fluid. Thus, as filtrate enters the ascending limb, Na+ and Cl- ions exit through ion channels present in the cell membrane. Further up, Na+ is actively transported out of the filtrate and Cl- follows. Osmolarity is given in units of milliosmoles per liter (mOsm/L).

Additional solutes and wastes are secreted into the kidney tubules during tubular secretion, which is the opposite process to tubular reabsorption. The collecting ducts collect filtrate coming from the nephrons and fuse in the medullary papillae. From here, the papillae deliver the filtrate, now called urine, into the minor calyces that eventually connect to the ureters through the renal pelvis.

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Key Points

- Glomerular filtration, tubular reabsorption, and tubular secretion are the three primary steps in which kidneys filter blood and maintain proper electrolyte balance.
- Glomerular filtration removes solutes from the blood; it is the first step of urine formation.
- In tubular reabsoption, the second step of urine formation, almost all nutrients are reabsorbed in the renal tubule by active or passive transport.
- Tubular secretion is the last step of urine formation, where solutes and waste are secreted into the collecting ducts, ultimately flowing to the bladder in the form of urine.

Key Terms

- **arteriole**: one of the small branches of an artery, especially one that connects with capillaries
- **countercurrent**: a current that flows against the prevailing one
- **electrolyte**: any of the various ions (such as sodium or chloride) that regulate the electric charge on cells and the flow of water across their membranes

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41.13: Hormonal Control of Osmoregulatory Functions - Epinephrine and Norepinephrine

Learning Objectives

- Describe hormonal control by epinephrine and norepinephrine of osmoregulatory functions

Epinephrine

As a hormone and neurotransmitter, epinephrine acts on nearly all body tissues. Its actions vary by tissue type and tissue expression of adrenergic receptors. For example, high levels of epinephrine cause smooth muscle relaxation in the airways, but cause contraction of the smooth muscle that lines most arterioles. Epinephrine acts by binding to a variety of adrenergic receptors. Epinephrine is a nonselective agonist of all adrenergic receptors, including the major subtypes α1, α2, β1, β2, and β3. Epinephrine's binding to these receptors triggers a number of metabolic changes. Binding to α-adrenergic receptors inhibits insulin secretion by the pancreas, stimulates glycogenolysis (the breakdown of glycogen) in the liver and muscle, and stimulates glycolysis (the metabolic pathway that converts glucose into pyruvate) in muscle. β-Adrenergic receptor binding triggers glucagon secretion in the pancreas, increased adrenocorticotropic hormone (ACTH) secretion by the pituitary gland, and increased lipolysis by adipose tissue. Together, these effects lead to increased blood glucose and fatty acids, providing substrates for energy production within cells throughout the body.

Norepinephrine

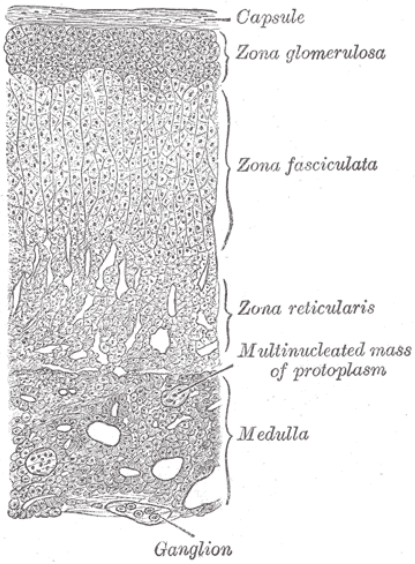


Figure 41.13.1: Adrenal gland: The adrenal medulla, located toward the bottom of this image, is responsible for the release of epinephrine and norepinephrine.

Norepinephrine is a catecholamine with multiple roles. It is the hormone and neurotransmitter most responsible for vigilant concentration in contrast to its most-chemically-similar hormone, dopamine, which is most responsible for cognitive alertness. Areas of the body that produce or are affected by norepinephrine are described as noradrenergic. One of the most important functions of norepinephrine is its role as the neurotransmitter released from the sympathetic neurons to affect the heart. An increase in norepinephrine from the sympathetic nervous system increases the rate of contractions in the heart. Norepinephrine also underlies the fight-or-flight response, along with epinephrine, directly increasing heart rate, triggering the release of glucose from energy stores, and increasing blood flow to skeletal muscle. When norepinephrine acts as a drug, it increases blood pressure by increasing vascular tone through α-adrenergic receptor activation. Norepinephrine is synthesized from dopamine by dopamine

β-hydroxylase in the secretory granules of the medullary chromaffin cells and is released from the adrenal medulla into the blood as a hormone. It is also a neurotransmitter in the central nervous system and sympathetic nervous system, where it is released from noradrenergic neurons in the locus coeruleus. The actions of norepinephrine are carried out via the binding to adrenergic receptors.

Role of Epinephrine and Norepinephrine in Kidney Function

Epinephrine and norepinephrine are released by the adrenal medulla and nervous system respectively. They are the flight/fight hormones that are released when the body is under extreme stress. During stress, much of the body's energy is used to combat imminent danger. Kidney function is halted temporarily by epinephrine and norepinephrine. These hormones function by acting directly on the smooth muscles of blood vessels to constrict them. Once the afferent arterioles are constricted, blood flow into the nephrons of the kidneys stops. These hormones go one step further and trigger the renin-angiotensin-aldosterone system, the hormone system that regulates blood pressure and water (fluid) imbalance.

Key Points

- Epinephrine, produced by the adrenal medulla, causes either smooth muscle relaxation in the airways or contraction of the smooth muscle in arterioles, which results in blood vessel constriction in the kidneys, decreasing or inhibiting blood flow to the nephrons.
- Norepinephrine, produced by the adrenal medulla, is a stress hormone that increases blood pressure, heart rate, and glucose from energy stores; in the kidneys, it will cause constriction of the smooth muscles, resulting in decreased or inhibited flow to the nephrons.
- Together, epinephrine and norepinephrine cause constriction of the blood vessels associated with the kidneys to inhibit flow to the nephrons.

Key Terms

- **epinephrine**: (adrenaline) an amino acid-derived hormone secreted by the adrenal gland in response to stress
- **norepinephrine**: a neurotransmitter found in the locus coeruleus which is synthesized from dopamine
- **catecholamine**: any of a class of aromatic amines derived from pyrocatechol that are hormones produced by the adrenal gland
- **adrenergic**: containing or releasing adrenaline

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41.14: Hormonal Control of Osmoregulatory Functions - Other Hormonal Controls for Osmoregulation

Learning Objectives

- Describe hormonal control by the renin-angiotensin-aldosterone system

Renin-Angiotensin-Aldosterone

The renin-angiotensin-aldosterone system (RAAS) is a hormone system that regulates blood pressure and water (fluid) balance. This system proceeds through several steps to produce angiotensin II, which acts to stabilize blood pressure and volume. Renin is secreted by a part of the juxtaglomerular complex and produced by the granular cells of the afferent and efferent arterioles. Renin is a circulating enzyme that acts on angiotensinogen, which is made in the liver, converting it to angiotensin I. Defective renin production can cause a continued decrease in blood pressure and cardiac output. After renin facilitates the production of angiotensis I, angiotensin converting enzyme (ACE) then converts angiotensin I to angiotensin II. Angiotensin II raises blood pressure by constricting blood vessels and also triggers the release of the mineralocorticoid aldosterone from the adrenal cortex. This, in turn, stimulates the renal tubules to reabsorb more sodium. Angiotensin II also triggers the release of anti-diuretic hormone (ADH) from the hypothalamus, leading to water retention in the kidneys. It acts directly on the nephrons, decreasing glomerular filtration rate. Thus, via the RAAS, the kidneys control blood pressure and volume directly. Medically, blood pressure can be controlled by drugs that inhibit ACE (called ACE inhibitors).

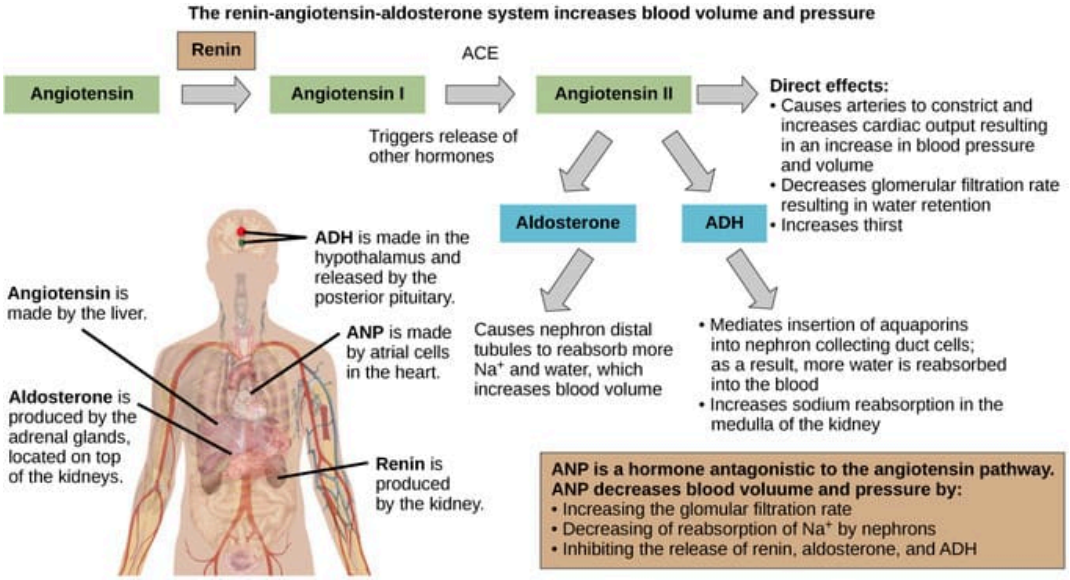


Figure 41.14.1: Renin-angiotensin-aldosterone system: The renin-angiotensin-aldosterone system increases blood pressure and volume. The hormone ANP has antagonistic effects.

Mineralocorticoids

Mineralocorticoids are hormones synthesized by the adrenal cortex that affect osmotic balance. One type of mineralocorticoid, known as aldosterone, regulates sodium levels in the blood. Almost all of the sodium in the blood is reclaimed by the renal tubules under the influence of aldosterone. As sodium is always reabsorbed by active transport and water follows sodium to maintain osmotic balance, aldosterone manages not only sodium levels, but also the water levels in body fluids. Aldosterone also stimulates potassium secretion concurrently with sodium reabsorption. By contrast, absence of aldosterone means that no sodium is reabsorbed in the renal tubules; all of it is excreted in the urine. In addition, the daily dietary potassium load is not secreted; retention of potassium ions (K+) can cause a dangerous increase in plasma K+ concentration. Patients who have

Addison's disease have a failing adrenal cortex and cannot produce aldosterone. They constantly lose sodium in their urine; if the supply is not replenished, the consequences can be fatal.

Antidiurectic Hormone

Antidiuretic hormone or ADH (also called vasopressin) helps the body conserve water when body fluid volume, especially that of blood, is low. It is formed by the hypothalamus, but is stored and released from the posterior pituitary gland. It acts by inserting aquaporins in the collecting ducts, promoting reabsorption of water. ADH also acts as a vasoconstrictor (constricting blood vessels) and increases blood pressure during hemorrhaging.

Atrial Natriuretic Peptide Hormone

The atrial natriuretic peptide (ANP) hormone lowers blood pressure by acting as a vasodilator (dilating or widening blood vessels). It is released by cells in the atrium of the heart in response to high blood pressure and in patients with sleep apnea. ANP affects salt release; because water passively follows salt to maintain osmotic balance, it also has a diuretic effect. ANP also prevents sodium reabsorption by the renal tubules, decreasing water reabsorption (thus acting as a diuretic) and lowering blood pressure. Its actions suppress the actions of aldosterone, ADH, and renin.

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42: THE IMMUNE SYSTEM

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42.1: Innate Immune Response - Innate Immune Response

Learning Objectives

- Explain the purpose of the immune system

The environment surrounding all of us consists of numerous pathogens: agents (usually microorganisms) that cause disease(s) in their hosts. A host is the organism that is invaded and often harmed by a pathogen. Pathogens, which include bacteria, protists, fungi, and other infectious organisms, can be found in food and water, on surfaces, and in the air. Concern over pathogens is one of the main reasons that we wash our hands after going to the bathroom or touching raw meat.

Mammalian immune systems evolved for protection from such pathogens. They are composed of an extremely-diverse array of specialized cells and soluble molecules that coordinate a rapid, flexible defense system capable of providing protection from a majority of these disease agents. Central to this goal, the immune system must be capable of recognizing “self” from “other” so that when it destroys cells, it destroys pathogen cells and not host cells.

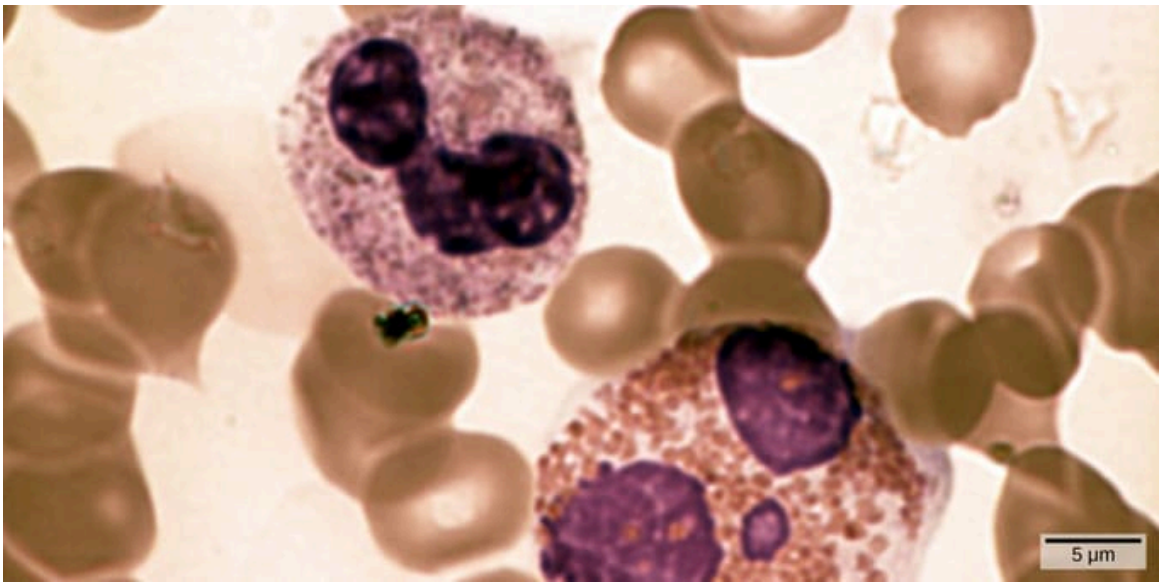


Figure 42.1.1: Neutrophils and eosinophils: In this compound light micrograph, purple-stained neutrophil (upper left) and eosinophil (lower right) are white blood cells that float among red blood cells in this blood smear. Neutrophils provide an early, rapid, and nonspecific defense against invading pathogens. Eosinophils play a variety of roles in the immune response.

The immune response that defends against pathogens can be classified as either innate or active. The innate immune response is present in its final state from birth and attempts to defend against all pathogens. Conversely, the adaptive immune response stores information about past infections and mounts pathogen-specific defenses. It expands over time, gaining more information about past targets so that it can respond quickly to future pathogens. The adaptive immune response functions throughout the body to combat specific pathogens that it has encountered before (a process known as reactivation). However, we are born with only innate immunity, developing our adaptive immune response after birth.

Components of both immune systems constantly search the body for signs of pathogens. When pathogens are found, immune factors are mobilized to the site of an infection. The immune factors identify the nature of the pathogen, strengthen the corresponding cells and molecules to combat it efficiently, and then halt the immune response after the infection is cleared to avoid unnecessary host cell damage. Features of the immune system (e.g., pathogen identification, specific response, amplification, retreat, and remembrance) are essential for survival against pathogens.

Key Points

- The mammalian immune system has evolved an extremely-diverse array of specialized cells and soluble molecules that allow it to defend against a variety of pathogens, including bacteria, protists, fungi, and other infectious organisms.
- The innate immune response serves as a general defense against all pathogens, but has no capacity to adapt or learn when new pathogens attack.
- The adaptive immune response has a “memory” about previously encountered pathogens and is able to mount pathogen-specific defenses based on this memory.

Key Terms

- **pathogen**: any organism or substance, especially a microorganism, capable of causing disease, such as bacteria, viruses, protozoa, or fungi
- **immune system**: the system that differentiates self from non-self and protects the body from foreign substances and pathogenic organisms by producing an immune response

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42.2: Innate Immune Response - Physical and Chemical Barriers

Learning Objectives

- Describe physical and chemical barriers in the innate immune response

The immune system comprises both innate and adaptive immune responses. Innate immunity occurs naturally due to genetic factors or physiology. It is not induced by infection or vaccination, but is constantly available to reduce the workload for the adaptive immune response. The adaptive immune response expands over time, storing information about past infections and mounting pathogen-specific defenses. Both the innate and adaptive levels of the immune response involve secreted proteins, receptor-mediated signaling, and intricate cell -to-cell communication. From an historical perspective, the innate immune system developed early in animal evolution, roughly a billion years ago, as an essential response to infection. In the innate immune response, any pathogenic threat triggers a consistent sequence of events that can identify the type of pathogen and either clear the infection independently or mobilize a highly-specialized adaptive immune response.

Before any immune factors are triggered, the skin (also known as the epithelial surface) functions as a continuous, impassable barrier to potentially-infectious pathogens. The skin is considered the first defense of the innate immune system; it is the first of the nonspecific barrier defenses. Pathogens are killed or inactivated on the skin by desiccation (drying out) and by the skin's acidity. In addition, beneficial microorganisms that coexist on the skin compete with invading pathogens, preventing infection. Desquamation, or peeling skin, also serves to dislodge organisms that have adhered to the surface of the body and are awaiting entry. Regions of the body that are not protected by skin (such as the eyes and mucous membranes) have alternative methods of defense. These include tears in the eyes; mucous membranes that provide partial protection despite having to allow absorption and secretion; mucus secretions that trap and rinse away pathogens; and cilia (singular cilium) in the nasal passages and respiratory tract that push the mucus with the pathogens out of the body. Furthermore, tears and mucus secretions contain microbicidal factors that prevent many infections from entering via these routes.

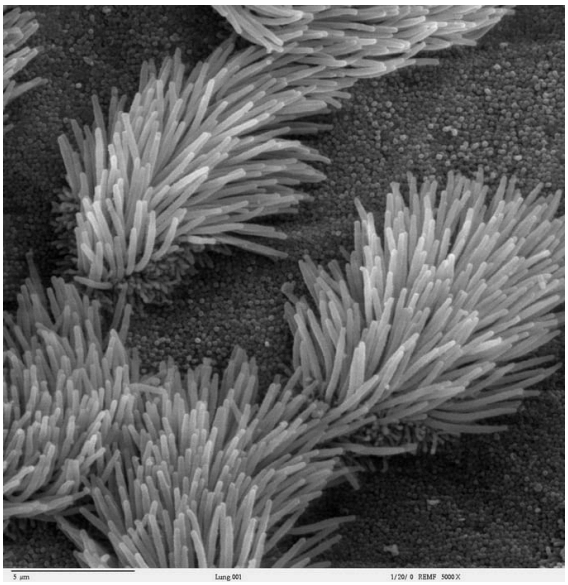


Figure 42.2.1: Cilia up close: Cilia are a type of organelle found in eukaryotic cells. In the innate immune system, they serve to move pathogens out of the respiratory system via a concerted sweeping motion.

Despite these barriers, pathogens may enter the body through skin abrasions or punctures, or by collecting on mucosal surfaces in large numbers that overcome the mucus or cilia. Some pathogens have evolved specific mechanisms that allow them to overcome physical and chemical barriers.

Once inside, the body still has many other defenses, including chemical barriers. Some of these include the low pH of the

stomach, which inhibits the growth of pathogens; blood proteins that bind and disrupt bacterial cell membranes; and the process of urination, which flushes pathogens from the urinary tract. The blood-brain barrier also protects the nervous system from pathogens that have already entered the blood stream, but would do significantly more damage if they entered the central nervous system.

Key Points

- The skin, or epithelial surface, serves as the primary barrier to microbial entry into the body; skin peeling, drying out, and the skin's acidity all serve to dislodge or kill foreign pathogens.
- Orifices such as the eyes and mouth, which are not covered by skin, have other mechanisms by which they prevent entry; tears wash away microbes, while cilia in the nasal passages and respiratory tract push mucus (which traps pathogens) out of the body.
- Many chemical barriers also exist once pathogens make it past the outer physical barriers; the acidity of the stomach ensures that few organisms arriving with food survive the digestive system.

Key Terms

- **cilium**: a hairlike organelle projecting from a eukaryotic cell (such as unicellular organism or one cell of a multicelled organism), which serves either for locomotion by moving or as sensors
- **microbicidal**: functioning to reduce the infectivity of microbes

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42.3: Innate Immune Response - Pathogen Recognition

Learning Objectives

- Describe the role of PAMPs and PRRs, interferons, and other cytokines in innate immunity

When a pathogen enters the body, cells in the blood and lymph detect the specific pathogen-associated molecular patterns (PAMPs) on the pathogen's surface. PAMPs are carbohydrate, polypeptide, and nucleic acid "signatures" that are expressed by viruses, bacteria, and parasites, but which differ from molecules on host cells. These PAMPs allow the immune system to recognize "self" from "other" so as not to destroy the host.

The immune system has specific cells with receptors that recognize these PAMPs. A macrophage is a large, phagocytic cell that engulfs foreign particles and pathogens. Macrophages recognize PAMPs via complementary pattern recognition receptors (PRRs). PRRs are molecules on macrophages and dendritic cells which are in contact with the external environment and can thus recognize PAMPs when present. A monocyte, a type of leukocyte (white blood cell) that circulates in the blood and lymph, differentiates into macrophages after it moves into infected tissue. Dendritic cells bind molecular signatures of pathogens, promoting pathogen engulfment and destruction.

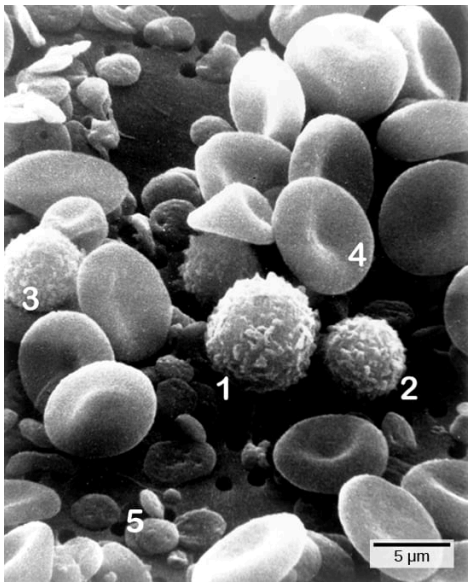


Figure 42.3.1: Blood cells related to the innate immune response: Cells of the blood include (1) monocytes, (2) lymphocytes, (3) neutrophils, (4) red blood cells, and (5) platelets. Leukocytes (1, 2, 3) are white blood cells that play an important role in the body's immune system.

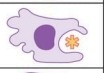
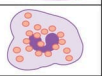
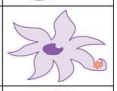
Cell type	Characteristics	Location	Image
Mast cell	Dilates blood vessels and induces inflammation through release of histamines and heparin. Recruits macrophages and neutrophils. Involved in wound healing and defense against pathogens but can also be responsible for allergic reactions.	Connective tissues, mucous membranes	
Macrophage	Phagocytic cell that consumes foreign pathogens and cancer cells. Stimulates response of other immune cells.	Migrates from blood vessels into tissues.	
Natural killer cell	Kills tumor cells and virus-infected cells.	Circulates in blood and migrates into tissues.	
Dendritic cell	Presents antigens on its surface, thereby triggering adaptive immunity.	Present in epithelial tissue, including skin, lung and tissues of the digestive tract. Migrates to lymph nodes upon activation.	
Monocyte	Differentiates into macrophages and dendritic cells in response to inflammation.	Stored in spleen, moves through blood vessels to infected tissues.	
Neutrophil	First responders at the site of infection or trauma, this abundant phagocytic cell represents 50-60 percent of all leukocytes. Releases toxins that kill or inhibit bacteria and fungi and recruits other immune cells to the site of infection.	Migrates from blood vessels into tissues.	
Basophil	Responsible for defense against parasites. Releases histamines that cause inflammation and may be responsible for allergic reactions.	Circulates in blood and migrates to tissues.	
Eosinophil	Releases toxins that kill bacteria and parasites but also causes tissue damage.	Circulates in blood and migrates to tissues.	

Figure 42.3.1: Cells involved in the innate immune system: The immune system has specific cells whose job is to recognize pathogen-associated molecular patterns. The characteristics and location of cells involved in the innate immune system are described in this chart.

Once a pathogen is detected, the immune system must also track whether it is replicating intracellularly (inside the cell, as with most viruses and some bacteria) or extracellularly (outside of the cell, as with other bacteria, but not viruses). The innate immune system must respond accordingly by identifying the extracellular pathogen and/or by identifying host cells that have already been infected.

Cytokine release affect

The binding of PRRs with PAMPs triggers the release of cytokines, which signal that a pathogen is present and needs to be destroyed along with any infected cells. A cytokine is a chemical messenger that regulates cell differentiation (form and function), proliferation (production), and gene expression to affect immune responses. At least 40 types of cytokines exist in humans that differ in terms of the cell type that produces them, the cell type that responds to them, and the changes they produce.

One subclass of cytokines is the interleukin (IL), which mediates interactions between leukocytes (white blood cells). Interleukins are involved in bridging the innate and adaptive immune responses. In addition to being released from cells after PAMP recognition, cytokines are released by the infected cells which bind to nearby uninfected cells, inducing those cells to release cytokines, resulting in a cytokine burst.

A second class of cytokines is interferons, which are released by infected cells as a warning to nearby uninfected cells. A function an interferons is to inhibit viral replication, making them particularly effective against viruses. They also have other important functions, such as tumor surveillance. Interferons work by signaling neighboring uninfected cells to destroy RNA (often a very important biomolecule for viruses) and reduce protein synthesis; signaling neighboring infected cells to undergo apoptosis (programmed cell death); and activating immune cells.

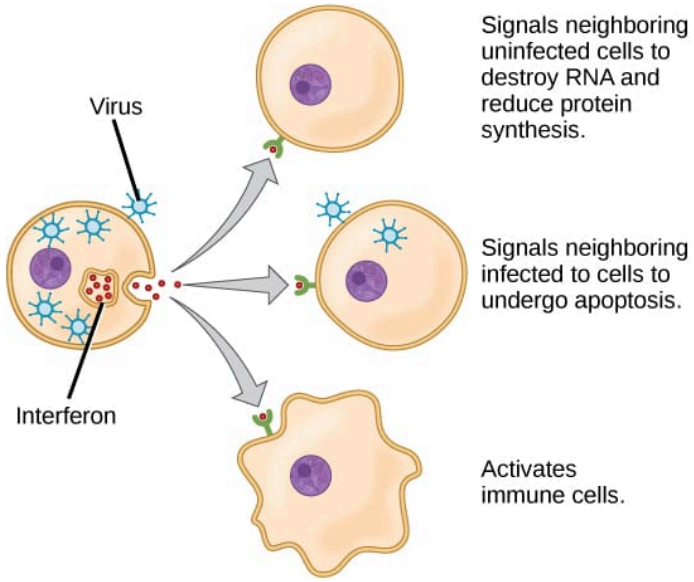


Figure 42.3.1: Interferon release: Interferons are cytokines that are released by a cell infected with a virus. The response of neighboring cells to interferons helps stem the infection.

Cytokines also send feedback to cells of the nervous system to bring about the overall symptoms of feeling sick, which include lethargy, muscle pain, and nausea. These effects may have evolved because the symptoms encourage the individual to rest, preventing them from spreading the infection to others. Cytokines also increase the core body temperature, causing a fever, which causes the liver to withhold iron from the blood. Without iron, certain pathogens (such as some bacteria) are unable to replicate; this is called nutritional immunity.

Phagocytosis and inflammation

The first cytokines to be produced are pro-inflammatory; that is, they encourage inflammation, or the localized redness, swelling (edema), heat, loss of function, and pain that result from the movement of leukocytes and fluid through increasingly-permeable capillaries to a site of infection. The population of leukocytes that arrives at an infection site depends on the nature of the infecting pathogen. Both macrophages and dendritic cells engulf pathogens and cellular debris through phagocytosis. A neutrophil is also a phagocytic leukocyte that engulfs and digests pathogens. Neutrophils, the most-abundant leukocytes of the immune system, have a nucleus with two to five lobes and contain organelles (lysosomes) that digest engulfed pathogens. An eosinophil is a leukocyte that works with other eosinophils to surround a parasite. It is involved in the allergic response and in protection against helminthes (parasitic worms).

Neutrophils and eosinophils are particularly important leukocytes that engulf large pathogens, such as bacteria and fungi. A mast cell is a leukocyte that produces inflammatory molecules, such as histamine, in response to large pathogens. A basophil is a leukocyte that, like a neutrophil, releases chemicals to stimulate the inflammatory response. Basophils are also involved in allergy and hypersensitivity responses and induce specific types of inflammatory responses. Eosinophils and basophils produce additional inflammatory mediators to recruit more leukocytes. A hypersensitive immune response to harmless antigens, such as in pollen, often involves the release of histamine by basophils and mast cells; this is why many anti-allergy medications are anti-histamines.

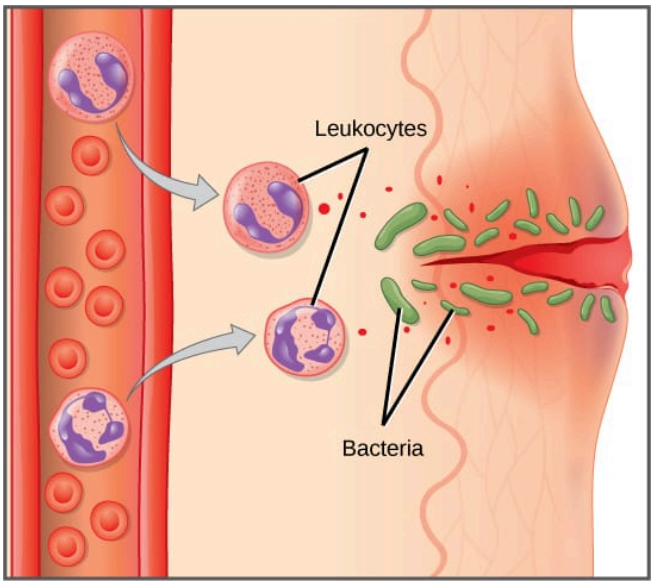


Figure 42.3.1: Innate immune response to cuts: In response to a cut, mast cells secrete histamines that cause nearby capillaries to dilate. Neutrophils and monocytes leave the capillaries. Monocytes mature into macrophages. Neutrophils, dendritic cells, and macrophages release chemicals to stimulate the inflammatory response. Neutrophils and macrophages also consume invading bacteria by phagocytosis.

Key Points

- Pathogens are recognized by a variety of immune cells, such as macrophages and dendritic cells, via pathogen-associated molecular patterns (PAMPs) on the pathogen surface, which interact with complementary pattern-recognition receptors (PRRs) on the immune cells' surfaces.
- Upon binding of PRRs with PAMPs (pathogen recognition), immune cells release cytokines to tell other cells to start fighting back.
- One class of cytokines, interferons, warn nearby uninfected cells of impending infection, cause cells to start cleaving RNA and reduce protein synthesis, and signal nearby infected cells to undergo apoptosis.
- Another class of cytokines, called inerleukins, mediate interactions between white blood cells (leukocytes) and help bridge the innate and adaptive immune responses.
- Inflammation (hot, red, swollen, painful tissue associated with infection) is encouraged by cytokines that are produced immediately upon pathogen recognition; the increase in blood flow associated with inflammation allows more leukocytes (a type of innate immune cell) to reach the infected area.

Key Terms

- **macrophage**: a white blood cell that phagocytizes necrotic cell debris and foreign material, including viruses, bacteria, and tattoo ink; part of the innate immune system
- **phagocytosis**: the process where a cell incorporates a particle by extending pseudopodia and drawing the particle into a vacuole of its cytoplasm
- **cytokine**: any of various small regulatory proteins that regulate the cells of the immune system; they are released upon binding of PRRs to PAMPS

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42.4: Innate Immune Response - Natural Killer Cells

Learning Objectives

- Describe the role of natural killer cells in the immune response

Lymphocytes are leukocytes (white blood cells) that are histologically identifiable by their large, darkly-staining nuclei; they are small cells with very little cytoplasm. After a pathogen enters the body, infected cells are identified and destroyed by natural killer (NK) cells, which are a type of lymphocyte that can kill cells infected with viruses or tumor cells (abnormal cells that uncontrollably divide and invade other tissue). While NK cells are part of the innate immune response, they are best understood relative to their counterparts in the adaptive immune response,T cells, which are also classified as lymphocytes.

T cells are lymphocytes that mature in the thymus gland and identify intracellular infections, especially from viruses, by the altered expression of major histocompatibility class (MHC) I molecules on the surface of infected cells. MHC I molecules are proteins on the surfaces of all nucleated cells which help the immune system distinguish between “self” and “non-self.” If the cell is infected, the MHC I molecules display fragments of proteins from the infectious agents to T-cells. Healthy cells do not display any proteins and will be ignored by the immune system, while the cells identified as “non-self” by foreign proteins will be attacked by the immune system.

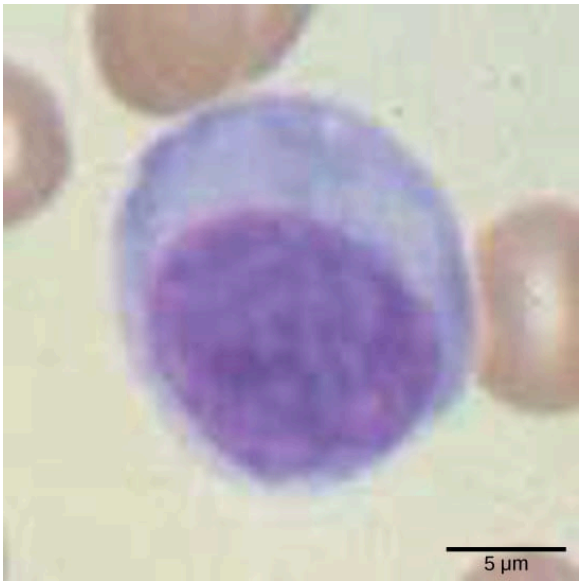


Figure 42.4.1: Lymphocytes: Lymphocytes, such as NK cells, are characterized by their large nuclei that actively absorb Wright stain and, therefore, appear dark colored under a microscope.

An infected cell (or a tumor cell) is often incapable of synthesizing and displaying MHC I molecules appropriately. The metabolic resources of cells infected by some viruses produce proteins that interfere with MHC I processing and/or trafficking to the cell surface. The reduced MHC I on host cells varies from virus to virus and results from active inhibitors being produced by the viruses. This process can deplete host MHC I molecules on the cell surface, which prevents T-cells from recognizing them, but which NK cells detect as “unhealthy” or “abnormal” while searching for cellular MHC I molecules. As such, NK cells offer a complementary check for unhealthy cells, relative to T cells. Similarly, the dramatically-altered gene expression of tumor cells leads to expression of extremely- deformed or absent MHC I molecules that also signal “unhealthy” or “abnormal.”

NK cells are always active; an interaction with normal, intact MHC I molecules on a healthy cell disables the killing sequence, causing the NK cell to move on. After the NK cell detects an infected or tumor cell, its cytoplasm secretes granules comprised of perforin: a destructive protein that creates a pore in the target cell. Granzymes are released along with the perforin in the immunological synapse. A granzyme, a protease that digests cellular proteins, induces the target cell to undergo programmed cell death, or apoptosis. Phagocytic cells then digest the cell debris left behind. NK cells are constantly patrolling the body. They are an effective mechanism for controlling potential infections and preventing cancer progression.

Key Points

- Natural killer (NK) cells are lymphocytes (a subclass of white blood cells) that recognize infected or tumorogenic cells and kill them.
- Unlike the related T cells, NK cells do not recognize fragments of the infecting particle, but rather the incorrect display of major histocompatibility complex (MHC) I molecules.
- NK cells are always active, but will not perform their killing function on cells with intact MHC I molecules.
- When NK cells detect an infected or tumor cell, they secrete granules that contain perforin, creating a pore in the target cell; granzymes then pass through these pores, degrading cellular proteins, causing cells to undergo apoptosis.

Key Terms

- **lymphocyte**: a type of white blood cell or leukocyte that is divided into two principal groups and a null group: B-cells, T-cells, and natural killer (NK) cells
- **major histocompatibility complex**: a protein present on the extracellular surface of the cell that displays portions of the proteins that are degraded inside the cell
- **T cell**: a lymphocyte, from the thymus, that can recognize specific antigens and can activate or deactivate other immune cells

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42.5: Innate Immune Response - The Complement System

Learning Objectives

- Explain how the complement system aids antibody response

Complement

The innate immune system serves as a first responder to pathogenic threats that bypass natural physical and chemical barriers of the body. Using a combination of cellular and molecular attacks, the innate immune system identifies the nature of a pathogen and responds with inflammation, phagocytosis (where a cell engulfs a foreign particle), cytokine release, destruction by NK cells, and/or a complement system. In this concept, we will discuss the complement system.

An array of approximately 20 types of soluble proteins, called a complement system, functions to destroy extracellular pathogens. Cells of the liver and macrophages synthesize complement proteins continuously. These proteins are abundant in the blood serum and are capable of responding immediately to infecting microorganisms. The complement system is so named because it is complementary to the antibody response of the adaptive immune system. Complement proteins bind to the surfaces of microorganisms and are particularly attracted to pathogens that are already bound by antibodies. Binding of complement proteins occurs in a specific and highly-regulated sequence, with each successive protein being activated by cleavage and/or structural changes induced upon binding of the preceding protein(s). After the first few complement proteins bind, a cascade of sequential binding events follows in which the pathogen rapidly becomes coated in complement proteins.

Complement proteins perform several functions. They serve as a marker to indicate the presence of a pathogen to phagocytic cells, such as macrophages and B cells, to enhance engulfment. This process is called opsonization. Certain complement proteins can combine to form attack complexes that open pores in microbial cell membranes. These structures destroy pathogens by causing their contents to leak. When innate mechanisms are insufficient to clear an infection, the adaptive immune response is informed and mobilized.

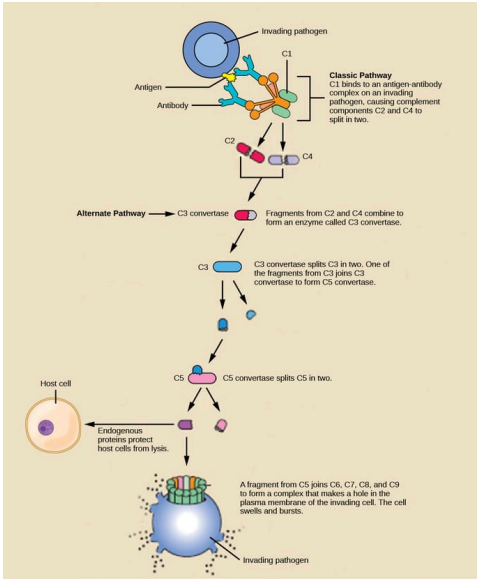


Figure 42.5.1: Complement cascade in the innate immune response: The classic pathway for the complement cascade involves the attachment of several initial complement proteins to an antibody-bound pathogen, followed by rapid activation and binding of many more complement proteins and the creation of destructive pores in the microbial cell envelope and cell wall. The alternate pathway does not involve antibody activation. Rather, C3 convertase spontaneously breaks down C3. Endogenous regulatory proteins prevent the complement complex from binding to host cells. Pathogens lacking these regulatory proteins are lysed.

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Key Points

- The complement system is so named because it is complementary to the antibody response of the adaptive immune system.
- The complement system proteins are produced continuously by the liver and macrophages, are abundant in the blood serum, and are capable of immediate response to infecting microorganisms.
- The complement system works by first having several proteins bind to a target; this binding event then begins a series of highly-specific and regulated sequences wherein successive proteins are activated by cleavage and/or structural changes of the preceding proteins.
- The complement system serves as a marker to indicate targets for phagocytic cells; complement proteins can also combine to form attack complexes capable of opening pores in microbial cell membranes.

Key Terms

- **opsonization**: the process by which a pathogen is marked for ingestion and destruction by a phagocyte
- **complement system**: an aspect of the innate immune system that supplements the actions of the antibodies and phagocytic cells in clearing out pathogens from an organism

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42.6: Adaptive Immune Response - Antigen-presenting Cells- B and T cells

Learning Objectives

- Explain the role played by B and T cells in the adaptive immune system

Introduction

The adaptive, or acquired, immune response to an initial infection takes days or even weeks to become established, much longer than the innate response. However, adaptive immunity is more specific to an invading pathogen and can fight back much more quickly than the innate response if it has seen the pathogen before. Adaptive immunity occurs after exposure to an antigen either from a pathogen or a vaccination. An antigen is a molecule that binds to a specific antibody, often stimulating a response in the immune system as a result.

The adaptive immune response activates when the innate immune response insufficiently controls an infection. In fact, without information from the innate immune system, the adaptive response could not be mobilized. There are two types of adaptive responses: the cell-mediated immune response, which is controlled by activated T cells, and the humoral immune response, which is controlled by activated B cells and antibodies. Upon infection, activated T and B cells that have surface binding sites with specificity to the molecules on the pathogen greatly increase in number and attack the invading pathogen. Their attack can kill pathogens directly or they can secrete antibodies that enhance the phagocytosis of pathogens and disrupt the infection. Adaptive immunity also involves a memory, which gives the host long-term protection from reinfection by the same type of pathogen; upon re-exposure, this host memory will facilitate a rapid and powerful response.

B and T Cells

Lymphocytes, which are white blood cells, are formed with other blood cells in the red bone marrow found in many flat bones, such as the shoulder or pelvic bones. The two types of lymphocytes of the adaptive immune response are B and T cells. Whether an immature lymphocyte becomes a B cell or T cell depends on where in the body it matures. The B cells remain in the bone marrow to mature (hence the name “B” for “bone marrow”), while T cells migrate to the thymus, where they mature (hence the name “T” for “thymus”).

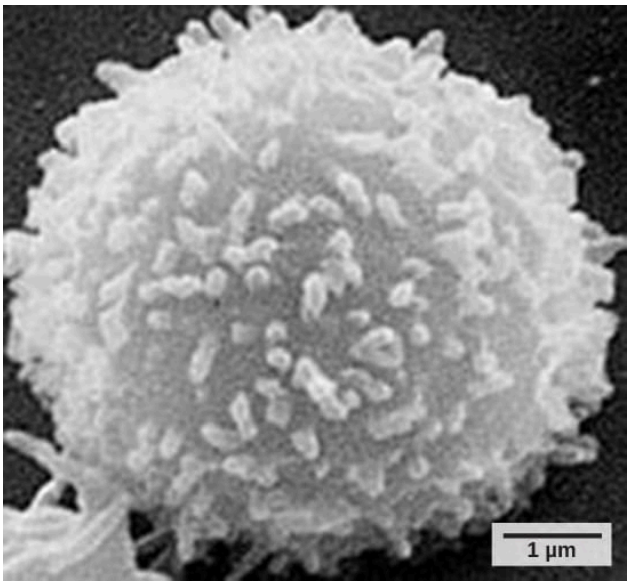


Figure 42.6.1: T cell by SEM: This scanning electron micrograph shows a T lymphocyte. T and B cells are indistinguishable by light microscopy, but can be differentiated experimentally by probing their surface receptors.

B Cell Receptors

The maturation of a B or T cell involves becoming immunocompetent, meaning that it can recognize and bind to a specific molecule or antigen. This recognition, which is central to the functioning of the adaptive immune response, results from the presence of highly specific receptors on the surfaces of B and T cells. On B cells, these receptors contain antibodies, which are responsible for antigen binding. An antibody is specific for one particular antigen; typically, it will not bind to anything else. Upon antigen binding to a B cell receptor, a signal is sent into the B cell to turn on an immune response.

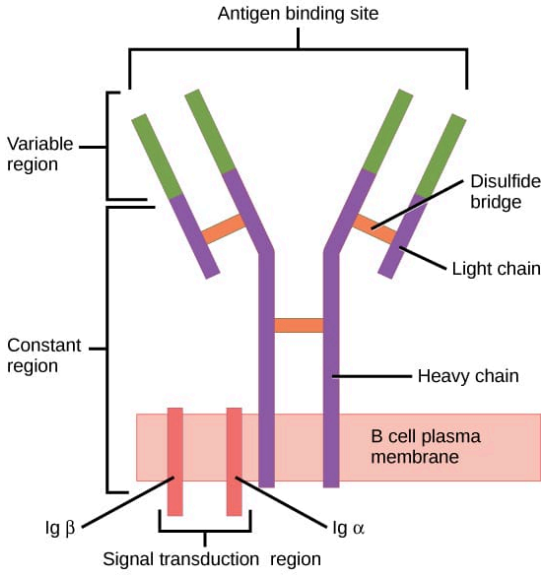


Figure 42.6.1: B cell receptors: B cell receptors are embedded in the membranes of B cells and bind a variety of antigens through their variable regions, or antibodies. The signal transduction region transfers the signal into the cell.

T Cell Receptors

Meanwhile, T cell receptors are responsible for the recognition of pathogenic antigens by T cells. Unlike B cells, T cells do not directly recognize antigens. Instead, they recognize antigens presented on major histocompatibility complexes (MHCs) that cells use to display which proteins are inside of them. If a cell is infected, it will present antigenic portions of the infecting pathogen on

its MHC for recognition by T cells, which will then mount an appropriate immune response. Unlike antibodies, which can typically bind one and only one antigen, T cell receptors have more flexibility in their capacity to recognize antigens presented by MHCs.

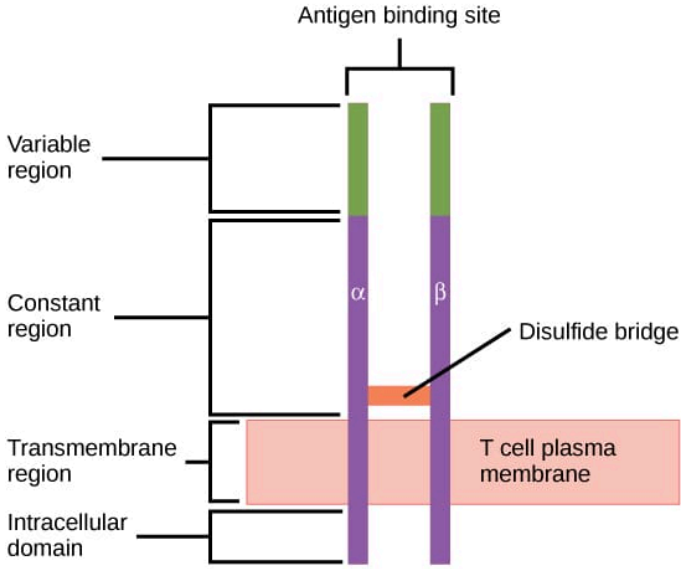


Figure 42.6.1: T cell receptors (TCRs): A T cell receptor spans the membrane and projects variable binding regions into the extracellular space to bind processed antigens via MHC molecules on APCs.

It is the specific pathogen recognition (via binding antigens) of B and T cells that allows the adaptive immune response to adapt. During the maturation process, B and T cells that bind too strongly to the body's own cells' antigens are eliminated in order to minimize an immune response against the body's own tissues. Only those cells that react weakly to the body's own cells will remain. This process occurs during fetal development and continues throughout life. Once they are immunocompetent, the T and B cells migrate to the spleen and lymph nodes where they remain until they are called on during an infection. B cells are involved in the humoral immune response, which targets pathogens loose in blood and lymph, while T cells are involved in the cell-mediated immune response, which targets infected cells.

Key Points

- The adaptive immune response is slower to develop than the innate immune response, but it can act much more powerfully and quickly than the innate immune response against pathogens that it has seen before.
- B and T cells are lymphocytes, or white blood cells, which are able to recognize antigens that distinguish "self" from "other" in the body.
- B and T cells that recognize "self" antigens are destroyed before they can mature; this helps to prevent the immune system from attacking its own body.

Key Terms

- **B cell**: a lymphocyte, developed in the bursa of birds and the bone marrow of other animals, that produces antibodies and is responsible for the immune system
- **T cell**: a lymphocyte, from the thymus, that can recognize specific antigens and can activate or deactivate other immune cells
- **antigen**: a substance that binds to a specific antibody; may cause an immune response

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42.7: Adaptive Immune Response - Humoral Immune Response

Learning Objectives

- Summarize the humoral immune response

The humoral immune response fights pathogens that are free in the bodily fluids, or “humours”. It relies on antigens (which are also often free in the humours) to detect these pathogens. An antigen is a biomolecule, such as a protein or sugar, that binds to a specific antibody. An antibody/antigen interaction may stimulate an immune response. Not every biomolecule is antigenic and not all antigens produce an immune response. B cells are the major cell type involved in the humoral immune response. When a foreign antigen (one coming from a pathogen, for example) is detected, B cells in the body that recognize that antigen will begin to produce antibodies as a means of fighting off the foreign invader.

B cell maturation

During maturation, B cells gain antigen receptor molecules, termed B cell receptors (BCRs), which are displayed in large numbers, extracellularly on their membrane. These membrane-bound protein complexes contain antibodies, which enable specific antigen recognition. Each B cell initially produced has only one kind of antibody (antigen receptor), which makes every B cell unique. It is the immense number of B cells in the body, each of which produces a unique antibody, that allows the immune system to detect such a wide variety of pathogenic antigens. B cells containing antibodies that recognize “self” antigens are destroyed before they can mature, preventing the immune system from attacking the host. Once B cells mature in the bone marrow, they migrate to lymph nodes or other lymphatic organs, where they may begin to encounter pathogens.

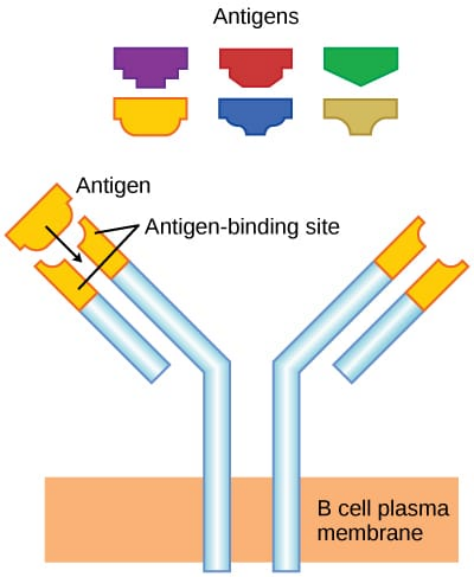


Figure 42.7.1: B cell receptors: B cell receptors, containing antibodies (termed antigen-binding site in the picture) are embedded in the membranes of B cells and bind a variety of antigens through their variable regions.

B cell activation

When a B cell encounters the antigen that binds to its receptor, the antigen molecule is brought into the cell by endocytosis, reappearing on the surface of the cell bound to an MHC class II molecule. When this process is complete, the B cell is sensitized. In most cases, the sensitized B cell must then encounter a specific kind of T cell, called a helper T cell, before it is activated. This activation of the helper T cell occurs when a dendritic cell presents an antigen on its MHC II molecule, allowing the T cell to

recognize it and mature.

The helper T cell binds to the antigen-MHC class II complex and is induced to release cytokines that induce the B cell to divide rapidly, making thousands of identical (clonal) cells. These daughter cells become either plasma cells or memory B cells. The memory B cells remain inactive at this point. A later encounter with the antigen, caused by a reinfection by the same bacteria or virus, will result in them dividing into a new population of plasma cells. The plasma cells, on the other hand, produce and secrete large quantities, up to 100 million molecules per hour, of antibody molecules. An antibody, also known as an immunoglobulin (Ig), is a protein that is produced by plasma cells after stimulation by an antigen. Antibodies are the agents of humoral immunity. Antibodies occur in the blood, in gastric and mucus secretions, and in breast milk. Antibodies in these bodily fluids can bind pathogens and mark them for destruction by phagocytes before they are able to infect cells.

Antibodies

These antibodies circulate in the blood stream and lymphatic system, binding with the antigen whenever it is encountered. The binding can fight infection in several ways. Antibodies can bind to viruses or bacteria, which interferes with the chemical interactions required for them to infect or bind to other cells. The antibodies may create bridges between different particles containing antigenic sites, clumping them all together and preventing their proper functioning. Antibody neutralization can prevent pathogens from entering and infecting host cells. The neutralized antibody-coated pathogens can then be filtered by the spleen to be eliminated in urine or feces. The antigen-antibody complex stimulates the complement system described previously, destroying the cell bearing the antigen. Antibodies also opsonize pathogen cells, wherein they mark them for destruction by phagocytic cells, such as macrophages or neutrophils. Additionally, antibodies stimulate inflammation, while their presence in mucus and on the skin prevents pathogen attack.

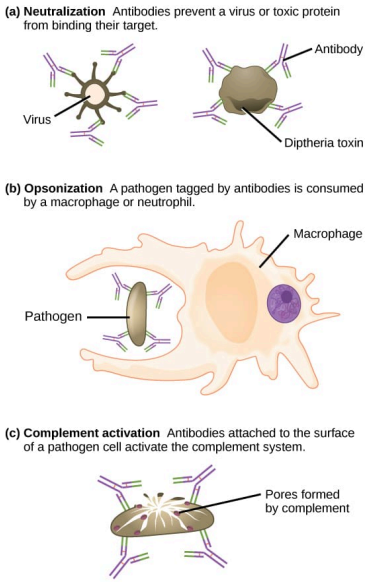


Figure 42.7.1: Methods by which antibodies inhibit infection: Antibodies may inhibit infection by (a) preventing the antigen from binding its target, (b) tagging a pathogen for destruction by macrophages or neutrophils, or (c) activating the complement cascade.

The production of antibodies by plasma cells in response to an antigen is called active immunity. This describes the host's active response of the immune system to an infection or to a vaccination. There is also a passive immune response wherein antibodies are introduced into the host from an outside source, instead of the individual's own plasma cells. For example, antibodies circulating in a pregnant woman's body move across the placenta into the developing fetus. The child benefits from the presence of these antibodies for up to several months after birth. In addition, a passive immune response is possible by injecting antibodies into an individual in the form of an antivenom to a snake-bite toxin or antibodies in blood serum to help fight a hepatitis infection, giving immediate relief.

Key Points

- Antigens are proteins and other macromolecules that bind to a specific antibody and are used by the immune system to recognize pathogens.

- B cells express receptors (BCRs) on their membrane which contain antibodies; these antibodies allow B cells to detect pathogens and release further antibodies to fight the infection.
- Antibodies fight infections in three ways: they mark pathogens for destruction by phagocytic cells in a process known as opsonization, they coat key sites on pathogens necessary for infection, and they induce the complement cascade to occur against antibody-bound pathogens.
- Once the adaptive immune response has encountered an antigen, B cells will divide to produce plasma cells, which rapidly secrete antibodies to that antigen in a process called active immunity.

Key Terms

- **antibody**: a protein produced by B-lymphocytes that binds to a specific antigen
- **opsonize**: to make (bacteria or other cells) more susceptible to the action of phagocytes by use of opsonins
- **MHC**: an acronym for major histocompatibility complex; these extracellular protein receptors display antigens derived from extracellular (class I) or intracellular (class II) proteins and other biomolecules

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42.8: Adaptive Immune Response - Cell-Mediated Immunity

Learning Objectives

- Summarize the cell-mediated immune response

T cells

Just as the humoral immune response has B cells which mediate its response, the cellular immune response has T cells, which recognize infected cells and destroy them before the pathogen inside can replicate and spread to infect other cells. Unlike B cells, T lymphocytes (T cells) are unable to recognize pathogens without assistance. First, an antigen-presenting cell (APC, such as a dendritic cell or a macrophage) detects, engulfs (via phagocytosis in the case of macrophages or by entry of the pathogen of its own accord in the case of dendritic cells), and digests pathogens into hundreds or thousands of antigen fragments. These fragments are then transported to the surface of the APC, where they are presented on proteins known as Major Histocompatibility Complexes class II (MHC II, see). T cells become activated towards a certain antigen once they encounter it displayed on an MHC II. After a virus or bacteria enters a cell, it can no longer be detected by the humoral immune response. Instead, the cellular immune response must take over. To do so, a T cell will become activated by interacting with an antigen of the infecting cell or virus presented on the MHC II of an APC.

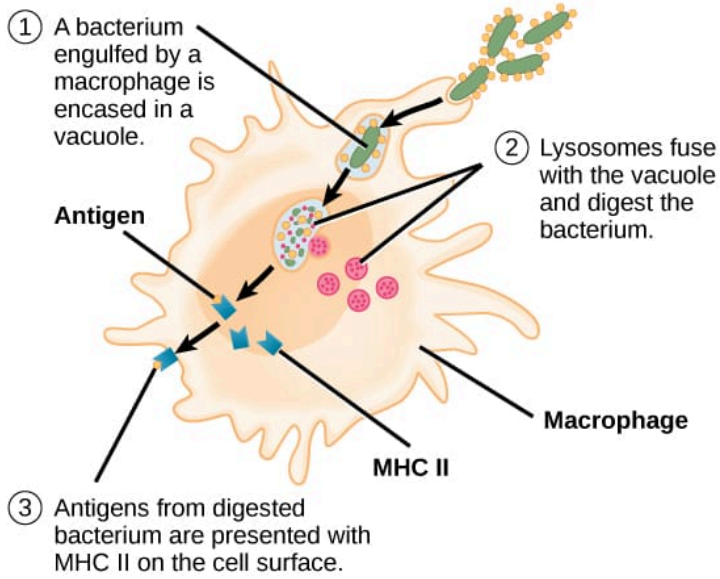


Figure 42.8.1: APCs, MHCs and lymphocytes: An antigen-presenting cell (APC), such as a macrophage, engulfs a foreign antigen, partially digests it in a lysosome, and then embeds it in an MHC class II molecule for presentation at the cell surface. Lymphocytes of the adaptive immune response must interact with antigen-embedded MHC class II molecules to mature into functional immune cells.

Cytotoxic T cells mediate one arm of the cellular immune response

There are two main types of T cells: helper T lymphocytes (T_H) and the cytotoxic T lymphocytes (T_C). The T_H lymphocytes function indirectly to tell other immune cells about potential pathogens, while cytotoxic T cells (T_C) are the key component of the cell-mediated part of the adaptive immune system which attacks and destroys infected cells. T_C cells are particularly important in protecting against viral infections because viruses replicate within cells where they are shielded from extracellular contact with circulating antibodies. Once activated, the T_C creates a large clone of cells with one specific set of cell-surface receptors, similar to the proliferation of activated B cells. As with B cells, the clone includes active T_C cells and inactive memory T_C cells. The resulting active T_C cells then identify infected host cells.

T_C cells attempt to identify and destroy infected cells by triggering apoptosis (programmed cell death) before the pathogen can replicate and escape, thereby halting the progression of intracellular infections. To recognize which cells to pursue, T_C recognize antigens presented on MHC I complexes, which are present on all nucleated cells. MHC I complexes display a current readout of intracellular proteins inside a cell and will present pathogen antigens if the pathogen is present in the cell. T_C cells also support NK lymphocytes to destroy early cancers.

Cytokines released by T_H cells recruit NK cells and phagocytes

Cytokines are signaling molecules secreted by a T_H cell in response to a pathogen-infected cell; they stimulate natural killer cells and phagocytes such as macrophages. Phagocytes will then engulf infected cells and destroy them. Cytokines are also involved in stimulating T_C cells, enhancing their ability to identify and destroy infected cells and tumors. A summary of how the humoral and cell-mediated immune responses are activated appears in. B plasma cells and T_C cells are collectively called effector cells because they are involved in “effecting” (bringing about) the immune response of killing pathogens and infected host cells.

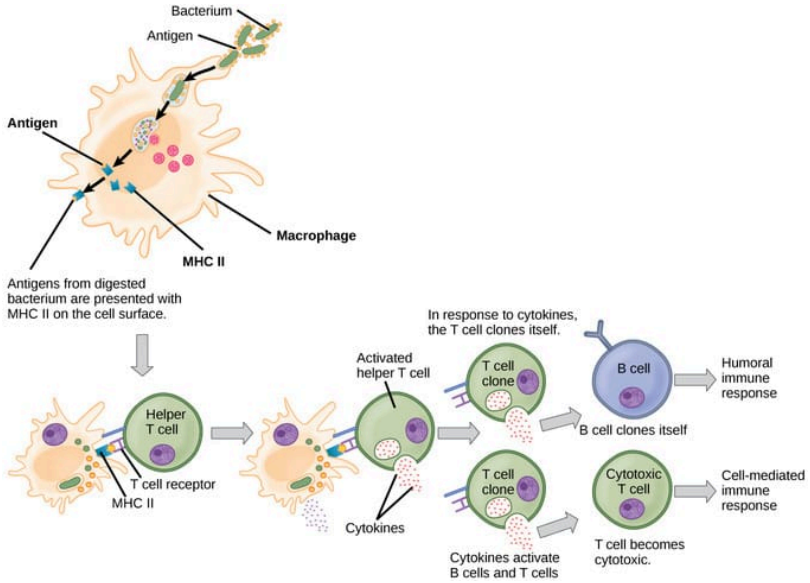


Figure 42.8.1: Helper T cells in the immune response: A helper T cell becomes activated by binding to an antigen presented by an APC via the MHCII receptor, causing it to release cytokines. Depending on the cytokines released, this activates either the humoral or the cell-mediated immune response.

Key Points

- Once a pathogen enters a cell, it can no longer be detected by the humoral immune response; instead, the cell-mediated immune response must take over to kill the infected cell before it can allow the virus or bacteria to replicate and spread.
- T cells recognize infected cells by interacting with antigen present on their MHC II molecules; before a T cell can do so, it must be activated via interaction with an antigen presenting cell, or APC.
- Once a cytotoxic T cell (T_C) is activated, it will clone itself, producing many T_C cells with the correct receptors; some portion of the cells are active and will help destroy infected cells, while others are inactive memory cells that will create more active T_C cells if the infection returns.
- Helper T cells (T_H cells) also aid in cell-mediated immunity by releasing signaling molecules known as cytokines which can recruit natural killer cells and phagocytes to destroy infected cells and further activate T_C cells; they do not directly destroy pathogens.

Key Terms

- **cytotoxic T cell**: a subgroup of lymphocytes (white blood cells) that are capable of inducing death to infected somatic or tumor cells; part of cell-mediated immunity
- **cytokine**: any of various small regulatory proteins that regulate the cells of the immune system; they are released upon

binding of PRRs to PAMPS

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42.9: Adaptive Immune Response - Cytotoxic T Lymphocytes and Mucosal Surfaces

Learning Objectives

- Describe the features of the lymphatic system as they relate to the immune response

Lymphatic system

Lymph, the watery fluid that bathes tissues and organs, contains protective white blood cells, but does not contain erythrocytes (red blood cells). Lymph moves about the body through the lymphatic system, which is made up of vessels, lymph ducts, lymph glands, and organs such as tonsils, adenoids, thymus, and spleen. Although the immune system is characterized by circulating cells throughout the body, the regulation, maturation, and intercommunication of immune factors occur at specific sites that are known as lymph nodes.

The blood circulates immune cells, proteins, and other factors through the body. Approximately 0.1 percent of all cells in the blood are leukocytes, which include monocytes (the precursor of macrophages) and lymphocytes. Most cells in the blood are red blood cells. Cells of the immune system can travel between the distinct lymphatic and blood circulatory systems, which are separated by interstitial space, by a process called extravasation (passing through to surrounding tissue).

Recall that cells of the immune system originate from stem cells in the bone marrow. B cell maturation occurs in the bone marrow, whereas progenitor cells migrate from the bone marrow and develop and mature into naïve T cells in the organ called the thymus. On maturation, T and B lymphocytes circulate to various destinations. Lymph nodes scattered throughout the body house large populations of T and B cells, dendritic cells, and macrophages. Lymph gathers antigens as it drains from tissues. These antigens are filtered through lymph nodes before the lymph is returned to circulation. Antigen-presenting cells (APCs) in the lymph nodes capture and process antigens, informing nearby lymphocytes about potential pathogens.

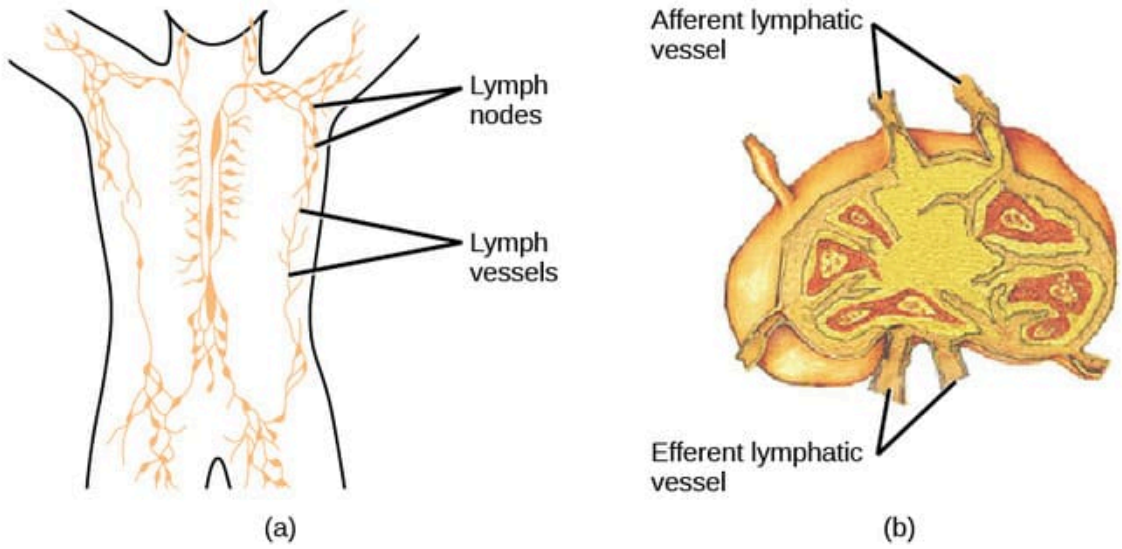


Figure 42.9.1: Lymphatic system: (a) Lymphatic vessels carry a clear fluid called lymph throughout the body. The liquid passes through (b) lymph nodes that filter the lymph that enters the node through afferent vessels, leaving through efferent vessels. Lymph nodes are filled with lymphocytes that purge infecting cells.

The spleen houses B and T cells, macrophages, dendritic cells, and NK cells. The spleen is also the site where APCs that have trapped foreign particles in the blood can communicate with lymphocytes. Antibodies are synthesized and secreted by activated plasma cells in the spleen, which filters foreign substances and antibody-complexed pathogens from the blood. Functionally, the

spleen is to the blood as lymph nodes are to the lymph.

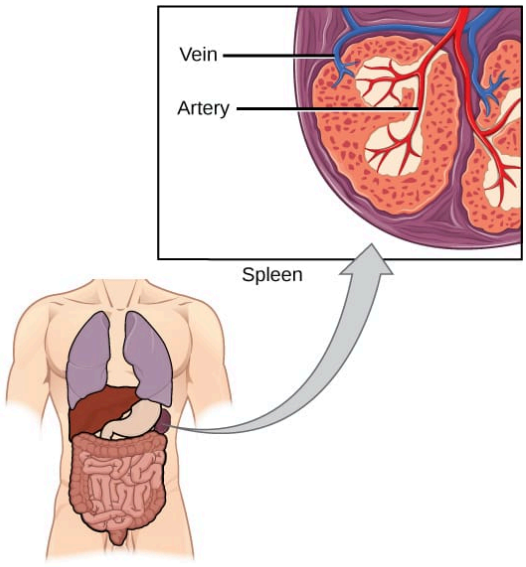


Figure 42.9.1: Spleen in the lymphatic system: The spleen functions to immunologically filter the blood and allow for communication between cells corresponding to the innate and adaptive immune responses.

Key Points

- The lymphatic system contains lymph: a fluid that bathes tissues and organs and contains white blood cells (not red blood cells).
- Once B and T cells mature, the majority of them enter the lymphatic system, where they are stored in lymph nodes until needed.
- Lymph nodes also store dendritic cells and macrophages; as antigens are filtered through the lymphatic system, these cells collect them so as to present them to B and T cells.
- The spleen, which is to blood what lymph nodes are to lymph, filters foreign substances and antibody -complexed pathogens from the blood.

Key Terms

- **lymph**: a colorless, watery, bodily fluid carried by the lymphatic system, consisting mainly of white blood cells

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42.10: Adaptive Immune Response - Immunological Memory

Learning Objectives

- Describe the role of memory B and T cells in immunological memory

The adaptive immune system has a memory component that allows for a rapid and large response upon re-invasion of the same pathogen. During the adaptive immune response to a pathogen that has not been encountered before, known as the primary immune response, plasma cells secreting antibodies and differentiated T cells increase, then plateau over time. As B cells and T cells mature into effector cells, a subset of the naïve populations differentiates into B and T memory cells with the same antigen specificities. A memory cell is an antigen-specific B or T lymphocyte that does not differentiate into an effector cell during the primary immune response, but that can immediately become an effector cell on re-exposure to the same pathogen. As the infection is cleared and pathogenic stimuli subside, the effector cells are no longer needed; they undergo apoptosis. In contrast, the memory cells persist in circulation.

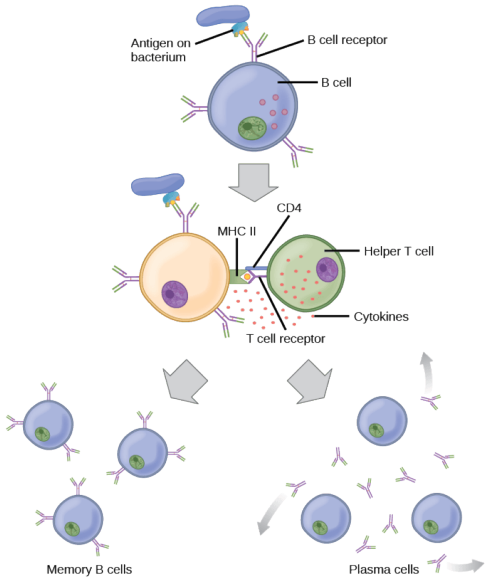


Figure 42.10.1: Formation of memory B cells and plasma cells: After initially binding an antigen to the B cell receptor (BCR), a B cell internalizes the antigen and presents it on MHC II. A helper T cell recognizes the MHC II–antigen complex and activates the B cell. As a result, memory B cells and plasma cells are made.

If the pathogen is not encountered again during the individual's lifetime, B and T memory cells will circulate for a few years or even several decades, gradually dying off, having never functioned as effector cells. However, if the host is re-exposed to the same pathogen type, circulating memory cells will immediately differentiate into plasma cells and T_C cells without input from APCs or T_H cells. This is known as the secondary immune response. One reason why the adaptive immune response is delayed is that it takes time for naïve B and T cells with the appropriate antigen specificities to be identified, activated, and proliferate. On reinfection, this step is skipped. The result is a more rapid production of immune defenses. Memory B cells that differentiate into plasma cells output ten to hundred-fold greater antibody amounts than were secreted during the primary response. This rapid and dramatic antibody response may stop the infection before it can even become established. Individuals may not realize they had been exposed.

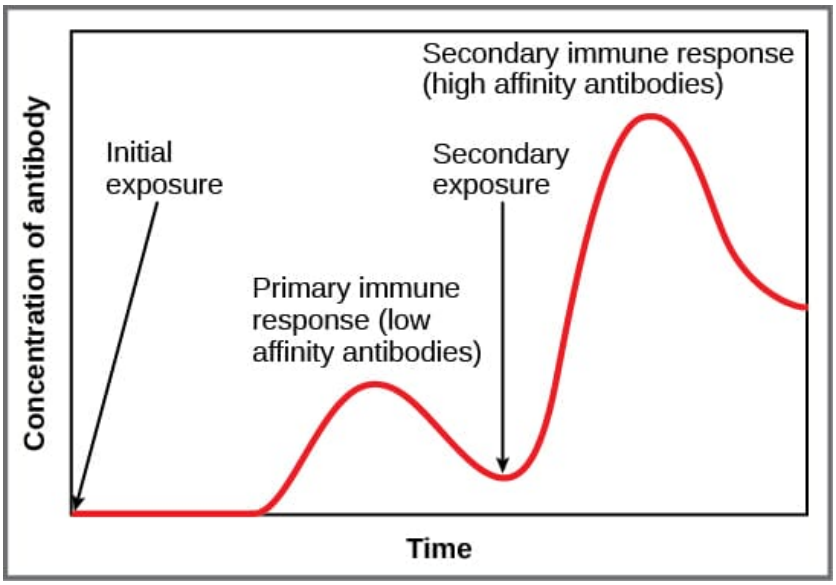


Figure 42.10.1: Primary versus secondary immune response: In the primary response to infection, antibodies are secreted first from plasma cells. Upon re-exposure to the same pathogen, memory cells differentiate into antibody-secreting plasma cells that output a greater amount of antibody for a longer period of time.

Vaccination is based on the knowledge that exposure to noninfectious antigens, derived from known pathogens, generates a mild primary immune response. The immune response to vaccination may not be perceived by the host as illness, but still confers immune memory. When exposed to the corresponding pathogen to which an individual was vaccinated, the reaction is similar to a secondary exposure. Because each reinfection generates more memory cells and increased resistance to the pathogen, some vaccine courses involve one or more booster vaccinations to mimic repeat exposures.



Figure 42.10.1: Vaccination: Vaccines, often delivered by injection into the arm, result in a secondary immune response if the vaccinated individual is later exposed to that pathogen.

Key Points

- During the adaptive immune response to a pathogen that the body has not previously encountered (the primary immune response), the level of plasma cells that secrete antibodies to the new pathogen and T cells that recognize the pathogen will increase at a modest pace.
- If a pathogen is re-encountered, memory B and T cells can immediately differentiate into plasma cells and cytotoxic T cells without input from APCs or T_H cells; this secondary immune response occurs much more rapidly than the primary immune

response.
- Vaccination can be used to generate a mild, primary immune response against an inactivated pathogen, which will allow the secondary immune response to function the first time the immune system encounters the actual pathogen.

Key Terms

- **vaccination**: inoculation in order to protect against a particular disease or strain of disease; causes a primary immune response without illness, allowing the secondary response to destroy subsequent infection
- **effector cell**: a plasma B cell or cytotoxic T cell, which are the main types of cells responsible for the humoral and cellular immune responses, respectively

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42.11: Adaptive Immune Response - Regulating Immune Tolerance

Learning Objectives

- Describe the process by which immune tolerance is acquired

Mucosal surfaces

The innate and adaptive immune responses discussed thus far comprise the systemic immune system (affecting the whole body), which is distinct from the mucosal immune system. Mucosa are another name for mucous membranes. Mucosal immunity is formed by mucosa-associated lymphoid tissue, or MALT, which functions independently of the systemic immune system; it has its own innate and adaptive components. MALT is a collection of lymphatic tissue that combines with epithelial tissue lining the mucosa throughout the body. This tissue functions as the immune barrier and immune response in areas of the body in direct contact to the external environment. The systemic and mucosal immune systems use many of the same cell types. Foreign particles that make their way to MALT are taken up by absorptive epithelial cells called M cells and delivered to APCs (antigen-presenting cells) located directly below the mucosal tissue. M cells are located in the Peyer's patch, which is a lymphoid nodule. APCs of the mucosal immune system are primarily dendritic cells, with B cells and macrophages playing minor roles. Processed antigens displayed on APCs are detected by T cells in the MALT and at various mucosal induction sites, such as the tonsils, adenoids, appendix, or the mesenteric lymph nodes of the intestine. Activated T cells then migrate through the lymphatic system and into the circulatory system to mucosal sites of infection.

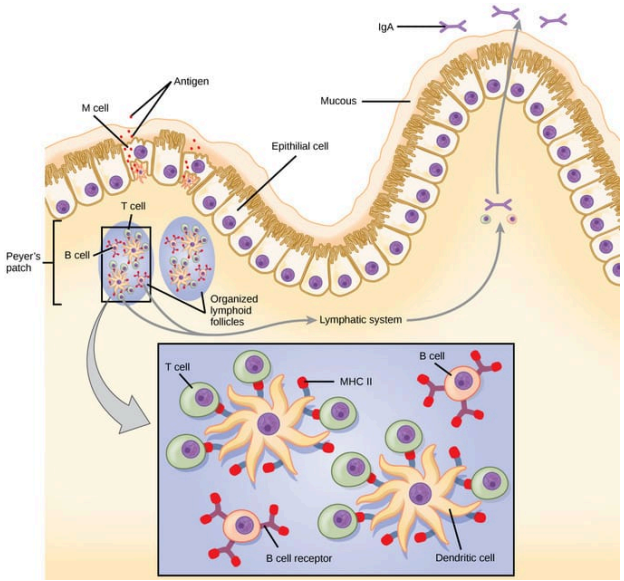


Figure 42.11.1: MALT tissue: The topology and function of intestinal MALT is shown. Pathogens are taken up by M cells in the intestinal epithelium and excreted into a pocket formed by the inner surface of the cell. The pocket contains antigen-presenting cells, such as dendritic cells, which engulf the antigens, then present them with MHC II molecules on the cell surface. The dendritic cells migrate to an underlying tissue called a Peyer's patch. Antigen-presenting cells, T cells, and B cells aggregate within the Peyer's patch, forming organized lymphoid follicles. There, some T cells and B cells are activated. Other antigen-loaded dendritic cells migrate through the lymphatic system where they activate B cells, T cells, and plasma cells in the lymph nodes. The activated cells then return to MALT tissue effector sites. IgA and other antibodies are secreted into the intestinal lumen.

MALT is a crucial component of a functional immune system because mucosal surfaces, such as the nasal passages, are the first tissues onto which inhaled or ingested pathogens are deposited. This allows the immune system to detect and deal with pathogens very quickly after they enter the body through various mucous membranes. The mucosal tissue includes the mouth, pharynx, and esophagus, along with the gastrointestinal, respiratory, and urogenital tracts.

Immune tolerance

The immune system has to be regulated to prevent wasteful, unnecessary responses to harmless substances and, more importantly, so that it does not attack “self.” The acquired ability to prevent an unnecessary or harmful immune response to a detected foreign substance known not to cause disease or to self-antigens is described as immune tolerance. The primary mechanism for developing immune tolerance to self-antigens occurs during the selection for weakly, self-binding cells during T and B lymphocyte maturation. Any T or B lymphocytes that recognize harmless foreign or “self” antigens are deleted before they can fully mature into immunocompetent cells.

There are populations of T cells that suppress the immune response to self-antigens. They also suppress the immune response after the infection has cleared to minimize host cell damage induced by inflammation and cell lysis. Immune tolerance is especially well developed in the mucosa of the upper digestive system because of the tremendous number of foreign substances (such as food proteins) that APCs of the oral cavity, pharynx, and gastrointestinal mucosa encounter. Immune tolerance is brought about by specialized APCs in the liver, lymph nodes, small intestine, and lung that present harmless antigens to a diverse population of regulatory T (T_{reg}) cells: specialized lymphocytes that suppress local inflammation and inhibit the secretion of stimulatory immune factors. The combined result of T_{reg} cells is to prevent immunologic activation and inflammation in undesired tissue compartments, allowing the immune system to focus on hazardous pathogens instead.

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Key Points

- Mucosal surfaces are those that are in contact with air, but, unlike the skin, allow fluid to flow in and out of them.
- Due to the location of mucosal surfaces, they are often the first sites to encounter new antigens.

- The immune system has to be regulated to prevent wasteful, unnecessary responses to harmless substances and, more importantly, so that it does not attack “self”.
- Mucosal-associated lymphoid tissue, or MALT, is involved in immune tolerance to harmless, foreign antigens.

Key Terms

- **self-antigen**: antigens (substances that bind to antibodies) that are usually well tolerated by the immune system, which has been educated to non-reactivity against the structures
- **mucous membrane**: a membrane which secretes mucus; it forms the lining of body passages that contact the air, such as the respiratory and genitourinary tracts including the mouth, nasal passages, vagina and urethra

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42.12: Antibodies - Antibody Structure

Learning Objectives

- Differentiate among the classes of antibodies

An antibody is a molecule that recognizes a specific antigen; this recognition is a vital component of the adaptive immune response. Antibodies are composed of four polypeptides: two identical heavy chains (large peptide units) that are partially bound to each other in a “Y” formation, which are flanked by two identical light chains (small peptide units). The area where the antigen is recognized on the antibody is known as the variable domain or variable region. This is why there are numerous antibodies that can each recognize a different antigen. The antibody base is known as the constant domain or constant region. The portion of an antigen that is recognized by the antibody is known as the epitope.

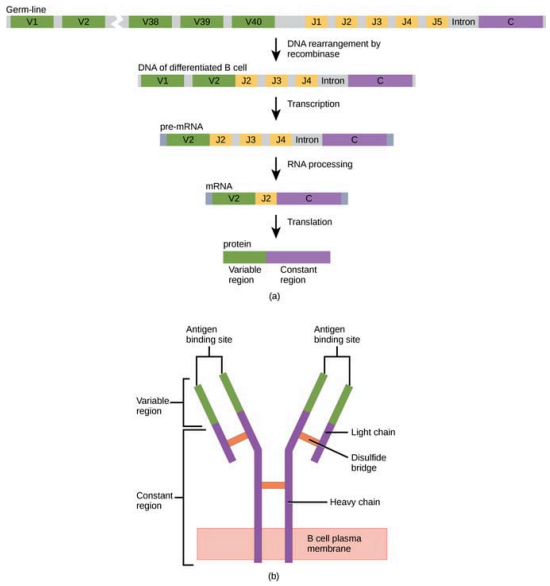


Figure 42.12.1: Antibodies: (a) As a germ-line B cell matures, an enzyme called DNA recombinase randomly excises V and J segments from the light chain gene. Splicing at the mRNA level results in further gene rearrangement. As a result, (b) each antibody has a unique variable region capable of binding a different antigen.

Antibody variation

In B cells, the variable region of the light chain gene has 40 variable (V) and five joining (J) segments. An enzyme called DNA recombinase randomly excises most of these segments out of the gene, splicing one V segment to one J segment. During RNA processing, all but one V and J segment are spliced out. Recombination and splicing may result in over 10^6 possible VJ combinations. As a result, each differentiated B cell in the human body typically has a unique variable chain. The constant domain, which does not bind to an antibody, is the same for all antibodies. The large diversity of antibody structure translates into the large diversity of antigens that antibodies can bind and recognize.

Similar to TCRs (T cell receptors) and BCRs (B cell receptors), antibody diversity is produced by the mutation and recombination of approximately 300 different gene segments encoding the light and heavy chain variable domains in precursor cells that are destined to become B cells. The variable domains from the heavy and light chains interact to form the binding site through which an antibody can bind a specific epitope on an antigen. The numbers of repeated constant domains in Ig classes (discussed below) are the same for all antibodies corresponding to a specific class. Antibodies are structurally similar to the extracellular component of the BCRs. The maturation of B cells into plasma cells occurs when the cells gain the ability to secrete the antibody portion of its BCR in large quantities.

Antibody Classes

Antibodies can be divided into five classes (IgM, IgG, IgA, IgD, and IgE) based on their physiochemical, structural, and immunological properties. Ig stands for immunoglobulin, another term for an antibody. IgGs, which make up about 80 percent of all antibodies in circulation, have heavy chains that consist of one variable domain and three identical constant domains. IgA and IgD also have three constant domains per heavy chain, whereas IgM and IgE each have four constant domains per heavy chain. The variable domain determines binding specificity, while the constant domain of the heavy chain determines the immunological mechanism of action of the corresponding antibody class. It is possible for two antibodies to have the same binding specificities, but be in different classes and, therefore, to be involved in different functions.

After an adaptive defense is produced against a pathogen, typically plasma cells first secrete IgM into the blood. BCRs on naïve B cells are of the IgM class and, occasionally, the IgD class. IgM molecules comprise approximately ten percent of all antibodies. Prior to antibody secretion, plasma cells assemble IgM molecules into pentamers (five individual antibodies) linked by a joining (J) chain. The pentamer arrangement means that these macromolecules can bind ten identical antigens. However, IgM molecules released early in the adaptive immune response do not bind to antigens as stably as do IgGs, which are one of the possible types of antibodies secreted in large quantities upon re-exposure to the same pathogen. The properties of immunoglobulins and their basic structures are shown in the table.

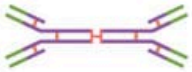
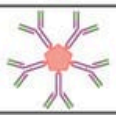
Name	Properties	Structure
IgA	Found in mucous, saliva, tears, and breast milk. Protects against pathogens.	
IgD	Part of the B cell receptor. Activates basophils and mast cells.	
IgE	Protects against parasitic worms. Responsible for allergic reactions.	
IgG	Secreted by plasma cells in the blood. Able to cross the placenta into the fetus.	
IgM	May be attached to the surface of a B cell or secreted into the blood. Responsible for early stages of immunity.	

Figure 42.12.1: Classes of antibodies: Immunoglobulins (antibody classes) have different functions, but all are composed of light and heavy chains that form a Y-shaped structure.

IgAs populate the saliva, tears, breast milk, and mucus secretions of the gastrointestinal, respiratory, and genitourinary tracts. Collectively, these bodily fluids coat and protect the extensive mucosa (4000 square feet in humans). The total number of IgA molecules in these bodily secretions is greater than the number of IgG molecules in the blood serum. A small amount of IgA is also secreted into the serum in monomeric form. Conversely, some IgM is secreted into bodily fluids of the mucosa. Similarly to IgM, IgA molecules are secreted as polymeric structures linked with a J chain. However, IgAs are secreted mostly as dimeric molecules, not pentamers.

IgE is present in the serum in small quantities and is best characterized in its role as an allergy mediator. IgD is also present in small quantities. Similarly to IgM, BCRs containing the IgD class of antibodies are found on the surface of naïve B cells. This class supports antigen recognition and subsequent maturation of B cells to plasma cells.

Key Points

- Antibodies contain four polypeptides: two identical (to each other) heavy chains in a “Y” formation and two idenitical (to each other) light chains on the outside of the top of the “Y” portion.
- Each antibody has a unique variable region, which is responsible for antigen detection and specificity.
- There are five classes of antibodies, each utilized by the body under different conditions, including IgM, IgG, IgA, IgD, and

IgE; Ig stands for immunoglobulin.
- IgAs, secreted in the milk, tears and mucous, are the most numerous antibodies produced; inside of the body, circulating IgGs are the most abundant.

Key Terms

- **immunoglobulin**: any of the glycoproteins in blood serum that respond to invasion by foreign antigens and that protect the host by removing pathogens; also known as an antibody
- **antigen**: a substance that binds to a specific antibody; may cause an immune response
- **B cell**: a lymphocyte, developed in the bursa of birds and the bone marrow of other animals, that produces antibodies and is responsible for the immune system
- **epitope**: that part of a biomolecule (such as a protein) that is the target of an immune response; the part of the antigen recognized by the immune system

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42.13: Antibodies - Antibody Functions

Learning Objectives

- Differentiate among affinity, avidity, and cross-reactivity in antibodies

Differentiated plasma cells are crucial players in the humoral immunity response. The antibodies they secrete are particularly significant against extracellular pathogens and toxins. Once secreted, antibodies circulate freely and act independently of plasma cells. Sometimes, antibodies can be transferred from one individual to another. For instance, a person who has recently produced a successful immune response against a particular disease agent can donate blood to a non-immune recipient, confering temporary immunity through antibodies in the donor's blood serum. This phenomenon, called passive immunity, also occurs naturally during breastfeeding, which makes breastfed infants highly resistant to infections during the first few months of life.

Antibodies coat extracellular pathogens and neutralize them by blocking key sites on the pathogen that enhance their infectivity, such as receptors that "dock" pathogens on host cells. Antibody neutralization can prevent pathogens from entering and infecting host cells, as opposed to the cytotoxic T-cell-mediated approach of killing cells that are already infected to prevent progression of an established infection. The neutralized antibody-coated pathogens can then be filtered by the spleen and eliminated in urine or feces.

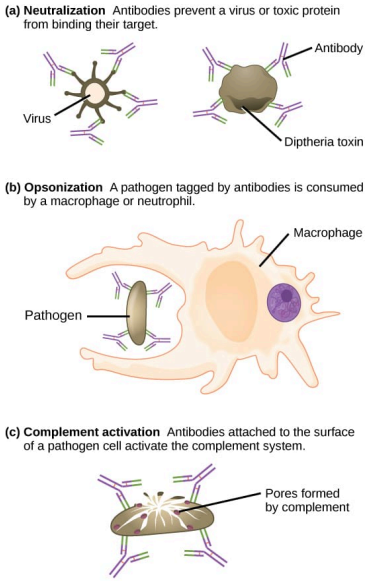


Figure 42.13.1: Mechanisms of antibody action: Antibodies may inhibit infection by (a) preventing the antigen from binding to its target, (b) tagging a pathogen for destruction by macrophages or neutrophils, or (c) activating the complement cascade.

Antibodies also mark pathogens for destruction by phagocytic cells, such as macrophages or neutrophils, because they are highly attracted to macromolecules complexed with antibodies. Phagocytic enhancement by antibodies is called opsonization. In another process, complement fixation, IgM and IgG in serum bind to antigens, providing docking sites onto which sequential complement proteins can bind. The combination of antibodies and complement enhances opsonization even further, promoting rapid clearing of pathogens.

Affinity, avidity, and cross reactivity

Not all antibodies bind with the same strength, specificity, and stability. In fact, antibodies exhibit different affinities (attraction) depending on the molecular complementarity between antigen and antibody molecules. An antibody with a higher affinity for a particular antigen would bind more strongly and stably. It would be expected to present a more challenging defense against the pathogen corresponding to the specific antigen.

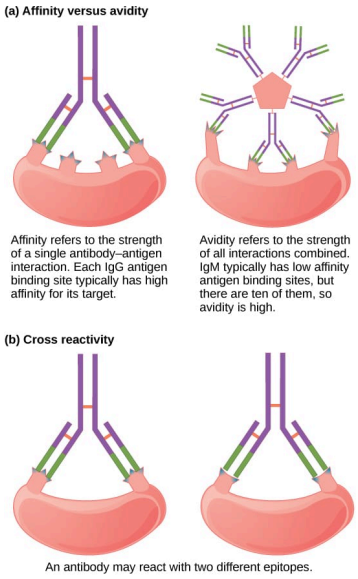


Figure 42.13.1: Antibody affinity, avidity, and cross reactivity: (a) Affinity refers to the strength of single interactions between antigen and antibody, while avidity refers to the strength of all interactions combined. (b) An antibody may cross-react with different epitopes.

The term avidity describes binding by antibody classes that are secreted as joined, multivalent structures (such as IgM and IgA). Although avidity measures the strength of binding, just as affinity does, the avidity is not simply the sum of the affinities of the antibodies in a multimeric structure. The avidity depends on the number of identical binding sites on the antigen being detected, as well as other physical and chemical factors. Typically, multimeric antibodies, such as pentameric IgM, are classified as having lower affinity than monomeric antibodies, but high avidity. Essentially, the fact that multimeric antibodies can bind many antigens simultaneously balances their slightly-lower-binding strength for each antibody/antigen interaction.

Antibodies secreted after binding to one epitope on an antigen may exhibit cross reactivity for the same or similar epitopes on different antigens. Cross reactivity occurs when an antibody binds not to the antigen that elicited its synthesis and secretion, but to a different antigen. Because an epitope corresponds to such a small region (the surface area of about four to six amino acids), it is possible for different macromolecules to exhibit the same molecular identities and orientations over short regions.

Cross reactivity can be beneficial if an individual develops immunity to several related pathogens despite having been exposed to or vaccinated against only one of them. For instance, antibody cross reactivity may occur against the similar surface structures of various Gram-negative bacteria. Conversely, antibodies raised against pathogenic molecular components that resemble self molecules may incorrectly mark host cells for destruction, causing autoimmune damage. Patients who develop systemic lupus erythematosus (SLE) commonly exhibit antibodies that react with their own DNA. These antibodies may have been initially raised against the nucleic acid of microorganisms, but later cross-reacted with self-antigens. This phenomenon is also called molecular mimicry.

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Key Points

- Antibodies are produced by plasma cells, but, once secreted, can act independently against extracellular pathogen and toxins.
- Antibodies bind to specific antigens on pathogens; this binding can inhibit pathogen infectivity by blocking key extracellular sites, such as receptors involved in host cell entry.
- Antibodies can also induce the innate immune response to destroy a pathogen, by activating phagocytes such as macrophages or neutrophils, which are attracted to antibody-bound cells.
- Affinity describes how strongly a single antibody binds a given antigen, while avidity describes the binding of a multimeric antibody to multiple antigens.
- A multimeric antibody may have individual arms with low affinity, but have high overall avidity due to synergistic effects between binding sites.
- Cross reactivity occurs when an antibody binds to a different-but-similar antigen than the one for which it was raised; this can increase pathogen resistance or result in an autoimmune reaction.

Key Terms

- **avidity**: the measure of the synergism of the strength individual interactions between proteins
- **affinity**: the attraction between an antibody and an antigen

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42.14: Disruptions in the Immune System - Immunodeficiency

Learning Objectives

- Explain the problems associated with immunodeficiency

Immunodeficiency

Failures, insufficiencies, or delays at any level of the immune response can allow pathogens or tumor cells to gain a foothold to replicate or proliferate to high enough levels that the immune system becomes overwhelmed, leading to immunodeficiency; it may be acquired or inherited. Immunodeficiency can be acquired as a result of infection with certain pathogens (such as HIV), chemical exposure (including certain medical treatments), malnutrition, or, possibly, by extreme stress. For instance, radiation exposure can destroy populations of lymphocytes, elevating an individual's susceptibility to infections and cancer. Dozens of genetic disorders result in immunodeficiencies, including Severe Combined Immunodeficiency (SCID), bare lymphocyte syndrome, and MHC II deficiencies. Rarely, primary immunodeficiencies that are present from birth may occur. Neutropenia is one form in which the immune system produces a below-average number of neutrophils, the body's most abundant phagocytes. As a result, bacterial infections may go unrestricted in the blood, causing serious complications.

HIV/AIDS

Human immunodeficiency virus infection / acquired immunodeficiency syndrome (HIV/AIDS), is a disease of the human immune system caused by infection with human immunodeficiency virus (HIV). During the initial infection, a person may experience a brief period of influenza-like illness. This is typically followed by a prolonged period without symptoms. As the illness progresses, it interferes more and more with the immune system. The person has a high probability of becoming infected, including from opportunistic infections and tumors that do not usually affect people who have working immune systems.

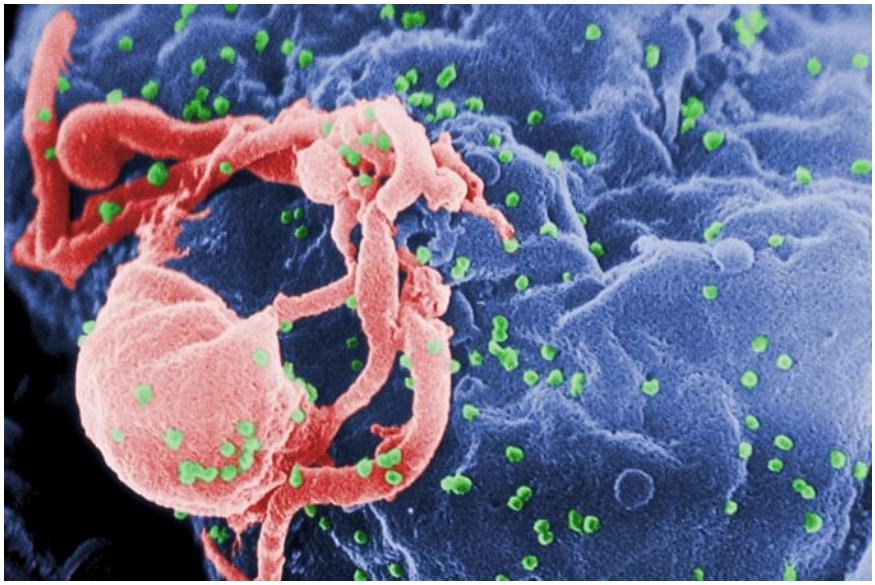


Figure 42.14.1: Image of HIV: scanning electron micrograph of HIV-1 budding (in green, color added) from cultured lymphocyte: Multiple round bumps on cell surface represent sites of assembly and budding of HIV. During primary infection, the level of HIV may reach several million virus particles per milliliter of blood.

After the virus enters the body, there is a period of rapid viral replication, leading to an abundance of virus in the peripheral blood. During primary infection, the level of HIV may reach several million virus particles per milliliter of blood. This response is

accompanied by a marked drop in the number of circulating CD4+ T cells, cells that are or will become helper T cells. The acute viremia, or spreading of the virus, is almost invariably associated with activation of CD8+ T cells (which kill HIV-infected cells) and, subsequently, with antibody production. The CD8+ T cell response is thought to be important in controlling virus levels, which peak and then decline, as the CD4+ T cell counts recover.

Ultimately, HIV causes AIDS by depleting CD4+ T cells (helper T cells). This weakens the immune system, allowing opportunistic infections. T cells are essential to the immune response; without them, the body cannot fight infections or kill cancerous cells. The mechanism of CD4+ T cell depletion differs in the acute and chronic phases. During the acute phase, HIV-induced cell lysis and killing of infected cells by cytotoxic T cells accounts for CD4+ T cell depletion, although apoptosis (programmed cell death) may also be a factor. During the chronic phase, the consequences of generalized immune activation coupled with the gradual loss of the ability of the immune system to generate new T cells appear to account for the slow decline in CD4+ T cell numbers.

Key Points

- If a pathogen is allowed to proliferate to certain levels, the immune system can become overwhelmed; immunodeficiency occurs when the immune system fails to respond sufficiently to a pathogen.
- Immunodeficiency can be caused by many factors, including certain pathogens, malnutrition, chemical exposure, radiation exposure, or even extreme stress.
- HIV is a virus that causes immunodeficiency by infecting helper T cells, causing cytotoxic T cells to destroy them.

Key Terms

- **phagocyte**: a cell of the immune system, such as a neutrophil, macrophage or dendritic cell, that engulfs and destroys viruses, bacteria, and waste materials
- **lysis**: the disintegration or destruction of cells
- **immunodeficiency**: a depletion in the body's natural immune system, or in some component of it

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42.15: Disruptions in the Immune System - Hypersensitivities

Learning Objectives

- Distinguish between the disruptions to the immune system caused by allergies and autoimmunity

Maladaptive immune responses toward harmless foreign substances or self antigens that occur after tissue sensitization are termed hypersensitivities. This can potentially be very dangerous for an individual, as the immune response can be very powerful; it can destroy host tissue if not kept in check. The types of hypersensitivities include immediate, delayed, and autoimmunity hypersensitivities. A large proportion of the population is affected by one or more types of hypersensitivity.

Allergies

The immune reaction that results from immediate hypersensitivities, in which an antibody-mediated immune response occurs within minutes of exposure to a harmless antigen, is called an allergy. In the United States, 20 percent of the population exhibits symptoms of allergy or asthma, whereas 55 percent test positive against one or more allergens. Upon initial exposure to a potential allergen, an allergic individual synthesizes antibodies of the IgE class; this class of antibodies also mediates the immune response to parasitic worms. The constant domain of the IgE molecules interacts with mast cells embedded in connective tissues. This process primes, or sensitizes, the tissue. Upon subsequent exposure to the same allergen, IgE molecules on mast cells bind the antigen via their variable domains, stimulating the mast cell to release the modified amino acids histamine and serotonin. These chemical mediators then recruit eosinophils which mediate allergic responses. The effects of an allergic reaction range from mild symptoms such as sneezing and itchy, watery eyes, to more severe or even life-threatening reactions involving intensely-itchy welts known as hives, airway contraction with severe respiratory distress, and plummeting blood pressure. This extreme reaction is known as anaphylactic shock. If not treated with epinephrine to counter the blood pressure and breathing effects, this condition can be fatal.

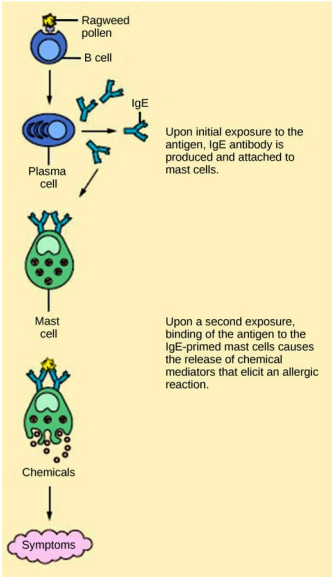


Figure 42.15.1: Allergens: This image shows an example of an allergic response to ragweed pollen. On first exposure to an allergen, an IgE antibody is synthesized by plasma cells in response to a harmless antigen. The IgE molecules bind to mast cells. On secondary exposure, the mast cells release histamines and other modulators that affect the symptoms of allergy.

Delayed hypersensitivity is a cell-mediated immune response that takes approximately one to two days after secondary exposure for a maximal reaction to be observed. This type of hypersensitivity involves the T_H1 cytokine -mediated inflammatory response. It may manifest as local tissue lesions or contact dermatitis (rash or skin irritation). Delayed hypersensitivity occurs in some

individuals in response to contact with certain types of jewelry or cosmetics. It also facilitates the immune response to poison ivy and is the reason why the skin test for tuberculosis results in a small region of inflammation on individuals who were previously exposed to *Mycobacterium tuberculosis*. Cortisone is typically used to treat such responses as it inhibits cytokine production.

Autoimmunity

Autoimmunity is a type of hypersensitivity to self antigens that affects approximately five percent of the population. Most types of autoimmunity involve the humoral immune response. Antibodies that inappropriately mark self components as foreign are termed autoantibodies. In patients with the autoimmune disease myasthenia gravis, muscle cell receptors that induce contraction in response to acetylcholine are targeted by antibodies. The result is muscle weakness that may include marked difficultly with fine and/or gross motor functions. In systemic lupus erythematosus, a diffuse autoantibody response to the individual's own DNA and proteins results in various systemic diseases. Systemic lupus erythematosus may affect the heart, joints, lungs, skin, kidneys, central nervous system, or other tissues, causing tissue damage via antibody binding, complement recruitment, lysis, and inflammation.

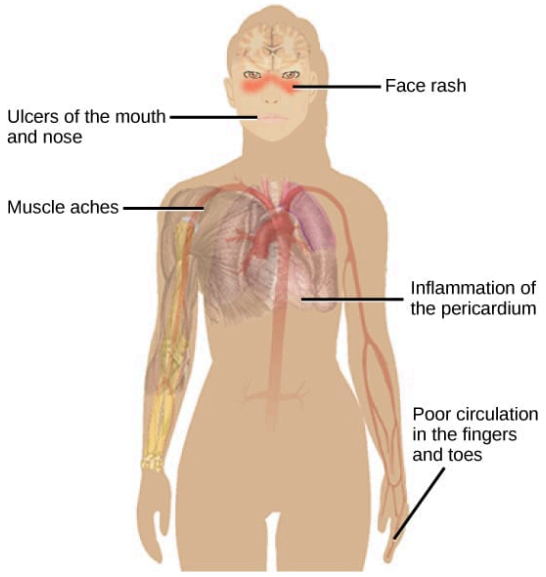


Figure 42.15.1: SLE and autoimmunity: Systemic lupus erythematosus is characterized by autoimmunity to the individual's own DNA and/or proteins, which leads to varied dysfunction of the organs.

Autoimmunity can develop with time; its causes may be rooted in molecular mimicry. Antibodies and TCRs may bind self antigens that are structurally similar to pathogen antigens, which the immune receptors first raised. As an example, infection with *Streptococcus pyogenes* (bacterium that causes strep throat) may generate antibodies or T cells that react with heart muscle, which has a similar structure to the surface of *S. pyogenes*. These antibodies can damage heart muscle with autoimmune attacks, leading to rheumatic fever. Insulin -dependent (Type 1) diabetes mellitus arises from a destructive inflammatory T_H1 response against insulin-producing cells of the pancreas. Patients with this autoimmunity must be injected with insulin that originates from other sources.

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Key Points

- While the immune system is normally very tightly controlled to disregard “self” and harmless antigens, a condition known as hypersensitivity can override this control, causing illness and injury to an individual.
- Allergies result when the immune system recognizes harmless antigens, such as pollen or dust; they are characterized by red, swollen eyes, sneezing and itching, and can also encompass more serious symptoms such as anaphylactic shock.
- Autoimmunity occurs when the immune system recognizes “self” antigens and begins attacking them; antibodies that recognize self are termed autoantibodies.

Key Terms

- **autoantibody**: an antibody formed in response to an agent (autoantigen) produced by the organism itself
- **histamine**: an amine that causes dilatation of capillaries, contraction of smooth muscle, and stimulation of gastric acid secretion; it is released during allergic reactions

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43: ANIMAL REPRODUCTION AND DEVELOPMENT

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43.1: REPRODUCTION METHODS

- Topic hierarchy

43.1A: Methods of Reproducing

43.1B: Types of Sexual and Asexual Reproduction

43.1C: Sex Determination

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43.1A: Methods of Reproducing

Learning Objectives

- Describe reproduction in animals

Animal Reproduction

Reproduction (or procreation) is the biological process by which new “offspring” (individual organisms) are produced from their “parents. ” It is a fundamental feature of all known life that each individual organism exists as the result of reproduction. Most importantly, reproduction is necessary for the survival of a species. The known methods of reproduction are broadly grouped into two main types: sexual and asexual.

In asexual reproduction, an individual can reproduce without involvement with another individual of that species. The division of a bacterial cell into two daughter cells is an example of asexual reproduction. This type of reproduction produces genetically-identical organisms (clones), whereas in sexual reproduction, the genetic material of two individuals combines to produce offspring that are genetically different from their parents.

During sexual reproduction, the male gamete (sperm) may be placed inside the female’s body for internal fertilization, or the sperm and eggs may be released into the environment for external fertilization. Humans provide an example of the former, while seahorses provide an example of the latter. Following a mating dance, the female seahorse lays eggs in the male seahorse’s abdominal brood pouch where they are fertilized. The eggs hatch and the offspring develop in the pouch for several weeks.



Figure 43.1A.1: Sexual reproduction in seahorses: Female seahorses produce eggs for reproduction that are then fertilized by the male. Unlike almost all other animals, the male seahorse then gestates the young until birth.

Asexual versus Sexual Reproduction

Organisms that reproduce through asexual reproduction tend to grow in number exponentially. However, because they rely on mutation for variations in their DNA, all members of the species have similar vulnerabilities. Organisms that reproduce sexually yield a smaller number of offspring, but the large amount of variation in their genes makes them less susceptible to disease.

Many organisms can reproduce sexually as well as asexually. Aphids, slime molds, sea anemones, and some species of starfish are examples of animal species with this ability. When environmental factors are favorable, asexual reproduction is employed

to exploit suitable conditions for survival, such as an abundant food supply, adequate shelter, favorable climate, disease, optimum pH, or a proper mix of other lifestyle requirements. Populations of these organisms increase exponentially via asexual reproductive strategies to take full advantage of the rich supply resources. When food sources have been depleted, the climate becomes hostile, or individual survival is jeopardized by some other adverse change in living conditions, these organisms switch to sexual forms of reproduction.

Sexual reproduction ensures a mixing of the gene pool of the species. The variations found in offspring of sexual reproduction allow some individuals to be better suited for survival and provide a mechanism for selective adaptation to occur. In addition, sexual reproduction usually results in the formation of a life stage that is able to endure the conditions that threaten the offspring of an asexual parent. Thus, seeds, spores, eggs, pupae, cysts, or other "over-wintering" stages of sexual reproduction ensure the survival during unfavorable times as the organism can "wait out" adverse situations until a swing back to suitability occurs.

Key Points

- Reproduction (or procreation) is the biological process by which new "offspring" are produced from their "parents".
- Asexual reproduction yields genetically-identical organisms because an individual reproduces without another.
- In sexual reproduction, the genetic material of two individuals from the same species combines to produce genetically-different offspring; this ensures mixing of the gene pool of the species.
- Organisms that reproduce through asexual reproduction tend to grow exponentially and rely on mutations for DNA variation, while those that reproduce sexually yield a smaller number of offspring, but have larger genetic variation.

Key Terms

- **reproduction**: the act of producing new individuals biologically
- **clone**: a living organism produced asexually from a single ancestor, to which it is genetically identical

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43.1B: Types of Sexual and Asexual Reproduction

Learning Objectives

- Discuss sexual and asexual reproduction methods

Asexual Reproduction

Asexual reproduction produces offspring that are genetically identical to the parent because the offspring are all clones of the original parent. This type of reproduction occurs in prokaryotic microorganisms (bacteria) and in some eukaryotic single-celled and multi-celled organisms. Animals may reproduce asexually through fission, budding, fragmentation, or parthenogenesis.

Fission

Fission, also called binary fission, occurs in prokaryotic microorganisms and in some invertebrate, multi-celled organisms. After a period of growth, an organism splits into two separate organisms. Some unicellular eukaryotic organisms undergo binary fission by mitosis. In other organisms, part of the individual separates, forming a second individual. This process occurs, for example, in many asteroid echinoderms through splitting of the central disk. Some sea anemones and some coral polyps also reproduce through fission.



Figure $43.1B.1$: Fission: Coral polyps reproduce asexually by fission, where an organism splits into two separate organisms.

Budding

Budding is a form of asexual reproduction that results from the outgrowth of a part of a cell or body region leading to a separation from the original organism into two individuals. Budding occurs commonly in some invertebrate animals such as corals and hydras. In hydras, a bud forms that develops into an adult, which breaks away from the main body; whereas in coral budding, the bud does not detach and multiplies as part of a new colony.

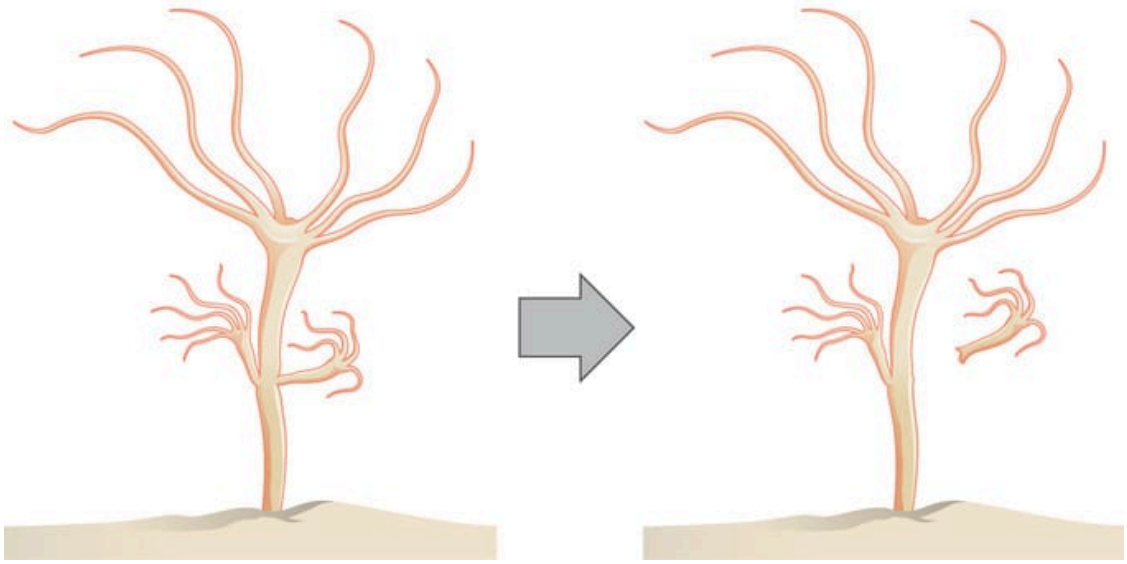


Figure $43.1B.1$: Budding: Hydra reproduce asexually through budding, where a bud forms that develops into an adult and breaks away from the main body.

Fragmentation

Fragmentation is the breaking of the body into two parts with subsequent regeneration. If the animal is capable of fragmentation, and the part is big enough, a separate individual will regrow.

Many sea stars reproduce asexually by fragmentation. For example, if the arm of an individual sea star is broken off it will regenerate a new sea star. Fishery workers have been known to try to kill the sea stars that eat 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. Fragmentation also occurs in annelid worms, turbellarians, and poriferans.



Figure $43.1B.1$: Fragmentation: Sea stars can reproduce through fragmentation. The large arm, a fragment from another sea star, is developing into a new individual.

Note that in fragmentation, there is generally a noticeable difference in the size of the individuals, whereas in fission, two individuals of approximately the same size are formed.

Parthenogenesis

Parthenogenesis is a form of asexual reproduction where an egg develops into a complete individual without being fertilized. The resulting offspring can be either haploid or diploid, depending on the process and the species. Parthenogenesis occurs in invertebrates such as water fleas, rotifers, aphids, stick insects, some ants, wasps, and bees. Bees use parthenogenesis to produce haploid males (drones) and diploid females (workers). If an egg is fertilized, a queen is produced. The queen bee controls the reproduction of the hive bees to regulate the type of bee produced.

Some vertebrate animals, such as certain reptiles, amphibians, and fish, also reproduce through parthenogenesis. Although more common in plants, parthenogenesis has been observed in animal species that were segregated by sex in terrestrial or marine zoos. Two Komodo dragons, a bonnethead shark, and a blacktip shark have produced parthenogenic young when the females have been isolated from males.

Sexual Reproduction

Sexual reproduction is the combination of (usually haploid, or having a single set of unpaired chromosomes) reproductive cells from two individuals to form a third (usually diploid, or having a pair of each type of chromosome) unique offspring. Sexual reproduction produces offspring with novel combinations of genes. This can be an adaptive advantage in unstable or unpredictable environments. As humans, we are used to thinking of animals as having two separate sexes, male and female, determined at conception. However, in the animal kingdom, there are many variations on this theme.

Hermaphroditism

Hermaphroditism occurs in animals where one individual has both male and female reproductive parts. Invertebrates, such as earthworms, slugs, tapeworms and snails, are often hermaphroditic. Hermaphrodites may self-fertilize or may mate with another of their species, fertilizing each other and both producing offspring. Self fertilization is common in animals that have limited mobility or are not motile, such as barnacles and clams.

Key Points

- Asexual reproduction includes fission, budding, fragmentation, and parthenogenesis, while sexual reproduction is achieved through the combination of reproductive cells from two individuals.
- The ability of a species to reproduce through fragmentation depends on the size of part that breaks off, while in binary fission, an individual splits off and forms two individuals of the same size.
- Budding may lead to the production of a completely new adult that forms away from the original body or may remain attached to the original body.
- Observed in invertebrates and some vertebrates, parthenogenesis produce offspring that may be either haploid or diploid.
- Sexual reproduction, the production of an offspring with a new combination of genes, may also involve hermaphroditism in which an organism can self-fertilize or mate with another individual of the same species.

Key Terms

- **binary fission**: the process whereby a cell divides asexually to produce two daughter cells
- **hermaphroditism**: having sexual organs of both sexes
- **parthenogenesis**: a form of asexual reproduction where growth and development of embryos occur without fertilization

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43.1C: Sex Determination

Learning Objectives

- Differentiate among the various ways animals determine the sex of offspring

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

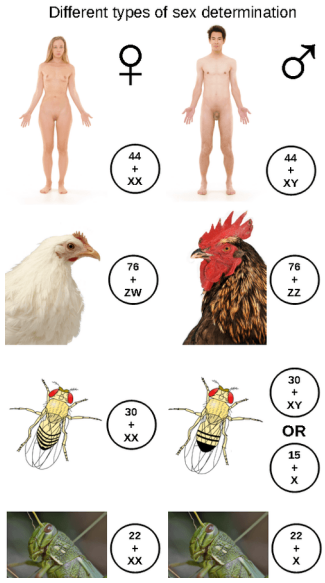


Figure $43.1C.1$: Sex determination: The presence of X and Y chromosomes are one of the factors responsible for sex determination in mammals, with males being the heterozygous sex. In birds, Z and W chromosomes determine sex, with females being the heterozygous sex.

Avian sex determination is dependent on the presence of Z and W chromosomes. Homozygous for Z (ZZ) results in a male, while heterozygous (ZW) results in a female. 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 this system.

The sex of some species is not determined by genetics, but by some aspect of the environment. Sex determination in some crocodiles and turtles, for example, is often dependent on the temperature during critical periods 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, while warm temperatures produce females. In some crocodiles, moderate temperatures produce males, while both warm and cool temperatures produce females. In some species, sex is both genetic- and temperature-dependent.

Individuals of some species change their sex during their lives, alternating between male and female. 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, for example, are born male, grow, become female, and lay eggs; some oyster species change sex multiple times.

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Key Points

- Mammals, birds, and some other animal species depend on heterozygous or homozygous chromosome combinations for sex determination.
- Cool or warm temperatures affect sex determination in species such as crocodiles and turtles.
- Some species, such as oysters, have the capability of alternating their sex several times within their life span.

Key Terms

- **protandry**: the condition in which an organism begins life as a male and then changes into a female
- **protogyny**: the condition in which an organism begins life as a female and then changes into a male
- **homozygous**: of an organism in which both copies of a given gene have the same allele

- **heterozygous**: of an organism which has two different alleles of a given gene

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43.2: FERTILIZATION



- Topic hierarchy

43.2A: External and Internal Fertilization

43.2B: The Evolution of Reproduction

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43.2A: External and Internal Fertilization

Learning Objectives

- Compare and contrast external and internal methods of fertilization

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 can then take 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 release of the reproductive material may be triggered by 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). Pairs of fish that are not broadcast spawners may exhibit courtship behavior. This allows the female to select a particular male. The trigger for egg and sperm release (spawning) causes the egg and sperm to be placed in a small area, enhancing the possibility of fertilization.



Figure $43.2A.1$: Anemone fish protecting its spawn: An image of an Anemone fish protecting its spawn. The anemone fish utilizes a form of external fertilization.

External fertilization in an aquatic environment protects the eggs from drying out. Broadcast spawning can result in a greater mixture of the genes within a group, leading to higher genetic diversity and a greater chance of species survival in a hostile environment. For sessile aquatic organisms such as sponges, broadcast spawning is the only mechanism for fertilization and colonization of new environments. The presence of the fertilized eggs and developing young in the water provides opportunities for predation, resulting in a loss of offspring. Therefore, millions of eggs must be produced by individuals. The offspring produced through this method must mature rapidly. The survival rate of eggs produced through broadcast spawning is low.

Internal Fertilization

Internal fertilization occurs most often in land-based animals, although some aquatic animals also use this method. There are three ways that offspring are produced following internal fertilization: oviparity, ovoviparity, and viviparity.

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. This occurs in most bony fish, many reptiles, some cartilaginous fish, most amphibians, two mammals, and all birds.

Reptiles and insects produce leathery eggs, while birds and turtles produce eggs with high concentrations of calcium carbonate in the shell, making them hard. These animals are classified as oviparous.

In ovoviparity, fertilized eggs are retained in the female, but the embryo obtains its nourishment from the egg's yolk; the young are fully developed when they are hatched. This occurs in some bony fish (such as the guppy, *Lebistes reticulatus*), some sharks, some lizards, some snakes (such as the garter snake, *Thamnophis sirtalis*), some vipers, and some invertebrate animals (such as the Madagascar hissing cockroach, *Gromphadorhina portentosa*).

In viviparity, the young develop within the female, receiving nourishment from the mother's blood through a placenta. The offspring develops in the female and is born alive. This occurs in most mammals, some cartilaginous fish, and a few reptiles, making these animals viviparous.

Internal fertilization has the advantage of protecting the fertilized egg from dehydration on land. The embryo is isolated within the female, which limits predation on the young. Internal fertilization also enhances the fertilization of eggs by a specific male. Even though fewer offspring are produced through this method, their survival rate is higher than that for external fertilization.

Key Points

- External fertilization is characterized by the release of both sperm and eggs into an external environment; sperm will fertilize the egg outside of the organism, as seen in spawning.
- Internal fertilization is characterized by sperm fertilizing the egg within the female; the three methods include: oviparity (egg laid outside female body), ovoviparity (egg held within female), and viviparity (development within female followed by live birth).
- Internal fertilization protects the fertilized egg or embryo from predation and harsh environments, which results in higher survival rates than can occur with external fertilization.
- Ovoviparity is characterized by an organism retaining a fertilized egg inside the body where development occurs and nourishment is received from the yolk.
- Viparity is characterized by an organism which has its young develop within the female and nourishment is received directly from the mother via a placenta.

Key Terms

- **oviparous**: egg-laying; depositing eggs that develop and hatch outside the body as a reproductive strategy
- **viviparous**: being born alive, as are most mammals, some reptiles, and a few fish (as opposed to being laid as an egg)
- **ovoviparity**: eggs are retained in the female, but the embryo obtains its nourishment from the egg's yolk

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43.2B: The Evolution of Reproduction

Learning Objectives

- Differentiate among the types of reproductive systems that have evolved

Several competing scientific hypotheses have been proposed to explain the evolution of sexual reproduction. All sexually-reproducing eukaryotic organisms derive from a common ancestor that was a single-celled eukaryotic species. Many protists reproduce sexually, as do multicellular plants, animals, and fungi. However, there are a few species which have secondarily lost this feature. The evolution of sex contains two related, yet distinct, themes: its origin and its maintenance. However, since the hypotheses for the origins of sex are difficult to test experimentally, most current work has been focused on the maintenance of sexual reproduction.

Once multicellular organisms evolved and developed specialized cells, some also developed tissues and organs with specialized functions. The evolution of reproductive organs arrived with the development of gonads that produced sperm and eggs. These cells develop through meiosis, an adaption of mitosis, which reduced the number of chromosomes in each reproductive cell by half, while increasing the number of cells through cell division. The development of specialized gonads to produce sperm and egg was a major step in the evolutionary process.

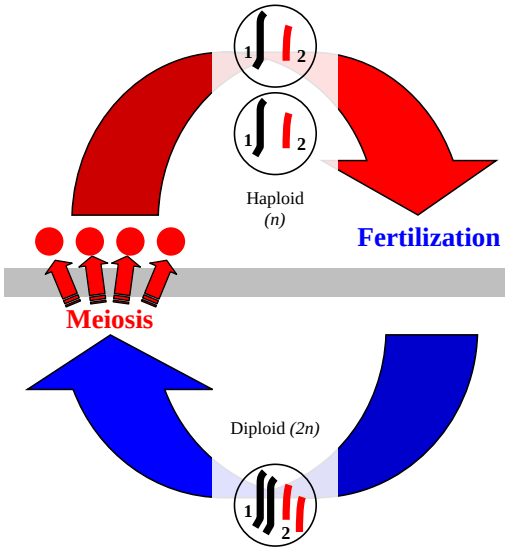


Figure $43.2B.1$: Meiosis: The development of sperm and eggs occurs via the process of meiosis which reduces the number of chromosomes in each cell by half.

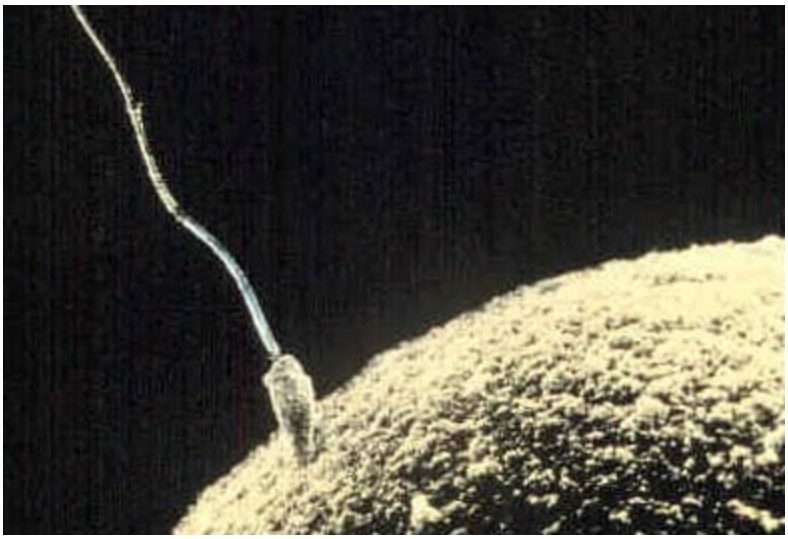


Figure $43.2B.1$: Sperm fertilizing an egg: The evolution of sex-specific gonads led to the development of sperm (male) and eggs (female). When fertilized, if the conditions are favorable, the egg may develop into a new organism.

An early development in reproduction occurred in the Annelids. These organisms produce sperm and eggs from undifferentiated cells in their coelom, storing them in that cavity. When the coelom becomes filled, the cells are released through an excretory opening or by the body splitting open. Further evolution of reproductive systems resulted in the development of reproductive systems that are sex specific. In these more advanced systems, sperm is made in the testes and then travels through coiled tubes to the epididymis for storage. Additionally, in these more advanced systems, eggs are matured in the ovary; when released, they travel to the uterine tubes for fertilization. These types of reproductive systems developed in insects (compared to annelids which have a coelom for storage). Specifically, in the insect reproductive system, a specialized sac developed, called a spermatheca, which is used to store sperm for later use, sometimes up to a year. This was a key development since fertilization in insects can be timed with environmental or food conditions that are optimal for offspring survival.

Vertebrates have similar structures (i.e., gonads that specialize in sex cell production) with a few differences in their reproductive systems. Non-mammals, such as birds and reptiles, have a common body opening, called a cloaca, for the digestive, excretory, and reproductive systems. Coupling between birds usually involves positioning the cloaca openings opposite each other for transfer of sperm. In mammals, there are separate openings for the systems in the female and a uterus for support of developing offspring. Depending on the type of species, there are differences in the uterus. In species that produce large numbers of offspring, the uterus has two chambers. In other species that produce one offspring, such as in primates, there is a single uterus.

Another development in the evolution of reproduction is the means by which sperm is transferred. During reproduction, sperm transfer from the male to the female ranges from releasing the sperm into the watery environment for external fertilization, to the joining of cloaca in birds, to the development of a penis for direct delivery into the female's vagina in mammals. All of these methods of sperm transfer represent the varying ways reproduction has evolved and become specialized to specific organisms.

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Key Points

- Annelids undergo sexual reproduction by producing sperm or eggs within the coelom and storing them within the cavity until they are ready to be released through an excretory opening.
- Insects have developed complete reproductive systems for the separate sexes and will often have a specialized sac for sperm called the spermatheca.
- Non-mammals will utilize a common body opening called the cloaca to transfer sperm between animals.
- The means by which sperm is transferred varies and can include releasing sperm into the environment as well as direct delivery to the vagina.

Key Terms

- **coelom**: a fluid-filled cavity within the body of an animal; the digestive system is suspended within the cavity, which is lined by a tissue called the peritoneum
- **gonad**: a sex organ that produces gametes; specifically, a testicle or ovary
- **cloaca**: the common duct in fish, reptiles, birds, and some primitive mammals that serves as the anus as well as the genital opening
- **spermatheca**: a small sac within the reproductive tract of some female invertebrates, such as insects, which stores sperm until it is used to fertilize the ova

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43.3: HUMAN REPRODUCTIVE ANATOMY AND GAMETOGENESIS

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- Topic hierarchy

43.3A: Male Reproductive Anatomy

43.3B: Female Reproductive Anatomy

43.3C: Gametogenesis (Spermatogenesis and Oogenesis)

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43.3A: Male Reproductive Anatomy

Learning Objectives

- Diagram the structures of human male reproductive anatomy

Human Reproductive Anatomy

The reproductive tissues of male and female humans develop similarly *in utero* until a low level of the hormone testosterone is released from male gonads. Testosterone causes the undeveloped tissues to differentiate into male sexual organs. Primitive gonads become testes; other tissues produce a penis and scrotum in males.

Male Reproductive Anatomy

In the male reproductive system, the scrotum houses the testicles or testes, providing passage for blood vessels, nerves, and muscles related to testicular function. The testes, a pair of male reproductive organs, produce sperm and male sex hormones, including the steroid testosterone. Coiled in each testis are seminiferous tubules that produce sperm.

Sperm

Sperm are immobile at body temperature; therefore, the scrotum and penis are external to the body so that a proper temperature is maintained for motility. In land mammals, the pair of testes must be suspended outside the body at about 2° C lower than body temperature to produce viable sperm.

Sperm develop in the seminiferous tubules that are coiled inside the testes. The walls of the seminiferous tubules are composed of the developing sperm cells, with the least-developed sperm at the periphery of the tubule and the fully-developed sperm in the lumen. The sperm cells are mixed with “nursemaid” cells called Sertoli cells which protect the germ cells and promote their development. Other cells mixed in the wall of the tubules are the interstitial cells of Leydig; these cells produce high levels of testosterone once the male reaches adolescence.

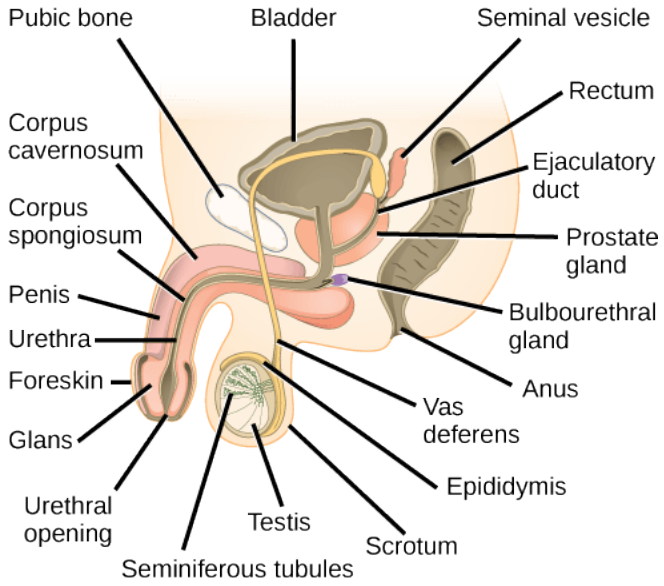


Figure 43.3A.1: Male reproductive system: The reproductive structures of the human male are shown. Sperm are produced in the seminiferous tubules, mature in the epididymis, and then are forced out into the vas deferens and out of the body through the urethra during ejaculation.

Sperm consist of a flagellum (as a tail), a neck that contains the cell's energy-producing mitochondria, and a head that contains the genetic material. When the sperm have developed flagella, or lash-like appendages that protrude from the cell body, and are nearly mature, they leave the testicles and enter the epididymis. This structure lies along the top and posterior portion of the testes; it is the site of sperm maturation. The sperm leave the epididymis and enter the vas deferens, which is the duct in the testicle that carries sperm from the epididymis to the ejaculatory duct.

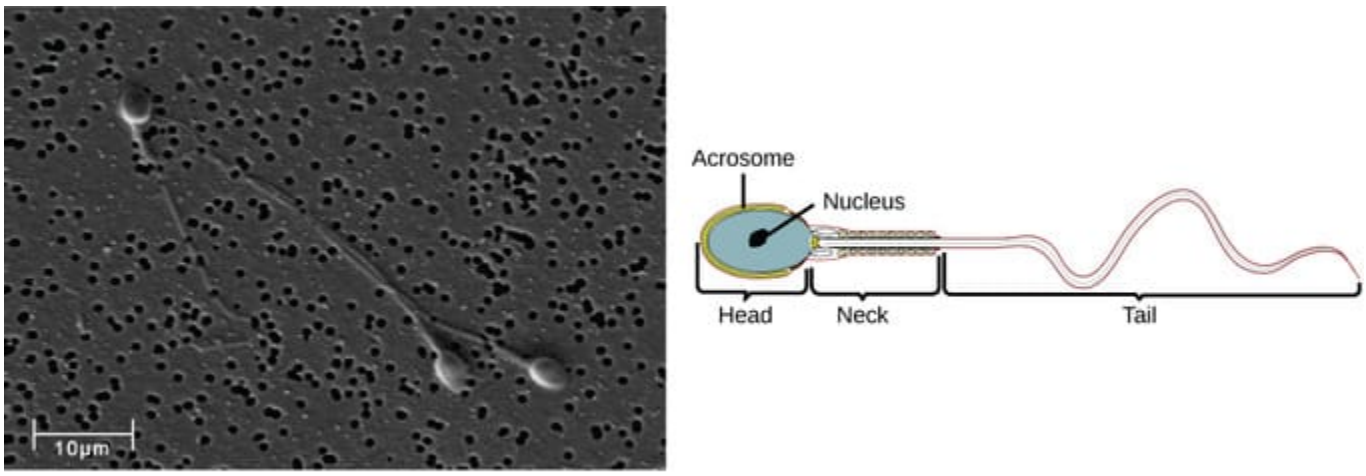


Figure 43.3A.1: Structure of a human sperm: Human sperm, visualized using scanning electron microscopy, have a flagellum, neck, and head.

Semen is a mixture of sperm and spermatic duct secretions (about 10 percent of the total), along with fluids from accessory glands, that contribute most of the semen's volume. An ejaculate will contain from two to five milliliters of fluid with from 50–120 million sperm per milliliter. The bulk of the semen comes from the accessory glands associated with the male reproductive system, including the seminal vesicles, the prostate gland, and the bulbourethral gland.

Seminal vesicles, penis, prostate, and bulbourethral gland

The seminal vesicles are a pair of glands that lie along the posterior border of the urinary bladder. The glands make a solution that is thick, yellowish, and alkaline. As sperm are only motile in an alkaline environment, a basic pH is important to reverse the acidity of the vaginal environment. The solution also contains mucus, fructose (a sperm mitochondrial nutrient), a coagulating enzyme, ascorbic acid, and local-acting hormones called prostaglandins.

The penis is an organ that drains urine from the renal bladder and functions as a copulatory organ during intercourse. The penis contains three tubes of erectile tissue running through the length of the organ. These consist of a pair of tubes on the dorsal side, called the corpus cavernosum, and a single tube of tissue on the ventral side, called the corpus spongiosum. This tissue, when engorged with blood, becomes erect and hard, in preparation for intercourse. The organ is inserted into the vagina, culminating with an ejaculation, which is the forcible ejection of semen from the urethra. An orgasm is a two-stage process: first, glands and accessory organs connected to the testes contract; second, semen (containing sperm) is expelled through the urethra during ejaculation. After intercourse, the blood drains from the erectile tissue and the penis becomes flaccid.

The walnut-shaped prostate gland surrounds the urethra, the connection to the urinary bladder. It has a series of short ducts that directly connect to the urethra. The gland is a mixture of smooth muscle and glandular tissue. The muscle provides much of the force needed for ejaculation to occur.

The bulbourethral gland, or Cowper's gland, is an exocrine gland which secretes a clear fluid known as pre-ejaculate that is generated upon sexual arousal. This gland releases its secretion prior to the release of the bulk of the semen. It neutralizes any acid residue in the urethra left over from urine. This usually accounts for a couple of drops of fluid in the total ejaculate and may contain a few sperm. Withdrawal of the penis from the vagina before ejaculation to prevent pregnancy may not work if sperm are present in the bulbourethral gland secretions.

Key Points

- The male gonads, or testes, produce sperm within the seminiferous tubules; the sperm are housed here until they are nearly mature, at which point they enter the epidydimis for full maturation.
- The testes are housed in the scrotum, an external sac that keeps the sperm at a temperature lower than that of the body.
- At ejaculation, sperm leave the epidydimis and enter the vas deferens, a duct which carries the sperm out of the body through the urethra, along with the fluids of various glands of the male reproductive system.
- The seminal vesicles produce a thick fluid that is alkaline in order to protect sperm from the acidic nature of the female vagina; it also contains sugars to nourish the sperm.
- The prostate gland produces the force necessary to push the sperm out of the epididymis at ejaculation, while the bulbourethral gland emits a fluid just prior to ejaculation that neutralizes acid from any urine left over in the urethra.
- During sexual arousal, the spongy tissue inside the penis (the corpus spongiosum) fills with blood, causing the penis to become erect and hard; after ejaculation, the blood flows back out of the penis, leaving it flaccid.

Key Terms

- **epididymis**: a narrow, tightly-coiled tube connecting the efferent ducts from the rear of each testicle to its vas deferens, where sperm are stored during maturation
- **prostate gland**: a gland in male mammals surrounding the urethra just below the urinary bladder that controls the release of urine from the bladder and produces a secretion that is the fluid part of semen
- **seminiferous tubule**: any of many threadlike structures, located in the testes, that are the specialized areas of sperm production

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43.3B: Female Reproductive Anatomy

Learning Objectives

- Diagram the structures of human female reproductive anatomy

Female reproductive anatomy

Female reproductive anatomy includes both external and internal structures. Among the external structures are the vulva, which consists of the mons pubis, clitoris, labia majora, labia minora, and the vestibular glands. The vulva is an area associated with the vestibule that includes the structures found in the inguinal (groin) area of women. The mons pubis is a round, fatty area that overlies the pubic symphysis. The clitoris is a structure with erectile tissue that contains a large number of sensory nerves and serves as a source of stimulation during intercourse. The labia majora are a pair of elongated folds of tissue that run posterior from the mons pubis and enclose the other components of the vulva. The labia majora derive from the same tissue that produces the scrotum in a male. The labia minora are thin folds of tissue centrally located within the labia majora. These labia protect the openings to the vagina and urethra. The mons pubis and the anterior portion of the labia majora become covered with hair during adolescence; the labia minora is hairless. The greater vestibular glands are found at the sides of the vaginal opening and provide lubrication during intercourse.

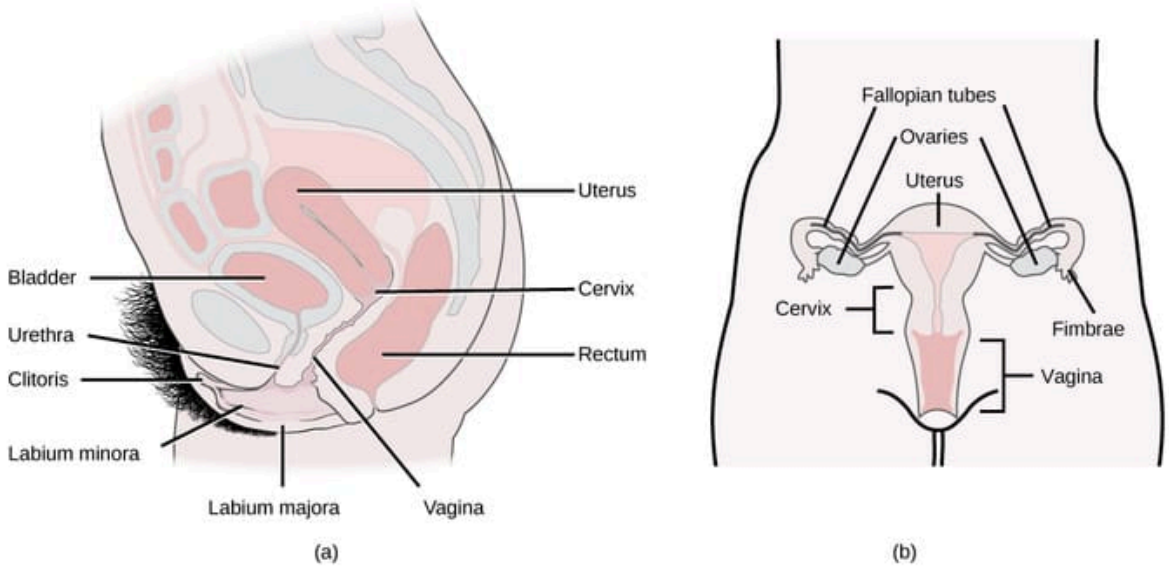


Figure $43.3B.1$: Female reproductive anatomy: The reproductive structures of the human female are shown. Several structures are on the outside of the body, such as the labia, vulva, and clitoris, while others, such as the ovaries and uterus, are internal.

Internal female reproductive structures include ovaries, oviducts, the uterus, and the vagina. An ovary consists of a medulla and cortex: the medulla contains nerves and blood vessels to supply the cortex with nutrients and remove waste. The outer layers of cells of the cortex are the functional parts of the ovaries. The cortex is made up of follicular cells that surround eggs. During the menstrual cycle, a batch of follicular cells develops, preparing the eggs for release. At ovulation, one follicle ruptures and one egg is released.

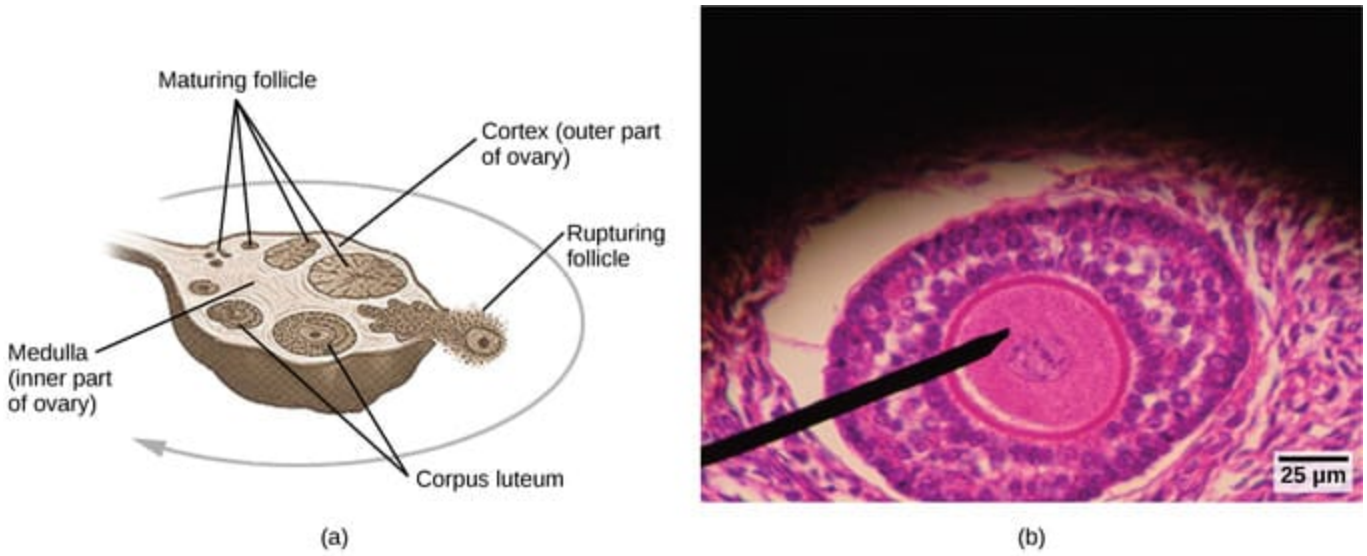


Figure $43.3B.1$: Oocyte development: Oocytes develop in (a) follicles, located in the ovary. At the beginning of the menstrual cycle, the follicle matures. At ovulation, the follicle ruptures, releasing the egg. The follicle becomes a corpus luteum, which eventually degenerates. The (b) follicle in this light micrograph has an oocyte at its center.

The oviducts, or fallopian tubes, extend from the uterus in the lower abdominal cavity to the ovaries, but they are not in contact with the ovaries. The lateral ends of the oviducts flare out into a trumpet-like structure and have a fringe of finger-like projections called fimbriae. When an egg is released at ovulation, the fimbrae help the non-motile egg enter into the tube, the passage to the uterus. The walls of the oviducts are ciliated (covered in cilia) and are primarily smooth muscle. The cilia beat toward the middle, while the smooth muscle contracts in the same direction, moving the egg toward the uterus. Fertilization usually takes place within the oviducts. The embryo is moved toward the uterus for further development. It usually takes the egg or embryo a week to travel through the oviduct.

The uterus, a structure about the size of a woman's fist, is lined with an endometrium that is rich in blood vessels and mucus glands. The uterus supports the developing embryo and fetus during gestation. The thickest portion of the wall of the uterus is made of smooth muscle. Contractions of the smooth muscle in the uterus aid in passing the baby through the vagina during labor. A portion of the lining of the uterus sloughs off during each menstrual period if an egg has not been fertilized; it builds up again in preparation for an implantation. Part of the uterus, called the cervix, protrudes into the top of the vagina, which functions as the birth canal.

The vagina is a muscular tube that serves several purposes. It allows menstrual flow to leave the body, is the receptacle for the penis during intercourse, and serves as the vessel for the delivery of offspring. It is lined by stratified squamous epithelial cells to protect the underlying tissue.

Key Points

- The external anatomy of the female reproductive system is referred to as the vulva; it includes the labia minora, which protects the vagina and urethra, and the labia majora, which surrounds it.
- Internal female reproductive structures include ovaries, oviducts, the uterus, and the vagina.
- The eggs develop in structures called follicles, which are located on the surface of the ovaries; at maturity, one of the follicles will rupture and release the egg, which is captured by the fimbrae of the oviduct.
- If fertilization occurs, it generally does so in the oviduct; the fertilized egg then travels down the oviduct and enters the uterus, where it will implant in the lining of the uterus, known as the endometrium.
- If fertilization does not occur, the endometrium of the uterus will slough off at the end of the menstrual period and is shed through the vagina, which is also the opening through which the penis enters during intercourse and through which the baby will exit during birth.

Key Terms

- **clitoris**: a small sensitive elongated erectile organ at the anterior part of the vulva in female mammals, homologous with the

penis
- **ovary**: a female reproductive organ, often paired, that produces ova and in mammals secretes the hormones estrogen and progesterone
- **vagina**: the passage leading from the opening of the vulva to the cervix of the uterus for copulation and childbirth in female mammals
- **uterus**: an organ of the female reproductive system in which the young are conceived and develop until birth; the womb
- **vulva**: the external female sexual organs, collectively

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43.3C: Gametogenesis (Spermatogenesis and Oogenesis)

Learning Objectives

- Distinguish between spermatogenesis and oogenesis

Gametogenesis (Spermatogenesis and Oogenesis)

Gametogenesis, the production of sperm and eggs, takes place through the process of meiosis. During meiosis, two cell divisions separate the paired chromosomes in the nucleus and then separate the chromatids that were made during an earlier stage of the cell's life cycle, resulting in gametes that each contain half the number of chromosomes as the parent. The production of sperm is called spermatogenesis and the production of eggs is called oogenesis.

Oogenesis

Oogenesis occurs in the outermost layers of the ovaries. As with sperm production, oogenesis starts with a germ cell, called an oogonium (plural: oogonia), but this cell undergoes mitosis to increase in number, eventually resulting in up to one to two million cells in the embryo.

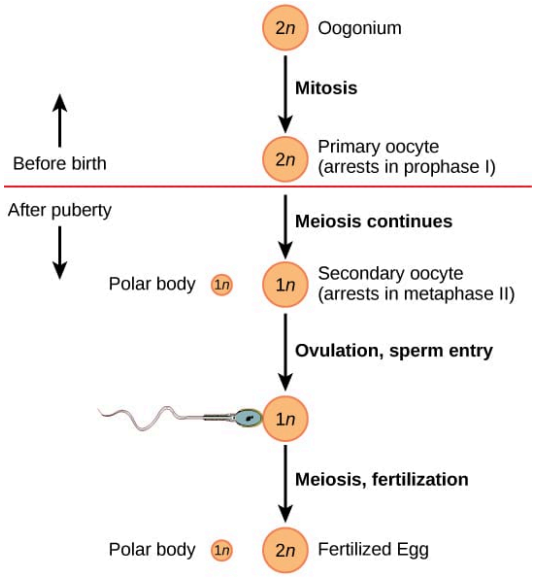


Figure $43.3C.1$: Oogenesis: The process of oogenesis occurs in the ovary's outermost layer. A primary oocyte begins the first meiotic division, but then arrests until later in life when it will finish this division in a developing follicle. This results in a secondary oocyte, which will complete meiosis if it is fertilized.

The cell starting meiosis is called a primary oocyte. This cell will begin the first meiotic division, but be arrested in its progress in the first prophase stage. At the time of birth, all future eggs are in the prophase stage. At adolescence, anterior pituitary hormones cause the development of a number of follicles in an ovary. This results in the primary oocyte finishing the first meiotic division. The cell divides unequally, with most of the cellular material and organelles going to one cell, called a secondary oocyte, and only one set of chromosomes and a small amount of cytoplasm going to the other cell. This second cell is called a polar body and usually dies. A secondary meiotic arrest occurs, this time at the metaphase II stage. At ovulation, this secondary oocyte will be released and travel toward the uterus through the oviduct. If the secondary oocyte is fertilized, the cell continues through the meiosis II, completing meiosis, producing a second polar body and a fertilized egg containing all 46 chromosomes of a human being, half of them coming from the sperm.

Spermatogenesis

Spermatogenesis occurs in the wall of the seminiferous tubules, with stem cells at the periphery of the tube and the spermatozoa at the lumen of the tube. Immediately under the capsule of the tubule are diploid, undifferentiated cells. These stem cells, called spermatogonia (singular: spermatagonium), go through mitosis with one offspring going on to differentiate into a sperm cell, while the other gives rise to the next generation of sperm.

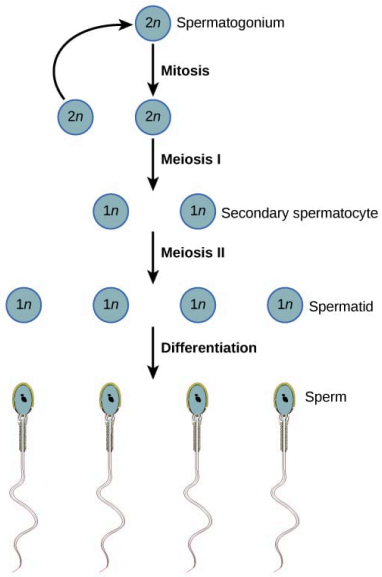


Figure $43.3C.1$: Spermatogenesis: During spermatogenesis, four sperm result from each primary spermatocyte, which divides into two haploid secondary spermatocytes; these cells will go through a second meiotic division to produce four spermatids.

Meiosis begins with a cell called a primary spermatocyte. At the end of the first meiotic division, a haploid cell is produced called a secondary spermatocyte. This haploid cell must go through another meiotic cell division. The cell produced at the end of meiosis is called a spermatid. When it reaches the lumen of the tubule and grows a flagellum (or "tail"), it is called a sperm cell. Four sperm result from each primary spermatocyte that goes through meiosis.

Stem cells are deposited during gestation and are present at birth through the beginning of adolescence, but in an inactive state. During adolescence, gonadotropic hormones from the anterior pituitary cause the activation of these cells and the production of viable sperm. This continues into old age.

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Key Points

- Gametogenesis, the production of sperm (spermatogenesis) and eggs (oogenesis), takes place through the process of meiosis.
- In oogenesis, diploid oogonium go through mitosis until one develops into a primary oocyte, which will begin the first meiotic division, but then arrest; it will finish this division as it develops in the follicle, giving rise to a haploid secondary oocyte and a smaller polar body.
- The secondary oocyte begins the second meiotic division and then arrests again; it will not finish this division unless it is fertilized by a sperm; if this occurs, a mature ovum and another polar body is produced.
- In spermatogenesis, diploid spermatogonia go through mitosis until they begin to develop into gametes; eventually, one develops into a primary spermatocyte that will go through the first meiotic division to form two haploid secondary spermatocytes.
- The secondary spermatocytes will go through a second meiotic division to each produce two spermatids; these cells will eventually develop flagella and become mature sperm.

Key Terms

- **spermatocyte**: a male gametocyte, from which a spermatozoon develops
- **oocyte**: a cell that develops into an egg or ovum; a female gametocyte
- **polar body**: one of the small cells that are by-products of the meiosis that forms an egg
- **mitosis**: the division of a cell nucleus in which the genome is copied and separated into two identical halves. It is normally followed by cell division
- **meiosis**: cell division of a diploid cell into four haploid cells, which develop to produce gametes

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43.4: HORMONAL CONTROL OF HUMAN REPRODUCTION

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- Topic hierarchy

43.4A: Male Hormones

43.4B: Female Hormones

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43.4A: Male Hormones

Learning Objectives

- Explain the function of male hormones in reproduction

Male Hormones

Puberty is a period of several years in which rapid physical growth and psychological changes occur, culminating in sexual maturity. The average onset of puberty is age 11 or 12 for boys. Some of the most significant parts of pubertal development involve distinctive physiological changes in individuals' height, weight, body composition, and circulatory and respiratory systems. These changes are largely influenced by hormonal activity. Hormones play an organizational role, priming the body to behave in a certain way once puberty begins, and an activational role, referring to changes in hormones during adolescence that trigger behavioral and physical changes.

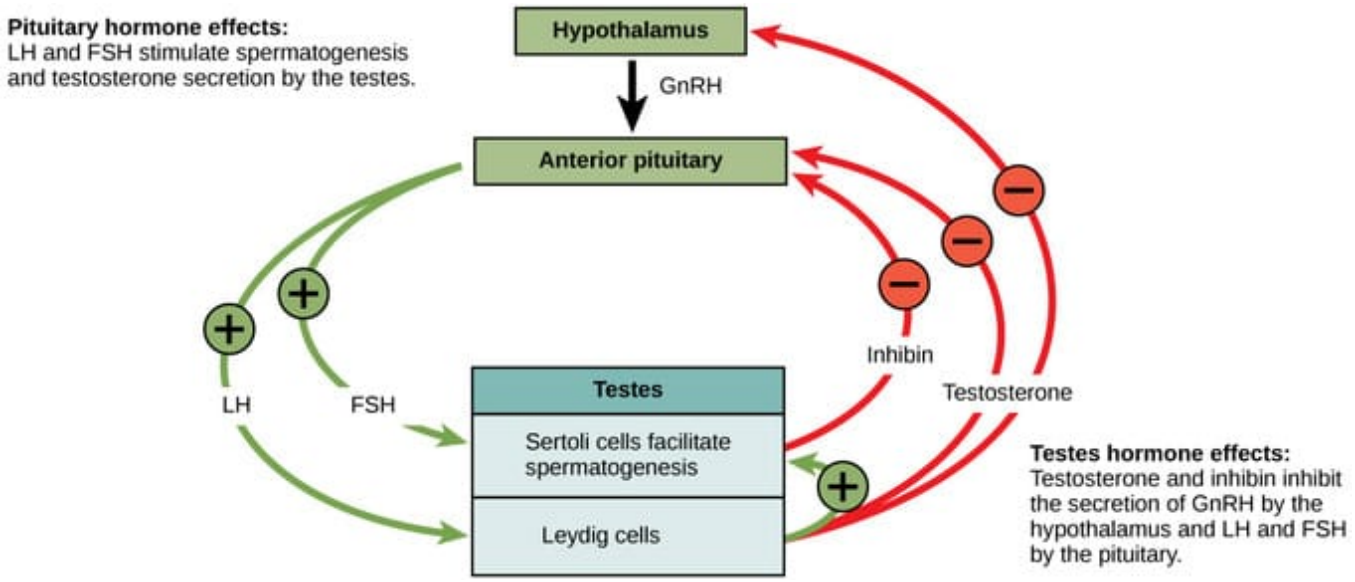


Figure 43.4A.1: Hormonal regulation of the male reproductive system: GnRH stimulates the production of FSH and LH, which act on the testes to begin spermatogenesis and to develop secondary sex characteristics in the male. In turn, the testes production of testosterone and the hormone inhibin inhibit the release of GnRH, FSH, and LH in a negative feedback loop.

At the onset of puberty, the hypothalamus begins secreting high pulses of GnRH, or gonadotropin-releasing hormone. In response, the pituitary gland releases follicle stimulating hormone (FSH) and luteinizing hormone (LH) into the male system for the first time. FSH enters the testes, stimulating the Sertoli cells, which help to nourish the sperm cells that the testes produce, to begin facilitating spermatogenesis. LH also enters the testes, stimulating the interstitial cells, called Leydig cells, to make and release testosterone into the testes and the blood.

Testosterone, the hormone responsible for the secondary sexual characteristics that develop in the male during adolescence, stimulates spermatogenesis, or the process of sperm production in the testes. Secondary sex characteristics include a deepening of the voice, the growth of facial, axillary, and pubic hair, and the beginnings of the sex drive.

A negative feedback system occurs in the male with rising levels of testosterone acting on the hypothalamus and anterior pituitary to inhibit the release of GnRH, FSH, and LH. The Sertoli cells produce the hormone inhibin, which is released into the blood when the sperm count is too high. This inhibits the release of GnRH and FSH, which will cause spermatogenesis to slow down. If the sperm count reaches 20 million/ml, the Sertoli cells cease the release of inhibin, allowing the sperm count to increase.

Key Points

- The onset of puberty is signaled by high pulses of GnRH secreted by the hypothalamus; this in turn signals the release of FSH and LH from the pituitary gland.
- FSH causes the Sertoli cells of the testes (which help nurse developing sperm cells) to begin the process of spermatogenesis in the testes.
- LH triggers the production of testosterone from the Leydig cells of the testis; testosterone causes the development of secondary sex characteristics in the male.
- As spermatogenesis and testosterone production increase, the Sertoli cells produce inhibin, which, together with rising levels of testosterone, inhibit the release of FSH and LH from the pituitary gland.

Key Terms

- **puberty**: the age at which a person is first capable of sexual reproduction
- **Sertoli cell**: a kind of sustentacular cell which serves as a “nurse” cell of the testes and which is part of a seminiferous tubule
- **Leydig cell**: one of the interstitial cells, located next to the seminiferous tubules inside the testicle, that produce testosterone
- **follicle stimulating hormone**: a gonadotropic glycoprotein hormone, secreted in the anterior pituitary, that stimulates the growth of ovarian follicles in female mammals, and induces spermatogenesis in male mammals
- **luteinizing hormone**: a hormone, produced by part of the pituitary gland, that stimulates ovulation and the development of the corpus luteum in female mammals, and the production of androgens by male mammals
- **inhibin**: a peptide hormone, secreted by the gonads, which inhibits the secretion of follicle-stimulating hormone
- **testosterone**: steroid hormone produced primarily in the testes of the male; it is responsible for the development of secondary sex characteristics in the male

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43.4B: Female Hormones

Learning Objectives

- Explain the function of female hormones in reproduction

Female Hormones

The control of reproduction in females is more complex than that of the male. As with the male, the hypothalamic hormone GnRH (gonadotropin-releasing hormone) causes the release of the hormones FSH (follicle stimulating hormone) and LH (luteinizing hormone) from the anterior pituitary. In addition, estrogens and progesterone are released from the developing follicles, which are structures on the ovaries that contain the maturing eggs.

In females, FSH stimulates the development of egg cells, called ova, which develop in structures called follicles. Follicle cells produce the hormone inhibin, which inhibits FSH production. LH also plays a role in the development of ova, as well as in the induction of ovulation and stimulation of estradiol and progesterone production by the ovaries. Estradiol and progesterone are steroid hormones that prepare the body for pregnancy. Estradiol is the reproductive hormone in females that assists in endometrial regrowth, ovulation, and calcium absorption; it is also responsible for the secondary sexual characteristics of females. These include breast development, flaring of the hips, and a shorter period necessary for bone maturation. Progesterone assists in endometrial re-growth and inhibition of FSH and LH release.

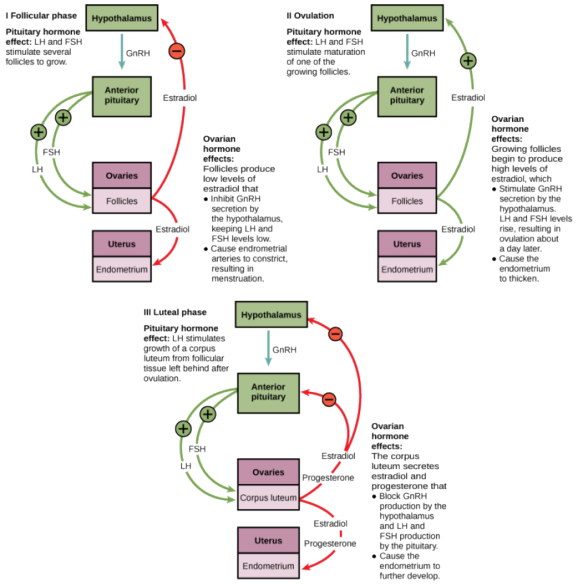


Figure $43.4B.1$: Hormonal control of the female reproductive cycle: The ovarian and menstrual cycles of female reproduction are regulated by hormones produced by the hypothalamus, pituitary, and ovaries. The pattern of activation and inhibition of these hormones varies between phases of the reproductive cycle.

The Ovarian Cycle and the Menstrual Cycle

The ovarian cycle governs the preparation of endocrine tissues and release of eggs, while the menstrual cycle governs the preparation and maintenance of the uterine lining. These cycles occur concurrently and are coordinated over a 22–32 day cycle, with an average length of 28 days.

The first half of the ovarian cycle is the follicular phase. Slowly-rising levels of FSH and LH cause the growth of follicles on the surface of the ovary, which prepares the egg for ovulation. As the follicles grow, they begin releasing estrogens and a low level of progesterone. Progesterone maintains the endometrium, the lining of the uterus, to help ensure pregnancy. Just prior to the

middle of the cycle (approximately day 14), the high level of estrogen causes FSH and, especially, LH to rise rapidly and then fall. The spike in LH causes ovulation: the most mature follicle ruptures and releases its egg. The follicles that did not rupture degenerate and their eggs are lost. The level of estrogen decreases when the extra follicles degenerate.

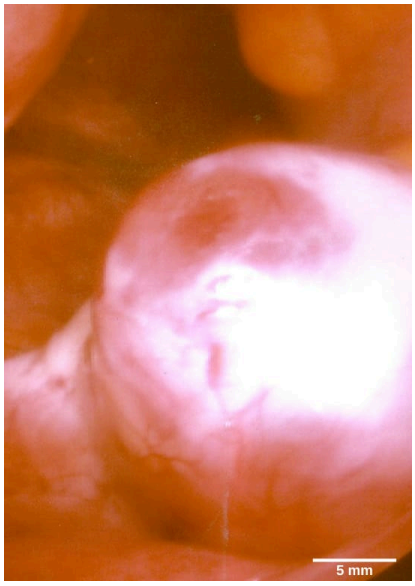


Figure $43.4B.1$: Follicle: This mature egg follicle may rupture and release an egg in response to a surge of LH.

If pregnancy implantation does not occur, the lining of the uterus is sloughed off, a process known as menstruation. After about five days, estrogen levels rise and the menstrual cycle enters the proliferative phase. The endometrium begins to regrow, replacing the blood vessels and glands that deteriorated during the end of the last cycle.

Following ovulation, the ovarian cycle enters its luteal phase and the menstrual cycle enters its secretory phase, both of which run from about day 15 to 28. The luteal and secretory phases refer to changes in the ruptured follicle. The cells in the follicle undergo physical changes, producing a structure called a corpus luteum, which produces estrogen and progesterone. The progesterone facilitates the regrowth of the uterine lining and inhibits the release of further FSH and LH. The uterus is again being prepared to accept a fertilized egg, should it occur during this cycle. The inhibition of FSH and LH prevents any further eggs and follicles from developing. The level of estrogen produced by the corpus luteum increases to a steady level for the next few days.

If no fertilized egg is implanted into the uterus, the corpus luteum degenerates and the levels of estrogen and progesterone decrease. The endometrium begins to degenerate as the progesterone levels drop, initiating the next menstrual cycle. The decrease in progesterone also allows the hypothalamus to send GnRH to the anterior pituitary, releasing FSH and LH to start the cycles again.

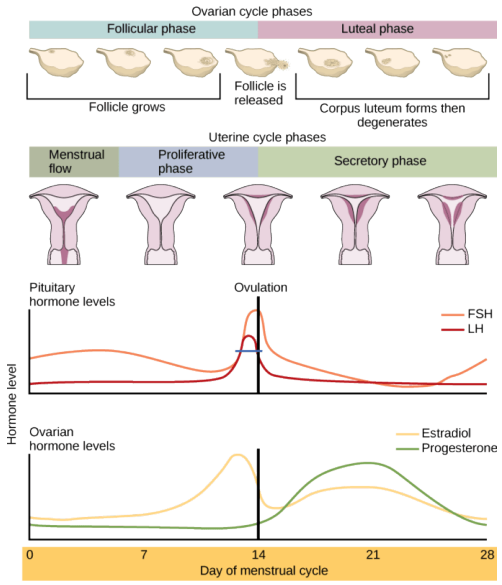


Figure $43.4B.1$: Stages of the menstrual cycle: Rising and falling hormone levels result in progression of the ovarian and menstrual cycles.

Menopause

As women approach their mid-40s to mid-50s, their ovaries begin to lose their sensitivity to FSH and LH. Menstrual periods become less frequent and finally cease; this process is known as menopause. There are still eggs and potential follicles on the ovaries, but without the stimulation of FSH and LH, they will not produce a viable egg to be released. The outcome of this is the inability to have children.

Various symptoms are associated with menopause, including hot flashes, heavy sweating, headaches, some hair loss, muscle pain, vaginal dryness, insomnia, depression, weight gain, and mood swings. Estrogen is involved in calcium metabolism and, without it, blood levels of calcium decrease. To replenish the blood, calcium is lost from bone, which may decrease the bone density and lead to osteoporosis. Supplementation of estrogen in the form of hormone replacement therapy (HRT) can prevent bone loss, but the therapy can have negative side effects, such as an increased risk of stroke or heart attack, blood clots, breast cancer, ovarian cancer, endometrial cancer, gall bladder disease, and, possibly, dementia.

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Key Points

- As in males, GnRH secreted by the hypothalamus triggers the release of FSH and LH from the pituitary; however, in females, this signals the ovaries to produce estradiol and progesterone.
- FSH stimulates the growth and maturation of follicles on the ovaries, which house and nourish the developing eggs; the follicle, in turn, releases inhibin, which inhibits the production of FSH.
- Progesterone stimulates the growth of the endometrial lining of the uterus in order to prepare it for pregnancy; a strong surge of LH at around day 14 of the cycle triggers ovulation of an egg from the most mature follicle.
- After ovulation, the ruptured follicle becomes a corpus luteum, which secretes progesterone to either regrow the uterine lining or to support the pregnancy if it occurs.
- During middle age, a woman's ovaries become less sensitive to FSH and LH and, therefore, cease to mature follicles and undergo ovulation; this is known as menopause.

Key Terms

- **corpus luteum**: a yellow mass of cells that forms from an ovarian follicle during the luteal phase of the menstrual cycle in mammals; it secretes steroid hormones
- **menopause**: the ending of menstruation; the time in a woman's life when this happens
- **endometrium**: the mucous membrane that lines the uterus in mammals and in which fertilized eggs are implanted
- **estradiol**: a potent estrogenic hormone produced in the ovaries of all vertebrates; the synthetic compound is used medicinally to treat estrogen deficiency and breast cancer
- **menstruation**: the periodic discharging of the menses, the flow of blood and cells from the lining of the uterus in females of humans and other primates

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43.5: FERTILIZATION AND EARLY EMBRYONIC DEVELOPMENT

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- Topic hierarchy

43.5A: Fertilization

43.5B: Cleavage, the Blastula Stage, and Gastrulation

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43.5A: Fertilization

Learning Objectives

- Describe the process of fertilization

Fertilization

Fertilization is the process in which gametes (an egg and sperm) fuse to form a zygote. The egg and sperm are haploid, which means they each contain one set of chromosomes; upon fertilization, they will combine their genetic material to form a zygote that is diploid, having two sets of chromosomes. A zygote that has more than two sets of chromosomes will not be viable; therefore, to ensure that the offspring has only two sets of chromosomes, only one sperm must fuse with one egg.

In mammals, the egg is protected by a layer of extracellular matrix consisting mainly of glycoproteins called the zona pellucida. When a sperm binds to the zona pellucida, a series of biochemical events, called the acrosomal reaction, take place. In placental mammals, the acrosome contains digestive enzymes that initiate the degradation of the glycoprotein matrix protecting the egg and allowing the sperm plasma membrane to fuse with the egg plasma membrane. The fusion of these two membranes creates an opening through which the sperm nucleus is transferred into the ovum. Fusion between the oocyte plasma membrane and sperm follows and allows the sperm nucleus, centriole, and flagellum, but not the mitochondria, to enter the oocyte. The nuclear membranes of the egg and sperm break down and the two haploid genomes condense to form a diploid genome. This process ultimately leads to the formation of a diploid cell called a zygote. The zygote divides to form a blastocyst and, upon entering the uterus, implants in the endometrium, beginning pregnancy.

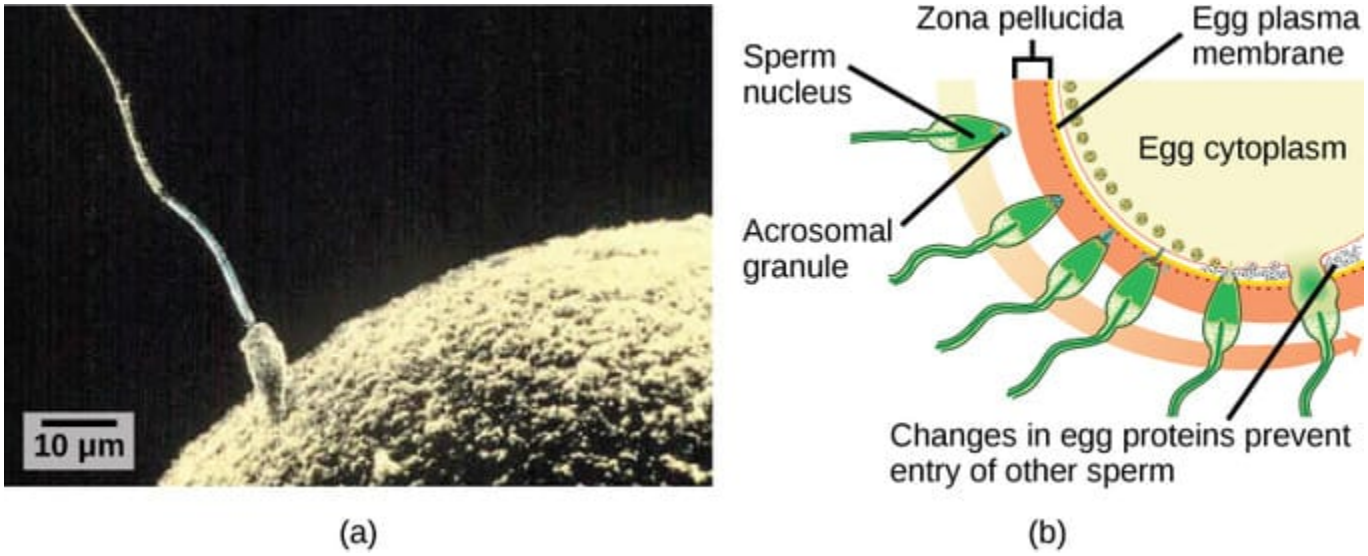


Figure 43.5A.1:

Process of fertilization: (a) Fertilization is the process in which sperm and egg fuse to form a zygote. (b) Acrosomal reactions help the sperm degrade the glycoprotein matrix protecting the egg and allow the sperm to transfer its nucleus.

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. If this mechanism fails, multiple sperm can fuse with the egg, resulting in polyspermy. The resulting embryo is not genetically viable and dies within a few days.

Key Points

- A mammalian egg is covered by a layer of glycoproteins called the zona pellucida, which the sperm must penetrate in order to fertilize the egg.
- Upon binding with the egg, the sperm initiates the acrosome reaction, in which it releases digestive enzymes that degrade the zona pellucida, allowing the plasma membrane of the sperm to fuse with that of the egg.
- Upon fusion of the two plasma membranes, the sperm's nucleus enters the egg and fuses with the nucleus of the egg.
- Both the sperm and the egg each contain one half the normal number of chromosomes, so when they fuse the resulting zygote is a diploid organism with a complete set of chromosomes.
- When the egg is successfully fertilized, it releases proteins that prevent it from being fertilized by another sperm, a condition known as polyspermy.

Key Terms

- **fertilization**: the act of fecundating or impregnating animal or vegetable gametes
- **zona pellucida**: a glycoprotein membrane surrounding the plasma membrane of an oocyte
- **acrosome**: a structure forming the end of the head of a spermatozoon
- **polyspermy**: the penetration of an ovum by more than one sperm

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43.5B: Cleavage, the Blastula Stage, and Gastrulation

Learning Objectives

- Describe the events that occur from the formation of a zygote to gastrulation

Cleavage and Blastula Stage

The development of multi-cellular organisms begins from a single-celled zygote, which undergoes rapid cell division to form the blastula. The rapid, multiple rounds of cell division are termed cleavage. After the cleavage has produced over 100 cells, the embryo is called a blastula. The blastula is usually a spherical layer of cells (the blastoderm) surrounding a fluid-filled or yolk-filled cavity (the blastocoel). Mammals at this stage form a structure called the blastocyst, characterized by an inner cell mass that is distinct from the surrounding blastula. During cleavage, the cells divide without an increase in mass; that is, one large single-celled zygote divides into multiple smaller cells. Each cell within the blastula is called a blastomere.

Cleavage can take place in two ways: holoblastic (total) cleavage or meroblastic (partial) cleavage. The type of cleavage depends on the amount of yolk in the eggs. In placental mammals (including humans) where nourishment is provided by the mother's body, the eggs have a very small amount of yolk and undergo holoblastic cleavage. Other species, such as birds, with a lot of yolk in the egg to nourish the embryo during development, undergo meroblastic cleavage.

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 is also known as the embryoblast; this mass of cells will go on to form the embryo. At this stage of development, the inner cell mass consists of embryonic stem cells that will differentiate into the different cell types needed by the organism. The trophoblast will contribute to the placenta and nourish the embryo.

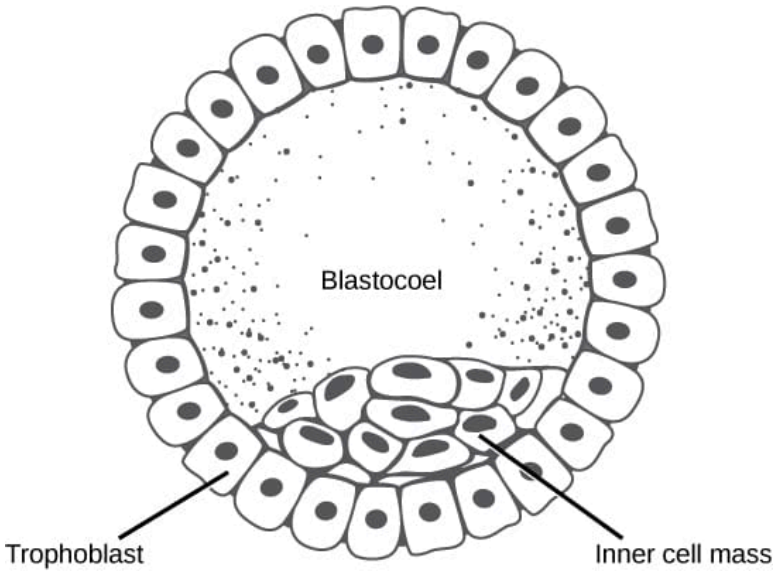


Figure $43.5B.1$: Formation of the blastocyst: The rearrangement of the cells in the mammalian blastula to two layers, the inner cell mass and the trophoblast, results in the formation of the blastocyst.

Gastrulation

The typical blastula is a ball of cells. The next stage in embryonic development is the formation of the body plan. The cells in the blastula rearrange themselves spatially to form three layers of cells in a process known as gastrulation. During gastrulation, the blastula folds upon itself to form the three layers of cells. Each of these layers is called a germ layer, which differentiate into

different organ systems.

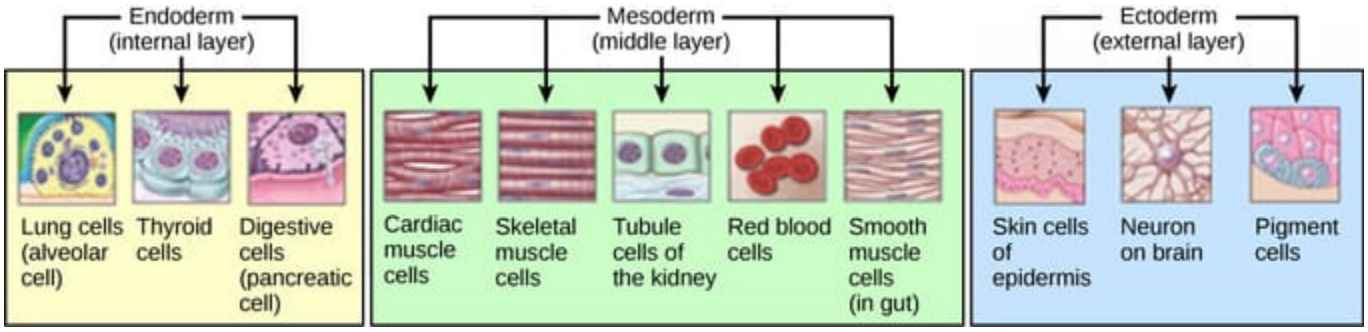


Figure $43.5B.1$:

Differentiation of germ layers: The three germ layers give rise to different cell types in the animal body: the ectoderm forms the nervous system and the outer layer of skin, the mesoderm gives rise to muscles and connective tissues, and the endoderm gives rise to the lining of the digestive system and other internal organs.

The three germs layers are the endoderm, the ectoderm, and the mesoderm. The ectoderm gives rise to the nervous system and the epidermis; the mesoderm gives rise to the muscle cells and connective tissue in the body; and the endoderm gives rise to columnar cells found in the digestive system and many internal organs.

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Key Points

- A single-celled zygote will undergo multiple rounds of cleavage, or cell division, in order to produced a ball of cells, called a blastula, with a fluid-filled cavity in its center, called a blastocoel.
- In animals with little yolk in the egg, the zygote undergoes holoblastic cleavage, in which the entire zygote is cleaved repeatedly; in animals with a lot of yolk in the egg, the zygote undergoes meroblastic cleavage, in which only part of the zygote is cleaved.
- The blastula eventually organizes itself into two layers: the inner cell mass (which will become the embryo) and the outer layer or trophoblast (which will become the placenta); the structure is now called a blastocyst.
- During gastrulation, the blastula folds in on itself to form three germ layers, the ectoderm, the mesoderm, and the endoderm, that will give rise to the internal structures of the organism.

Key Terms

- **blastula**: a 6-32-celled hollow structure that is formed after a zygote undergoes cell division
- **blastomere**: any cell that results from division of a fertilized egg
- **meroblastic**: undergoing only partial cleavage
- **holoblastic**: cleaving, and separating into separate blastomeres
- **inner cell mass**: a mass of cells within a primordial embryo that will eventually develop into the distinct form of a fetus in most eutherian mammals
- **gastrulation**: the stage of embryo development at which a gastrula is formed from the blastula by the inward migration of cells
- **trophoblast**: the membrane of cells that forms the wall of a blastocyst during early pregnancy, providing nutrients to the embryo and later developing into part of the placenta

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43.6: ORGANOGENESIS AND VERTEBRATE FORMATION

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- Topic hierarchy

43.6A: Organogenesis
43.6B: Vertebrate Axis Formation

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43.6A: Organogenesis

Learning Objectives

- Describe the process of organogenesis in vertebrates

Organogenesis

Organogenesis is the process by which the three germ tissue layers of the embryo, which are the ectoderm, endoderm, and mesoderm, develop into the internal organs of the organism. Organs form from the germ layers through the differentiation: the process by which a less-specialized cell becomes a more-specialized cell type. This must occur many times as a zygote becomes a fully-developed organism. During differentiation, the embryonic stem cells express specific sets of genes which 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 differentiate into epidermal cells. Therefore, the process of differentiation is regulated by cellular signaling cascades.

In vertebrates, one of the primary steps during organogenesis is the formation of the neural system. The ectoderm forms epithelial cells and tissues, as well as neuronal tissues. During the formation of the neural system, special signaling molecules called growth factors signal some cells at the edge of the ectoderm to become epidermis cells. The remaining cells in the center form the neural plate. If the signaling by growth factors were disrupted, then the entire ectoderm would differentiate into neural tissue. The neural plate undergoes a series of cell movements where it rolls up and forms a tube called the neural tube. In further development, the neural tube will give rise to the brain and the spinal cord.

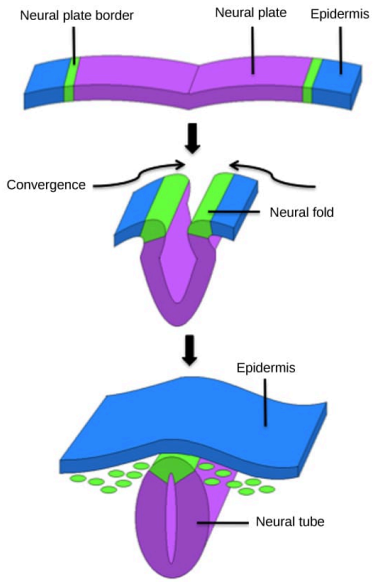


Figure 43.6A.1: Neural tube formation: The central region of the ectoderm forms the neural tube, which gives rise to the brain and the spinal cord.

The mesoderm that lies on either side of the vertebrate neural tube will develop into the various connective tissues of the animal body. A spatial pattern of gene expression reorganizes the mesoderm into groups of cells called somites, with spaces between them. The somites will further develop into the ribs, lungs, and segmental (spine) muscle. The mesoderm also forms a structure called the notochord, which is rod-shaped and forms the central axis of the animal body.

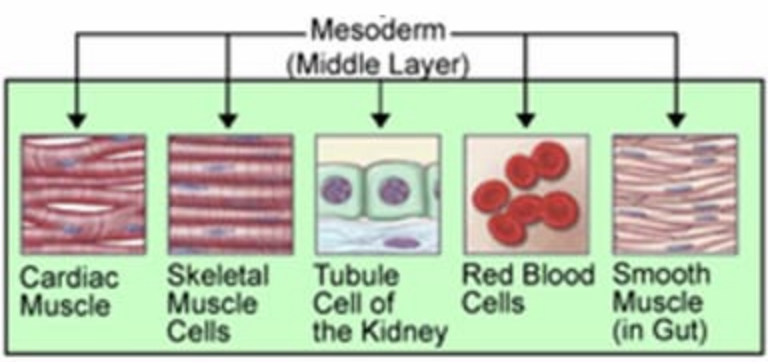


Figure 43.6A.1: Mesoderm: The mesoderm aids in the production of cardiac muscles, skeletal muscle, smooth muscle, tissues within the kidneys, and red blood cells.

The endoderm consists, at first, of flattened cells, which subsequently become columnar. It forms the epithelial lining of the whole of the digestive tube (except part of the mouth and pharynx) and the terminal part of the rectum (which is lined by involutions of the ectoderm). It also forms the lining cells of all the glands which open into the digestive tube, including those of the liver and pancreas; the epithelium of the auditory tube and tympanic cavity; the trachea, bronchi, and air cells of the lungs; the urinary bladder and part of the urethra; and the follicle lining of the thyroid gland and thymus. Additionally, the endoderm forms internal organs including the stomach, the colon, the liver, the pancreas, the urinary bladder, the epithelial parts of trachea, the lungs, the pharynx, the thyroid, the parathyroid, and the intestines.

Key Points

- Cells in the ectoderm are signaled by molecules called growth factors to form the neural plate, which rolls up to form a structure called the neural tube; the neural tube will eventually develop into the brain and spinal cord.
- The differing expression of various genes controls the differentiation of the mesoderm into connective tissue, as well as the ribs, spine, skeletal muscle, and lungs.
- The endoderm forms the lining of the digestive tract, as well as the linings of all the glands that will empty into the digestive tract; it also forms a wide variety of internal organs.

Key Terms

- **organogenesis**: the formation and development of the organs of an organism from embryonic cells
- **ectoderm**: outermost of the three tissue layers in the embryo of a metazoan animal, which will produce the epidermis (skin) and nervous system of the adult
- **mesoderm**: one of the three tissue layers in the embryo of a metazoan animal, which will produce many internal organs of the adult such as the muscles, spine and circulatory system
- **endoderm**: one of the three tissue layers in the embryo of a metazoan animal, which will produce the digestive system and other internal organs of the adult
- **neural plate**: a thick, flat bundle of ectoderm formed in vertebrate embryos after induction by the notochord

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43.6B: Vertebrate Axis Formation

Learning Objectives

- Describe the formation of body axes in vertebrates

Vertebrate Axis Formation

Even as the germ layers form, the ball of cells still retains its spherical shape. However, animal bodies have lateral-medial (toward the side-toward the midline), dorsal-ventral (toward the back-toward the belly), and anterior-posterior (toward the front-toward the back) axes. As the body forms, it must develop in such a way that cells, tissues, and organs are organized correctly along these axes.

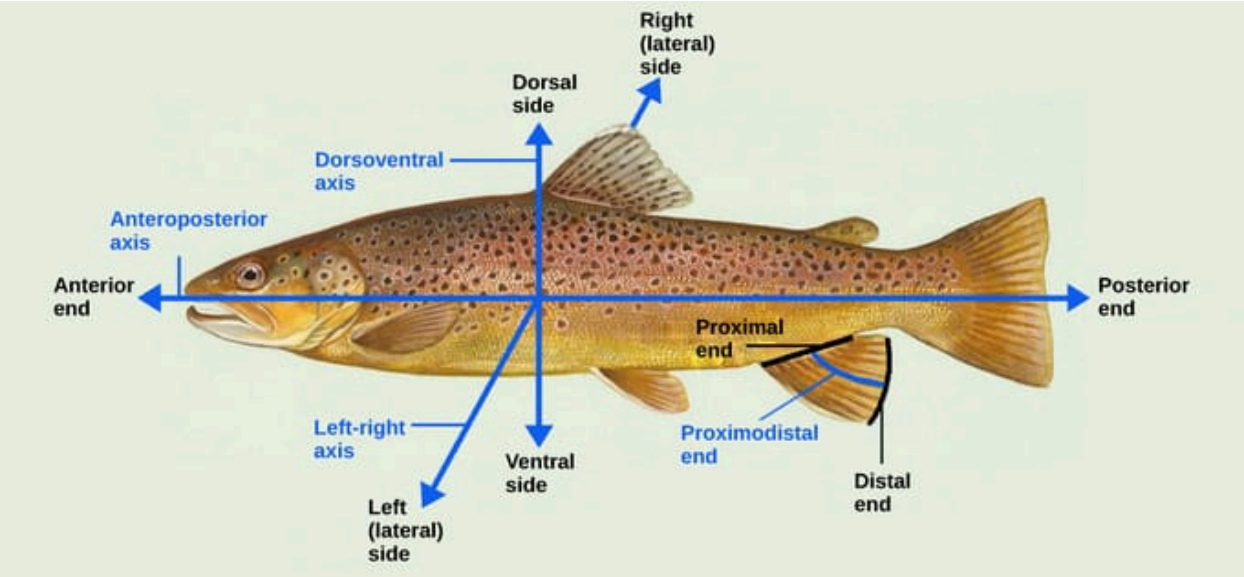


Figure $43.6B.1$: Body axes: Animal bodies have three axes for symmetry: anterior/posterior (front/behind), dorsal/ventral (back/belly), and lateral/medial (side/middle).

How are these established? In one of the most seminal experiments ever to be carried out in developmental biology, Spemann and Mangold took dorsal cells from one embryo and transplanted them into the belly region of another embryo. They found that the transplanted embryo now had two notochords: one at the dorsal site from the original cells and another at the transplanted site. This suggested that the dorsal cells were genetically programmed to form the notochord and define the dorsal-ventral axis. Since then, researchers have identified many genes that are responsible for axis formation. Mutations in these genes leads to the loss of symmetry required for organism development. Many of these genes are involved in the Wnt signaling pathway.

In early embryonic development, the formation of the primary body axes is a crucial step in establishing the overall body plan of each particular organism. Wnt signaling can be implicated in the formation of the anteroposterior and dorsoventral axes. Wnt signaling activity in anterior-posterior development can be seen in several organisms including mammals, fish, and frogs. Wnt signaling is also involved in the axis formation of specific body parts and organ systems that are a part of later development. In vertebrates, sonic hedgehog (Shh) and Wnt morphogenetic signaling gradients establish the dorsoventral axis of the central nervous system during neural tube axial patterning. High Wnt signaling establishes the dorsal region while high Shh signaling indicates in the ventral region. Wnt is also involved in the dorsal-ventral formation of the central nervous system through its involvement in axon guidance. Wnt proteins guide the axons of the spinal cord in an anterior-posterior direction. Wnt is also involved in the formation of the limb dorsal-ventral axis. Specifically, Wnt7a helps produce the dorsal patterning of the developing limb.

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Key Points

- As an animal develops, it must organize its internal and external structures such that the anterior/posterior (forward/backward), dorsal / ventral (back/belly), and lateral/medial (side/middle) axes are correctly determined.
- Proteins that are part of the Wnt signaling pathway help determine the anterior/posterior axis by guiding the axons of the spinal cord in an anterior/posterior direction.
- Together with the sonic hedgehog (Shh) protein, Wnt determines the dorsal/ventral axis; Wnt levels are highest in the dorsal region and lessen toward the ventral region, while Shh levels are highest in the ventral region and lessen toward the dorsal region.

Key Terms

- **dorsal**: with respect to, or concerning the side in which the backbone is located, or the analogous side of an invertebrate
- **ventral**: on the front side of the human body, or the corresponding surface of an animal, usually the lower surface
- **notochord**: a flexible rodlike structure that forms the main support of the body in the lowest chordates; a primitive spine
- **Wnt signaling pathway**: a group of signal transduction pathways made of proteins that pass signals from outside of a cell through cell surface receptors to the inside of the cell

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43.7: HUMAN PREGNANCY AND BIRTH

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- Topic hierarchy

43.7A: Human Gestation

43.7B: Labor and Birth

43.7C: Contraception and Birth Control

43.7D: Infertility

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43.7A: Human Gestation

Learning Objectives

- Describe the development of the human fetus from fertilization through the third trimester

Human gestation

Twenty-four hours before fertilization, the egg has finished meiosis and become a mature oocyte. When fertilized (at conception), the egg, now known as a zygote, travels through the oviduct to the uterus. The developing embryo must implant into the wall of the uterus within seven days or it will deteriorate and die. The outer layers of the zygote (blastocyst) grow into the endometrium by digesting the endometrial cells. Wound healing of the endometrium closes up the blastocyst into the tissue. Another layer of the blastocyst, the chorion, begins releasing a hormone called human chorionic gonadotropin (hCG) which makes its way to the corpus luteum, keeping it active. This ensures adequate levels of progesterone that will maintain the endometrium of the uterus for the support of the developing embryo. Pregnancy tests determine the level of hCG in urine or serum: if the hormone is present, the test is positive.

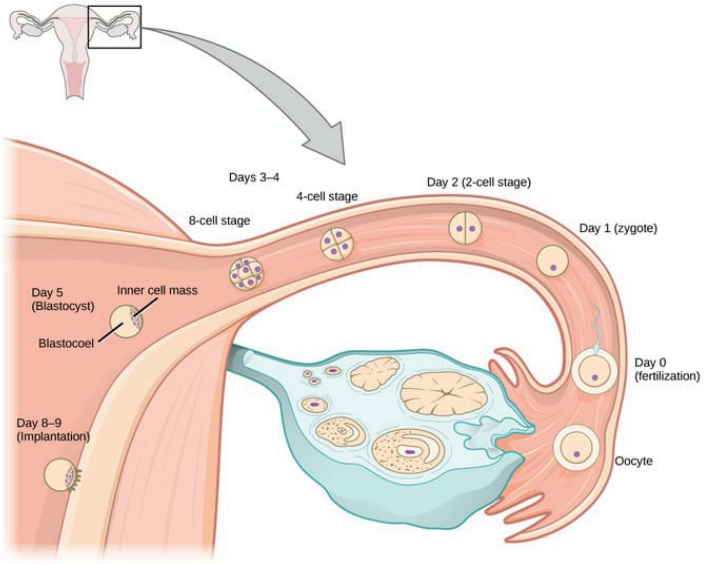


Figure 43.7A.1: Development of the embryo: In humans, fertilization occurs soon after the oocyte leaves the ovary. Implantation occurs eight or nine days later. The embryo divides several times as it travels.

First trimester

The gestation period is divided into three equal periods or trimesters. During the first two to four weeks of the first trimester, nutrition and waste are handled by the endometrial lining through diffusion. As the trimester progresses, the outer layer of the embryo begins to merge with the endometrium and the placenta forms. This organ takes over the nutrient and waste requirements of the embryo and fetus, with the mother's blood passing nutrients to the placenta and removing waste from it. Chemicals from the fetus, such as bilirubin, are processed by the mother's liver for elimination. Some of the mother's immunoglobulins will pass through the placenta, providing passive immunity against some potential infections.

Internal organs and body structures begin to develop during the first trimester. By five weeks, limb buds, eyes, the heart, and liver have been basically formed. By eight weeks, the term fetus applies; the body is essentially formed. The individual is about five centimeters (two inches) in length and many of the organs, such as the lungs and liver, are not yet functioning. Exposure to any toxins is especially dangerous during the first trimester, as all of the body's organs and structures are going through initial development. Anything that affects that development can have a severe effect on the fetus' survival.



Figure 43.7A.1: First trimester: Fetal development is shown at nine weeks gestation. At this stage, the body is essentially formed; however many of the organs are not yet functioning.

Second trimester

During the second trimester, the fetus grows to about 30 cm (12 inches). As it becomes active, the mother usually feels the first movements. All organs and structures continue to develop. The placenta has taken over the functions of nutrition and waste, along with the production of estrogen and progesterone from the corpus luteum, which has degenerated. The placenta will continue functioning up through the delivery of the fetus.



Figure 43.7A.1: Second trimester: This fetus is just entering the second trimester, when the placenta takes over more of the functions performed as the baby develops.

Third trimester

During the third trimester, the fetus grows to 3 to 4 kg (6 ½ -8 ½ lbs.) and about 50 cm (19-20 inches) long. This is the period of the most rapid growth during the pregnancy. Organ development continues to birth (and some systems, such as the nervous system and liver, continue to develop after birth). The mother will be at her most uncomfortable during this trimester. She may urinate frequently due to pressure on the bladder from the fetus. There may also be intestinal blockage and circulatory problems,

especially in her legs. Clots may form in her legs due to pressure from the fetus on returning veins as they enter the abdominal cavity.

Key Points

- After fertilization, the zygote implants itself in the uterine wall; its outer layer grows into the endometrium, where it begins to produce human chorionic gonadotropin.
- During the first trimester, the placenta forms along with the internal organs and structures; however, not all of the internal organs function at this point.
- During the second trimester, internal organs continue to develop and the fetus becomes active.
- The third trimester is one of rapid growth, in which the fetus reaches its full size; pregnancy often becomes uncomfortable for the mother.

Key Terms

- **zygote**: a diploid fertilized egg cell
- **chorion**: allows exchange of oxygen and carbon dioxide between the embryo and the egg's external environment
- **human chorionic gonadotropin**: a peptide hormone, produced during pregnancy, that prevents the breakdown of the corpus luteum and maintains progesterone production
- **placenta**: a vascular organ in mammals that supplies food and oxygen from the mother to the fetus, while passing back waste; it is implanted in the wall of the uterus

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43.7B: Labor and Birth

Learning Objectives

- Describe the process of labor and birth in humans

Labor and Birth

Labor is the physical effort of expulsion of the fetus and the placenta from the uterus during birth (parturition). The total gestation period from fertilization to birth is about 38 weeks (birth usually occurring 40 weeks after the last menstrual period). Toward the end of the third trimester, estrogen causes receptors on the uterine wall to develop and bind the hormone oxytocin. At this time, the baby reorients, facing forward and down with the back or crown of the head engaging the cervix (uterine opening). This causes the cervix to stretch, sending nerve impulses to the hypothalamus, which signals for the release of oxytocin from the posterior pituitary. The oxytocin causes the smooth muscle in the uterine wall to contract. At the same time, the placenta releases prostaglandins into the uterus, increasing the contractions. A positive feedback relay occurs between the uterus, hypothalamus, and the posterior pituitary to assure an adequate supply of oxytocin. As more smooth muscle cells are recruited, the contractions increase in intensity and force.

There are three stages to labor. During stage one, the cervix thins and dilates. This is necessary for the baby and placenta to be expelled during birth. The cervix will eventually dilate to about 10 cm, a process that may take many hours, especially in a woman bearing her first child. At some point, the amniotic sac bursts and the amniotic fluid escapes. During stage two, the baby is expelled from the uterus with the umbilical cord still attached. The uterus contracts and the mother pushes as she compresses her abdominal muscles to aid the delivery. The last stage is the passage of the placenta after the baby has been born and the organ has completely disengaged from the uterine wall, usually within a few minutes. If labor should stop before stage two is reached, synthetic oxytocin, known as Pitocin, can be administered to restart and maintain labor.

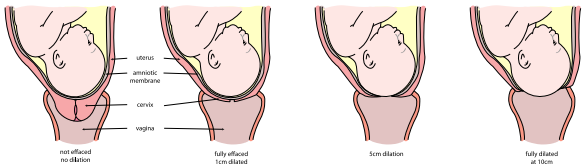


Figure $43.7B.1$: Cervix dilation: During the first stage of labor, the cervix, which is normally closed, must open and widen to accommodate the passage of the baby. A cervix is considered fully dilated at 10 centimeters.

The mother's mammary glands go through changes during the third trimester to prepare for lactation and breastfeeding. When the baby begins suckling at the breast, signals are sent to the hypothalamus causing the release of prolactin from the anterior pituitary, which signals the mammary glands to produce milk. Oxytocin is also released, promoting the release of the milk. The milk contains nutrients for the baby's development and growth as well as immunoglobulins to protect the child from bacterial and viral infections.

Key Points

- At the end of gestation, estrogen receptors on the uterine wall bind oxytocin, which causes the uterine muscles to contract; as the muscles contract, they signal for the release of more oxytocin in a positive feedback loop.
- During the first stage of labor, the cervix thins and dilates to allow passage of the baby into the birth canal; typically over the course of several hours, the cervix will dilate to its full width of 10 centimeters.
- During the second stage of labor, contractions become very strong and, aided by the pushing of the mother, the baby is expelled from the uterus.
- During the third stage of labor, the placenta, amniotic sac, and the remainder of the umbilical cord are expelled from the uterus, usually within a few minutes after birth.
- When the baby begins suckling at the breast after delivery, prolactin signals the release of milk from the mammary glands, providing nutrition and immunity against disease to the infant.

Key Terms

- **prolactin**: a peptide gonadotrophic hormone secreted by the pituitary gland; it stimulates growth of the mammary glands and lactation in females
- **parturition**: the act of giving birth; childbirth
- **oxytocin**: a hormone that stimulates contractions during labor, and then the production of milk

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43.7C: Contraception and Birth Control

Learning Objectives

- Describe the various methods of birth control and their associated failure rates

Contraception and Birth Control

Contraception, also known as birth control, is methods or devices used to prevent pregnancy. Strictly speaking, contraception aims to prevent the sperm and egg from joining, while birth control can refer to methods used to prevent a fertilized egg from developing into a fetus. Both terms are, however, frequently used interchangeably.

There are many methods of birth control, including barriers to sperm, hormones that prevent ovulation, sterilization procedures, and "natural" methods. Each method has an associated "failure rate", which is the number of pregnancies resulting from the method's use over a twelve-month period.

Barrier methods include those that prevent the sperm from reaching the egg. These include condoms, diaphragms, cervical caps, sponges, and spermicides; they have a failure rate of 15-24%. Barrier methods such as condoms, cervical caps, and diaphragms serve to block sperm from entering the uterus, thereby preventing fertilization. Chemicals such as spermicides, which are designed to kill sperm, are often used in conjunction; sponges, for example, are saturated with spermicides and are placed in the vagina at the cervical opening. Combinations of spermicidal chemicals and barrier methods achieve lower failure rates than do the methods when used separately.

Hormonal methods use synthetic progesterone (sometimes in combination with estrogen) to inhibit the hypothalamus from releasing FSH or LH, preventing an egg from being available for fertilization. The method of administering the hormone affects failure rate, although, in general, hormonal methods have a failure rate of 8%. The most reliable method, with a failure rate of less than 1 percent, is the implantation of the hormone under the skin. The same rate can be achieved through the sterilization procedures of vasectomy in the man or of tubal ligation in the woman, or by using an intrauterine device (IUD). IUDs are inserted into the uterus where they establish an inflammatory condition that prevents fertilized eggs from implanting into the uterine wall.

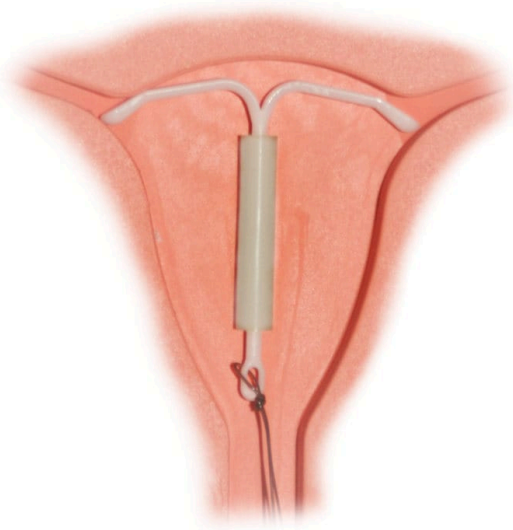


Figure $43.7C.1$: Intrauterine device: An intrauterine device, or IUD, is implanted inside a woman's uterus, causing the uterus to respond with slight inflammation. This inflammation prevents a fertilized egg from implanting in the uterine wall.

Sterilization is a one-time, permanent, surgical procedure. In a vasectomy, the vasa deferentia of a male are severed and then tied/sealed in a manner that prevents sperm from entering into the seminal stream (ejaculate). Tubal ligation or tubectomy is a

surgical procedure for sterilization in which a woman's fallopian tubes are clamped and blocked, or severed and sealed; either method prevents eggs from reaching the uterus for fertilization. Both of these procedures have a less than 1% failure rate.

Natural methods include avoiding intercourse when ovulation is occurring ("natural family planning) or withdrawing the penis from the vagina before ejaculation. Nearly 25% of the couples using natural family planning or withdrawal can expect a failure of the method. Natural family planning is based on the monitoring of the menstrual cycle and having intercourse only during times when the egg is not available. A woman's body temperature may rise a degree Celsius at ovulation and the cervical mucus may increase in volume, becoming more pliable. These changes give a general indication of when intercourse is more or less likely to result in fertilization. Withdrawal involves the removal of the penis from the vagina during intercourse, before ejaculation occurs; it has a failure rate of 27%. This is, therefore, a risky method. The high failure rate is due to the possible presence of sperm in the bulbourethral gland's secretion, which may enter the vagina prior to removing the penis.

Termination of an existing pregnancy can be spontaneous or voluntary. Spontaneous termination in the first trimester is referred to as spontaneous abortion, while in the second and third trimesters is referred to as a miscarriage. Spontaneous abortion usually occurs very early in the pregnancy (typically within the first few weeks). Pregnancy loss occurs when the embryo/fetus cannot develop properly so the gestation is naturally terminated. Voluntary termination of a pregnancy is called an elective abortion. Laws regulating elective abortion vary between states; the laws tend to view fetal viability as the criteria for allowing or preventing the procedure.

Key Points

- Barrier methods include those that prevent the sperm from reaching the egg (condoms, diaphragms, cervical caps, sponges, and spermicides); these methods have a failure rate of 15-24%.
- Hormonal methods include those that prevent a woman from ovulating (oral birth control pills, hormone injections, and hormone implants); these have a failure rate of 8%.
- Sterilization, such as a tubal ligation in a woman or a vasectomy in a man, is an extremely effective (although permanent) method of contraception, with a failure rate of 1%.
- More "natural" methods of birth control include avoiding intercourse when a woman is ovulating, or withdrawing the penis from the vagina before ejaculation; these methods are much less successful, with a failure rate of around 25%.

Key Terms

- **condom**: a flexible sleeve made of latex or other impermeable material such as sheepskin, worn over an erect penis during intercourse as a contraceptive or as a way to prevent the spread of STDs
- **intrauterine device**: a contraceptive device consisting of a spiral or similar shape of plastic or metal inserted through the vagina into the uterus in order to prevent the implantation of a fertilized egg
- **vasectomy**: the surgical removal of all or part of the vas deferens, usually as a means of male sterilization
- **contraception**: the use of a device or procedure to prevent conception as a result of sexual activity
- **spermicide**: a substance used for killing sperm

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43.7D: Infertility

Learning Objectives

- Define infertility and discuss ways in which it can be treated

Infertility is the inability to conceive or carry a fetus to birth. About 75% of causes of infertility can be identified. These include diseases (such as sexually-transmitted diseases that can cause scarring of the reproductive tubes in either men or women) or developmental problems frequently related to abnormal hormone levels in one of the individuals. Inadequate nutrition, especially starvation, can delay menstruation. Stress can also lead to infertility. Short-term stress can affect hormone levels, while long-term stress can delay puberty, causing less-frequent menstrual cycles. Other factors that affect fertility include toxins (such as cadmium), tobacco smoking, marijuana use, gonadal injuries, and aging.

If the cause of infertility is identified, several assisted reproductive technologies (ART) are available to aid conception. A common type of assisted reproductive technology is *in vitro* fertilization (IVF) where an egg and sperm are combined outside the body and then placed in the uterus. Eggs are obtained from the woman after extensive hormonal treatments that prepare mature eggs for fertilization and prepare the uterus for implantation of the fertilized egg. Sperm are obtained from the male and combined with the eggs, which are then supported through several cell divisions to ensure viability of the zygotes. When the embryos have reached the eight-cell stage, one or more is implanted into the woman's uterus. If fertilization is not accomplished by simple IVF, a procedure known as intracytoplasmic sperm injection (ICSI) can be used to inject the sperm into an egg. IVF procedures produce a surplus of fertilized eggs and embryos that can be frozen and stored for future use; the procedures can also result in multiple births.

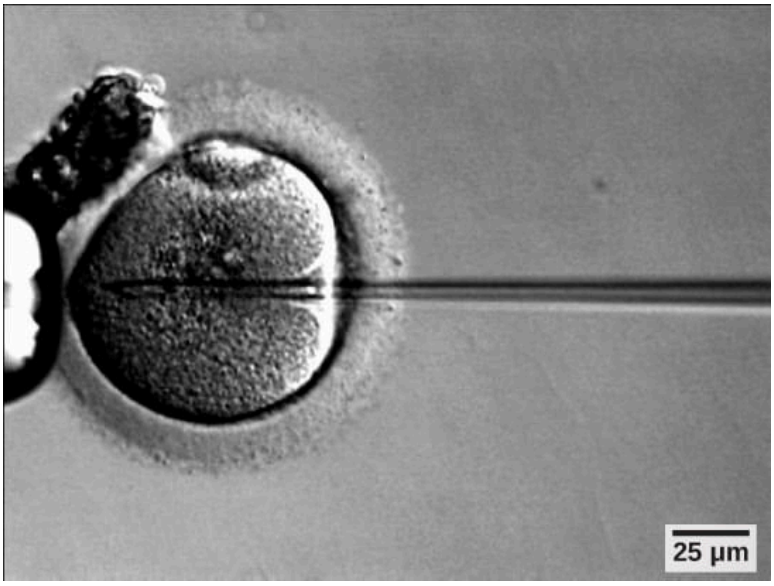


Figure $43.7D.1$: Intracytoplasmic sperm injection: A sperm is inserted into an egg for fertilization during intracytoplasmic sperm injection (ICSI).

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Key Points

- Infertility can have many causes, such as sexually transmitted diseases, toxins, malnutrition, drug use, stress, and age.
- Infertility can be treated by assisted reproductive technologies in which science intervenes, attempting to aid conception through artificial means.
- *In vitro* fertilization is a type of assisted reproductive technology in which an egg is fertilized by a sperm outside the body, grows to the eight- cell stage, and is then implanted in the uterus.

Key Terms

- **infertility**: the inability to conceive children
- **assisted reproductive technology**: the technological means of inducing pregnancy (by means of artificial insemination or other techniques)

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44: ECOLOGY AND THE BIOSPHERE

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44.1: THE SCOPE OF ECOLOGY

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- Topic hierarchy

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44.1A: Introduction to Ecology

Learning Objectives

- Describe the study of ecology

An Introduction to Ecology

Ecology is the study of the interactions of living organisms with their environment. Within the discipline of ecology, researchers work at four specific levels, sometimes discretely and sometimes with overlap. These levels are organism, population, community, and ecosystem. In ecology, ecosystems are composed of dynamically-interacting parts, which include organisms, the communities they comprise, and the non-living (abiotic) components of their environment. Ecosystem processes, such as primary production, pedogenesis (the formation of soil), nutrient cycling, and various niche construction activities, regulate the flux of energy and matter through an environment. These processes are sustained by organisms with specific life-history traits. The variety of organisms, called biodiversity, which refer to the differing species, genes, and ecosystems, enhances certain ecosystem services.

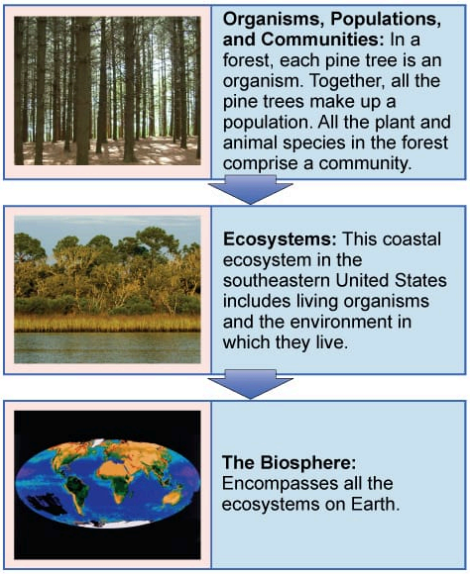


Figure 44.1A.1: Levels of ecological study: Ecologists study within several biological levels of organization, which include organism, population, community, and ecosystem.

In essence, ecologists seek to explain:

- life processes
- interactions, interrelationships, behaviors, and adaptations of organisms
- the movement of materials and energy through living communities
- the successional development of ecosystems
- the abundance and distribution of organisms and biodiversity in the context of the environment

There are many practical applications of ecology in conservation biology, wetland management, natural resource management (agroecology, agriculture, forestry, agroforestry, fisheries), city planning (urban ecology), community health, economics, basic and applied science, and human social interaction (human ecology). Organisms and resources comprise ecosystems which, in turn, maintain biophysical feedback mechanisms that moderate processes acting on living (biotic) and nonliving (abiotic) components of the planet. Ecosystems sustain life-supporting functions and produce natural capital, such as biomass production (food, fuel, fiber and medicine), the regulation of climate, global biogeochemical cycles, water filtration, soil formation, erosion control, flood protection, and many other natural features of scientific, historical, economic, or intrinsic value.

There are also many subcategories of ecology, such as ecosystem ecology, animal ecology, and plant ecology, which look at the differences and similarities of various plants in various climates and habitats. In addition, physiological ecology, or ecophysiology, studies the responses of the individual organism to the environment, while population ecology looks at the similarities and dissimilarities of populations and how they replace each other over time.

Finally, it is important to note that ecology is not synonymous with environment, environmentalism, natural history, or environmental science. It is also different from, though closely related to, the studies of evolutionary biology, genetics, and ethology.

Key Points

- In ecology, ecosystems are composed of organisms, the communities they comprise, and the non-living aspects of their environment.
- The four main levels of study in ecology are the organism, population, community, and ecosystem.
- Ecosystem processes are those that sustain and regulate the environment.
- Ecological areas of study include topics ranging from the interactions and adaptations of organisms within an ecosystem to the abiotic processes that drive the development of those ecosystems.

Key Terms

- **ecology**: the branch of biology dealing with the relationships of organisms with their environment and with each other
- **ecosystem**: a system formed by an ecological community and its environment that functions as a unit
- **ecophysiology**: the study of the relationships between, and adaptation of, the physiology of an organism and its environment

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44.1B: Organismal Ecology and Population Ecology

Learning Objectives

- Describe populations as studied in population ecology and organisms as studied in organismal ecology

Organismal Ecology



Figure $44.1B.1$: Karner blue butterfly: The Karner blue butterfly (Lycaeides melissa samuelis) is a rare butterfly that lives only in open areas with few trees or shrubs, such as pine barrens and oak savannas. It can only lay its eggs on lupine plants.

Researchers studying ecology at the organismal level are interested in the adaptations that enable individuals to live in specific habitats. These adaptations can be morphological (pertaining to the study of form or structure), physiological, and behavioral. For instance, the Karner blue butterfly (*Lycaeides melissa samuelis*) is considered a specialist because the females preferentially oviposit (that is, lay eggs) on wild lupine. This preferential adaptation means that the Karner blue butterfly is highly dependent on the presence of wild lupine plants for its continued survival.



Figure $44.1B.1$: Wild lupine: The wild lupine (Lupinus perennis) is the host plant for the Karner blue butterfly.

After hatching, the larval caterpillars emerge to spend four to six weeks feeding solely on wild lupine. The caterpillars pupate (undergo metamorphosis), emerging as butterflies after about four weeks. The adult butterflies feed on the nectar of flowers of wild lupine and other plant species. A researcher interested in studying Karner blue butterflies at the organismal level might, in addition to asking questions about egg laying, ask questions about the butterflies' preferred temperature (a physiological question) or the behavior of the caterpillars when they are at different larval stages (a behavioral question).

Population Ecology

A population is a group of interbreeding organisms that are members of the same species living in the same area at the same time. Organisms that are all members of the same species, a population, are called conspecifics. A population is identified, in part, by where it lives; its area of population may have natural or artificial boundaries. Natural boundaries might be rivers, mountains, or deserts, while examples of artificial boundaries include mowed grass or manmade structures such as roads. The study of population ecology focuses on the number of individuals in an area and how and why population size changes over time. Population ecologists are particularly interested in counting the Karner blue butterfly, for example, because it is classified as federally endangered. However, the distribution and density of this species is highly influenced by the distribution and abundance of wild lupine. Researchers might ask questions about the factors leading to the decline of wild lupine and how these affect Karner blue butterflies. For example, ecologists know that wild lupine thrives in open areas where trees and shrubs are largely absent. In natural settings, intermittent wildfires regularly remove trees and shrubs, helping to maintain the open areas that wild lupine requires. Mathematical models can be used to understand how wildfire suppression by humans has led to the decline of this important plant for the Karner blue butterfly.

Key Points

- Organismal ecology focuses on the morphological, physiological, and behavioral adaptations that let an organism survive in a specific habitat.
- Population ecology studies the number of individuals in an area, as well as how and why their population size changes over time.
- The Karner blue butterfly, an endangered species, makes a good model for both organismal and population ecology since it is dependent, as a population, on a specific plant that grows within specific areas, which, thus, influences butterfly distribution and numbers.

Key Terms

- **conspecific**: an organism belonging to the same species as another
- **population**: a collection of organisms of a particular species, sharing a particular characteristic of interest, most often that

of living in a given area
- **oviposit**: to lay eggs

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44.1C: Community Ecology and Ecosystem Ecology

Learning Objectives

- Distinguish between community ecology and ecosystem ecology

Key Points

- Community ecology focuses on the processes driving interactions between differing species and their overall consequences.
- Ecosystem ecology studies all organismal, population, and community components of an area, as well as the non-living counterparts.
- The mutualistic relationship between the Karner blue butterfly and ants are of interest to community ecology studies since both species interact within an area and affect each other's survival rate; in turn, they are both affected by nutrient -poor soils, which are part of the ecosystem ecology.

Key Terms

- **community**: a group of interdependent organisms inhabiting the same region and interacting with each other
- **conspecific**: an organism belonging to the same species as another
- **heterospecific**: an organism belonging to a different species to another

Community Ecology

A biological community consists of the different species within an area, typically a three-dimensional space, and the interactions within and among these species. Community ecologists are interested in the processes driving these interactions and their consequences. Questions about conspecific interactions often focus on competition among members of the same species for a limited resource. Ecologists also study interactions among various species; members of different species are called heterospecifics. Examples of heterospecific interactions include predation, parasitism, herbivory, competition, and pollination. These interactions can have regulating effects on population sizes and can impact ecological and evolutionary processes affecting diversity.

For example, the larvae of the Karner blue butterfly form mutualistic relationships with ants. Mutualism is a form of a long-term relationship that has coevolved between two species and from which each species benefits. For mutualism to exist between individual organisms, each species must receive some benefit from the other as a consequence of the relationship. Researchers have shown that there is an increase in the probability of survival when Karner blue butterfly larvae (caterpillars) are tended by ants. This might be because the larvae spend less time in each life stage when tended by ants, which provides an advantage for the larvae. Meanwhile, the Karner blue butterfly larvae secrete a carbohydrate-rich substance that is an important energy source for the ants. Both the Karner blue larvae and the ants benefit from their interaction.

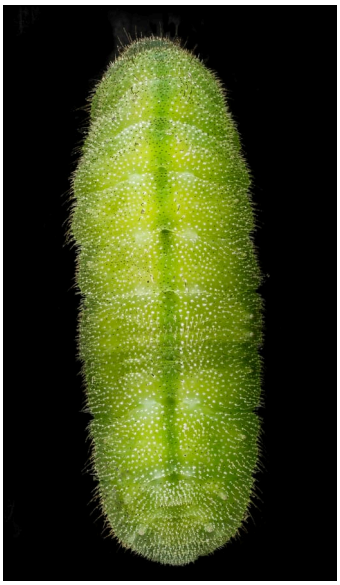


Figure 44.1C.1: Karner blue butterfly caterpillar: Karner blue butterfly caterpillars form beneficial interactions with ants. This mutualistic relationship is an example of a community ecological study, which aims to examine the interactions between different species living in an area.

Ecosystem Ecology

Ecosystem ecology is an extension of organismal, population, and community ecology. The ecosystem is composed of all the biotic components (living things) in an area along with that area's abiotic components (non-living things). Some of the abiotic components include air, water, and soil. Ecosystem biologists ask questions about how nutrients and energy are stored, along with how they move among organisms and the surrounding atmosphere, soil, and water.

The Karner blue butterflies and the wild lupine live in an oak-pine barren habitat. This habitat is characterized by natural disturbance and nutrient-poor soils that are low in nitrogen. The availability of nutrients is an important factor in the distribution of the plants that live in this habitat. Researchers interested in ecosystem ecology could ask questions about the importance of limited resources and the movement of resources, such as nutrients, though the biotic and abiotic portions of the ecosystem.

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44.2: BIOGEOGRAPHY

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- Topic hierarchy

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44.2B: Energy Sources

44.2C: Temperature and Water

44.2D: Inorganic Nutrients and Other Factors

44.2E: Abiotic Factors Influencing Plant Growth

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44.2A: Biogeography

Learning Objectives

- Explain the role of biogeography in the analysis of species distribution

Biogeography

Biogeography is the study of the geographic distribution of living things and the abiotic (non-living) factors that affect their distribution. Abiotic factors can include temperature, moisture, nutrients, oxygen, and energy availability, as well as disturbances from events such as wind and fire. Differences in temperature and rainfall are primarily based on latitude and elevation. As these abiotic factors change, the composition of plant and animal communities also changes. For example, if you were to begin a journey at the equator and walk north, you would notice gradual changes in plant communities. At the beginning of your journey, you would see tropical wet forests with broad-leaved evergreen trees, which are characteristic of plant communities found near the equator. As you continued to travel north, you would see these broad-leaved evergreen plants eventually give rise to seasonally-dry forests with scattered trees. You would also begin to notice changes in temperature and moisture. At about 30 degrees north, these forests would give way to deserts, which are characterized by low precipitation.

Moving farther north, you would see that deserts are replaced by grasslands or prairies. Eventually, grasslands are replaced by deciduous temperate forests. These deciduous forests give way to the boreal forests found in the subarctic, the area south of the Arctic Circle. Finally, you would reach the Arctic tundra, which is found at the most northern latitudes. This trek north reveals gradual changes in both climate and the types of organisms that have adapted to environmental factors associated with ecosystems found at different latitudes. However, different ecosystems exist at the same latitude due in part to abiotic factors such as jet streams, the Gulf Stream, and ocean currents. If you were to hike up a mountain, the changes you would see in the vegetation would parallel those as you move to higher latitudes.

Ecologists who study biogeography examine patterns of species distribution. No species exists everywhere. For example, the Venus flytrap is endemic to a small area in North and South Carolina. An endemic species is one which is naturally found only in a specific geographic area that is usually restricted in size. Other species are generalists, living in a wide variety of geographic areas. The raccoon, for example, is native to most of North and Central America.

Species distribution patterns are based on biotic and abiotic factors and the influences these factors have had during the very long periods of time required for species evolution. Therefore, early studies of biogeography were closely linked to the emergence of evolutionary thinking in the eighteenth century. Some of the most distinctive assemblages of plants and animals occur in regions that have been physically separated for millions of years by geographic barriers. Biologists estimate that Australia, for example, has between 600,000 and 700,000 species of plants and animals. Approximately 3/4 of living plant and mammal species are endemic species found solely in Australia.



Figure 44.2A.1: Endemic species of Australia: Australia is home to many endemic species. The (a) wallaby (Wallabia bicolor), a medium-sized member of the kangaroo family, is a pouched mammal, or marsupial. The (b) echidna (Tachyglossus aculeatus) is an egg-laying mammal.

Sometimes ecologists discover unique patterns of species distribution by determining where species are not found. Hawaii, for example, has no native land species of reptiles or amphibians and has only one native terrestrial mammal, the hoary bat. Most of New Guinea, as another example, lacks placental mammals.

Plants can be endemic or generalists. Endemic plants are found only in specific regions of the earth, while generalists are found in many regions. Isolated land masses, such as Australia, Hawaii, and Madagascar, often have large numbers of endemic plant species. Some of these plants are endangered due to human activity. The forest gardenia (*Gardenia brighamii*), for instance, is endemic to Hawaii; only an estimated 15–20 trees are thought to exist.



Figure 44.2A.1: Endangered forest gardenia: Listed as federally endangered, the forest gardenia is a small tree with distinctive flowers. It is found only in five of the Hawaiian Islands in small populations consisting of a few individual specimens.

Key Points

- The composition of plant and animal communities change as abiotic factors, which include temperature and altitude, start to vary.
- Some species exist only in specific geographical areas while others can thrive in a variety of areas; however, no single species

can be found everywhere in the world.
- Studying an area where a species is not found is also of importance to ecologists in determining unique patterns of species distribution.
- As with animals, plant species can also be either endemic, usually found in isolated land masses, or generalists, found in many regions.

Key Terms

- **biogeography**: the study of the geographical distribution of living things
- **generalist**: species which can thrive in a wide variety of environmental conditions
- **endemic**: unique to a particular area or region; not found in other places

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44.2B: Energy Sources

Learning Objectives

- Assess how energy availability affects species distribution within an ecosystem

Energy Availability & Nutrient Cycling as Abiotic Factors

Energy Sources

Energy from the sun is captured by green plants, algae, cyanobacteria, and photosynthetic protists. These organisms convert solar energy into the chemical energy needed by all living things. Light availability can be an important abiotic force directly affecting the evolution of adaptations in photosynthesizers. For instance, plants in the understory of a temperate forest are shaded when the trees above them in the canopy completely leaf out in the late spring. Not surprisingly, understory plants have adaptations to successfully capture available light. One such adaptation is the rapid growth of spring ephemeral plants, such as the spring beauty. These spring flowers achieve much of their growth and finish their life cycle (reproduce) early in the season before the trees in the canopy develop leaves.



Figure $44.2B.1$: Ephemeral plant: The spring beauty is an ephemeral spring plant that flowers early in the spring to avoid competing with larger forest trees for sunlight.

In aquatic ecosystems, the availability of light may be limited because sunlight is absorbed by water, plants, suspended particles, and resident microorganisms. Toward the bottom of a lake, pond, or ocean, there is a zone that light cannot reach. Photosynthesis cannot take place there and, as a result, a number of adaptations have evolved that enable living things to survive without light. For instance, aquatic plants have photosynthetic tissue near the surface of the water. The broad, floating leaves of a water lily cannot survive without light. In environments such as hydrothermal vents, some bacteria extract energy from inorganic chemicals because there is no light for photosynthesis.

Nutrient Cycling

The availability of nutrients in aquatic systems is also an important aspect of energy or photosynthesis. Many organisms sink to the bottom of the ocean when they die in the open water. When this occurs, the energy found in that organism is sequestered for some time unless ocean upwelling occurs. Ocean upwelling is the rising of deep ocean waters that occurs when prevailing winds

blow along surface waters near a coastline. As the wind pushes ocean waters offshore, water from the bottom of the ocean moves up to replace this water. As a result, the nutrients once contained in dead organisms become available for reuse by other living organisms.

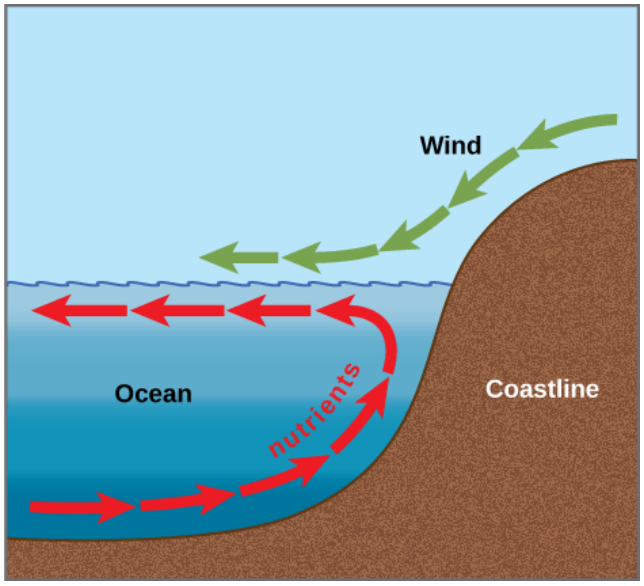


Figure $44.2B.1$: Upwelling: Ocean upwelling is an important process that recycles nutrients and energy in the ocean. As wind (green arrows) pushes offshore, it causes water from the ocean bottom (red arrows) to move to the surface, bringing up nutrients from the ocean depths.

In freshwater systems, the recycling of nutrients occurs in response to air temperature changes. The nutrients at the bottom of lakes are recycled twice each year: in the spring and fall turnover, which recycles nutrients and oxygen from the bottom of a freshwater ecosystem to the top of a body of water. These turnovers are caused by the formation of a thermocline: a layer of water with a temperature that is significantly different from that of the surrounding layers. In wintertime, the surface of lakes found in many northern regions is frozen. However, the water under the ice is slightly warmer, while the water at the bottom of the lake is warmer yet at 4 °C to 5 °C (39.2 °F to 41 °F). Water is densest at 4 °C; therefore, the deepest water is also the densest. The deepest water is oxygen poor because the decomposition of organic material at the bottom of the lake uses up available oxygen that cannot be replaced by means of oxygen diffusion into the water due to the surface ice layer.

In springtime, air temperatures increase and surface ice melts. When the temperature of the surface water begins to reach 4 °C, the water becomes heavier and sinks to the bottom. The water at the bottom of the lake, displaced by the heavier surface water, rises to the top. As it rises, the sediments and nutrients from the lake bottom are brought along with it. During the summer months, the lake water stratifies, or forms layers, with the warmest water at the lake surface.

As air temperatures drop in the fall, the temperature of the lake water cools to 4 °C; this causes fall turnover as the heavy cold water sinks and displaces the water at the bottom. The oxygen-rich water at the surface of the lake then moves to the bottom of the lake, while the nutrients at the bottom of the lake rise to the surface (). During the winter, the oxygen at the bottom of the lake is used by decomposers and other organisms requiring oxygen, such as fish.

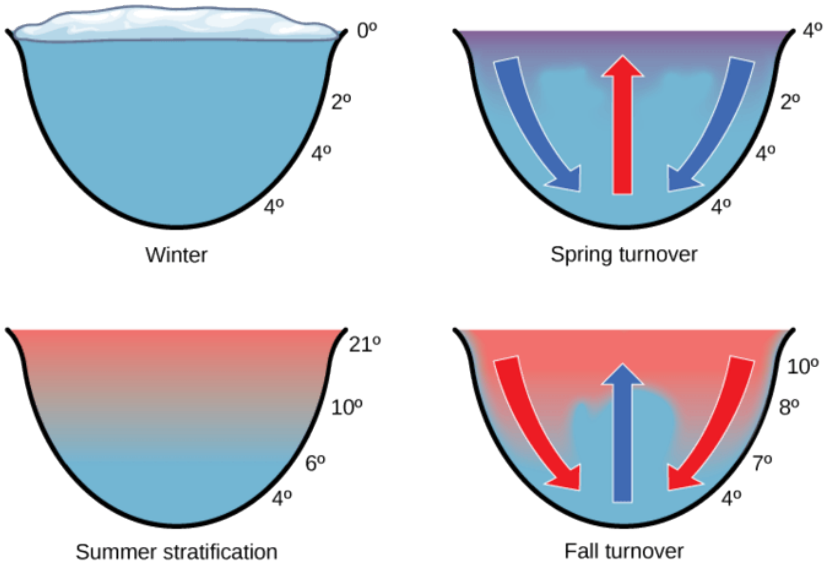


Figure $44.2B.1$: Nurient recycling in freshwater systems: The spring and fall turnovers are important processes in freshwater lakes that act to move the nutrients and oxygen at the bottom of deep lakes to the top. Turnover occurs because water has a maximum density at 4 °C. Surface water temperature changes as the seasons progress, causing denser water to sink.

Key Points

- In land habitats, plant adaptations include life cycles that are dependent on the availability of light; for example, species will flower or grow at varying times to ensure they capture enough available light suitable to their needs.
- In aquatic ecosystems, species growth and distribution are adapted to deal with the sometimes-limited availability of light due to its absorption by water, plants, suspended particles, microorganisms, and water depth.
- Ocean upwelling and spring and fall turnovers are important processes regulating the distribution of nutrients in an aquatic ecosystems.
- Nutrient availability is connected to the energy needs of organisms in aquatic ecosystems since sequestered energy is reused by living organisms from dead ones.

Key Terms

- **ephemeral**: lasting for a short period of time
- **upwelling**: the oceanographic phenomenon that occurs when strong, usually seasonal, winds push water away from the coast, bringing cold, nutrient-rich deep waters up to the surface
- **thermocline**: a layer within a body of water or air where the temperature changes rapidly with depth

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44.2C: Temperature and Water

Learning Objectives

- Describe species adaptations to temperature fluctuations and the availability of water

Temperature & Water as Abiotic Influences

Temperature

Temperature affects the physiology of living things as well as the density and state of water. It exerts an important influence on living organisms because few can survive at temperatures below 0 °C (32 °F) due to metabolic constraints. It is also rare for them to survive at temperatures exceeding 45 °C (113 °F). This is a reflection of evolutionary response to typical temperatures. Enzymes are most efficient within a narrow and specific range of temperatures; enzyme degradation can occur at higher temperatures. Therefore, organisms must either maintain an internal temperature or inhabit an environment that will keep the body within a temperature range that supports metabolism. Some animals have adapted to enable their bodies to survive significant temperature fluctuations, as seen in hibernation or reptilian torpor. Similarly, some bacteria have adapted to survive in extremely-hot temperatures found in places such as geysers. Such bacteria are examples of extremophiles: organisms that thrive in extreme environments.

Temperature can limit the distribution of living things. Animals faced with temperature fluctuations may respond with adaptations, such as migration, in order to survive. Migration, the movement from one place to another, is common in animals, including many that inhabit seasonally-cold climates. Migration solves problems related to temperature, locating food, and finding a mate. In migration, for instance, the arctic tern (*Sterna paradisaea*) makes a 40,000 km (24,000 mi) round trip flight each year between its feeding grounds in the southern hemisphere and its breeding grounds in the Arctic Ocean. Monarch butterflies (*Danaus plexippus*) live in the eastern United States in the warmer months, but migrate to Mexico and the southern United States in the wintertime. Some species of mammals also make migratory forays: reindeer (*Rangifer tarandus*) travel about 5,000 km (3,100 mi) each year to find food. Amphibians and reptiles are more limited in their distribution because they lack migratory ability. Not all animals that can migrate do so as migration carries risk and comes at a high energy cost.



Figure $44.2C.1$: Arctic tern: The arctic tern is an example of a species that must migrate yearly to deal with temperature fluctuations that exist in the regions where it is found.

Some animals hibernate or estivate to survive hostile temperatures. Hibernation enables animals to survive cold conditions,

while estivation allows animals to survive the hostile conditions of a hot, dry climate. Animals that hibernate or estivate enter a state known as torpor, a condition in which their metabolic rate is significantly lowered. This enables the animal to wait until its environment better supports its survival. Some amphibians, such as the wood frog (*Rana sylvatica*), have an antifreeze-like chemical in their cells, which retains the cells' integrity and prevents them from bursting.



Figure $44.2C.1$: Wood frog: The wood frog, like all other amphibians and reptiles, cannot migrate; as a result, the species survives extreme temperature changes through the antifreeze-like chemical found in their cells.

Water

Water is required by all living things because it is critical for cellular processes. Since terrestrial organisms lose water to the environment by simple diffusion, they have evolved many adaptations to retain water.

Examples of adaptations used by terrestrial and aquatic species include the following:

- Plants have a number of interesting features on their leaves, such as leaf hairs and a waxy cuticle, that serve to decrease the rate of water loss via transpiration.
- Freshwater organisms, surrounded by water, are constantly in danger of having water rush into their cells because of osmosis. Many adaptations of organisms living in freshwater environments have evolved to ensure that solute concentrations in their bodies remain within appropriate levels. One such adaptation is the excretion of dilute urine.
- Marine organisms are surrounded by water with a higher solute concentration than the organism and, thus, are in danger of losing water to the environment because of osmosis. These organisms have morphological and physiological adaptations to retain water and release solutes into the environment. For example, marine iguanas (*Amblyrhynchus cristatus*) sneeze out water vapor that is high in salt in order to maintain solute concentrations within an acceptable range while swimming in the ocean and eating marine plants.

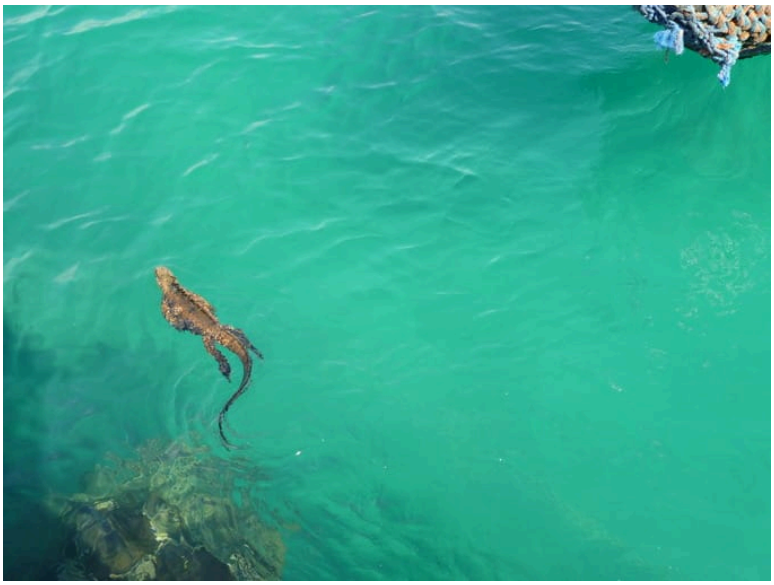


Figure $44.2C.1$: Marine iguanas: Marine iguanas have a special, salt-secretion adaption that allows them to minimize bodily water loss.

Key Points

- Temperature is a factor that influences species distribution because organisms must either maintain a specific internal temperature or inhabit an environment that will keep the body within a temperature range that supports their metabolism.
- Many species have developed adaptations, such as migration, hibernation, and estivation, to deal with temperature fluctuations in the environments in which they live.
- Water retention is vital to all living beings; adaptations have evolved within both terrestrial and aquatic species to minimize water loss.

Key Terms

- **osmosis**: The net movement of solvent molecules from a region of high solvent potential to a region of lower solvent potential through a partially permeable membrane
- **estivate**: to go into stasis or torpor in the summer months
- **extremophile**: an organism that lives under extreme conditions of temperature, salinity, etc; commercially important as a source of enzymes that operate under similar conditions
- **torpor**: a state of being inactive or stuporous
- **hibernation**: a state of inactivity and metabolic depression in animals during winter

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44.2D: Inorganic Nutrients and Other Factors

Learning Objectives

- Identify further abiotic factors that affect species distribution and abundance

Other Important Abiotic Factors

Inorganic nutrients, soil structure, and aquatic oxygen availability are further abiotic factors that affect species distribution in an ecosystem. The same is true for terrestrial factors, such as wind and fire, which can impact the types of species that inhabit regions exposed to these types of disturbances.

Inorganic Nutrients and Soil

Inorganic nutrients, such as nitrogen and phosphorus, are important in the distribution and the abundance of living things. Plants obtain these inorganic nutrients from the soil when water moves into the plant through the roots. Therefore, soil structure (the particle size of soil components), soil pH, and soil nutrient content play an important role in the distribution of plants. Animals obtain inorganic nutrients from the food they consume. Therefore, animal distributions are related to the distribution of what they eat. In some cases, animals will follow their food resource as it moves through the environment.

Oxygen Availability



Figure $44.2D.1$: Jack pine cones: The mature cones of the jack pine (Pinus banksiana) open only when exposed to high temperatures, such as during a forest fire. A fire will probably kill most vegetation, so a seedling that germinates after a fire is more likely to receive ample sunlight than one that germinates under normal conditions.

Some abiotic factors, such as oxygen, are important in aquatic ecosystems as well as terrestrial environments. Terrestrial animals obtain oxygen from the air they breathe. Oxygen availability can be an issue for organisms living at very high elevations, where there are fewer molecules of oxygen in the air. In aquatic systems, the concentration of dissolved oxygen is related to water temperature and the speed at which the water moves. Cold water has more dissolved oxygen than warmer water. In addition, salinity, water current, and tide can be important abiotic factors in aquatic ecosystems.

Other Terrestrial Factors

Wind can be an important abiotic factor because it influences the rate of evaporation and transpiration. The physical force of wind is also important because it can move soil, water, or other abiotic factors, as well as an ecosystem's organisms.

Fire is another terrestrial factor that can be an important agent of disturbance in terrestrial ecosystems. Some organisms are adapted to fire and, thus, require the high heat associated with fire to complete a part of their life cycle. For example, the jack pine, a coniferous tree, requires heat from fire for its seed cones to open. Through the burning of pine needles, fire adds nitrogen to the soil and limits competition by destroying undergrowth.

Key Points

- Soil structure, pH, and its nutrient content affect the distribution of plants, which in turn influences the distribution of the animals that feed on them.
- Oxygen availability is an important abiotic factor affecting species in both aquatic and terrestrial environments.
- Wind and fire impose physical disturbances that species must be adapted to in order to live in affected areas.

Key Terms

- **inorganic**: relating to a compound that does not contain carbon
- **transpiration**: the loss of water by evaporation in terrestrial plants, especially through the stomata; accompanied by a corresponding uptake from the roots

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44.2E: Abiotic Factors Influencing Plant Growth

Learning Objectives

- Identify the abiotic factors that affect plant growth

Abiotic Factors Influencing Plant Growth

Temperature and moisture are important influences on plant production (primary productivity) and the amount of organic matter available as food (net primary productivity). Primary production is the synthesis of organic compounds from atmospheric or aqueous carbon dioxide. It principally occurs through the process of photosynthesis, which uses light as its source of energy, but it also occurs through chemosynthesis, which uses the oxidation or reduction of chemical compounds as its source of energy. Almost all life on earth is directly or indirectly reliant on primary production. The organisms responsible for primary production, known as primary producers or autotrophs, form the base of the food chain. In terrestrial eco-regions, these are mainly plants, while in aquatic eco-regions, they are mainly algae.

Net primary productivity is an estimation of all of the organic matter available as food. It is calculated as the total amount of carbon fixed per year minus the amount that is oxidized during cellular respiration. In terrestrial environments, net primary productivity is estimated by measuring the aboveground biomass per unit area, which is the total mass of living plants, excluding roots. This means that a large percentage of plant biomass which exists underground is not included in this measurement. Net primary productivity is an important variable when considering differences in biomes. Very productive biomes have a high level of aboveground biomass.

Annual biomass production is directly related to the abiotic components of the environment. Environments with the greatest amount of biomass have conditions in which photosynthesis, plant growth, and the resulting net primary productivity are optimized. The climate of these areas is warm and wet. Photosynthesis can proceed at a high rate, enzymes can work most efficiently, and stomata can remain open without the risk of excessive transpiration. Together, these factors lead to the maximal amount of carbon dioxide (CO_2) moving into the plant, resulting in high biomass production. The aboveground biomass produces several important resources for other living things, including habitat and food. Conversely, dry and cold environments have lower photosynthetic rates and, therefore, less biomass. The animal communities living there will also be affected by the decrease in available food.

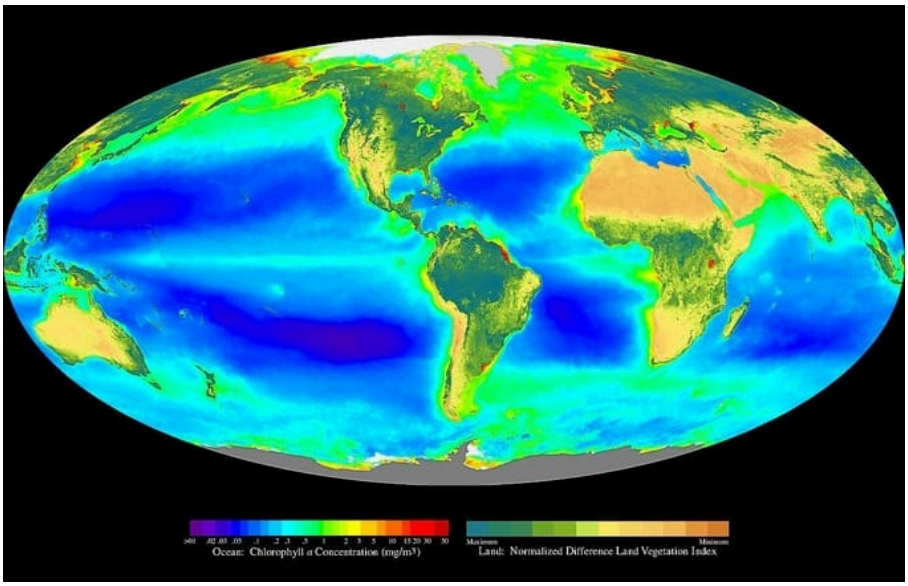


Figure $44.2E.1$: Primary productivity and biomass production: The magnitude and distribution of global primary production varies between biomes. However, warm and wet climates have the greatest amount of annual biomass production.

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Key Points

- Primary production, on which almost all of life on earth is dependent, occurs through either photosynthesis or chemosynthesis.
- Annual biomass production, used to estimate net primary productivity by plants in an area, is directly influenced by an environment's abiotic factors, which include temperature and moisture.
- Warm and wet climates have the greatest amount of plant biomass because they offer conditions in which photosynthesis, plant growth, and the resulting net primary productivity are highest.

Key Terms

- **biomass**: the total mass of all living things within a specific area, habitat, etc.
- **eco-region**: a region, smaller than an ecozone, that contains a distinct biodiversity of flora and fauna
- **chemosynthesis**: the production of carbohydrates and other compounds using the oxidation of chemical nutrients as a source of energy rather than sunlight; it is limited to certain bacteria and fungi

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44.3: TERRESTRIAL BIOMES

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- Topic hierarchy

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44.3B: Tropical Wet Forest and Savannas

44.3C: Subtropical Deserts and Chaparral

44.3D: Temperate Grasslands

44.3E: Temperate Forests

44.3F: Boreal Forests and Arctic Tundra

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44.3A: What constitutes a biome?

Learning Objectives

- Differentiate biomes from other levels of ecological classification, including habitat

What Constitutes a Biome?

A group of living organisms of the same kind that live in the same place simultaneously is known as a population. Populations live together in habitats, which together make up a community. An ecosystem is a community of living organisms interacting with the non-living components of that environment.

A biome is a community on a global scale, where habitats flank each other, and is usually defined by the temperature, precipitation, and types of plants and animals that inhabit it. The Earth's biomes are categorized into two major groups: terrestrial and aquatic. Terrestrial biomes are based on land, while aquatic biomes include both ocean and freshwater biomes. The major types of biomes include: aquatic, desert, forest, grassland, savannas, and tundra.

Biome Attributes

Generally, biome classification is determined by the climate and geography of an area. Each biome consists of communities that have adapted to the different climate and environment inside the biome. Specifically, there are special vegetation adaptations as well as physical and behavioral adaptions made by animals in order to accommodate the environment. The eight major terrestrial biomes on Earth are each distinguished by characteristic temperatures and amount of precipitation. Comparing the annual totals of precipitation and fluctuations in precipitation from one biome to another provides clues as to the importance of abiotic factors in the distribution of biomes. Temperature variation on a daily and seasonal basis is also important for predicting the geographic distribution of the biome and the vegetation type in the biome.

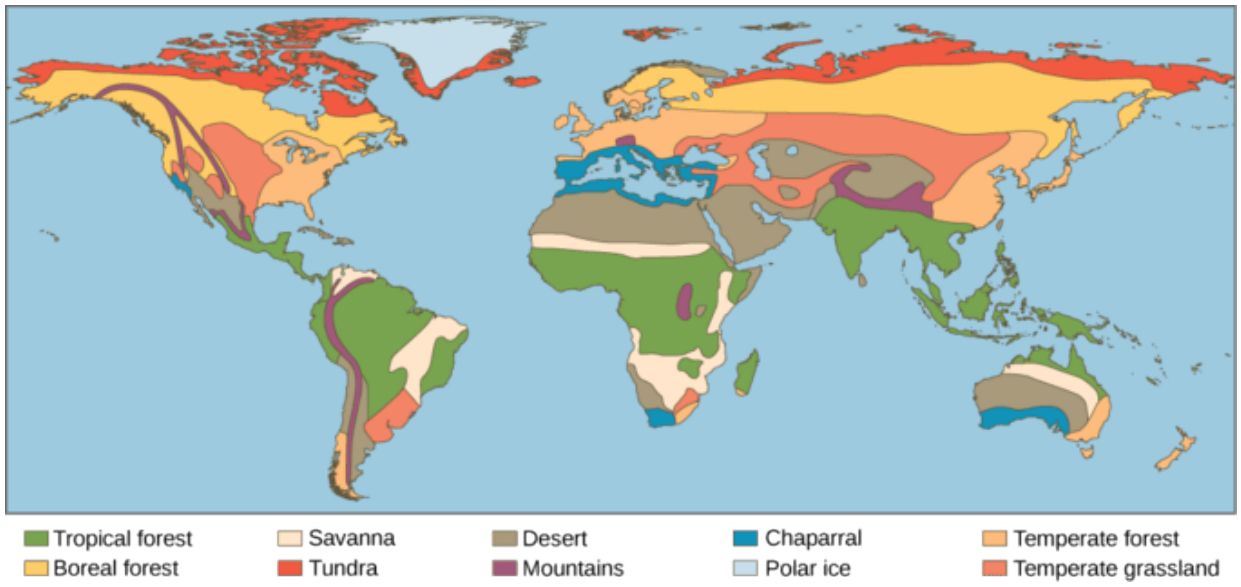


Figure 44.3A.1: Earth's Major Biomes: Each of the world's major biomes is distinguished by characteristic temperatures and amounts of precipitation. Each type of biome can be found in multiple places.

The distribution of these biomes shows that the same biome can occur in geographically distinct areas with similar climates. Biomes have no distinct boundaries. Instead, there is a transition zone called an ecotone, which contains a variety of plants and animals. For example, an ecotone might be a transition region between a grassland and a desert, with species from both.

Key Points

- The climate, including precipitation and temperature, and the geography control the type of biome found in a region.
- There are two major classifications of biomes, which are terrestial and aquatic, and these include the types of biomes known as deserts, forests, grasslands, savannas, tundra, and freshwater environments.
- A habitat is the location where a group of one type of organism (a population) lives, while a biome is a community made of all the habitats in a given region and climate.
- Different organisms inhabit different types of biomes.
- Each type of biome can be found in multiple locations on Earth depending on its climate, geography, and organisms.

Key Terms

- **biome**: any major regional biological community such as that of forest or desert
- **ecotone**: a transition area between two adjacent ecosystems
- **habitat**: a specific place or natural conditions in which a plant or animal lives
- **population**: a collection of organisms of a particular species, sharing a particular characteristic of interest, most often that of living in a given area
- **ecosystem**: a system formed by an ecological community and its environment that functions as a unit

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44.3B: Tropical Wet Forest and Savannas

Learning Objectives

- Recognize the distinguishing characteristics of tropical wet forests and savannas

Tropical Wet Forest

Tropical wet forests, also referred to as tropical rainforests, are found in equatorial regions. The vegetation is characterized by plants with broad leaves that fall off throughout the year. Unlike the trees of deciduous forests, the trees in this biome do not have a seasonal loss of leaves associated with variations in temperature and sunlight; these forests are “evergreen” year-round.

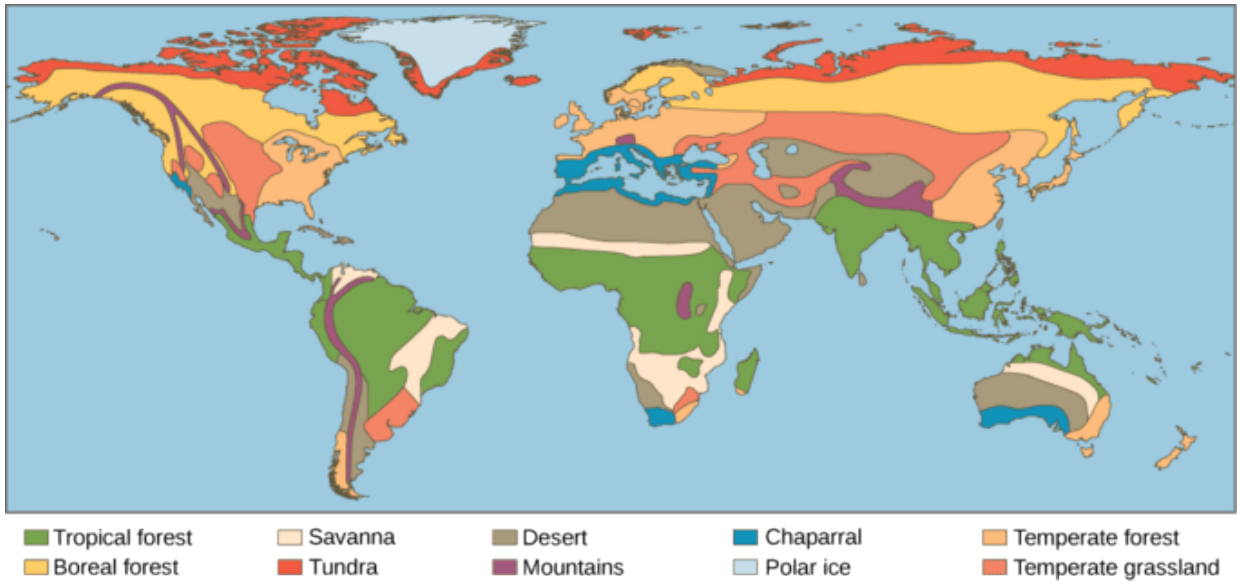


Figure $44.3B.1$: Terrestrial biomes: Each of the world’s major biomes is distinguished by characteristic temperatures and amounts of precipitation. Polar ice and mountains are also shown. Tropical wet forests are depicted in green and are usually found at equatorial regions. Savannas are depicted in light pink and are usually located in Africa, South America, and Northern Australia.

The temperature and sunlight profiles of tropical wet forests are very stable in comparison to that of other terrestrial biomes, with the temperatures ranging from 20°C – 34°C (68°F – 93°F). Compared to other forest biomes, tropical wet forests have little variation in seasonal temperatures. This lack of seasonality leads to year-round plant growth, rather than the seasonal (spring, summer, and fall) growth seen in other biomes. In contrast to other ecosystems, tropical ecosystems do not have long days and short days during the yearly cycle. Instead, a constant daily amount of sunlight (11–12 hrs per day) provides more solar radiation and, thereby, a longer period of time for plant growth.

The annual rainfall in tropical wet forests ranges from 125-660 cm (50–200 in), with some monthly variation. While sunlight and temperature remain fairly consistent, annual rainfall is highly variable. Tropical wet forests have wet months in which there can be more than 30 cm (11–12 in) of precipitation, as well as dry months in which there are fewer than 10 cm (3.5 in) of rainfall. However, the driest month of a tropical wet forest still exceeds the annual rainfall of some other biomes, such as deserts.

Tropical wet forests have high net primary productivity because the annual temperatures and precipitation values in these areas are ideal for plant growth. Therefore, the extensive biomass present in the tropical wet forest leads to plant communities with very high species diversity. Tropical wet forests have more species of trees than any other biome. On average, between 100 and 300 species of trees are present in a single hectare (2.5 acres) of South America. One way to visualize this is to compare the distinctive horizontal layers within the tropical wet forest biome. On the forest floor is a sparse layer of plants and decaying plant matter. Above that is an understory of short shrubby foliage. A layer of trees rising above this understory is topped by a closed upper canopy: the uppermost overhead layer of branches and leaves. Some additional trees emerge through this closed upper

canopy. These layers provide diverse and complex habitats for the variety of plants, fungi, animals, and other organisms within the tropical wet forests. For instance, epiphytes are plants that grow on other plants. Host plants are typically unharmed. Epiphytes are found throughout tropical wet forest biomes. Many species of animals use the variety of plants and the complex structure of the tropical wet forests for food and shelter. Some organisms live several meters above ground, having adapted to this arboreal lifestyle.



Figure $44.3B.1$: Tropical wet forests: Tropical wet forests, such as the forests of Madre de Dios near the Amazon River in Peru, have high species diversity.

Savannas

Savannas are grasslands with scattered trees located in Africa, South America, and northern Australia. Savannas are hot, tropical areas with temperatures averaging from 24°C – 29°C (75°F – 84°F) and an annual rainfall of 10–40 cm (3.9–15.7 in). They have an extensive dry season. For this reason, forest trees do not grow as well as they do in the tropical wet forest or other forest biomes. As a result, there are relatively few trees within the grasses and forbs (herbaceous flowering plants) that dominate the savanna. Since fire is an important source of disturbance in this biome, plants have evolved well-developed root systems that allow them to quickly re-sprout after a fire.



Figure $44.3B.1$: Savannas: Savannas, such as this one in Taita Hills Wildlife Sanctuary in Kenya, are dominated by grasses.

Animals commonly found in savannas in Africa include the African elephant, lions, gazelles, giraffes, ostriches, and many other mammals, birds, plants and invertebrates. The northern Australian savannas also have many types of plants, animals, insects, and reptiles, including marsupials (kangaroos and wallabies), bats, and rodents. In addition to the native animals such as foxes and Patagonian maras (rabbit-like rodents), savannas in South America are commonly used for grazing domestic livestock, such as sheep, goats, and cattle because of their open grasslands and herbaceous layer of plants.

Key Points

- Tropical wet forests, located near the equator, have temperatures that range from 20°C – 34°C (68°F – 93°F), with little variation in seasonal temperatures.
- The lack of seasonality, constant daily sunlight, ideal temperatures, and high rate of precipitation in tropical wet forests lead to increased plant growth and high species diversity.
- The annual rainfall in tropical wet forests ranges from 125 to 660 cm (50–200 in); there is a high rate of precipitation even in the dry months.
- Savannas, grasslands with scattered trees, are located in Africa, South America, and northern Australia.
- Temperatures in savannas range from 24°C – 29°C (75°F – 84°F), with annual rainfall ranges from 10–40 cm (3.9–15.7 in).
- Because savannas are very dry, trees do not grow as well as they do in other forest biomes and diversity is minimal.

Key Terms

- **deciduous**: of or pertaining to trees which lose their leaves in winter or the dry season
- **biome**: any major regional biological community such as that of forest or desert
- **understory**: the layer of plants that grow in the shade of the canopy of a forest

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44.3C: Subtropical Deserts and Chaparral

Learning Objectives

- Recognize the distinguishing characteristics of subtropical deserts and chaparrals

Subtropical Deserts

Subtropical deserts, which exist between 15° and 30° north and south latitude, are centered on the Tropics of Cancer and Capricorn. In some years, evaporation exceeds precipitation in this very dry biome. Subtropical hot deserts may have daytime soil surface temperatures above 60°C (140°F) and nighttime temperatures approaching 0°C (32°F). In cold deserts, temperatures may be as high as 25°C (77°F) and may drop below -30°C (-22°F). Subtropical deserts are characterized by low annual precipitation of fewer than 30 cm (12 in), with little monthly variation and lack of predictability in rainfall. In some cases, the annual rainfall can be as low as 2 cm (0.8 in), such as in central Australia (“the Outback”) and northern Africa.

Types of Deserts

There are several types of deserts including high-pressure deserts, mid-continent deserts, rain-shadow deserts, and upwelling deserts. In high-pressure deserts, the high atmospheric pressure enables the air to retain more moisture and there is little rainfall. High-pressure deserts include the Sahara, Arabian, Thar, and Kalahari deserts, and the desert regions within the Arctic and Antarctic circles. Areas in the middle of a continent can receive little rainfall because moisture tends to condense before it reaches the middle of a large continent. Modern examples of mid-continent deserts are the Turkmenistan, Gobi, and Great Australian deserts. Third, rain-shadow deserts are created when moisture from the ocean condenses on one side of a mountain range. These mountain ranges usually have a rainforest on one side and a desert on the other. Examples of rain-shadow deserts include the Mojave desert in the rain-shadow of the Sierra Nevada, the Patagonian desert in the rain-shadow of the Andes, and the Iranian desert in the rain-shadow of the Zagros mountains. Finally, upwelling deserts exist adjacent to areas where cold currents rise to the ocean surface, reducing evaporation. Examples include the Atacama desert, the Western Sahara, and the Namib desert.

Adaptations for Deserts

The type of vegetation and limited animal diversity of this biome are closely related to the low and unpredictable precipitation. Very dry deserts lack perennial vegetation that lives from one year to the next. Instead, many plants are annuals that grow quickly, reproduce when rainfall does occur, and then die. Many other plants in these areas are characterized by having a number of adaptations that conserve water, such as deep roots, reduced foliage, and water-storing stems. Seed plants in the desert produce seeds that can remain in dormancy for extended periods between rains. To reduce water loss and conserve energy, many desert animals like the fennec fox are nocturnal and burrow during the day.



Figure $44.3C.1$: Fennec fox: Fennec foxes live in the deserts of Northern Africa and have large ears for heat dissipation during the day. They stay in burrows during the day and are mostly active at night.



Figure $44.3C.1$: Desert plants: To reduce water loss, many desert plants have tiny leaves or no leaves at all. The leaves of ocotillo (*Fouquieria splendens*), shown here in the Sonora Desert near Gila Bend, Arizona, appear only after rainfall and then are shed.

Chaparral

The chaparral, also called the scrub forest, is found in California, along the Mediterranean Sea, and along the southern coast of Australia. The annual rainfall in this biome ranges from 65 cm to 75 cm (25.6–29.5 in), with the majority of rain falling in the winter. Due to the very dry summers, many chaparral plants are dormant during that season. The chaparral vegetation is dominated by shrubs and is adapted to periodic fires, with some plants producing seeds that only germinate after a hot fire. The ashes left behind after a fire are rich in nutrients, such as nitrogen, that fertilize the soil and promote plant regrowth.



Figure $44.3C.1$: Chaparrals: The chaparral, or scrub forest, is dominated by shrubs adapted to periodic fires. Some plants produce seeds that only germinate after a hot fire.

Key Points

- Subtropical deserts are centered on the Tropics of Cancer and Capricorn.
- Subtropical deserts can be hot or cold, but they are all very dry,having very low annual precipitation.
- Because precipitation is so low in subtropical deserts, most plants are annuals which utilize adaptations to conserve water.
- Chaparrals (scrub forests) are found in California, along the Mediterranean Sea, and along the southern coast of Australia.
- Chaparrals are very wet in the winter, but very dry in the summer months; most chaparral plants stay dormant during the summer.
- Most chaparral plants are shrubs adapted to fires; some seeds only germinate after a fire.

Key Terms

- **chaparral**: a region of shrubs, typically dry in the summer and rainy in the winter
- **subtropical desert**: dry region centered on the Tropics of Cancer and Capricorn where evaporation exceeds precipitation

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44.3D: Temperate Grasslands

Learning Objectives

- Recognize the distinguishing characteristics of temperate grasslands

Temperate Grasslands

Temperate grasslands are found throughout central North America, where they are also known as prairies, and within Eurasia, where they are known as steppes. Temperate grasslands have pronounced annual fluctuations in temperature, with hot summers and cold winters. The annual temperature variation produces specific growing seasons for plants. Plant growth is possible when temperatures are warm enough and when ample water is available to sustain it, which typically occurs in the spring, summer, and fall. During much of the winter, temperatures are low and water, which is stored in the form of ice, is not available for plant growth.



Figure $44.3D.1$: Temperate grasslands in New Zealand: Temperate tussock grasslands form expansive and distinctive landscapes in the South Island and to a lesser extent in the central plateau region of the North Island of New Zealand.

Annual precipitation ranges from 25 cm to 75 cm (9.8–29.5 in). Because of relatively-lower annual precipitation in temperate grasslands, there are few trees, except for those found growing along rivers or streams. The dominant vegetation tends to consist of grasses; some prairies sustain populations of grazing animals. The vegetation is very dense and the soils are fertile because the subsurface of the soil is packed with the roots and rhizomes (underground stems) of these grasses, which anchor plants into the ground and replenish the organic material (humus) in the soil when they die and decay.



Figure $44.3D.1$: Przewalski's horses on the Asian steppes: The Przewalski's horse is a rare and endangered subspecies of wild horse. By the end of the 1950s, only 12 individual Przewalski's horses were left in the world and several reintroduction programs have released populations back into the grasslands in Mongolia and Ukraine.

Fires, mainly caused by lightning, are a natural disturbance in temperate grasslands. When fire is suppressed, the vegetation eventually converts to scrub and dense forests. Often, the restoration or management of temperate grasslands requires the use of controlled burns to suppress the growth of trees and maintain the grasses. Burning causes new grass to grow, which brings back the grazing animals.

Organisms Found in Temperate Grasslands

Mites, insect larvae, nematodes and earthworms inhabit deep soil, which can reach 6 meters (20 ft) underground in undisturbed grasslands on the richest soils of the world. These invertebrates, along with symbiotic fungi, extend the root systems, break apart hard soil, enrich it with urea and other natural fertilizers, trap minerals and water, and promote growth. Some types of fungi make the plants more resistant to insect and microbial attacks. Grasslands also are home to a vast variety of mammals, reptiles, birds, and insects. Typical large mammals include the Giant Anteater and populations of grazing animals, such as the Blue Wildebeest, Przewalski's Horse, and the American Bison.



Figure $44.3D.1$: Grazing animals: The American bison (*Bison bison*), more commonly called the buffalo, is a grazing mammal that once populated American prairies in huge numbers.

Key Points

- Temperate grasslands are found throughout central North America, where they are also known as prairies; they are also found in Eurasia, where they are known as steppes.
- Temperate grasslands have hot summers and cold winters; the growing season occurs during the spring, summer, and fall.
- Because of the low annual precipitation, temperate grasslands have very few trees.
- Grasses are the dominant vegetation; their roots and rhizomes provide increased fertility to the soil.
- Fires caused by lightening occur often in grasslands; without fires grasslands are converted to scrub forests.

Key Terms

- **steppe**: the grasslands of Eastern Europe and Asia
- **prairie**: an extensive area of relatively flat grassland with few, if any, trees, especially in North America

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44.3E: Temperate Forests

Learning Objectives

- Recognize the distingushing chracteristics of temperate forests

Temperate Forests

Temperate forests are the most common biome in eastern North America, Western Europe, Eastern Asia, Chile, and New Zealand. This biome is found throughout mid-latitude regions. Temperatures ranging between -30°C – 30°C (-22°F – 86°F) drop below freezing on an annual basis, resulting in defined growing seasons during the spring, summer, and early fall. Precipitation is relatively constant throughout the year, ranging between 75 cm and 150 cm (29.5–59 in).

Because of the moderate, annual rainfall and temperatures, deciduous trees are the dominant plant in this biome. Deciduous trees lose their leaves each fall, remaining leafless in the winter; thus, no photosynthesis occurs during the dormant winter period. Each spring, new leaves appear as the temperature increases. Because of the dormant period, the net primary productivity of temperate forests is less than that of tropical wet forests. In addition, temperate forests show less diversity of tree species than do tropical wet forest biomes.



Figure $44.3E.1$: Deciduous trees: Deciduous trees, those that lose their leaves seasonally, are the dominant plant in the temperate forest.

The trees of the temperate forests leaf out and shade much of the ground; however, this biome is more open than tropical wet forests because trees in the temperate forests do not grow as tall as the trees in tropical wet forests. The soils of the temperate forests are rich in inorganic and organic nutrients due to the thick layer of leaf litter on forest floors. As this leaf litter decays, nutrients are returned to the soil. The leaf litter also protects soil from erosion, insulates the ground, and provides habitats for invertebrates (such as the pill bug or roly-poly, *Armadillidium vulgare*) and their predators, such as the red-backed salamander (*Plethodon cinereus*).

Organisms Found in Temperate Deciduous Forests

The leaf litter is home to invertebrates (such as the pill bug or roly-poly, *Armadillidium vulgare*) and their predators, including the red-backed salamander (*Plethodon cinereus*). Pileated woodpeckers depend upon dead or dying trees as a source of food and for constructing their nests, and many migratory birds, such as the spring warblers, time their arrival to coincide with the opening of the tree canopy, which provides the insects that are their principal food sources for raising young. Many well-known animals

are found in temperate deciduous forests including squirrels, deer, and bears. The top predators in deciduous forest were once wolves and cougars, but their populations have been in decline.



Figure $44.3E.1$: White-tailed deer: Deer such as the white-tailed deer of North America are common inhabitants of temperate forests.

Key Points

- Temperate forests are the most common biome in eastern North America, Western Europe, Eastern Asia, Chile, and New Zealand.
- Temperatures in temperate forests fluctuate; there are defined growing seasons during spring, summer, and early fall.
- Because temperate forests have moderate annual precipitation, the dominant plants are the deciduous trees.
- Deciduous trees experience a dormant period in the winter, which is why temperate forests have less net productivity than tropical forests.
- Temperate forests are more open than tropical wet forests since their trees do not grow as tall.
- The soils of the temperate forests are rich in inorganic and organic nutrients; this is due to the thick layer of leaf litter on forest floors, which returns nutrients to the soil.

Key Terms

- **deciduous**: of or pertaining to trees which lose their leaves in winter or the dry season
- **temperate forest**: forest concentrations formed in the northern and southern hemisphere, or in temperate regions; main characteristics include wide leaves, large and tall trees, and seasonal vegetation

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44.3F: Boreal Forests and Arctic Tundra

Learning Objectives

- Recognize the distinguishing characteristics of boreal forests and arctic tundra

Boreal Forests

The boreal forest, also known as taiga or coniferous forest, the world's largest terrestrial biome, is found south of the Arctic Circle and across most of Canada, Alaska, Russia, and northern Europe. This biome has cold, dry winters and short, cool, wet summers. Temperatures vary from –54°C – 30°C (-65°F – 86°F) throughout the whole year. The summers, while short, are generally warm and humid. In much of the taiga, -20°C (-4°F) would be a typical winter day temperature, while 18°C (64°F) would be an average summer day.The annual precipitation, from 40 cm -100 cm (15.7–39 in), usually takes the form of snow. Little evaporation occurs because of the cold temperatures.

The long and cold winters in the boreal forest have led to the predominance of cold-tolerant, cone-bearing plants. These are evergreen, coniferous trees such as pines, spruces, and firs, which retain their needle-shaped leaves year-round. Evergreen trees can photosynthesize earlier in the spring than can deciduous trees because less energy from the sun is required to warm a needle-like leaf than a broad leaf. This benefits evergreen trees, which grow faster than deciduous trees in the boreal forest. In addition, soils in boreal forest regions tend to be acidic, with little available nitrogen. Leaves are a nitrogen-rich structure that deciduous trees must produce yearly. Therefore, coniferous trees that retain nitrogen-rich needles may have a competitive advantage over the broad-leafed deciduous trees.

The net primary productivity of boreal forests is lower than that of temperate forests and tropical wet forests. The aboveground biomass of boreal forests is high because these slow-growing tree species are long-lived, accumulating standing biomass over time. Plant species diversity is less than that seen in temperate forests and tropical wet forests. Boreal forests lack the pronounced elements of the layered forest structure seen in tropical wet forests. The structure of a boreal forest is often only a tree layer and a ground layer. When conifer needles are dropped, they decompose more slowly than do broad leaves; therefore, fewer nutrients are returned to the soil to fuel plant growth.



Figure $44.3F.1$: Plants in the boreal forest: The boreal forest (taiga) has low-lying plants and conifer trees; it often consists of only a tree layer and a ground layer.

Arctic Tundra

The Arctic tundra, lying north of the subarctic boreal forest, is located throughout the Arctic regions of the northern hemisphere. The average winter temperature is -34°C (-29.2°F), while the average summer temperature is from 3°C – 12°C (37°F – 52°F). Plants in the arctic tundra have a very short growing season of approximately 10–12 weeks. However, during this time, there are almost 24 hours of daylight, so plant growth is rapid. The annual precipitation of the Arctic tundra is very low (about 15-25 cm), with little annual variation in precipitation. As in the boreal forests, there is little evaporation due to the cold temperatures.

Plants in the Arctic tundra are generally low to the ground. There is little species diversity, low net primary productivity, and low aboveground biomass. The soils of the Arctic tundra may remain in a perennially frozen state referred to as permafrost. The permafrost makes it impossible for roots to penetrate deep into the soil and slows the decay of organic matter, which inhibits the release of nutrients from organic matter. During the growing season, the ground of the Arctic tundra can be completely covered with plants or lichens.



Figure $44.3F.1$: Plants in the Arctic tundra: Low-growing plants such as shrub willow dominate the tundra landscape, shown here in the Arctic National Wildlife Refuge.

The biodiversity of the tundras is low: there are 1,700 species of vascular plants and only 48 species of land mammals. Notable animals in the Arctic tundra include caribou (reindeer), musk ox, arctic hare, arctic fox, snowy owl, lemmings, and polar bears. Due to the harsh climate, tundra regions have seen little human activity, even though they are sometimes rich in natural resources such as oil and uranium.



Figure $44.3F.1$: Caribou (reindeer) in the tundra: Some populations of the North American caribou migrate the farthest of any terrestrial mammal, traveling up to 5,000 km (3,100 mi) a year.

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Key Points

- The boreal forest is found across most of Canada, Alaska, Russia, and northern Europe; the arctic tundra lies north of the boreal forest.
- The boreal forest has cold, dry winters and short, cool, wet summers with precipitation that takes the form of snow; due to this environment, evergreen coniferous trees are the dominant plants.
- The soil in boreal forest regions is usually acidic and contains little available nitrogen.
- Boreal forests have lower productivity than tropical or temperate forests; they also have less diversity, with only a tree layer and ground layer.
- Temperatures in the arctic tundra are cold year-round and precipitation is very low.
- Plants in the arctic tundra have a very short growing season of approximately 10–12 weeks, but during this time, growth is rapid; plants are low to the ground and the soil is permanently frozen.

Key Terms

- **permafrost**: permanently frozen ground
- **arctic tundra**: a biome found in the far Northern Hemisphere, north of the boreal forests, where the subsoil is permanently frozen
- **boreal forest**: a biome found in the Northern Hemisphere and characterized by coniferous forests consisting mostly of pines, spruces, and larches

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44.4: AQUATIC BIOMES

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44.4A: Abiotic Factors Influencing Aquatic Biomes

44.4B: Marine Biomes

44.4C: Estuaries- Where the Ocean Meets Fresh Water

44.4D: Freshwater Biomes

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44.4A: Abiotic Factors Influencing Aquatic Biomes

Learning Objectives

- Differentiate among the abiotic factors that affect aquatic biomes

Abiotic Factors Influencing Aquatic Biomes

As with terrestrial biomes, aquatic biomes are influenced by a series of abiotic factors. However, these factors differ since water has different physical and chemical properties than does air. Even if the water in a pond or other body of water is perfectly clear (there are no suspended particles), water, on its own, absorbs light. As one descends into a deep body of water, there will eventually be a depth which the sunlight cannot reach. While there are some abiotic and biotic factors in a terrestrial ecosystem that might obscure light (such as fog, dust, or insect swarms), usually these are not permanent features of the environment. The importance of light in aquatic biomes is central to the communities of organisms found in both freshwater and marine ecosystems. In freshwater systems, stratification due to differences in density is perhaps the most critical abiotic factor and is related to the energy aspects of light. The thermal properties of water (rates of heating and cooling) are significant to the function of marine systems and have major impacts on global climate and weather patterns. Marine systems are also influenced by large-scale physical water movements, such as currents; these are less important in most freshwater lakes.

The ocean is categorized by several areas or zones. All of the ocean's open water is referred to as the pelagic realm (or zone). The benthic realm (or zone) extends along the ocean bottom from the shoreline to the deepest parts of the ocean floor. Within the pelagic realm is the photic zone, which is the portion of the ocean that light can penetrate (approximately 200 m or 650 ft). At depths greater than 200 m, light cannot penetrate; thus, this is referred to as the aphotic zone. The majority of the ocean is aphotic, lacking sufficient light for photosynthesis. The deepest part of the ocean, the Challenger Deep (in the Mariana Trench, located in the western Pacific Ocean), is about 11,000 m (about 6.8 mi) deep. To give some perspective on the depth of this trench, the ocean is, on average, 4267 m or 14,000 ft deep. These realms and zones are relevant to freshwater lakes as well, as they determine the types of organisms that will inhabit each region.

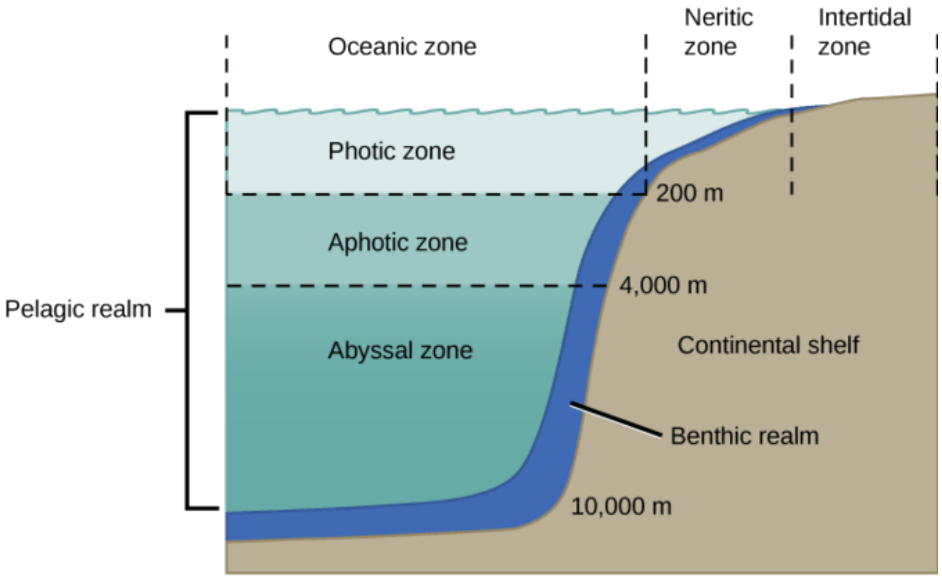


Figure 44.4A.1: Oceanic zones: The ocean is divided into different zones based on water depth, light availability, and distance from the shoreline.

Key Points

- In aquatic biomes, light is an important factor that influences the communities of organisms found in both freshwater and

marine ecosystems.
- In freshwater biomes, stratification, a major abiotic factor, is related to the energy aspects of light.
- Marine systems are influenced by the physical water movements, such as currents and tides, along with the thermal properties of water.
- Oceans zones can be categorized into photic or aphotic zones, depending on the presence or absence of light and photosynthesis.

Key Terms

- **stratification**: the process leading to the formation or deposition of layers
- **photic**: of, related to, or irradiated by light; especially describing that part of the near-surface ocean is which photosynthesis is possible
- **aphotic**: describing that part of the deep oceans and lakes where photosynthesis is not possible

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44.4B: Marine Biomes

Learning Objectives

- Describe coral reefs and the various zones in the ocean and the types of organisms living in each

Marine Biomes

The ocean is the largest marine biome. It is a continuous body of salt water that is relatively uniform in chemical composition; it is a weak solution of mineral salts and decayed biological matter. Within the ocean, coral reefs are a second kind of marine biome.

Ocean

Physical diversity has a significant influence on the ocean, which is categorized into different zones based on how far light reaches into the water. Each zone has a distinct group of species adapted to the biotic and abiotic conditions particular to that zone.

The intertidal zone (between high and low tide) is the oceanic region that is closest to land. It includes sandy beaches, but can also be rocky or muddy. This zone is an extremely variable environment because of tides. Organisms, exposed to air and sunlight at low tide, are underwater most of the time, especially during high tide. Therefore, living things that thrive in the intertidal zone are adapted to being dry for long periods of time. Since the shore of the intertidal zone is repeatedly struck by waves, the organisms found there are adapted to withstand damage from the pounding action of the waves. The exoskeletons of shoreline crustaceans are tough, protecting them from desiccation and wave damage.



Figure $44.4B.1$: Intertidal zone species: Sea urchins, mussel shells, and starfish, often found in the intertidal zone, are adapted to this rugged environment.

The neritic zone extends from the intertidal zone to depths of about 200 m (or 650 ft) at the edge of the continental shelf. Since light can penetrate this depth, photosynthesis can occur in the neritic zone. The water here contains silt, is well-oxygenated, low in pressure, and stable in temperature. Phytoplankton and floating *Sargassum*, a marine seaweed, provide a habitat for some sea life found in the neritic zone, including zooplankton, protists, small fishes, and shrimp, which are the base of the food chain for most of the world's fisheries.

Beyond the neritic zone is the open ocean area known as the oceanic zone. Within the oceanic zone there is thermal stratification where warm and cold waters mix because of ocean currents. Abundant plankton serve as the base of the food chain for larger animals. Nutrients are scarce in this less-productive part of the marine biome. When photosynthetic organisms and the protists and animals that feed on them die, their bodies fall to the bottom of the ocean where they remain. In contrast to freshwater lakes, the open ocean lacks a process for bringing the organic nutrients back up to the surface. The majority of organisms in the aphotic zone include sea cucumbers and other organisms that survive on the nutrients contained in the dead bodies of organisms in the photic zone.

A lower layer is the benthic realm, the deepwater region beyond the continental shelf. The bottom of the benthic realm comprises sand, silt, and dead organisms. Temperature decreases, remaining above freezing, as water depth increases. Due to the dead organisms that fall from the upper layers of the ocean, this nutrient-rich portion of the ocean allows a diversity of life to exist, including fungi, sponges, sea anemones, marine worms, sea stars, fishes, and bacteria.

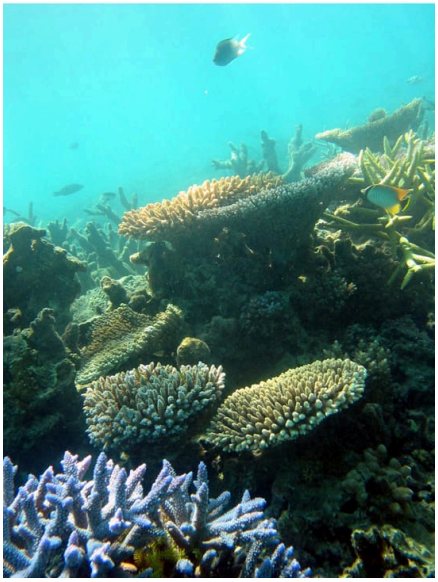


Figure $44.4B.1$: Coral reefs: Coral reefs are formed by the calcium carbonate skeletons of coral organisms, which are marine invertebrates in the phylum Cnidaria.

The deepest part of the ocean, the abyssal zone, at depths of 4000 m or greater, is very cold and has very high pressure, high oxygen content, and low nutrient content. There are a variety of invertebrates and fishes found in this zone, but the abyssal zone does not have plants due to the lack of light.

Coral Reefs

Coral reefs are ocean ridges formed by marine invertebrates living in warm, shallow waters of the ocean. They are found in the photic zone and are important in shore protection. Other coral reef systems are fringing islands, which are directly adjacent to land, or atolls, which are circular reef systems surrounding a former landmass that is now underwater. The coral organisms are colonies of cnidarian polyps that secrete a calcium carbonate skeleton, which slowly accumulates, forming the underwater reef. Corals found in shallower waters have a mutually symbiotic relationship with photosynthetic unicellular algae, which provides corals with the majority of the nutrition and the energy they require. The waters are nutritionally poor; therefore, without this mutualism, it would not be possible for large corals to grow. In contrast, corals living in deeper and colder water attain energy and nutrients by capturing prey using stinging cells on their tentacles.

Global Decline of Coral Reefs

Climate change and human activity pose dual threats to the long-term survival of the world's coral reefs. Corals evolved to survive at the upper limit of ocean water temperature. Excessive warmth induced by climate change causes reefs to expel their symbiotic, food-producing algae, resulting in a phenomenon known as bleaching. When bleaching occurs, the reefs lose much of their characteristic color as the algae and the coral animals die if loss of the symbiotic zooxanthellae is prolonged.

Key Points

- The ocean is divided into different zones with groups of species adapted to deal with the differences in light level, as well as other biotic and abiotic conditions particular to the zones.
- The intertidal zone is characterized by its high and low tides, as well as wave action; as the zone closest to land, it can be a sandy, rocky, or muddy beach.
- The neritic zone is silted, well-oxygenated, low in pressure, and stable in temperature; it is adjacent to the oceanic zone, in which warm and cold waters mix due to currents in the open ocean.
- The benthic zone is nutrient rich because of the sand, silt, and dead organisms that comprise the bottom of the region; as water depth increases, temperature within this deepwater region decreases.
- The abyssal zone is the deepest part of the ocean and, as such, it is cold, has very high pressure, high oxygen content, and low nutrient content.
- Coral reefs are ocean ridges formed by a mutualistic relationship between cnidarians and photosythetic algae; climate change and run-off are just two reasons why these important organisms are now in decline.

Key Terms

- **desiccation**: the state or process of drying-out
- **zooxanthellae**: animals of the genus Symbiodinium, a yellow dinoflagellate, notably found in coral reefs
- **photic**: of, related to, or irradiated by light; especially describing that part of the near-surface ocean is which photosynthesis is possible

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44.4C: Estuaries- Where the Ocean Meets Fresh Water

Learning Objectives

- Explain the ecology of estuaries

Estuaries: Where the Ocean Meets Fresh Water

Estuaries form a unique marine biome that occurs where a source of fresh water, such as a river, meets the ocean. Therefore, both fresh water and salt water are found in the same vicinity. Mixing results in a diluted (brackish) saltwater. Estuaries form protected areas where many of the young offspring of crustaceans, mollusks, and fish begin their lives. Salinity of estuaries is a very important factor that influences the organisms found there and their adaptations. The salinity, which varies, is based on the rate of flow of its freshwater sources. Once or twice a day, high tides bring salt water into the estuary. Low tides, occurring at the same frequency, reverse the current of salt water.



Figure $44.4C.1$: Low tide: The salinity levels within an estuary are dependent on the tides; during low tide, salt water influx levels are reduced.

The short-term and rapid variation in salinity due to the mixing of fresh water and salt water is a difficult physiological challenge for the plants and animals that inhabit estuaries. Many estuarine plant species are halophytes: plants that can tolerate salty water on their roots or sea spray. In some halophytes, filters in the roots remove the salt from the water that the plant absorbs. Other plants are able to pump oxygen into their roots. Animals, such as mussels and clams, have developed behavioral adaptations that expend a lot of energy to function in this rapidly-changing environment. When these animals are exposed to low salinity, they stop feeding, close their shells, and switch from aerobic respiration (in which they use gills) to anaerobic respiration (a process that does not require oxygen). When high tide returns to the estuary, the salinity and oxygen content of the water increases, causing these animals to open their shells, begin feeding, and to return to aerobic respiration.

Key Points

- Estuaries acts as nursery grounds for crustaceans, mollusks, and fish.
- Salinity, regulated by the influx of seawater and outflow of freshwater once or twice each day, is a determining factor in the types of organisms that can live there.
- To deal with the short-term and rapid variation in salinity, estuary species have developed specialized adaptations that enable them to live with the salty conditions; as a result, most plant species found in estuaries are halophytes.

Key Terms

- **brackish**: salty or slightly salty, as a mixture of fresh and sea water, such as that found in estuaries
- **halophyte**: any plant that tolerates an environment having a high salt content
- **estuary**: coastal water body where ocean tides and river water merge

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44.4D: Freshwater Biomes

Learning Objectives

- Differentiate among the freshwater biomes of lakes and ponds, rivers and streams, and wetlands

Freshwater Biomes

Freshwater biomes occur throughout the world's terrestrial biomes. They include lakes and ponds, rivers and streams, and wetlands.

Lakes and Ponds

Lakes and ponds can range in area from a few square meters to thousands of square kilometers. Temperature is an important abiotic factor affecting organisms found there. In the summer, thermal stratification of lakes and ponds occurs when the upper layer of water is warmed by the sun, but does not mix with deeper, cooler water. Light can penetrate within the photic zone of the lake or pond. Phytoplankton found here carry out photosynthesis, providing the base of the food web. At the bottom of lakes and ponds, bacteria in the aphotic zone break down dead organisms that sink to the bottom.

Nitrogen and phosphorus are important limiting nutrients. Because of this, they are determining factors in the amount of phytoplankton growth that occurs in lakes and ponds. When there is a large input of nitrogen and phosphorus (from sewage and run-off from fertilized lawns and farms, for example), the growth of algae skyrockets, resulting in a large accumulation called an algal bloom. These blooms can become so extensive that they reduce light penetration in water. As a result, the lake or pond becomes aphotic: photosynthetic plants cannot survive. When the algae die and decompose, severe oxygen depletion of the water occurs. Fish and other organisms that require oxygen are more likely to die. The resulting dead zones are found across the globe.



Figure $44.4D.1$: Algal blooms: The uncontrolled growth of algae in this lake has resulted in an algal bloom.

Rivers and Streams

Rivers and streams are continuously moving bodies of water that carry large amounts of water from the source, or headwater, to a lake or ocean. Abiotic features of a river or stream vary along its length. The origin point of streams (source water) is usually cold, low in nutrients, and clear.

Because the source channel is narrow, the current is often faster here than at any other point of the river or stream. This fast-moving water results in minimal silt accumulation at the bottom of the river or stream, resulting in clear water. Photosynthesis occurs primarily in algae growing on rocks since the swift current in channels inhibits the growth of phytoplankton. An additional input of energy can come from leaves or other organic material that falls into the river or stream from trees and other plants that border the water. When the leaves decompose, the organic material and nutrients in the leaves are returned to the water. Plants and animals have adapted to this fast-moving water. For instance, leeches have elongated bodies and suckers on both ends that attach to the substrate, keeping the leech anchored in place.

As the river or stream flows away from the source, the width of the channel gradually widens and the current slows. This slow-moving water, caused by the gradient decrease and the volume increase as tributaries unite, has more sedimentation. The water is as clear as it is near the source since phytoplankton can be suspended in slow-moving water. The water is also warmer. Worms and insects can be found burrowing into the mud. The higher order predator vertebrates, which include waterfowl, frogs, and fishes, often depend on taste or chemical cues to find prey due to the murkiness of the water.

Wetlands

Wetlands are environments in which the soil is either permanently or periodically saturated with water. They differ from lakes in that they are shallow bodies of water. Emergent vegetation consists of wetland plants that are rooted in the soil, but have portions of leaves, stems, and flowers extending above the water's surface. Types of wetlands include marshes, swamps, bogs, mudflats, and salt marshes. The three shared characteristics among these types are their hydrology, hydrophytic vegetation, and hydric soils.



Figure $44.4D.1$: Wetlands: Located in southern Florida, Everglades National Park is vast array of wetland environments, including sawgrass marshes, cypress swamps, and estuarine mangrove forests. Here, a great egret walks among cypress trees.

Freshwater marshes and swamps are characterized by slow and steady water flow. Bogs develop in depressions where water flow is low or non-existent. Bogs usually occur in areas where there is a clay bottom with poor percolation: the movement of water through the pores in the soil or rocks. The water found in a bog is stagnant and oxygen-depleted because the oxygen that is used during the decomposition of organic matter is not replaced, resulting in a slowing of decomposition. This leads to organic acids and other acids building up, which lower the pH of the water. At a lower pH, nitrogen becomes unavailable to plants, creating a challenge for them. Some types of bog plants capture insects and extract the nitrogen from their bodies.

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Key Points

- Temperature, as well as the availability of nitrogen and phosphorus, are factors that affect living things in lakes and ponds.
- When available in large amounts, nitrogen and phosphorus cause potentially-detrimental algal blooms in lakes; nitrogen is also a limiting factor for plant growth in bogs.
- The continuous movement of rivers and streams are their defining characteristic; these bodies of water carry large amounts of water from the source to a lake or ocean.
- Wetlands are shallow bodies of water with soil that is either permanently or periodically saturated with water; every type of wetland has three shared characteristics: their hydrology, hydrophytic vegetation, and hydric soils.

Key Terms

- **algal bloom**: a dense spread of algae on the surface of water
- **percolation**: the seepage or filtration of a liquid through a porous substance
- **hydrology**: the science of the properties, distribution, and effects of water on a planet's surface, in the soil and underlying rocks, and in the atmosphere

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44.5: CLIMATE AND THE EFFECTS OF GLOBAL CLIMATE CHANGE

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- Topic hierarchy

44.5A: Climate and Weather

44.5B: Causes of Global Climate Change

44.5C: Evidence of Global Climate Change

44.5D: Past and Present Effects of Climate Change

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44.5A: Climate and Weather

Learning Objectives

- Distinguish between climate and weather

Climate and Weather

A common misconception about global climate change is that a specific weather event occurring in a particular region (for example, a very cool week in June in central Indiana) is evidence of global climate change. However, a cold week in June is a weather-related event and not a climate-related one. These misconceptions often arise because of confusion over the terms climate and weather.

Climate refers to the long-term, predictable atmospheric conditions of a specific area. The climate of a biome is characterized by having consistent temperature and annual rainfall ranges. Climate does not address the amount of rain that fell on one particular day in a biome or the colder-than-average temperatures that occurred on one day. In contrast, weather refers to the conditions of the atmosphere during a short period of time. Weather forecasts are usually made for 48-hour cycles; while long-range weather forecasts are available, they can be unreliable.

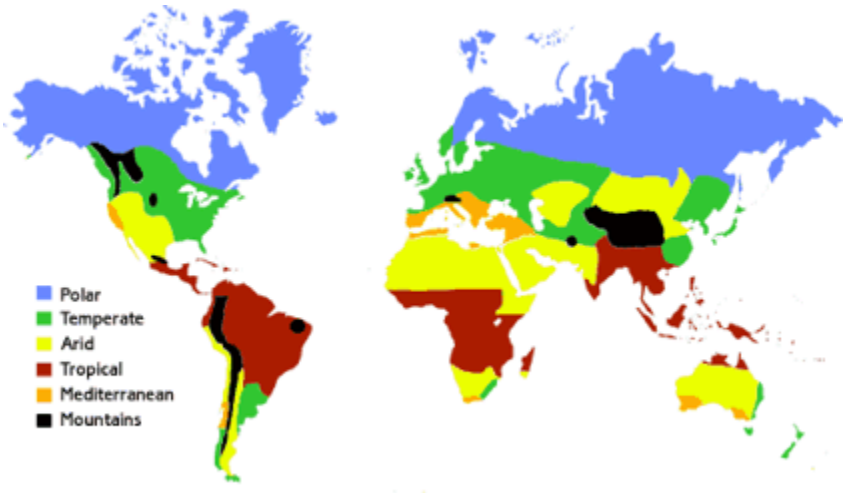


Figure 44.5A.1: Climate: Climate refers to long-term, predictable atmospheric conditions of a specific area. Weather, in contrast, refers to the conditions of the atmosphere during a short period of time. This map illustrates the various climate conditions around the world.

To better understand the difference between climate and weather, imagine that you are planning an outdoor event in northern Wisconsin. You would be thinking about climate when you plan the event in the summer rather than the winter because you have long-term knowledge that any given Saturday in the months of May to August would be a better choice for an outdoor event in Wisconsin than any given Saturday in January. However, you cannot determine the specific day that the event should be held because it is difficult to accurately predict the weather on a specific day. Climate can be considered “average” weather.

Key Points

- Climate refers to the long-term, predictable atmospheric conditions of a specific area; it does not address the amount of rain that fell on one particular day or the colder-than-average temperatures on a given day in a biome.
- Weather refers to the conditions of the atmosphere during a short period of time; weather forecasts are usually made for 48-hour cycles.
- Specific, one-off weather occurrences are not necessarily indicators of climate change.

Key Terms

- **biome**: any major regional biological community such as that of forest or desert
- **climate**: long-term manifestations of weather and other atmospheric conditions in a given area or country in a period long enough to ensure that representative values are obtained (generally 30 years)
- **weather**: the short term state of the atmosphere at a specific time and place, including the temperature, humidity, cloud cover, precipitation, wind, etc.

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44.5B: Causes of Global Climate Change

Learning Objectives

- Explain the drivers of climate change, past and present

Current and Past Drivers of Global Climate Change

Since it is not possible to go back in time to directly observe and measure climate, scientists use indirect evidence to determine the drivers, or factors, that may be responsible for climate change. The indirect evidence includes data collected using ice cores, boreholes (narrow shafts bored into the ground), tree rings, glacier lengths, pollen remains, and ocean sediments. The data shows a correlation between the timing of temperature changes and drivers of climate change. Before the Industrial Era (pre-1780), there were three drivers of climate change that were not related to human activity or atmospheric gases: the Milankovitch cycles, solar intensity, and volcanic eruptions.

Natural Causes of Climate Change

The Milankovitch cycles describe how slight changes in the earth's orbit affect the earth's climate. The length of the Milankovitch cycles ranges between 19,000 and 100,000 years. In other words, one could expect to see some predictable changes in the earth's climate associated with changes in the earth's orbit at a minimum of every 19,000 years.

The variation in the sun's intensity is the second natural factor responsible for climate change. Solar intensity is the amount of solar power or energy the sun emits in a given length of time. There is a direct relationship between solar intensity and temperature: as solar intensity increases (or decreases), the earth's temperature correspondingly increases (or decreases). Changes in solar intensity have been proposed as one of several possible explanations for the Little Ice Age.

Finally, volcanic eruptions are a third natural driver of climate change. Volcanic eruptions can last a few days, but the solids and gases released during an eruption can influence the climate over a period of a few years, causing short-term climate changes. The gases and solids released by volcanic eruptions can include carbon dioxide, water vapor, sulfur dioxide, hydrogen sulfide, hydrogen, and carbon monoxide.

Human Activity-Related Causes of Climate Change

Greenhouse gases are probably the most significant drivers of the climate. When heat energy from the sun strikes the earth, gases known as greenhouse gases trap the heat in the atmosphere, similar to how the glass panes of a greenhouse keep heat from escaping. The greenhouse gases that affect earth include carbon dioxide, methane, water vapor, nitrous oxide, and ozone. Approximately half of the radiation from the sun passes through these gases in the atmosphere, striking the earth. This radiation is converted into thermal radiation on the earth's surface; a portion of that energy is re-radiated into the atmosphere. Greenhouse gases, however, reflect much of the thermal energy back to the earth's surface. The more greenhouse gases there are in the atmosphere, the more thermal energy is reflected back to the earth's surface. Greenhouse gases, as they absorb and emit radiation, are an important factor in the greenhouse effect, or the warming of earth due to carbon dioxide and other greenhouse gases in the atmosphere.



Figure $44.5B.1$: Greenhouse gasses: The burning of fossil fuels in industry and by vehicles releases carbon dioxide and other greenhouse gases into the atmosphere.

Beginning recently, atmospheric carbon dioxide concentrations have increased beyond the historical maximum of 300 ppm. The current increases in atmospheric carbon dioxide have happened very quickly: in a matter of hundreds of years rather than thousands of years. A key factor that must be recognized when comparing the historical data and the current data is the presence of modern human society. No other driver of climate change has yielded changes in atmospheric carbon dioxide levels at this rate or to this magnitude.

Human activity releases carbon dioxide and methane, two of the most important greenhouse gases, into the atmosphere in several ways. The primary mechanism that releases carbon dioxide is the burning of fossil fuels, such as gasoline, coal, and natural gas. Deforestation, cement manufacture, animal agriculture, the clearing of land, and the burning of forests are other human activities that release carbon dioxide. Methane (CH_4) is produced when bacteria break down organic matter under anaerobic conditions (i.e., without oxygen), which can happen when organic matter is trapped underwater, as in rice paddies, or in the intestines of herbivores. Methane can also be released from natural gas fields and the decomposition that occurs in landfills. Another source of methane is the melting of clathrates: frozen chunks of ice and methane found at the bottom of the ocean. When water warms, these chunks of ice melt, releasing methane. As the ocean's water temperature increases, the rate at which clathrates melt is increasing, releasing even more methane. This leads to increased levels of methane in the atmosphere, which further accelerates the rate of global warming. This is an example of the positive feedback loop that is leading to the rapid rate of increase of global temperatures.

Key Points

- Data show a correlation between the timing of temperature changes and drivers of climate change.
- Prior to the Industrial Era (pre-1780), there were three drivers of climate change that were not related to human activity: Milankovitch cycles, sun intensity, and volcanic eruptions.
- Greenhouse gases, probably the most significant drivers of the climate, include carbon dioxide, methane, water vapor, nitrous oxide, and ozone.
- Human activity, such as the burning of fossil fuels, releases carbon dioxide and methane, two of the most important greenhouse gases, into the atmosphere.
- Deforestation, cement manufacture, animal agriculture, the clearing of land, and the burning of forests are other human activities that release carbon dioxide.

Key Terms

- **Milankovitch cycle**: any of the three cyclic variations in the earth's orbit around the sun, respectively the obliquity of its axis, the precession of the equinoxes, and the eccentricity of its orbit
- **greenhouse gas**: any gas, such as carbon dioxide, that contributes to the greenhouse effect (continued warming) when

released into the atmosphere
- **greenhouse effect**: the process by which a planet is warmed by its atmosphere

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44.5C: Evidence of Global Climate Change

Learning Objectives

- Evaluate the evidence for global climate change

Global Climate Change

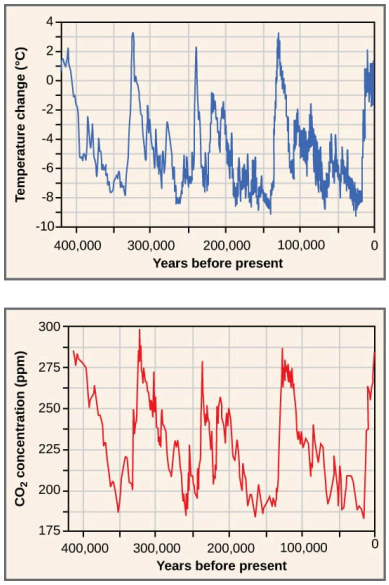


Figure $44.5C.1$: Measuring historical climate change: By measuring the amount of CO2 trapped in ice, scientists can determine past atmospheric CO2 concentrations. Temperatures relative to the present are determined from the amount of deuterium (an isotope of hydrogen) present.

Climate change can be understood by approaching three areas of study: (1) evidence of current and past global climate change, (2) causes of past and present-day global climate change, and (3) ancient and current results of climate change.

It is helpful to keep these three different aspects of climate change clearly separated when consuming media reports about global climate change. It is common for reports and discussions about global climate change to confuse the data showing that earth's climate is changing with the factors that drive this climate change.

Evidence for Global Climate Change

Since scientists cannot go back in time to directly measure climatic variables, such as average temperature and precipitation, they must, instead, indirectly measure temperature. To do this, scientists rely on historical evidence of earth's past climates.

Antarctic ice cores are a key example of such evidence. These ice cores are samples of polar ice obtained by means of drills that reach thousands of meters into ice sheets or high mountain glaciers. Viewing the ice cores is like traveling backwards through time; the deeper the sample, the earlier the time period. Trapped within the ice are bubbles of air and other biological evidence that can reveal temperature and carbon dioxide data. Antarctic ice cores have been collected and analyzed to indirectly estimate the temperature of the earth over the past 400,000 years.

Before the late 1800s, the earth had been as much as 9°C cooler and about 3°C warmer. Atmospheric concentration of carbon dioxide also rose and fell in periodic cycles; note the relationship between carbon dioxide concentration and temperature. Carbon dioxide levels in the atmosphere have historically cycled between 180 and 300 parts per million (ppm) by volume.

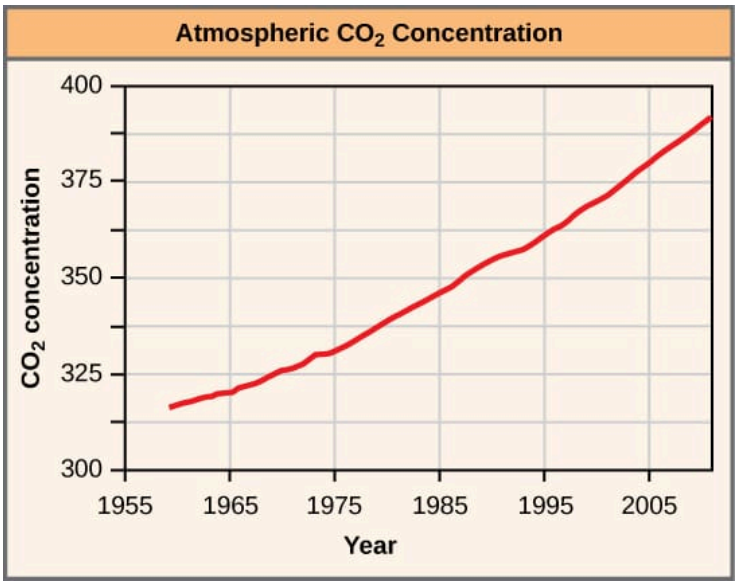


Figure 44.5C.1: Climate change and the Industrial Era: The atmospheric concentration of CO2 has risen steadily since the beginning of industrialization.The Industrial Revolution, which began around 1750, was characterized by changes in much of human society. Advances in agriculture increased the food supply, which improved the standard of living for people in Europe and the United States. New technologies were invented, providing jobs and cheaper goods. These new technologies were powered using fossil fuels, especially coal. The Industrial Revolution in the early nineteenth century ushered in the beginning of the Industrial Era, a period when atmospheric carbon dioxide began to rise. When a fossil fuel is burned, carbon dioxide is released.

Two significant temperature anomalies, or irregularities, have occurred in the last 2000 years. These are the Medieval Climate Anomaly (or the Medieval Warm Period) and the Little Ice Age. A third temperature anomaly aligns with the Industrial Era. The Medieval Climate Anomaly occurred between 900 and 1300 AD. During this time period, many climate scientists think that slightly-warmer conditions prevailed in many parts of the world; the higher-than-average temperature changes varied between 0.10 °C and 0.20 °C above the norm. Although 0.10 °C does not seem large enough to produce any noticeable change, it did free seas of ice. Because of this warming, the Vikings were able to colonize Greenland.

The Little Ice Age was a cold period that occurred between 1550 AD and 1850 AD. During this time, a slight cooling of a little less than 1 °C was observed in North America, Europe, and possibly other areas of the world. This 1 °C change is a seemingly-small deviation in temperature (as was observed during the Medieval Climate Anomaly); however, it also resulted in noticeable changes. Historical accounts reveal a time of exceptionally-harsh winters with much snow and frost.

Key Points

- Climate change can be understood by approaching three areas of study: (1) current and past global climate change, (2) causes of past and present-day global climate change, and (3) ancient and current results of climate change.
- Since we cannot go back in time to directly measure climatic variables, such as average temperature and precipitation, we must rely on historical evidence of earth's past climate, such as Antarctic ice cores.
- Three significant temperature anomalies, or irregularities, have occurred in the last 2000 years: the Medieval Climate Anomaly (or the Medieval Warm Period), the Little Ice Age, and the Industrial Era.
- With the beginning of the Industrial Era, atmospheric carbon dioxide began to rise.

Key Terms

- **fossil fuel**: any fuel derived from hydrocarbon deposits such as coal, petroleum, natural gas, and, to some extent, peat; these fuels are irreplaceable; their burning generates the greenhouse gas carbon dioxide

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44.5D: Past and Present Effects of Climate Change

Learning Objectives

- Describe the effects of current and geological climate change

Documented results of climate change: past and present

Scientists have geological evidence of the consequences of long-ago climate change. Modern-day phenomena, such as retreating glaciers and melting polar ice, cause a continual rise in sea level. Changes in climate can negatively affect organisms.

Geological climate change effects

Global warming has been associated with at least one planet-wide extinction event during the geological past. The Permian extinction event occurred about 251 million years ago toward the end of the roughly 50-million-year-long geological time span known as the Permian period. This geologic time period was one of the three warmest periods in earth's geologic history. Scientists estimate that approximately 70 percent of the terrestrial plant and animal species and 84 percent of marine species became extinct, vanishing forever near the end of the Permian period. Organisms that had adapted to wet and warm climatic conditions, such as annual rainfall of 300–400 cm (118–157 in) and 20 °C–30 °C (68 °F–86 °F) in the tropical wet forest, may not have been able to survive the Permian climate change.

Present climate change effects

A number of global events have occurred that may be attributed to recent climate change during our lifetimes. Glacier National Park in Montana, among others, is undergoing the retreat of many of its glaciers, a phenomenon known as glacier recession. In 1850, the area contained approximately 150 glaciers. By 2010, however, the park contained only about 24 glaciers greater than 25 acres in size. One of these glaciers is the Grinnell Glacier at Mount Gould. Between 1966 and 2005, the size of Grinnell Glacier shrank by 40 percent. Similarly, the mass of the ice sheets in Greenland and the Antarctic is decreasing: Greenland lost 150–250 km^3 of ice per year between 2002 and 2006. In addition, the size and thickness of the Arctic sea ice is decreasing.



Figure $44.5D.1$: Glacial recession: The effect of global warming can be seen in the continuing retreat of Grinnel Glacier. The loss of a glacier results in the loss of summer meltwaters, sharply reducing seasonal water supplies and severely affecting local ecosystems.

This loss of ice is leading to rises in the global sea level. On average, the sea is rising at a rate of 1.8 mm per year. However,

between 1993 and 2010, the rate of sea-level increase ranged between 2.9 and 3.4 mm per year. A variety of factors affect the volume of water in the ocean, including the temperature of the water (the density of water is related to its temperature) and the amount of water found in rivers, lakes, glaciers, polar ice caps, and sea ice. As glaciers and polar ice caps melt, there is a significant contribution of liquid water that was previously frozen.

In addition to some abiotic conditions changing in response to climate change, many organisms are also being affected by the changes in temperature. Temperature and precipitation play key roles in determining the geographic distribution and phenology of plants and animals. Phenology is the study of the effects of climatic conditions on the timing of periodic lifecycle events, such as flowering in plants or migration in birds. Researchers have shown that 385 plant species in Great Britain are flowering 4.5 days sooner than was recorded during the previous 40 years. In addition, insect-pollinated species were more likely to flower earlier than wind-pollinated species. The impact of changes in flowering date would be mitigated if the insect pollinators emerged earlier. This mismatched timing of plants and pollinators could result in injurious ecosystem effects because, for continued survival, insect-pollinated plants must flower when their pollinators are present.

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Key Points

- Global warming has been associated with at least one planet-wide extinction event during the geological past; scientists estimate that during the Permian period, approximately 70 percent of the terrestrial plant and animal species along with 84 percent of marine species became extinct.
- Glacier recession and melting ice caps are direct effects of current global climate change, ultimately leading to higher global sea levels; as glaciers and polar ice caps melt, there is a significant contribution of liquid water that was previously frozen.
- Changes in temperature and precipitation are causing plants to flower earlier, before their insect pollinators have emerged; mismatched timing of plants and pollinators could result in injurious ecosystem effects.
- This mismatched timing of plants and pollinators could result in injurious ecosystem effects because, for continued survival, insect-pollinated plants must flower when their pollinators are present.

Key Terms

- **phenology**: the study of the effect of climate on periodic biological phenomena
- **Permian**: of a geologic period within the Paleozoic era; comprises the Cisuralian, Guadalupian, and Lopingian epochs from about 280 to 248 million years ago

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45.1: POPULATION DEMOGRAPHY

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45.1A: Population Demography

Learning Objectives

- Explain the importance and function of population demography

Introduction

Imagine someone sailing down a river in a small motorboat on a warm day. She is enjoying the warm sunshine and cool breeze when suddenly a 20-pound silver carp hits her in the head. The presence of Asian carp in U.S. waterways make this risk very real on rivers and canal systems, particularly in Illinois and Missouri.



Figure 45.1A.1: Asian carp jump out of the water in response to electrofishing: The Asian carp in the inset photograph were harvested from the Little Calumet River in Illinois in May, 2010, using rotenone, also used as an insecticide.

The several types of Asian carp include the silver, black, grass, and big head carp. These have been farmed and eaten in China for over 1,000 years; it is among the top aquaculture foods worldwide. In the United States, however, Asian carp is considered to be an invasive species. It disrupts the structure and composition of native fish communities to the point of threatening native aquatic species.

Biologists are working to understand the biology and ecology of Asian carp. The aim is to develop methods of controlling the species without damaging native fish. Understanding the population dynamics of the carp will help biologists develop and implement measures that reduce its population, allowing scientists to model the statistics of carp populations.

Population demography

Populations are dynamic entities, consisting of all of the species living within a specific area. They fluctuate based on a number of factors: seasonal and yearly changes in the environment, natural disasters such as forest fires and volcanic eruptions, and competition for resources between and within species.

Demography, the statistical study of population dynamics, uses mathematical tools to investigate how populations respond to changes in their biotic and abiotic environments. Researchers originally designed demographic tools, such as life tables, to study human populations. To determine insurance rates, life insurance companies developed methods to analyze life expectancies of individuals in a population. The term “demographics” is often used in discussions of human populations, but demographic

approaches can be applied to all living populations.

Key Points

- Demographic studies help scientists understand the population dynamics of species, such as invasive species like the Asian carp.
- Population fluctuations depend on the weather, food availability, natural disasters such as forest fires or volcanic eruptions, predation, and biological competition.
- Researchers originally designed demographic tools to study human populations, but demographic approaches can be applied to all living populations.

Key Terms

- **demography**: the study of populations and how they change
- **population dynamics**: the variation of populations due to birth and death rates, by immigration and emigration, and concerning topics such as aging populations or population decline
- **statistics**: a systematic collection of data on measurements or observations, often related to demographic information such as population counts, incomes, population counts at different ages, etc.

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45.1B: Population Size and Density

Learning Objectives

- Choose the appropriate method to sample a population, given features of the organisms in that population

Population size and density

Population size and density are the two most important statistics scientists use to describe and understand populations. A population's size refers to the number of individuals (N) it comprises. Its density is the number of individuals within a given area or volume. These data allow scientists to model the fluctuations of a population over time. For example, a larger population may be more stable than a smaller population. With less genetic variation, a smaller population will have reduced capacity to adapt to environmental changes. Individuals in a low-density population are thinly dispersed; hence, they may have more difficulty finding a mate compared to individuals in a higher-density population. On the other hand, high-density populations often result in increased competition for food. Many factors influence density, but, as a rule-of-thumb, smaller organisms have higher population densities than do larger organisms.

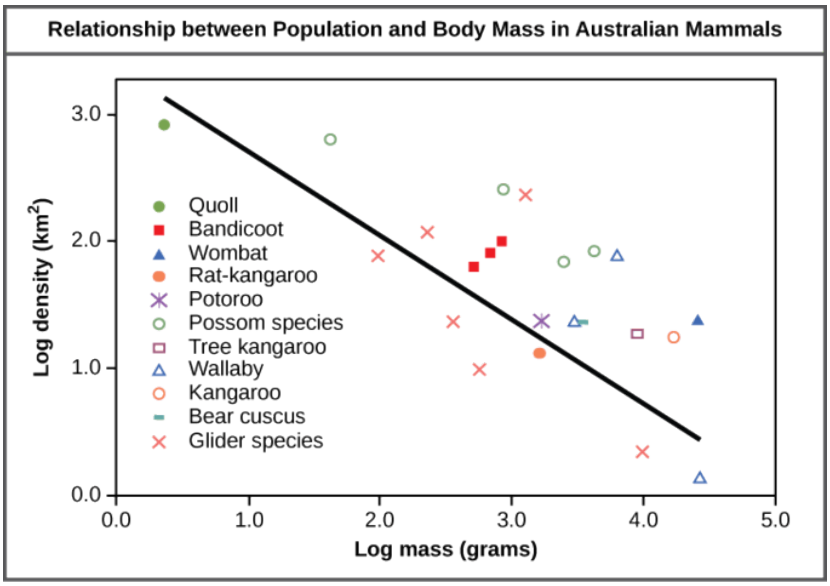


Figure $45.1B.1$: Population density is negatively correlated with body size: Australian mammals show a typical inverse relationship between population density and body size.

Population research methods

Counting all individuals in a population is the most accurate way to determine its size. However, this approach is not usually feasible, especially for large populations or extensive habitats. Instead, scientists study populations by sampling, which involves counting individuals within a certain area or volume that is part of the population's habitat. Analyses of sample data enable scientists to infer population size and population density about the entire population.

A variety of methods can be used to sample populations. Scientists usually estimate the populations of sessile or slow-moving organisms with the quadrat method. A quadrat is a square that encloses an area within a habitat. The area may be defined by staking it out with sticks and string, or using a square made of wood, plastic, or metal placed on the ground.

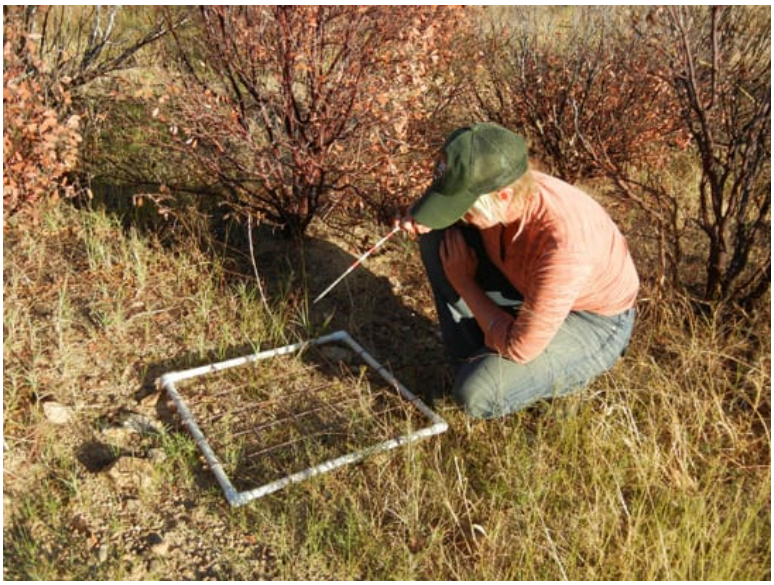


Figure $45.1B.1$: Scientist uses a quadrat to measure plant population size and density: A quadrat is a square frame of known area in which species of interest can be easily counted and measured.

A field study usually includes several quadrat samples at random locations or along a transect in representative habitat. After they place the quadrats, researchers count the number of individuals that lie within the quadrat boundaries. The researcher decides the quadrat size and number of samples from the type of organism, its spatial distribution, and other factors. For sampling daffodils, a 1 m^2 quadrat could be appropriate. Giant redwoods are larger and live further apart from each other, so a larger quadrat, such as 100 m^2, would be necessary. The correct quadrat size ensures counts of enough individuals to get a sample representative of the entire habitat.

Scientists typically use the mark and recapture technique for mobile organisms such as mammals, birds, or fish. With this method, researchers capture animals and mark them with tags, bands, paint, body markings, or some other sign. The marked animals are then released back into their environment where they mix with the rest of the population. Later, a new sample is collected, including some individuals that are marked (recaptures) and some individuals that are unmarked.

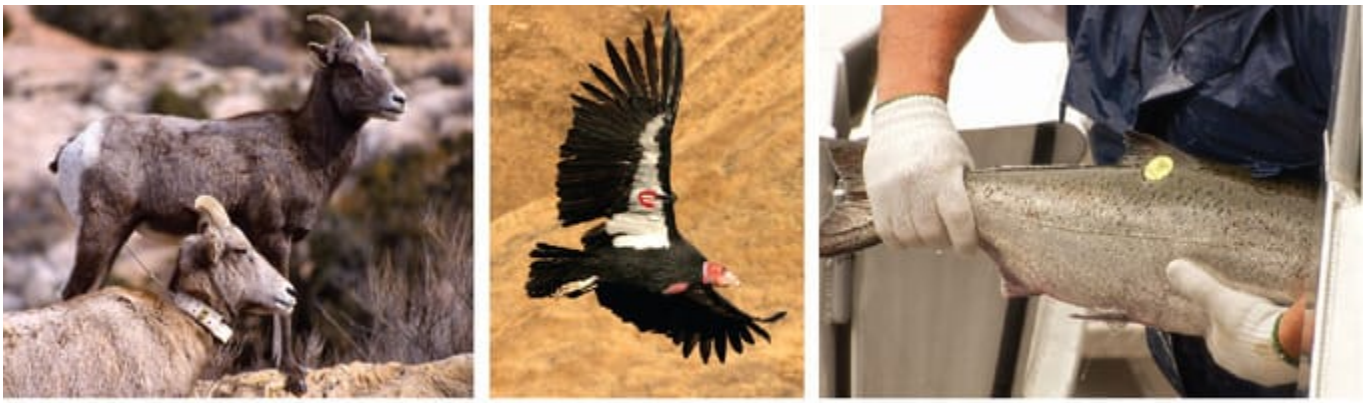


Figure $45.1B.1$: Mark and recapture is used to measure the population size of mobile animals.: With the mark and recapture method, researchers capture animals and mark them with tags, bands, paint, body markings or some other sign.

The ratio of marked to unmarked individuals allows scientists to calculate how many individuals are in the population as an estimate of total population size. This method assumes that the larger the population, the lower the percentage of tagged organisms that will be recaptured since they will have mixed with more untagged individuals. For example, if 80 deer are captured, tagged, and released into the forest, and later 100 deer are captured with 20 of them are already marked, we can determine the population size (N) using the following equation:

numbermarkedinfirstcatch×totalnumberofsecondcatchnumberofmarkedrecapturesinsecondcatchnumbermarkedinfirstcatch×total

Plugging the example data into the equation, the calculation gives an estimated total population size of 400.

$$80 \times 100 20 = 400 80 \times 100 20 = 400$$

Using the example data, if only 10 already-marked deer had been recaptured, the calculated total population size would be 800.

The mark and recapture method has limitations. Some animals from the first catch may learn to avoid capture in the second round. Such behavior would cause inflated population estimates. Alternatively, animals may preferentially be retrapped (especially if a food reward is offered), resulting in an underestimate of population size. Also, some species may be harmed by the marking technique, reducing their survival. A variety of other techniques have been developed, including the electronic tracking of animals tagged with radio transmitters and the use of data from commercial fishing and trapping operations to estimate the size and health of populations and communities.

Key Points

- A population ‘s size refers to the number of individuals (N) it comprises.
- Population density is the number of individuals within a given area or volume.
- Scientists usually study populations by sampling, which involves counting individuals within a certain area or volume that is part of the population’s habitat.
- The quadrat method is used to sample sessile organisms, using a square within which all individuals are counted; extrapolation of the data to the entire habitat results in a population size estimate.
- The mark and recapture technique is used for mobile organisms; it involves marking a sample of individuals and then estimating population size from the number of marked individuals in subsequent samples.

Key Terms

- **population density**: the average number of a population’s individuals that inhabit a unit area or volume
- **quadrat**: a square area, marked with boundaries for studying the population size and density of plants and sessile animals
- **mark and recapture**: a sample technique is used for study of the populations of mobile organisms, estimating population size from the number of marked individuals in samples

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45.1C: Species Distribution

Learning Objectives

- Differentiate among the ways in which species distribute themselves in space

Density and size are useful measures for characterizing populations. Scientists gain additional insight into a species' biology and ecology from studying how individuals are spatially distributed. Dispersion or distribution patterns show the spatial relationship between members of a population within a habitat. Patterns are often characteristic of a particular species; they depend on local environmental conditions and the species' growth characteristics (as for plants) or behavior (as for animals).

Individuals of a population can be distributed in one of three basic patterns: they can be more or less equally spaced apart (uniform dispersion), dispersed randomly with no predictable pattern (random dispersion), or clustered in groups (clumped dispersion).



Figure $45.1C.1$: Three patterns of distribution in populations of organisms: A population may have a uniform, random, or clumped distribution. Territorial birds, such as penguins, tend to have uniform distribution. Plants with wind-dispersed seeds, such as dandelions, are usually distributed randomly. Animals, such as elephants, that travel in groups exhibit clumped distribution.

Uniform dispersion is observed in plant species that inhibit the growth of nearby individuals. For example, the sage plant, *Salvia leucophylla*, secretes toxins, a phenomenon called negative allelopathy. The chemicals kill off surrounding plants in a circle around the individual sage plants, leading to a uniform distance between each plant. Animals that maintain defined territories, such as nesting penguins, also exhibit uniform dispersion.

Random dispersion occurs with dandelion and other plants that have wind-dispersed seeds that germinate wherever they happen to fall in a favorable environment. Clumped dispersion is seen in plants that drop their seeds straight to the ground, such as oak trees, or animals that live in groups, such as schools of fish or herds of elephants. Clumped dispersions may also result from habitat heterogeneity. If favorable conditions are localized, organisms will tend to clump around those, such as lions around a watering hole.

In this way, the dispersion pattern of the individuals within a population provides more information about how they interact with each other and their environment 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.

Key Points

- Dispersion or distribution patterns show the spatial relationship between members of a population within a habitat.

- Individuals of a population can be distributed in one of three basic patterns: uniform, random, or clumped.
- In a uniform distribution, individuals are equally spaced apart, as seen in negative allelopathy where chemicals kill off plants surrounding sages.
- In a random distribution, individuals are spaced at unpredictable distances from each other, as seen among plants that have wind-dispersed seeds.
- In a clumped distribution, individuals are grouped together, as seen among elephants at a watering hole.

Key Terms

- **dispersion pattern**: the spatial relationship between members of a population within a habitat, often characteristic of a particular species
- **allelopathy**: the release by a plant of a toxin to suppress growth of nearby competing plants, often resulting in a uniform dispersion pattern
- **habitat heterogeneity**: variation in physical environmental features within an area, such as topography, soil chemistry, temperature, moisture, and biological factors

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45.1D: The Study of Population Dynamics

Learning Objectives

- Distinguish between life tables and survivorship curves as used in demography

Demography

Population size, density, and distribution patterns describe a population at a fixed point in time. To study how a population changes over time, scientists must use the tools of demography: the statistical study of population changes over time. The key statistics demographers use are birth rates, death rates, and life expectancies; although, in practice, scientists also study immigration and emigration rates, which also affect populations.

These measures, especially birth rates, may be related to the population characteristics described in prior sections. For example, a large population would have a relatively-high birth rate if it has more reproductive individuals. Alternatively, a large population may also have a high death rate because of competition, disease, or waste accumulation. A high population density may lead to more reproductive encounters between individuals, as would a clumped distribution pattern. Such conditions would increase the birth rate.

Biological features of the population also affect population changes over time. Birth rates will be higher in a population with the ratio of males to females biased towards females, or in a population composed of relatively more individuals of reproductive age.

The demographic characteristics of a population are the basic determinants of how the population changes over time. If birth and death rates are equal, the population remains stable. The population will increase if birth rates exceed death rates, but will decrease if birth rates are lower than death rates. Life expectancy, another important factor, is the length of time individuals remain in the population. It is impacted by local resources, reproduction, and the overall health of the population. These demographic characteristics are often displayed in the form of a life table.

Life tables

Life tables, which provide important information about the life history of an organism, divide the population into age groups and often sexes; they show how long a member of that group will probably live. The tables are modeled after actuarial tables used by the insurance industry for estimating human life expectancy. Life tables may include:

- the probability of individuals dying before their next birthday (i.e., mortality rate)
- the percentage of surviving individuals at a particular age interval
- the life expectancy at each interval

The life table shown is from a study of Dall mountain sheep, a species native to northwestern North America. The population is divided into age intervals, as seen in the leftmost column. The mortality rate per 1,000 individuals is calculated by dividing the number of individuals dying during an age interval by the number of individuals surviving at the beginning of the interval, multiplied by 1,000.

Life Table of Dall Mountain Sheep[1]				
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

Table 1: This life table of *Ovis dalli* shows the number of deaths, number of survivors, mortality rate, and life expectancy at each age interval for the Dall mountain sheep.

Figure $45.1D.1$: Life table of Dall mountain sheep: This life table of *Ovis dalli* shows the number of deaths, number of survivors, mortality rate, and life expectancy at each age interval for the Dall mountain sheep.

For example, between ages three and four, 12 individuals die out of the 776 that were remaining from the original 1,000 sheep. This number is then multiplied by 1,000 to get the mortality rate per thousand.

As can be seen from the mortality rate data (column D), a high death rate occurred when the sheep were between 6 and 12 months old, which 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.

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 plotted versus time (usually with data compiled from a life table). These curves allow comparison of life histories of different populations.

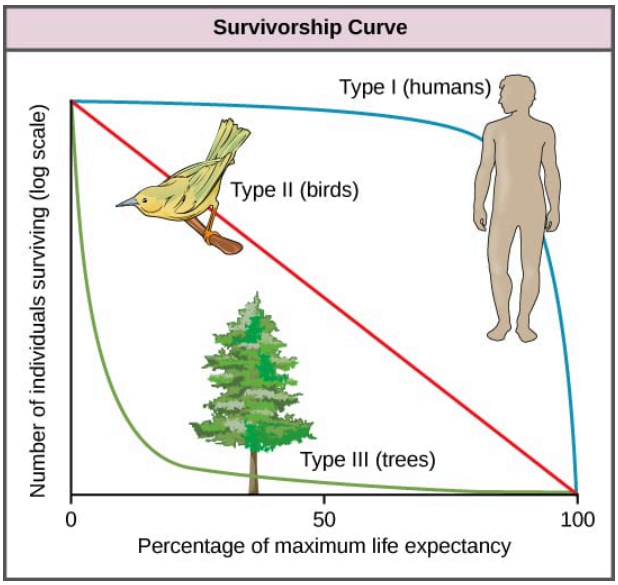


Figure 45.1D.1: Survivorship curves show the distribution of individuals in a population according to age: Humans and most mammals have a Type I survivorship curve because death primarily occurs in the older years. Birds have a Type II survivorship curve, as death at any age is equally probable. Trees 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.

Humans and most primates exhibit a Type I survivorship curve because a high percentage of offspring survive early and middle years; death occurs predominantly in older individuals. These species have few offspring as they invest in parental care to increase survival.

Birds show the Type II survivorship curve because equal numbers of birds tend to die at each age interval. These species may also have relatively-few offspring and provide significant parental care.

Trees, marine invertebrates, and most fishes exhibit a Type III survivorship curve. Very few individuals survive the younger years; however, those that live to old age are likely to survive for a relatively-long period. Organisms in this category usually have large numbers of offspring and provide little parental care. Such offspring are “on their own” and suffer high mortality due to predation or starvation; however, their abundance ensures that enough individuals survive to the next generation, perpetuating the population.

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Key Points

- The key statistics used in demography are birth rates, death rates, and life expectancies which may be influenced by population characteristics and biological factors.
- Birth rates, death rates, and life expectancies are the basic determinants of how a population changes over time.
- Life tables are demographic tools which shows a population's life expectancy and mortality within age groups.
- A survivorship curve is a graph of the number of individuals surviving at each age interval plotted versus time.

- The characteristics and behavior of a species, such as number of offspring produced, its percentage of surviving offspring, and degree of parental care, determine the shape of its survivorship curve.

Key Terms

- **life table**: a demographic tool which shows a population's life expectancy and mortality within age groups
- **survivorship curve**: a graph of the number of individuals surviving at each age interval plotted versus time
- **mortality rate**: the number of deaths per given unit of population over a given period of time

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45.2: ENVIRONMENTAL LIMITS TO POPULATION GROWTH

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- Topic hierarchy

45.2A: Exponential Population Growth

45.2B: Logistic Population Growth

45.2C: Density-Dependent and Density-Independent Population Regulation

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45.2A: Exponential Population Growth

Learning Objectives

- Describe exponential growth of a population size

Exponential growth

In his theory of natural selection, Charles Darwin was greatly influenced by the English clergyman Thomas Malthus. Malthus published a book in 1798 stating that populations with unlimited natural resources grow very rapidly, after which population growth decreases as resources become depleted. This accelerating pattern of increasing population size is called exponential growth.

The best example of exponential growth is seen in bacteria. Bacteria are prokaryotes that reproduce by prokaryotic fission. This division takes about an hour for many bacterial species. If 1000 bacteria are placed in a large flask with an unlimited supply of nutrients (so the nutrients will not become depleted), after an hour there will be one round of division (with each organism dividing once), resulting in 2000 organisms. In another hour, each of the 2000 organisms will double, producing 4000; after the third hour, there should be 8000 bacteria in the flask; and so on. The important concept of exponential growth is that the population growth rate, the number of organisms added in each reproductive generation, is accelerating; that is, it is increasing at a greater and greater rate. After 1 day and 24 of these cycles, the population would have increased from 1000 to more than 16 billion. When the population size, N, is plotted over time, a J-shaped growth curve is produced.

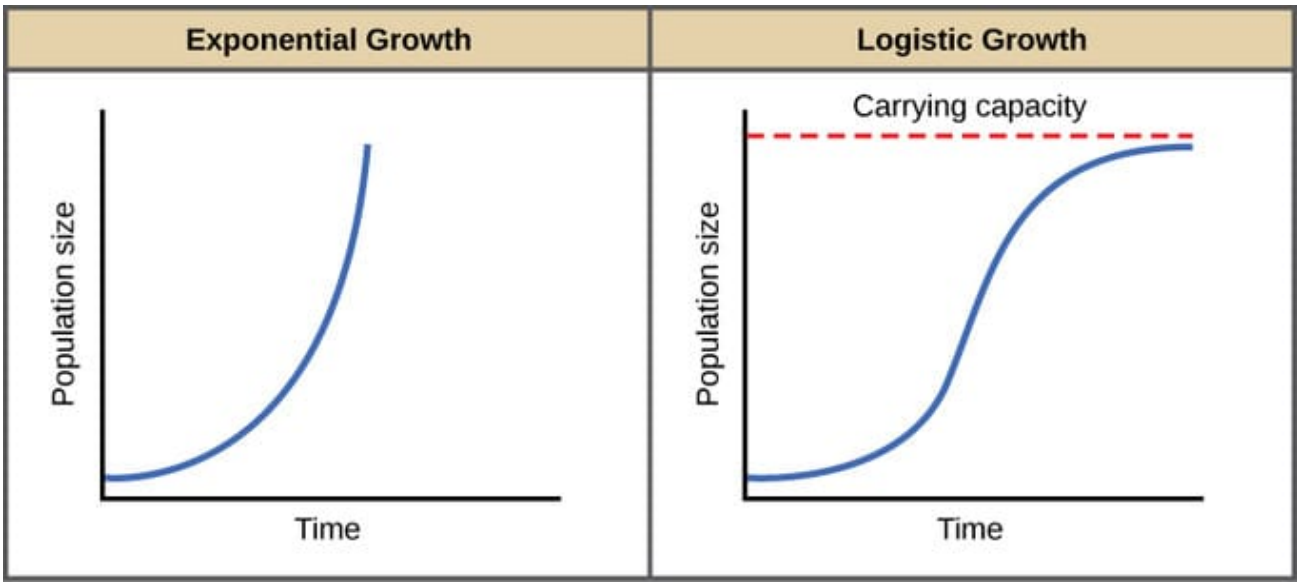


Figure $45.2A.1$: Exponential population growth: When resources are unlimited, populations exhibit exponential growth, resulting in a J-shaped curve. When resources are limited, populations exhibit logistic growth. In logistic growth, population expansion decreases as resources become scarce. It levels off when the carrying capacity of the environment is reached, resulting in an S-shaped curve.

The bacteria example is not representative of the real world where resources are limited. Furthermore, some bacteria will die during the experiment and, thus, not reproduce, lowering the growth rate. Therefore, when calculating the growth rate of a population, the death rate (D; the number organisms that die during a particular time interval) is subtracted from the birth rate (B; the number organisms that are born during that interval). This is shown in the following formula:

$$\frac{\Delta N}{\Delta T} = B - \frac{\Delta N}{\Delta T} = B - D \qquad (45.2A.1)$$

where ΔN = change in number, ΔT = change in time, B = birth rate, and D = death rate. The birth rate is usually expressed on a

per capita (for each individual) basis. Thus, B (birth rate) = bN (the per capita birth rate “b” multiplied by the number of individuals “N”) and D (death rate) = dN (the per capita death rate “d” multiplied by the number of individuals “N”). Additionally, ecologists are interested in the population at a particular point in time: an infinitely small time interval. For this reason, the terminology of differential calculus is used to obtain the “instantaneous” growth rate, replacing the change in number and time with an instant-specific measurement of number and time.

$$\frac{dN}{dT} = BNDN = (BD)NdN/dT = BNDN = (BD)N \tag{45.2A.2}$$

Notice that the “d” associated with the first term refers to the derivative (as the term is used in calculus) and is different from the death rate, also called “d.” The difference between birth and death rates is further simplified by substituting the term “r” (intrinsic rate of increase) for the relationship between birth and death rates:

$$\frac{dN}{dT} = rN\frac{dN}{dT} = rN \tag{45.2A.3}$$

The value “r” can be positive, meaning the population is increasing in size; negative, meaning the population is decreasing in size; or zero, where the population’s size is unchanging, a condition known as zero population growth. A further refinement of the formula recognizes that different species have inherent differences in their intrinsic rate of increase (often thought of as the potential for reproduction), even under ideal conditions. Obviously, a bacterium can reproduce more rapidly and have a higher intrinsic rate of growth than a human. The maximal growth rate for a species is its biotic potential, or r_{max}, thus changing the equation to:

$$\frac{dN}{dT} = r_{max}N \tag{45.2A.4}$$

Key Points

- To get an accurate growth rate of a population, the number that died in the time period (death rate) must be removed from the number born during the same time period (birth rate).
- When the birth rate and death rate are expressed in a per capita manner, they must be multiplied by the population to determine the number of births and deaths.
- Ecologists are usually interested in the changes in a population at either a particular point in time or over a small time interval.
- The intrinsic rate of increase is the difference between birth and death rates; it can be positive, indicating a growing population; negative, indicating a shrinking population; or zero, indicting no change in the population.
- Different species have a different intrinsic rate of increase which, when under ideal conditions, represents the biotic potential or maximal growth rate for a species.

Key Terms

- **fission**: the process by which a bacterium splits to form two daughter cells
- **per capita**: per person or individual

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45.2B: Logistic Population Growth

Learning Objectives

- Describe logistic growth of a population size

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 will survive to pass on their own characteristics and traits (which we know now are transferred by genes) to the next generation at a greater rate: a process known as 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 becomes large enough, resources will be depleted, slowing the growth rate. Eventually, the growth rate will plateau or level off. This population size, which represents the maximum population size that a particular environment can support, is called the **carrying capacity**, or K.

The formula we use to calculate logistic growth adds the carrying capacity as a moderating force in the growth rate. The expression “K – N” is indicative of how many individuals may be added to a population at a given stage, 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:

$$\begin{aligned}\frac{dN}{dT} &= r_{max}\frac{dN}{dT} \\ &= r_{max} \times N \times (\frac{K-N}{K})\frac{dN}{dT} \\ &= rmax * (dN/dT) = rmax * N * ((KN)/K)\end{aligned}$$

Notice that when N is very small, (K-N)/K becomes close to K/K or 1; the right side of the equation reduces to $r_{max}N$, which means the population is growing exponentially and is not influenced by carrying capacity. On the other hand, when N is large, $(K-N)/K$ come close to zero, which means that population growth will be slowed greatly or even stopped. Thus, population growth is greatly slowed in large populations by the carrying capacity K. This model also allows for negative population growth or a population decline. This occurs when the number of individuals in the population exceeds the carrying capacity (because the value of (K-N)/K is negative).

A graph of this equation yields an S-shaped curve; 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, growth levels off at the carrying capacity of the environment, with little change in population size over time.

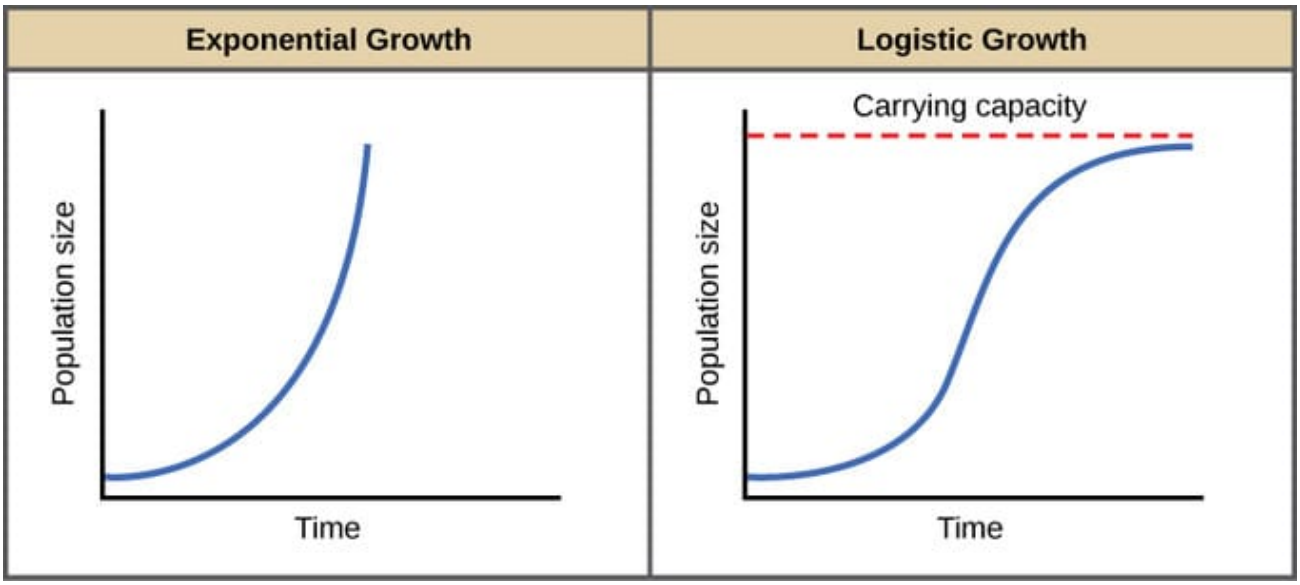


Figure $45.2B.1$: Exponential and logistical population growth: When resources are unlimited, populations exhibit exponential growth, resulting in a J-shaped curve. When resources are limited, populations exhibit logistic growth. In logistic growth, population expansion decreases as resources become scarce, leveling off when the carrying capacity of the environment is reached, resulting in an S-shaped curve.

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 the space to grow are the important resources, whereas in animals, important resources include food, water, shelter, nesting space, and mates.

In the real world, the variation of phenotypes among individuals within a population means that some individuals will be better adapted to their environment than others. The resulting competition between population members of the same species for resources is termed intraspecific competition (intra- = “within”; -specific = “species”). Intraspecific competition for resources 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 an environment’s carrying capacity.

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 (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 (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.

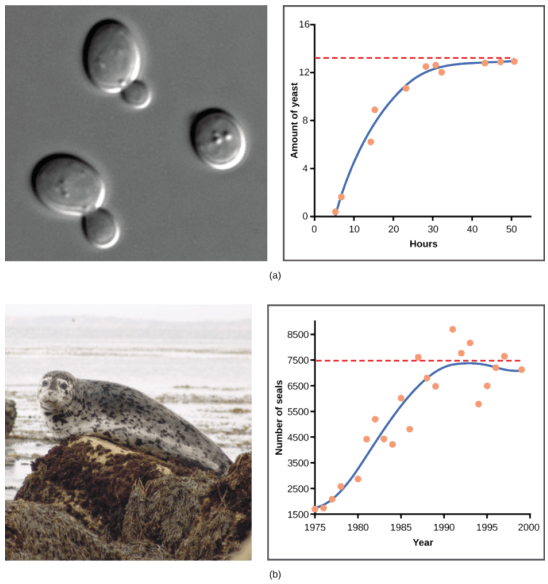


Figure $45.2B.1$: Logistic population growth: (a) Yeast grown in ideal conditions in a test tube show a classical S-shaped logistic growth curve, whereas (b) a natural population of seals shows real-world fluctuation.

Key Points

- The carrying capacity of a particular environment is the maximum population size that it can support.
- The carrying capacity acts as a moderating force in the growth rate by slowing it when resources become limited and stopping growth once it has been reached.
- As population size increases and resources become more limited, intraspecific competition occurs: individuals within a population who are more or less better adapted for the environment compete for survival.

Key Terms

- **phenotype**: the appearance of an organism based on a multifactorial combination of genetic traits and environmental factors, especially used in pedigrees
- **carrying capacity**: the number of individuals of a particular species that an environment can support; indicated by the letter "K"

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45.2C: Density-Dependent and Density-Independent Population Regulation

Learning Objectives

- Differentiate between density-dependent and density-independent population regulation.

Density-dependent regulation

In population ecology, density-dependent processes occur when population growth rates are regulated by the density of a population. Most density-dependent factors, which are biological in nature (biotic), include predation, inter- and intraspecific competition, accumulation of waste, and diseases such as those caused by parasites. Usually, the denser a population is, the greater its mortality rate. For example, during intra- and interspecific competition, the reproductive rates of the individuals will usually be lower, reducing their population's rate of growth. In addition, low prey density increases the mortality of its predator because it has more difficulty locating its food source.

An example of density-dependent regulation is shown with results from a study focusing on the giant intestinal roundworm (*Ascaris lumbricoides*), a parasite of humans and other mammals. The data shows that denser populations of the parasite exhibit lower fecundity: they contained fewer eggs. One possible explanation for this phenomenon was that females would be smaller in more dense populations due to limited resources so they would have fewer eggs. This hypothesis was tested and disproved in a 2009 study which showed that female weight had no influence. The actual cause of the density-dependence of fecundity in this organism is still unclear and awaiting further investigation.

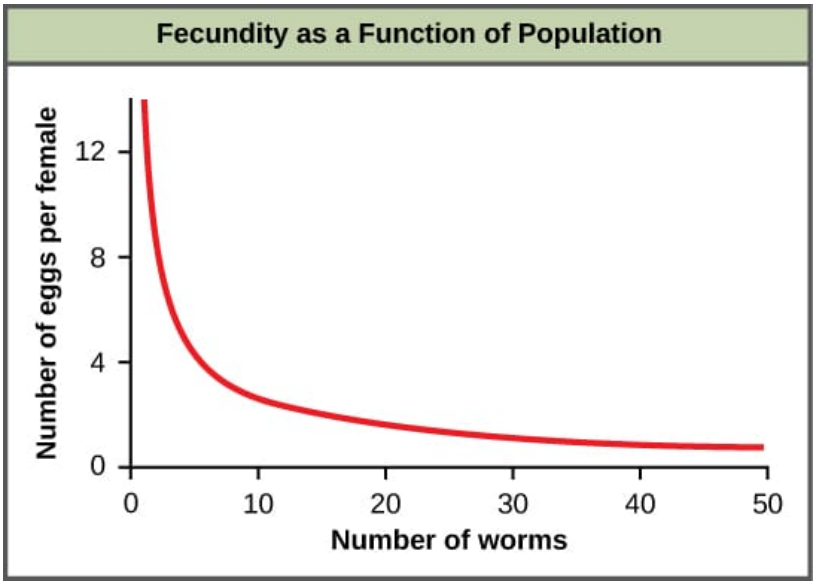


Figure 45.2C.1: Effect of population density on fecundity: In this population of roundworms, fecundity (number of eggs) decreases with population density.

Density-independent regulation and interaction with density-dependent factors

Many factors, typically physical or chemical in nature (abiotic), influence the mortality of a population regardless of its density. They include weather, natural disasters, and pollution. An individual deer may 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.

In real-life situations, population regulation is very complicated and density-dependent and independent factors can interact. A dense population that is reduced in a density-independent manner by some environmental factor(s) will be able to recover differently than would 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.

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Key Points

- The density of a population can be regulated by various factors, including biotic and abiotic factors and population size.
- Density-dependent regulation can be affected by factors that affect birth and death rates such as competition and predation.
- Density-independent regulation can be affected by factors that affect birth and death rates such as abiotic factors and environmental factors, i.e. severe weather and conditions such as fire.
- New models of life history incorporate ecological concepts that are typically included in r- and K-selection theory in combination with population age structures and mortality factors.

Key Terms

- **interspecific**: existing or occurring between different species
- **intraspecific**: occurring among members of the same species
- **fecundity**: number, rate, or capacity of offspring production

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45.3: LIFE HISTORY PATTERNS



- Topic hierarchy

45.3A: Life History Patterns and Energy Budgets

45.3B: Theories of Life History

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45.3A: Life History Patterns and Energy Budgets

Learning Objectives

- Describe the energy budgets of, and the life history strategies used in, reproduction

Life history patterns and energy budgets

Energy is required by all living organisms for their growth, maintenance, and reproduction. At the same time, energy is often a major limiting factor in determining an organism's survival. Plants, for example, acquire energy from the sun via photosynthesis, but must expend this energy to grow, maintain health, and produce energy-rich seeds to produce the next generation. Animals also have the additional burden of using some of their energy reserves to acquire food. In addition, some animals must expend energy caring for their offspring. Thus, all species have an energy budget in which they must balance energy intake with their use of energy for metabolism, reproduction, parental care, and energy storage, as when bears build up body fat for winter hibernation.

Parental care and fecundity

Fecundity is the potential reproductive capacity of an individual within a population. In other words, it describes how many offspring could ideally be produced if an individual has as many offspring as possible, repeating the reproductive cycle as soon as possible after the birth of the offspring. In animals, fecundity is inversely related to the amount of parental care given to an individual offspring. Species that produce a large number of offspring, such as many marine invertebrates, usually provide little if any care for those offspring, as they would not have the energy or the ability to do so. Most of their energy budget is used to produce many tiny offspring. Animals with this strategy are often self-sufficient at a very early age. This is because of the energy trade-off these organisms have made to maximize their evolutionary fitness. Since their energy is used for producing offspring instead of parental care, it makes sense that these offspring have some ability to be able to move within their environment to find food and perhaps shelter. Even with these abilities, their small size makes them extremely vulnerable to predation, so the production of many offspring allows enough of them to survive to maintain the species.

Animal species that have few offspring during a reproductive event usually give extensive parental care, devoting much of their energy budget to these activities, sometimes at the expense of their own health. This is the case with many mammals, such as humans, kangaroos, and pandas. The offspring of these species are relatively helpless at birth, needing to develop before they achieve self-sufficiency.

Plants with low fecundity produce few energy-rich seeds (such as coconuts and chestnuts) that have a good chance to germinate into a new organism. Plants with high fecundity usually have many small, energy-poor seeds (as do orchids) that have a relatively-poor chance of surviving. Although it may seem that coconuts and chestnuts have a better chance of surviving, the energy trade-off of the orchid is also very effective. It is a matter of where the energy is used: for large numbers of seeds or for fewer seeds with more energy.

Early versus late reproduction



Figure 45.3A.1: Semelparous species: Chinook salmon are an example of a population that uses its energy budget in one major reproductive event, dying shortly thereafter.

The timing of reproduction in a life history also affects species survival. Organisms that reproduce at an early age have a greater chance of producing offspring, but this is usually at the expense of their growth and the maintenance of their health. Conversely, organisms that start reproducing later in life often have greater fecundity or are better able to provide parental care, but they risk not surviving to reproductive age. Examples of this can be seen in fish. Small fish, such as guppies, use their energy to reproduce rapidly, but never attain the size that would give them defense against some predators. Larger fish, such as bluefin tuna and mako sharks, use their energy to attain a large size, but do so with the risk that they will die before they can reproduce or reproduce to their maximum. These different energy strategies and trade-offs are key to understanding the evolution of each species as it maximizes its fitness and fills its niche.

Single versus multiple reproductive events

Some life history traits, such as fecundity, timing of reproduction, and parental care, can be grouped together into general strategies that are used by multiple species. Semelparous species are those that only reproduce once during their lifetime and then die. Such species use most of their resource budget during a single reproductive event, sacrificing their health to the point that they do not survive. Examples of semelparity are bamboo, which flowers once and then dies, and the Chinook salmon, which uses most of its energy reserves to migrate from the ocean to its freshwater nesting area, where it reproduces and then dies. In contrast, iteroparous species reproduce repeatedly during their lives. Some animals are able to mate only once per year, but survive multiple mating seasons. Primates, including humans and chimpanzees, are examples of animals that display iteroparity.

Key Points

- The amount of parental care given to an individual offspring is inversely related to the reproductive capacity of an animal species.
- Animal species that produce many small, vulnerable offspring tend to provide little or no care for them due to their energy budget constraints; just enough offspring survive to maintain the species.
- Animal species that have few offspring expend large amounts of their energy budgets on caring for helpless offspring that need to develop before being on their own.
- Plants with low fecundity produce few energy-rich seeds with high germination rates, while plants with high fecundity usually have many small, energy-poor seeds with poor survival rates.
- Species that reproduce early ensure a greater chance of having surviving offspring than do those that must survive to a later reproductive age.
- Semelparous species use all of their reproductive budgets on one single reproductive event, while iteroparous species spend it on multiple mating seasons.

Key Terms

- **iteroparous**: reproducing more than once in a lifetime
- **semelparous**: reproducing only once in a lifetime
- **fecundity**: number, rate, or capacity of offspring production

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45.3B: Theories of Life History

Learning Objectives

- Distinguish between K- and r-selected species

Early theories about life history: *K*-selected and *r*-selected species

While reproductive strategies play a key role in life histories, they do not account for important factors such as limited resources and competition. The regulation of population growth by these factors can be used to introduce a classical concept in population biology: that of *K*-selected versus *r*-selected species.

By the second half of the twentieth century, the concept of K- and r-selected species was used extensively and successfully to study populations. The concept relates not only to reproductive strategies, but also to a species' habitat and behavior. This includes the way they obtain resources and care for their young, as well as length of life and survivorship factors. For this analysis, population biologists have grouped species into the two large categories, *K*-selected and *r*-selected, although they are really two ends of a continuum. The first variable is *K* (the carrying capacity of a population; density dependent), and the second variable is *r* (the intrinsic rate of natural increase in population size, density independent).

K-selected species

K-selected species are those in stable, predictable environments. Populations of *K*-selected species tend to exist close to their carrying capacity (hence the term *K*-selected) where intraspecific competition is high. These species produce few offspring, have a long gestation period, and often give long-term care to their offspring. While larger in size when born, the offspring are relatively helpless and immature at birth. By the time they reach adulthood, they must develop skills to compete for natural resources. Examples of *K*-selected species are primates including humans, other mammals such as elephants, and plants such as oak trees.



(a) K-selected species



(b) r-selected species

Figure $45.3B.1$: K- and r- selected species: (A) Elephants are considered K-selected species as they live long, mature late, and provide long-term parental care to few offspring. Oak trees produce many offspring that do not receive parental care, but are considered K-selected species based on longevity and late maturation. (B) Dandelions and jellyfish are both considered r-selected species as they mature early, have short lifespans, and produce many offspring that receive no parental care

In plants, scientists think of parental care more broadly: how long fruit takes to develop or how long it remains on the plant are determining factors in the time to the next reproductive event. Oak trees grow very slowly and take, on average, 20 years to

produce their first seeds, known as acorns. As many as 50,000 acorns can be produced by an individual tree, but the germination rate is low as many of these rot or are eaten by animals such as squirrels. In some years, oaks may produce an exceptionally large number of acorns; these years may be on a two- or three-year cycle depending on the species of oak (r-selection).

As oak trees grow to a large size (and for many years before they begin to produce acorns) they devote a large percentage of their energy budget to growth and maintenance. The tree's height and size allow it to dominate other plants in the competition for sunlight, the oak's primary energy resource. Furthermore, when it does reproduce, the oak produces large, energy-rich seeds that use their energy reserve to become quickly established (*K*-selection).

r-selected species

In contrast to K-selected species, *r*-selected species have a large number of small offspring (hence their *r* designation). This strategy is often employed in unpredictable or changing environments. Animals that are *r*-selected do not give long-term parental care and the offspring are relatively mature and self-sufficient at birth. Examples of *r*-selected species are marine invertebrates, such as jellyfish, and plants, such as the dandelion. Dandelions have small seeds that are dispersed long distances by wind; many seeds are produced simultaneously to ensure that at least some of them reach a hospitable environment. Seeds that land in inhospitable environments have little chance for survival since the seeds are low in energy content. Note that survival is not necessarily a function of energy stored in the seed itself.

Modern theories of life history

The r- and K-selection theory, although accepted for decades and used for much groundbreaking research, has now been reconsidered. Many population biologists have abandoned or modified it. Over the years, several studies attempted to confirm the theory, but these attempts have largely failed. Many species were identified that did not follow the theory's predictions. Furthermore, the theory ignored the age-specific mortality of the populations which scientists now know is very important. New demographic-based models of life history evolution have been developed which incorporate many ecological concepts included in r- and K-selection theory, as well as population age structure and mortality factors.

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Key Points

- K-selection species are defined as those present in stable and predictable environments that produce fewer offspring, have longer gestation periods, and provide long-term care after birth.
- r-selected species are defined as those present in fluctuating environments that have large numbers of offspring and do not provide long-term care after birth.
- Based on evidence that shows not all species follow solely the K- or r-selection theories, new models of life history are being developed which incorporate K- and r-selection theories with additional factors that affect life and survivorship such as population age structure and mortality factors.

Key Terms

- **carrying capacity**: the number of individuals of a particular species that an environment can support; indicated by the letter "K"
- **intraspecific**: occurring among members of the same species

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45.4: HUMAN POPULATION GROWTH

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- Topic hierarchy

45.4A: Human Population Growth

45.4B: Overcoming Density-Dependent Regulation

45.4C: Age Structure, Population Growth, and Economic Development

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45.4A: Human Population Growth

Learning Objectives

- Predict the long-term consequences of exponential human population growth

Human Population Growth

Global human population growth is around 75 million annually, or 1.1% per year. The global population has grown from 1 billion in 1800 to 7 billion in 2012. It is expected to keep growing, though predictions differ as to when and if this growth will plateau.

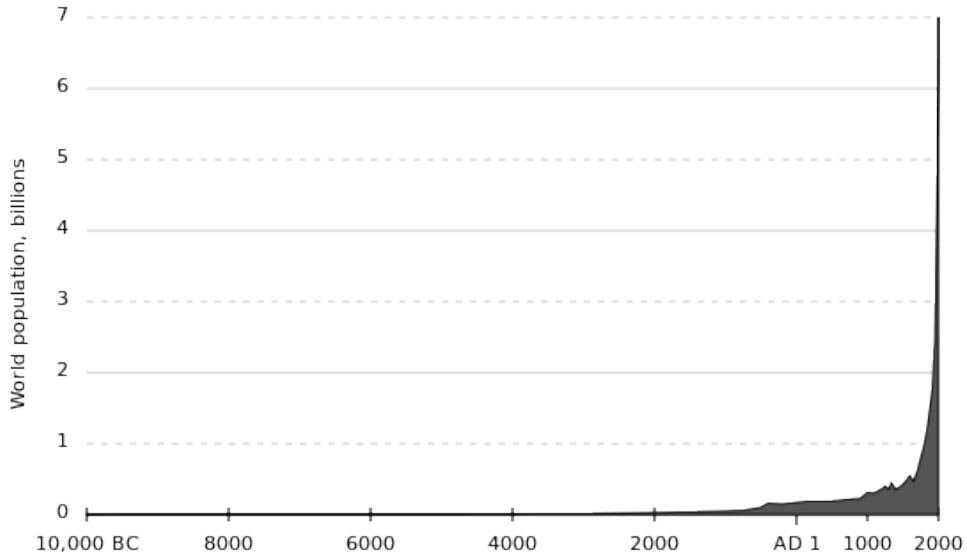


Figure 45.4A.1: The estimated growth of the human population from 10,000 BCE–2000 CE.: The human population has grown most sharply in the past 200 years.

The "population growth rate" is the rate at which the number of individuals in a population increases in a given time period as a fraction of the initial population. Specifically, population growth rate refers to the change in population over a time period, often expressed as a percentage of the number of individuals in the population at the beginning of that period. This can be written as the formula:

population growth rate=P(t2)–P(t1)P(t1)population growth rate=P(t2)–P(t1)P(t1)

Globally, the growth rate of the human population has been declining since 1962 and 1963, when it was 2.20% per annum. In 2009, the estimated annual growth rate was 1.1%. The CIA World Factbook gives the world annual birthrate, mortality rate, and growth rate as 1.89%, 0.79%, and 1.096% respectively. The last 100 years have seen a rapid increase in population due to medical advances and massive increase in agricultural productivity.

Each region of the globe has seen reductions in growth rate in recent decades, though growth rates remain above 2% in some countries of the Middle East and Sub-Saharan Africa, and also in South Asia, Southeast Asia, and Latin America. This does not mean that the population is declining;
rather, it means the population is growing more slowly. However, some countries do experience negative population growth, mainly due to low fertility rates, high death rates and emigration.

According to the UN's 2010 revision to its population projections, world population will peak at 10.1 billion in 2100 compared to 7 billion in 2011. However, some experts dispute the UN's forecast and have argued that birthrates will fall below replacement rates (the number of births needed to maintain a stable population) in the 2020s. According to these forecasters, population growth

will be only sustained until the 2040s by rising longevity, but will peak below 9 billion by 2050, followed by a long decline.

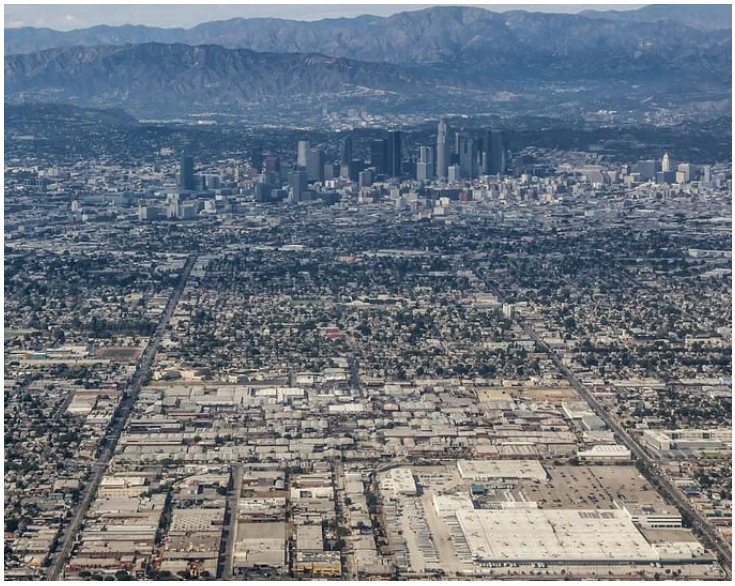


Figure 45.4A.1: Growing Population Rate and Resource Scarcity: Greater Los Angeles lies on a coastal Mediterranean Savannah with a small watershed that is able to support at most one million people on its own water; as of 2015, the area has a population of over 18 million. Researchers predict that similar cases of resource scarcity will grow more common as the world population increases.

Long-term Consequences of Population Growth

The “population explosion” seen in the last century has led to dire predictions. In 1968, biologist Paul Ehrlich wrote, “The battle to feed all of humanity is over. In the 1970s, hundreds of millions of people will starve to death in spite of any crash programs embarked upon now. At this late date, nothing can prevent a substantial increase in the world death rate. ” Although many critics view Ehrlich’s view as an exaggeration, the human population continues to grow exponentially. The laws of nature dictate that exponential growth cannot continue indefinitely.

Despite efforts to curb population growth, such as the “one-child policy” in China (introduced in 1979 but relaxed in the early 2000s), the human population continues to grow. A primary concern regarding this growth is that the demand for ever-more food will lead to widespread shortages, as forecast by Ehrlich.

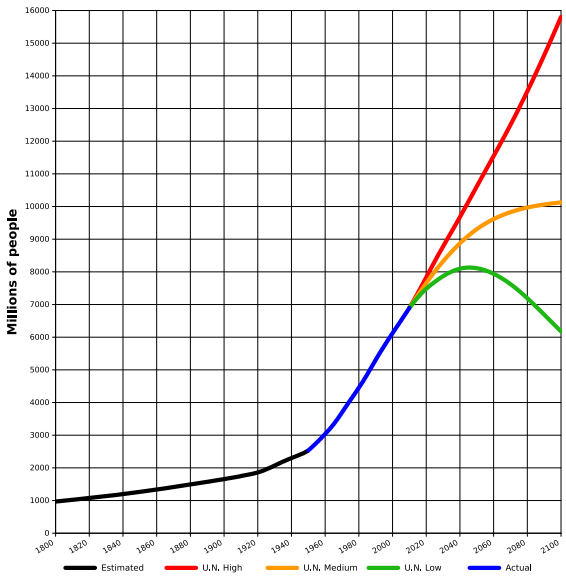


Figure 45.4A.1: World population growth from 1800 to 2100: United Nations projections in 2010 give "high" (red line), "medium" (orange) and "low" (green) scenarios for world population growth. The highest estimate projects the world population may rise to 16 billion by 2100 or it may decline to 6 billion, according to the lowest estimate.

In addition to the threat of food shortages, human population growth is damaging to the environment in potentially permanent ways. Most scientists agree that climate change caused by the emission of the greenhouse gas carbon dioxide (CO_2) is a significant consequence of human activities. In a series of treaties in the late 20th century, many countries committed to reducing their CO_2emissions to prevent continuous global warming; however these treaties have not been ratified by every country, largely due to economic and political concerns. The role of human activity in climate change is hotly debated in some circles. The future holds considerable uncertainty for curbing human population growth and protecting the environment.

Key Points

- Global human population growth is around 75 million annually, or 1.1% per year. The global population has grown from 1 billion in 1800 to 7 billion in 2012.
- Although the direst consequences of human population growth have not yet been realized, exponential growth cannot continue indefinitely.
- In the late 1970s, China's "one-child" policy tried to control population growth, but restrictions were relaxed in the early 2000s.
- One of the major consequences of population growth is the potential for widespread food shortages.
- Most scientists agree that humans and human population growth are causing climate change by emission of the greenhouse gas carbon dioxide (CO_2).
- International treaties to limit greenhouse gas emissions have not been ratified by every country due to economic and political concerns.

Key Terms

- **greenhouse gas**: Any gas, such as carbon dioxide, that contributes to the greenhouse effect (continued warming) when released into the atmosphere.
- **climate change**: Changes in the earth's climate, especially those said to be produced by global warming.

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45.4B: Overcoming Density-Dependent Regulation

Learning Objectives

- Describe ways in which humans overcome density-dependent regulation of population size

Humans are uniquely able to consciously alter their environment to increase its carrying capacity. This capability is an underlying reason for human population growth as humans are able to overcome density-dependent limits on population growth, in contrast with all other organisms.

Human intelligence, society, and communication have enabled this capacity. For instance, people can construct shelters to protect them from the elements; food supply has increased because of agriculture and domestication of animals; and humans use language to pass on technology to new generations, allowing continual improvement upon previous accomplishments. Migration has also contributed to human population growth. Originating from Africa, humans have migrated to nearly every inhabitable area on the planet.

Public health, sanitation, and the use of antibiotics and vaccines have lessened the impact of infectious disease on human populations. In the fourteenth century, the bubonic plague killed as many as 100 million people: between 30 to 60 percent of Europe's population. Today, however, the plague and other infectious diseases have much less of an impact. Through vaccination programs, better nutrition, and vector control (carriers of disease), international agencies have significantly reduced the global infectious disease burden. For example, reported cases of measles in the United States dropped from around 700,000 a year in the 1950s to practically zero by the late 1990s. Globally, measles fell 60 percent from an estimated 873,000 deaths in 1999 to 164,000 in 2008. This advance is attributed entirely to a comprehensive vaccination program.

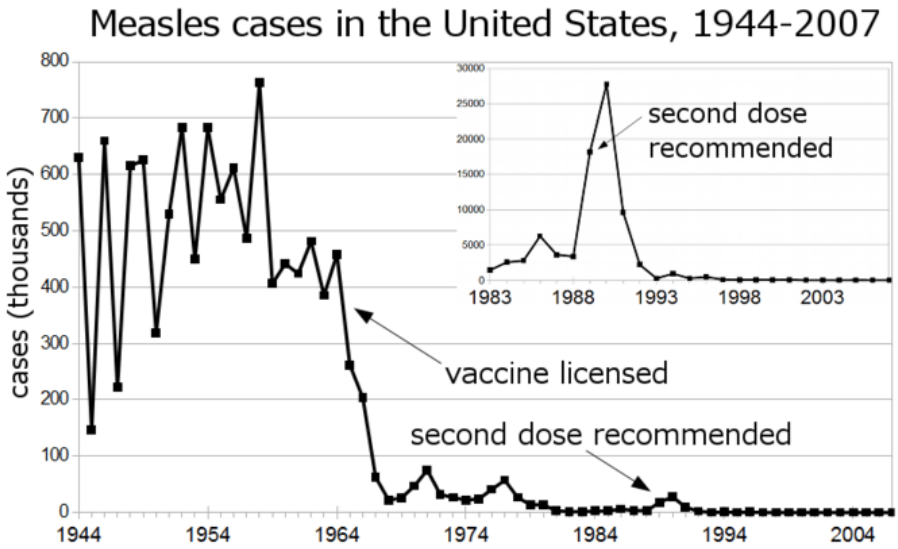


Figure $45.4B.1$: Measles cases reported in the United States, 1944-2007: Measles cases reported in the United States, represented as thousands of cases per year, declined sharply after the measles vaccine was introduced, in 1964.

Developing countries have also made advances in curbing mortality from infectious disease. For example, deaths from infectious and parasitic diseases in Brazil fell from second place as the most important causes of death in 1977 to fifth place in 1984. The improvement is attributed in part to increased access to essential goods and services, reflecting the country's rising prosperity. Through changes in economic status, as in Brazil, as well as global disease control efforts, human population growth today is less limited by infectious disease than has been the case historically.

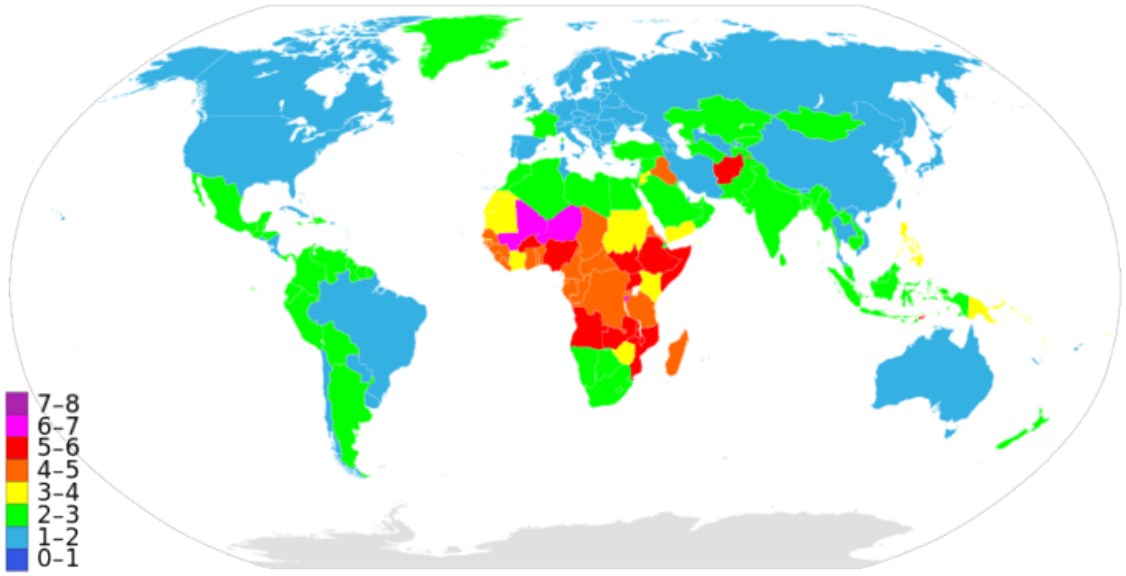


Figure 45.4B.1: Countries by Fertility Rate Comparison: The advent of modern medicine is very closely tied to childhood mortality, as well as the number of children per mother (Fertility Rate). As modern medicine decrease child mortality, the birth rate decreases.

Key Points

- Humans' ability to alter their environment is an underlying reason for human population growth, enabling people to overcome density-dependent limits on growth, in contrast with all other organisms.
- Abilities, such as construction of shelter, food cultivation, and the sharing of technology, have helped humans overcome factors that would have otherwise limited their population growth.
- Originating from Africa, human migration to nearly every inhabitable area of the globe has enabled colonization of areas where people were previously absent.
- Advances in medicine, notably vaccines and antibiotics, as well as improvements in nutrition and vector control, have significantly curbed mortality from disease.

Key Terms

- **density-dependent**: Processes that occur when population growth rates are regulated by the size of a population in a given amount of resources such as food or habitat area.
- **vaccine**: A substance given to stimulate the body's production of antibodies and provide immunity against a disease, prepared from the agent that causes the disease, or a synthetic substitute.
- **infectious disease**: Illness caused by introduction of a pathogen or parasite into the body via contact with a transmitting agent such as vector organism or an infected person.

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45.4C: Age Structure, Population Growth, and Economic Development

Learning Objectives

- Explain how age structure in a population is associated with population growth and economic development

The variation of populations over time, also known as population dynamics, depends on biological and environmental processes that determine population changes. A population's growth rate is strongly influenced by the proportions of individuals of particular ages. With knowledge of this age structure, population growth can be more accurately predicted. Age structure data allow the rate of growth (or decline) to be associated with a population's level of economic development.

For example, the population of a country with rapid growth has a triangle-shaped age structure with a greater proportion of younger individuals who are at or close to reproductive age. This pattern typically occurs where fewer people live to old age because of sub-optimal living standards, such as occurs in underdeveloped countries.

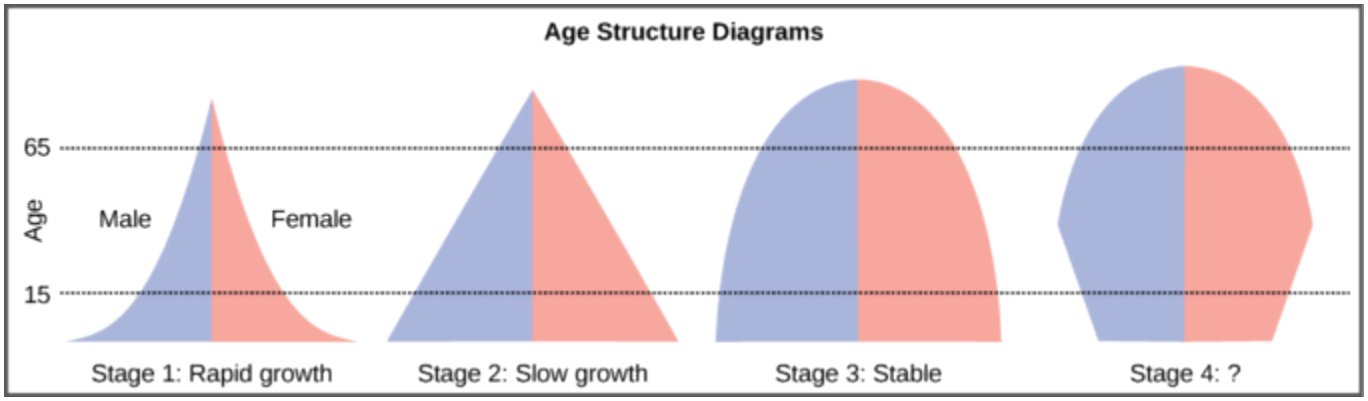


Figure $45.4C.1$: Population bar graphs for stages of demographic change from expansion to contraction: The leftmost diagram (representing the age structure of a rapidly-growing population) indicates that the number of individuals decreases rapidly with age. The slow-growth model shows that the proportion of individuals decreases steadily with age. The stable population diagram is rounded on top; the older part of the population is a larger proportion of the population than in the other age diagrams. The rightmost diagram represents a population that may be stable or even declining. The relatively few young people may not be making up for the mortality among the older age groups.

YouTube Video

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

Changing Population Age Structure: This 3:28 minute movie discusses age structures and gives examples.

Some developed countries, including the United States, have a slowly-growing population. This results in a column-shaped age structure diagram with steeper sides. In these cases, the population has fewer young and reproductive-aged individuals, with a greater proportion of older individuals. Some developed countries, such as Italy, have zero population growth. Countries with declining populations, such as Japan, have a bulge in the middle of their age structure diagram. The bulge indicates relatively-few young individuals, and a higher proportion of middle-aged and older individuals.

Globally, less-economically developed countries in Africa and Asia have the highest growth rates, leading to populations

consisting mostly of younger people. Improved health care, beginning in the 1960s, is one of the leading causes of the increased growth rates that created the population explosion. For example, in the Middle East and North Africa, around 65 percent of the population is under the age of 30. These high growth rates lead to the so-called “youth bulge,” which some experts believe is a cause of social unrest and economic problems such as high unemployment.

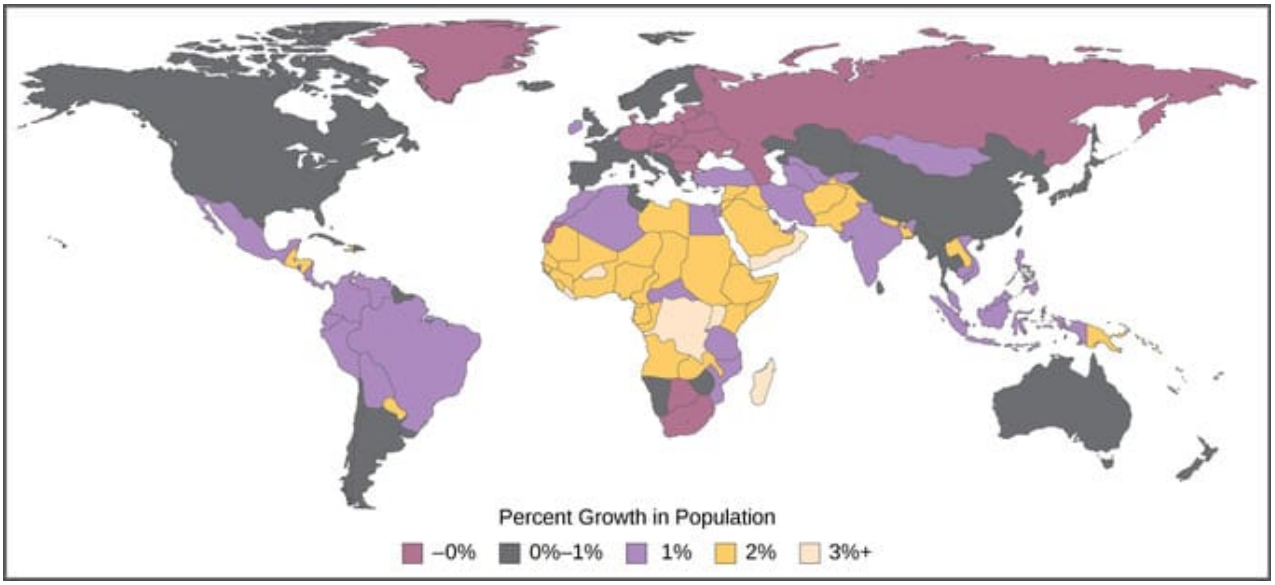


Figure $45.4C.1$: Global percent growth rate of population: The percent growth rate of population in different countries shows that the highest growth rates are in underdeveloped regions of Africa and Asia.

All of the factors above also have an impact on the average life expectancy. As economic development and quality of health care increase, the life expectancy also increases.

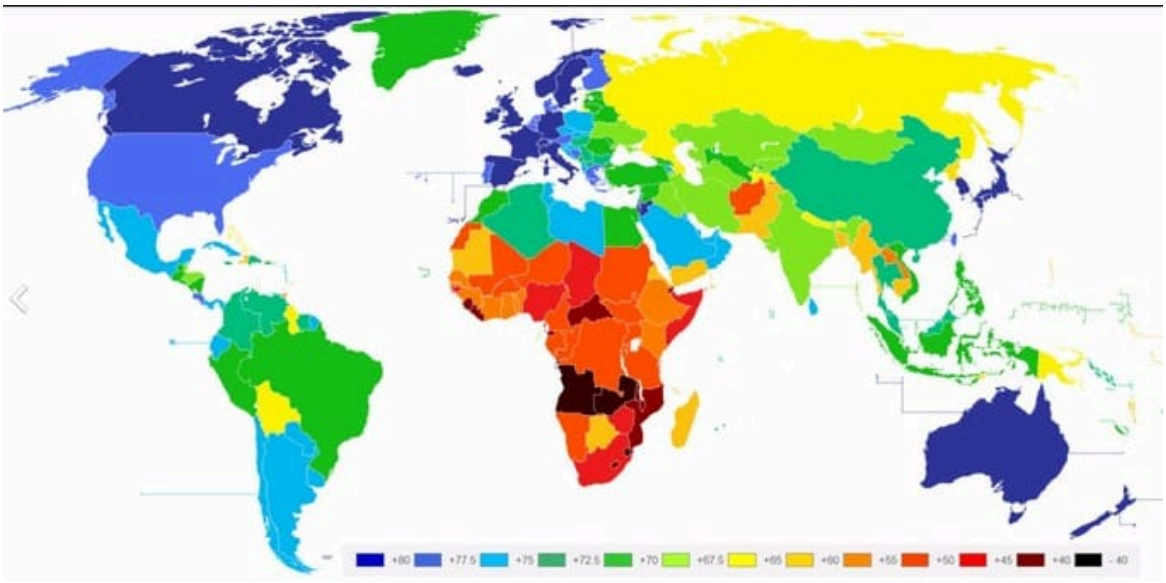


Figure $45.4C.1$: Worldwide Life Expectancy by Country: 2012 map showing average life expectancy by country in years. In 2012, the World Health Organization estimated the average global life expectancy as 70.5 years.

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Key Points

- Population dynamics are influenced by age structure, which is characteristic for populations growing at different rates.
- Age structure varies according to the age distribution of individuals within a population.
- Fast-growing populations with a high proportion of young people have a triangle-shaped age structure, representing younger ages at the bottom and older ages at the top.
- Slow-growing populations with a smaller proportion of young people have a column-shaped age structure, representing a relatively even distribution of ages.
- Improvements in health care have led to the population explosion in underdeveloped countries, causing a “youth bulge” which is associated with social unrest.

Key Terms

- **population dynamics**: Variation among populations due to birth and death rates, by immigration and emigration, and concerning topics such as aging populations or population decline.
- **youth bulge**: Age structure typical of fast-growing populations in which a majority of the population are relatively young.
- **age structure**: The composition of a population in terms of the proportions of individuals of different ages; represented as a bar graph with younger ages at the bottom and males and females on either side.

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45.5: COMMUNITY ECOLOGY



-  Topic hierarchy 

45.5A: The Role of Species within Communities

45.5B: Predation, Herbivory, and the Competitive Exclusion Principle

45.5C: Symbiosis

45.5D: Ecological Succession

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45.5A: The Role of Species within Communities

Learning Objectives

- Distinguish between foundation, keystone, and invasive species

Characteristics of Communities

Communities are complex entities that can be characterized by their structure (the types and numbers of species present) and dynamics (how communities change over time). Understanding community structure and dynamics enables community ecologists to manage ecosystems more effectively. There are three main types of species that serve as the basis for a community. These include the foundation species, keystone species, and invasive species. Each of these has a specific role in how communities are formed.

Foundation Species

Foundation species are considered the “base” or “bedrock” of a community, having the greatest influence on its overall structure. They are usually the primary producers: organisms that bring most of the energy into the community. Kelp, a 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. An example is the photosynthetic corals of the coral reef. Corals themselves are not photosynthetic, but harbor symbionts within their body tissues (dinoflagellates called zooxanthellae) that perform photosynthesis; this is another example of a mutualism. 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 $45.5A.1$: Foundation species: Coral is the foundation species of coral reef ecosystems. The photosynthetic algae within the corals provides energy for them so that they can build the reefs.

Keystone Species

A keystone species is one whose presence is key to maintaining biodiversity within an ecosystem and to upholding an ecological community’s structure. The intertidal sea star, *Pisaster ochraceus*, of the northwestern United States is a keystone species.

Studies have shown that when this organism is removed from communities, populations of their natural prey (mussels) increase, completely altering the species composition and reducing 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. If these fish were to become extinct, the community would be greatly affected.



Figure 45.5A.1: Keystone species maintain biodiveristy: The *Pisaster ochraceus* sea star is a keystone species. When this animal is removed from certain areas, its prey species greatly alters the dynamics of the ecosystem, reducing biodiversity.

Invasive Species

Invasive species are foreign species whose introduction can cause harm to the economy and the environment. These species have many ways of entering foreign environments, including through ship's ballast water: when planes take off, organisms can sometimes become stuck in the cargo area. When the plane arrives in its destination, the organisms are now in a foreign environment. Travelers sometimes illegally smuggle items, such as fruits, plants, or even animals as pets, from one state or country to another..

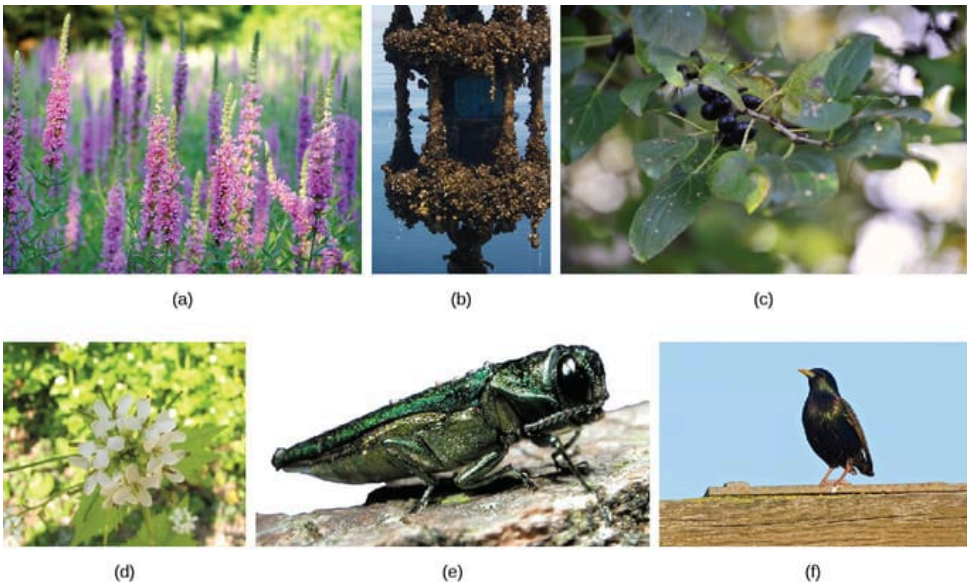


Figure 45.5A.1: Invasive species threaten ecosystems: In the United States, invasive species such as (a) purple loosestrife (*Lythrum salicaria*) and the (b) zebra mussel (*Dreissena polymorpha*) threaten certain ecosystems. Some forests are threatened by the spread of (c) common buckthorn (*Rhamnus cathartica*), (d) garlic mustard (*Alliaria petiolata*), and (e) the emerald ash borer (*Agrilus planipennis*). The (f) European starling (*Sturnus vulgaris*) may compete with native bird species for nest holes.

Invasive species are often better competitors than native species, resulting in population explosions. These new species usually overtake the native populations, driving them to localized extinctions.

One of the many recent proliferations of an invasive species concerns the growth of Asian carp populations. Asian carp were introduced to the United States in the 1970s by fisheries and sewage treatment facilities that used the fish's excellent filter feeding capabilities to clean their ponds of excess plankton. Some of the fish escaped, however, and by the 1980s, they had colonized many waterways of the Mississippi River basin, including the Illinois and Missouri Rivers.

Voracious eaters and rapid reproducers, Asian carp may outcompete native species for food, potentially leading to native species extinctions. For example, black carp are voracious eaters of native mussels and snails, limiting this food source for native fish species. Silver carp eat plankton that native mussels and snails feed upon, reducing this food source by a different alteration of the food web. In some areas of the Mississippi River, Asian carp species have become predominant, effectively outcompeting native fish for habitat. 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 a desirable food in the United States. Moreover, their presence 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 the boaters.

One infested waterway of particular importance is the Chicago Sanitary and Ship Channel, the major supply waterway linking the Great Lakes to the Mississippi River. To prevent the Asian carp from leaving the canal, a series of electric barriers have been successfully 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, but no one knows whether the Asian carp will ultimately be considered a nuisance, like other invasive species, such as the water hyacinth and zebra mussel, or whether it will be the destroyer of the largest freshwater fishery of the world.

Key Points

- A community is defined by the structure of different species that occupy it and how those structures change over time.
- Foundation species change the environment where other species live, modifying it to benefit the organisms that live there.
- Keystone species maintain biodiversity; their removal can greatly alter the dynamics within the community.
- Invasive species are non-native organisms introduced into an area that may be better competitors and reproduce faster than native species; they tend to upset the natural balance.

Key Terms

- **invasive species**: any species that has been introduced to an environment where it is not native and has since become a nuisance through rapid spread and increase in numbers, often to the detriment of native species
- **community**: a group of interdependent organisms inhabiting the same region and interacting with each other
- **keystone species**: a species that exerts a large, stabilizing influence throughout an ecological community, despite its relatively small numerical abundance

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45.5B: Predation, Herbivory, and the Competitive Exclusion Principle

Learning Objectives

- Distinguish between predation and herbivory and describe defense mechanisms against each

Predation and Herbivory

Most animals fall into one of two major categories when it comes to obtaining the energy they need to survive in the environment: predation or herbivory. An animal that hunts, kills, and eats other animals is called a predator. Examples of predators include tigers, snakes, and hawks. Herbivory, on the other hand, refers to animals that eat plant matter. Deer, mice, and most song birds are examples. To protect themselves against these feeding mechanisms, many organisms have developed methods that keep them from being eaten.

Predation is the hunting of prey by its predator. Populations of predators and prey in a community are not constant over time; in most cases, they vary in cycles that appear to be related. The most-often-cited example of predator-prey dynamics is seen in the cycling of the lynx (predator) and the snowshoe hare (prey), which is based on nearly 200-year-old trapping data from North American forests. This cycle of predator and prey lasts approximately 10 years, with the predator population lagging 1–2 years behind that of the prey population. 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, they kill so many hares that the hare population begins to decline. This is 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, at least in part, to low predation pressure, starting the cycle anew.

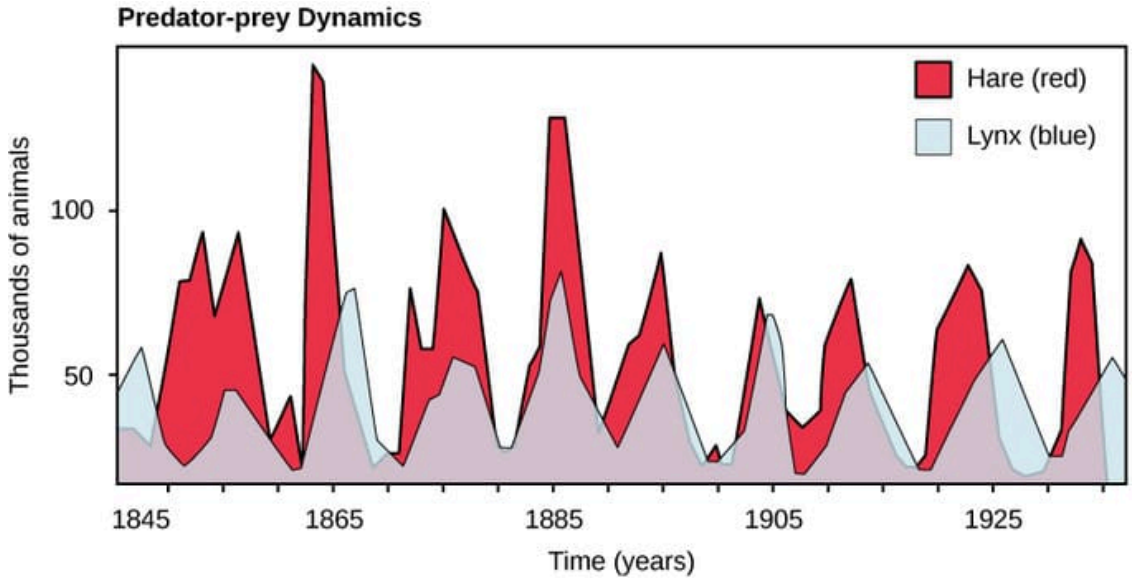


Figure $45.5B.1$: Predator and prey population cycling: The cycling of lynx and snowshoe hare populations in Northern Ontario is an example of predator-prey dynamics. As hare populations increase,the lynx populations also increase due to increased food supplies. Many lynx eating many hares causes a decline in the hare population size. This results in a decrease in the lynx population. Then the cycle begins again.

Herbivory describes the consumption of plants by insects and other animals. Unlike animals, plants cannot outrun predators or use mimicry to hide from hungry animals. Some plants have developed mechanisms to defend against herbivory. Other species have developed mutualistic relationships; for example, herbivory provides a mechanism of seed distribution that aids in plant reproduction.

Defense Mechanisms against Predation and Herbivory

The study of communities must consider evolutionary forces that act on the members of the various populations contained within it. Species are not static, but slowly changing and adapting to their environment by natural selection and other evolutionary forces. Species have evolved numerous mechanisms to escape predation and herbivory. These defenses may be mechanical, chemical, physical, or behavioral.

Mechanical defenses, such as the presence of thorns on plants or the hard shell on turtles, discourage animal predation and herbivory by causing physical pain to the predator or by physically preventing the predator from being able to eat the prey. Chemical defenses are produced by many animals as well as plants, such as the foxglove which is extremely toxic when eaten.

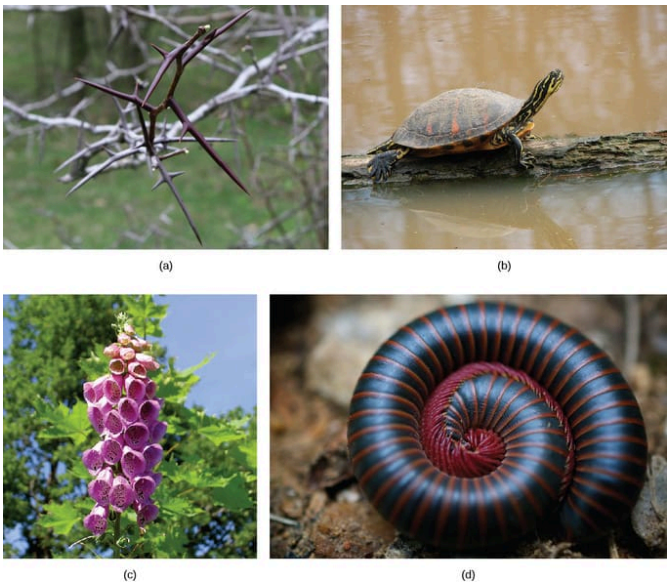


Figure $45.5B.1$: Defenses against predation and herbivory: The (a) honey locust tree (*Gleditsia triacanthos*) uses thorns, a mechanical defense, against herbivores, while the (b) Florida red-bellied turtle (*Pseudemys nelsoni*) uses its shell as a mechanical defense against predators. (c) Foxglove (*Digitalis* sp.) uses a chemical defense: toxins produced by the plant can cause nausea, vomiting, hallucinations, convulsions, or death when consumed. (d) The North American millipede (*Narceus americanus*) uses both mechanical and chemical defenses: when threatened, the millipede curls into a defensive ball, producing a noxious substance that irritates eyes and skin.

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 stationary against a background of real twigs. In another example, the chameleon can change its color to match its surroundings. Both of these are examples of camouflage: avoiding detection by blending in with the background.

Some species use coloration as a way of warning predators they are not good to eat. For example, the cinnabar moth caterpillar, the fire-bellied toad, and many species of beetle have bright colors that warn of a foul taste, the presence of toxic chemical, and/or the ability to sting or bite, respectively. Predators that ignore this coloration and eat the organisms will experience their unpleasant taste or presence of toxic chemicals and learn not to eat them in the future. This type of defensive mechanism is called aposematic coloration, or warning coloration.



Figure $45.5B.1$: Examples of aposematic coloration: (a) The strawberry poison dart frog (*Oophaga pumilio*) uses aposematic coloration to warn predators that it is toxic, while the (b) striped skunk (*Mephitis mephitis)*uses aposematic coloration to warn predators of the unpleasant odor it produces.

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 Batesian mimicry, a harmless species imitates the warning coloration of a harmful one. Assuming they share the same predators, this coloration then protects the harmless ones, even though they do not have the same level of physical or chemical defenses against predation as the organism they mimic. Many insect species mimic the coloration of wasps or bees, which are stinging, venomous insects, thereby discouraging predation.

Key Points

- Predation, the hunting and consuming of animals by other animals, often shows cyclical patterns of predator/prey population sizes; predators increase in numbers when prey species are plentiful.
- Herbivory is the eating of plant material for energy and can assist the plants with seed distribution.
- Plants have evolved spines and toxins to defend against being eaten by herbivores.
- Animals use bright colors to advertise that they are toxic; mimicry to hide from predators; or have spines, shells, and scales to protect themselves.
- Batesian mimicry is when a non-toxic species looks similar to a poisonous one, which deters predator attacks.

Key Terms

- **camouflage**: resemblance of an organism to its surroundings for avoiding detection
- **herbivory**: the consumption of living plant tissue by animals
- **Batesian mimicry**: the resemblance of one or more non-poisonous species to a poisonous species, for example, the scarlet king snake and the coral snake

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45.5C: Symbiosis

Learning Objectives

- Differentiate among the types of symbiosis: commensalism, mutualism, and parasitism

Symbiotic relationships, or symbioses (plural), are close interactions between individuals of different species over an extended period of time which impact the abundance and distribution of the associating populations. Most scientists accept this definition, but some restrict the term to only those species that are mutualistic, where both individuals benefit from the interaction.

Commensalism

A commensalistic relationship occurs when one species benefits from the close, prolonged interaction, while the other neither benefits nor is harmed. Birds nesting in trees provide an example of a commensal relationship. 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. Most of the leaves, which the tree uses to obtain 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.



Figure $45.5C.1$: Commensalistic relationship: The southern masked-weaver bird 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.

Mutualism

A second type of symbiotic relationship, mutualism, is where two species both benefit from their interaction. Some scientists believe that these are the only true examples of symbiosis. For example, termites have a mutualistic relationship with protozoa that live in the insect's gut. The termite benefits from the ability of bacterial symbionts within the protozoa to digest cellulose. 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 and the bacterial symbionts benefit by having a protective environment and a constant supply of food from the wood-chewing actions of the termite.

Parasitism

A parasite is an organism that lives in or on another living organism, deriving nutrients from it. 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. The parasite, however, is unlikely to kill the host. This is because the parasite needs the host to complete its reproductive cycle by spreading to another host.

The reproductive cycles of parasites are often very complex, sometimes requiring more than one host species. A tapeworm is a parasite that causes disease in humans when contaminated, undercooked meat such as pork, fish, or beef is consumed. The tapeworm can live inside the intestine of the host for several years, benefiting from the food the host is bringing into its gut by eating; it may grow to be over 50 ft long by adding segments. The parasite moves from species to species as it requires two hosts to complete its life cycle.

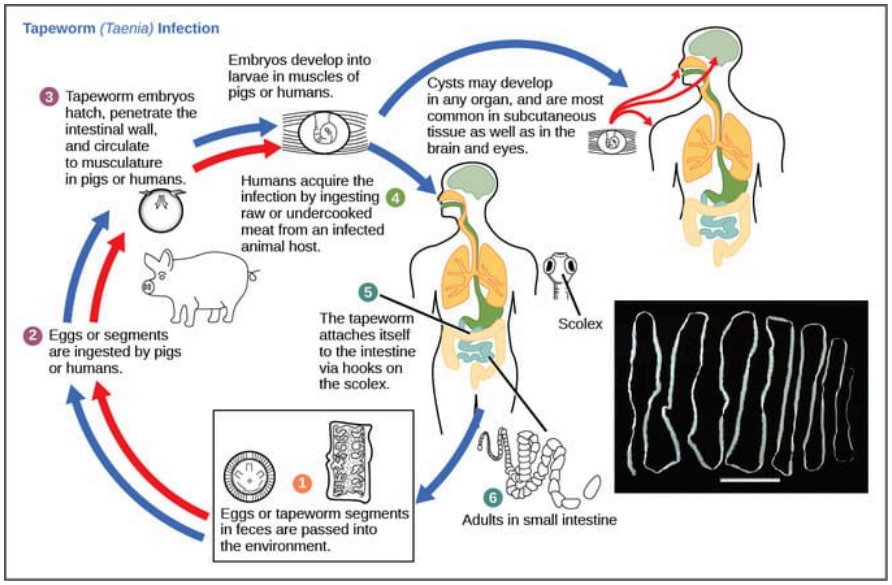


Figure $45.5C.1$: Lifecycle of a parasitic tapeworm: This diagram shows the life cycle of a pork tapeworm (*Taenia solium*), a human worm parasite. The eggs of the tapeworm are ingested by the host. When they hatch, the worms travel through the wall of the intestine and begin to grow. Here, the parasite will absorb the nutrition from the host and continue to grow.

Key Points

- Commensalism is when two organisms share the same environment, where one benefits and the other is unharmed.
- Trees and birds have a commensalistic relationship; the birds benefit from having a place to build their nests, while the trees are unharmed and not impacted by the bird's presence.
- Mutualism is when two species sharing the same environment both benefit from their interactions.
- The protozoans living within the intestines of termites create a mutualistic relationship with them; the protozoans get a safe place to live while the termites get help digesting the cellulose in their diet.
- Parasitism occurs when two organisms interact, but while one benefits, the other experiences harm.
- Parasites harm their hosts, as with the tapeworm attaching itself to the intestine of a cow; the tapeworm absorbs the nutrients from the cow's diet, preventing them from being absorbed by the cow.

Key Terms

- **mutualism**: Any interaction between two species that benefits both.
- **commensalism**: A sharing of the same environment by two organisms where one species benefits and the other is unaffected; e.g., barnacles on whales.
- **parasitism**: Interaction between two organisms, in which one organism (the parasite) benefits and the other (the host) is harmed.

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45.5D: Ecological Succession

Learning Objectives

- Distinguish between primary and secondary succession following disturbances to communities

Community dynamics

Community dynamics are the changes in community structure and composition over time. Sometimes these changes are induced by environmental disturbances such as volcanoes, earthquakes, storms, fires, and climate change. Communities with a stable structure are said to be at equilibrium. 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. In primary succession, newly-exposed or newly-formed land is colonized by living things. In secondary succession, part of an ecosystem is disturbed, but remnants of the previous community remain.

Primary succession and pioneer species

Primary succession occurs when new land is formed or rock is exposed; 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 are added each year. First, weathering and other natural forces break down the substrate enough for the establishment of certain hearty plants and lichens with few soil requirements, known as pioneer species. These species help to further break down the mineral-rich lava into soil where other, less-hardy species will grow, eventually replacing the pioneer species. In addition, as these early species grow and die, they add to an ever-growing layer of decomposing organic material, contributing to soil formation. Over time, the area will reach an equilibrium state with a set of organisms quite different from the pioneer species.



Figure $45.5D.1$: Pioneer species are the first to colonize: During primary succession in lava on Maui, Hawaii, succulent plants are the pioneer species. After weathering breaks down the lava into soil, the plants are able to take root. These plants will help to further change the soil by adding nutrients to it.

Secondary succession

A classic example of secondary succession occurs in oak and hickory forests cleared by wildfire. Wildfires will burn most vegetation and kill those animals unable to flee the area. Their nutrients, however, are returned to the ground in the form of ash. Thus, even when areas are devoid of life due to severe fires, they will soon be ready for new life to take hold.

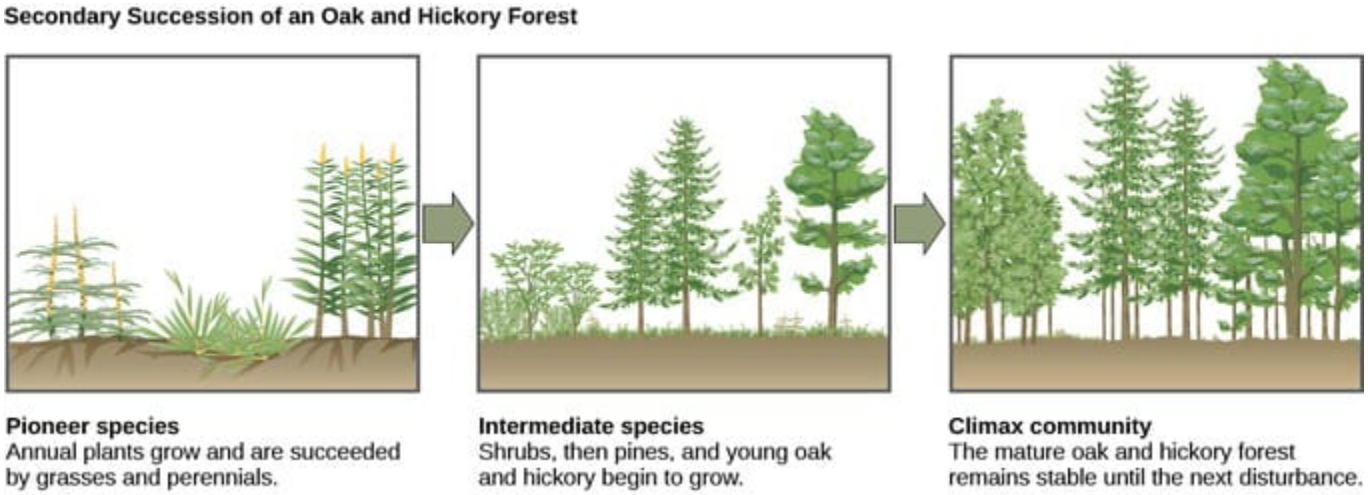


Figure $45.5D.1$: Secondary succession in the forest: Secondary succession is shown in an oak and hickory forest after a forest fire. Those organisms that could not escape are killed, but their bodies decompose, adding nutrients to the soil. These nutrients provide the basis for new plants to grow.

Before a wildfire, vegetation is often dominated by tall trees with access to the major plant energy resource: sunlight. Their height gives them access to sunlight while also shading the ground and other low-lying species. After the fire, however, 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 along with other pioneer species. Due to changes in the environment brought on by the growth of the grasses and other species, over many years, shrubs will 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 where species composition is no longer changing and resembles the community before the fire. This equilibrium state is referred to as the climax community, which will remain stable until the next disturbance.

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Key Points

- After an environmental disturbance such as a volcanic eruption or forest fire, communities are able to replace lost species through the process of succession.
- Primary succession occurs after a volcanic eruption or earthquake; it involves the breakdown of rocks by lichens to create new, nutrient -rich soils.
- The first species to colonize an area after a major disturbance are called pioneer species; they help to form the new environment.
- Secondary succession occurs after a disturbance such as a forest fire, where there is still some organic matter to allow new plants to grow.
- Both types of succession take place over long periods of time and result in the communities reaching a state of equilibrium.

Key Terms

- **succession**: an act of following in sequence
- **equilibrium**: the condition of a system in which competing influences are balanced, resulting in no net change

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45.6: INNATE ANIMAL BEHAVIOR



- Topic hierarchy

45.6A: Introduction to Animal Behavior

45.6B: Movement and Migration

45.6C: Animal Communication and Living in Groups

45.6D: Altruism and Populations

45.6E: Mating Systems and Sexual Selection

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45.6A: Introduction to Animal Behavior

Learning Objectives

- Distinguish between innate and learned behaviors

Behavior is the change in activity of an organism in response to a stimulus. Behavioral biology is the study of the biological and evolutionary bases for such changes. The idea that behaviors evolved as a result of the pressures of natural selection is not new.

Animal behavior has been studied for decades, by biologists in the science of ethology, by psychologists in the science of comparative psychology, and by scientists of many disciplines in the study of neurobiology. Although there is overlap between these disciplines, scientists in these behavioral fields take different approaches. Comparative psychology is an extension of work done in human and behavioral psychology. Ethology is an extension of genetics, evolution, anatomy, physiology, and other biological disciplines. One cannot study behavioral biology without touching on both comparative psychology and ethology.



Figure 45.6A.1: A Range of Animal Behaviors: Ethology has many aspects ranging from animal communication, emotions, culture, learning and sexuality.

One goal of behavioral biology is to distinguish the innate behaviors, which have a strong genetic component and are largely independent of environmental influences, from the learned behaviors, which result from environmental conditioning.

Innate behavior, or instinct, is important because there is no risk of an incorrect behavior being learned. These behaviors are “hard wired” into the system. In contrast, learned behaviors are flexible, dynamic, and can be altered relative to changes in the environment. Learned behaviors, even though they may have instinctive components, allow an organism to adapt to changes in the environment and are modified by previous experiences. Simple learned behaviors include habituation and imprinting—both are important to the maturation process of young animals.

Key Points

- Behavioral biology is the study of the biological and evolutionary bases for changes in activity in response to a stimulus.
- Comparative psychology is an extension of work done in human and behavioral psychology. Ethology is an extension of genetics, evolution, anatomy, physiology, and other biological disciplines.
- Innate behaviors have a strong genetic component and are largely independent of environmental influences; they are “hard wired.”
- Learned behaviors result from environmental conditioning; they allow an organism to adapt to changes in the environment

and are modified by previous experiences..

Key Terms

- **behavioral biology**: A systematic approach to the understanding of human and animal behavior assuming that the behavior of a human or animal is a consequence of that individual's history.
- **comparative psychology**: The scientific study of the behavior and mental processes of non-human animals, especially as these relate to the phylogenetic history, adaptive significance, and development of behavior.

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45.6B: Movement and Migration

Learning Objectives

- Distinguish between kinesis, taxis, and migration in response to stimuli

Innate behaviors: movement and migration

Innate or instinctual behaviors rely on response to stimuli. The simplest example of this is a reflex action: an involuntary and rapid response to stimulus. To test the “knee-jerk” reflex, a doctor taps the patellar tendon below the kneecap with a rubber hammer. The stimulation of the nerves there leads to the reflex of extending the leg at the knee. This is similar to the reaction of someone who touches a hot stove and instinctually pulls his or her hand away. Even humans, with our great capacity to learn, still exhibit a variety of innate behaviors.

Kinesis and taxis

Another activity or movement of innate behavior is kinesis: undirected movement in response to a stimulus. Orthokinesis is the increased or decreased speed of movement of an organism in response to a stimulus. Woodlice, for example, increase their speed of movement when exposed to high or low temperatures. This movement, although random, increases the probability that the insect spends less time in the unfavorable environment. Another example is klinokinesis, an increase in turning behaviors. It is exhibited by bacteria such as *E. coli* which, in association with orthokinesis, helps the organisms randomly find a more hospitable environment.

A similar, but more-directed version of kinesis is taxis: the directed movement towards or away from a stimulus. This movement can be in response to light (phototaxis), chemical signals (chemotaxis), or gravity (geotaxis). It can be directed toward (positive) or away (negative) from the source of the stimulus. An example of a positive chemotaxis is exhibited by the unicellular protozoan *Tetrahymena thermophila*. This organism swims using its cilia, at times moving in a straight line and at other times making turns. The attracting chemotactic agent alters the frequency of turning as the organism moves directly toward the source, following the increasing concentration gradient.

Migration as innate behavior

Migration is the long-range seasonal movement of animals. An evolved, adapted response to variation in resource availability, it is a common phenomenon found in all major groups of animals. Birds fly south for the winter to get to warmer climates with sufficient food, while salmon migrate to their spawning grounds. The popular 2005 documentary *March of the Penguins* followed the 62-mile migration of emperor penguins through Antarctica to bring food back to their breeding site and to their young. Wildebeests migrate over 1800 miles each year in search of new grasslands.



Figure $45.6B.1$: Migration: Wildebeests migrate in a clockwise fashion over 1800 miles each year in search of rain-ripened grass.

Although migration is thought of as an innate behavior, only some migrating species always migrate (obligate migration). Animals that exhibit facultative migration can choose to migrate or not. Additionally, in some animals, only a portion of the population migrates, whereas the rest does not migrate (incomplete migration). For example, owls that live in the tundra may migrate in years when their food source, small rodents, is relatively scarce, but not migrate during the years when rodents are plentiful.

Key Points

- Innate behaviors are instinctual, relying on responses to stimuli.
- Kinesis is the undirected movement in response to a stimulus, which can include orthokinesis (related to speed) or klinokinesis (related to turning).
- Taxis is the directed movement towards or away from a stimulus, which can be in response to light (phototaxis), chemical signals (chemotaxis), or gravity (geotaxis).
- Migration is an innate behavior characterized as the long-range seasonal movement of animals; it is an evolved, adapted response to variation in resource availability.
- Migration is a variable innate behavior as some migrating species always migrate (obligate migration) while in other animals, only a portion of the population migrates (incomplete migration).

Key Terms

- **orthokinesis**: the speed of movement of the individual is dependent upon the intensity of the stimulus
- **taxis**: the movement of an organism in response to a stimulus; similar to kinesis, but more direct
- **kinesis**: the undirected movement of an organism in response to an external stimulus

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45.6C: Animal Communication and Living in Groups

Learning Objectives

- Differentiate among the ways in which animals communicate

Innate behaviors: living in groups

Not all animals live in groups, but even those that live relatively-solitary lives (with the exception of those that can reproduce asexually) must mate. Mating usually involves one animal signaling another so as to communicate the desire to mate. There are several types of energy-intensive behaviors or displays associated with mating called mating rituals. Other behaviors found in populations that live in groups are described in terms of which animal benefits from the behavior. In selfish behavior, only the animal in question benefits; in altruistic behavior, one animal's actions benefit another animal; cooperative behavior occurs when both animals benefit. All of these behaviors involve some sort of communication between population members.

Communication within a species

Animals communicate with each other using stimuli known as signals. These signals are chemical (pheromones), aural (sound), visual (courtship and aggressive displays), or tactile (touch). These types of communication may be instinctual, learned, or a combination of both. These are not the same as the communication we associate with language, which has been observed only in humans and, perhaps, in some species of primates and cetaceans.

A pheromone is a secreted, chemical signal used to obtain a response from another individual of the same species. The purpose of pheromones is to elicit a specific behavior from the receiving individual. Pheromones are especially common among social insects, but they are used by many animal species to attract the opposite sex, to sound alarms, to mark food trails, and to elicit other, more-complex behaviors. Even humans are thought to respond to certain pheromones called axillary steroids. These chemicals influence human perception of other people. In one study, they were responsible for a group of women synchronizing their menstrual cycles. The role of pheromones in human-to-human communication is still somewhat controversial and continues to be researched.

Songs are an example of an aural signal: one that needs to be heard by the recipient. Perhaps the best known of these are songs of birds, which identify the species and are used to attract mates. Other well-known songs are those of whales, which are of such low frequency that they can travel long distances underwater. Dolphins communicate with each other using a wide variety of vocalizations. Male crickets make chirping sounds using a specialized organ to attract a mate, repel other males, and to announce a successful mating.

Courtship displays are a series of ritualized visual behaviors (signals) designed to attract and convince a member of the opposite sex to mate. These displays are ubiquitous in the animal kingdom. They often involve a series of steps, including an initial display by one member followed by a response from the other. If at any point the display is performed incorrectly or a proper response is not given, the mating ritual is abandoned and the mating attempt will be unsuccessful.



Figure $45.6C.1$: Courtship displays: A male peacock's extravagant, eye-spotted tail is used in courtship displays to attract a mate.

Aggressive displays are also common in the animal kingdom. As, for example, when a dog bares its teeth to get another dog to back down. Presumably, these displays communicate not only the willingness of the animal to fight, but also its fighting ability. Although these displays do signal aggression on the part of the sender, it is thought that they are actually a mechanism to reduce the amount of fighting that occurs between members of the same species: they allow individuals to assess the fighting ability of their opponent and thus decide whether it is "worth the fight."

Distraction displays are seen in birds and some fish. They are designed to attract a predator away from the nest that contains their young. This is an example of an altruistic behavior: it benefits the young more than the individual performing the display, which is putting itself at risk by doing so.

Many animals, especially primates, communicate with other members in the group through touch. Activities such as grooming, touching the shoulder or root of the tail, embracing, lip contact, and greeting ceremonies have all been observed in the Indian langur, an Old World monkey. Similar behaviors are found in other primates, especially in the great apes.

Key Points

- Animals need to communicate with one another in order to successfully mate, which usually involves one animal signaling another; the energy-intensive behaviors or displays associated with mating are called mating rituals.
- Animal signaling is not the same as the communication we associate with language, which has been observed only in humans, but may also occur in some non-human primates and cetaceans.
- Animal communication by stimuli known as signals may be instinctual, learned, or a combination of both.

Key Terms

- **pheromone**: a chemical secreted by an animal that affects the development or behavior of other members of the same species, functioning often as a means of attracting a member of the opposite sex

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45.6D: Altruism and Populations

Learning Objectives

- Explain how altruistic behaviors can benefit populations

Altruistic Behaviors

Behaviors that lower the fitness of the individual engaging in the behavior, but increase the fitness of another individual, are termed altruistic. Examples of such behaviors are seen widely across the animal kingdom. Social insects, such as worker bees, have no ability to reproduce, yet they maintain the queen so she can populate the hive with her offspring. Meerkats keep a sentry standing guard to warn the rest of the colony about intruders, even though the sentry is putting itself at risk. Wolves and wild dogs bring meat to pack members not present during a hunt. Lemurs take care of infants unrelated to them. Although on the surface these behaviors appear to be altruistic, it may not be so simple.

Why Does Altruism Exist?

There has been much discussion over why altruistic behaviors exist. Do these behaviors lead to overall evolutionary advantages for their species ? Do they help the altruistic individual pass on its own genes? And what about such activities between unrelated individuals? One explanation for altruistic-type behaviors is found in the genetics of natural selection. In the 1976 book, *The Selfish Gene,* scientist Richard Dawkins attempted to explain many seemingly-altruistic behaviors from the viewpoint of the gene itself. Although a gene obviously cannot be selfish in the human sense, it may appear that way if the sacrifice of an individual benefits related individuals that share genes that are identical by descent (present in relatives because of common lineage). Mammal parents make this sacrifice to take care of their offspring. Emperor penguins migrate miles in harsh conditions to bring food back for their young. Selfish gene theory has been controversial over the years and is still discussed among scientists in related fields.



Figure $45.6D.1$: Altruistic actions: Emperor penguins migrate miles in harsh conditions to bring back food for their young. Are extreme, altruistic actions such as these motivated by the selfish need to pass on genes?

Even less-related individuals (those with less genetic identity than that shared by parent and offspring) benefit from seemingly altruistic behavior. The activities of social insects such as bees, wasps, ants, and termites are good examples. Sterile workers in these societies take care of the queen because they are closely related to it; as the queen has offspring, she is passing on genes from the workers indirectly. Thus, it is of fitness benefit for the worker to maintain the queen without having any direct

chance of passing on its genes due to its sterility. The lowering of individual fitness to enhance the reproductive fitness of a relative and, thus, one's inclusive fitness evolves through kin selection. This phenomenon can explain many superficially-altruistic behaviors seen in animals. However, these behaviors may not be truly defined as altruism in these cases because the actor is actually increasing its own fitness either directly (through its own offspring) or indirectly (through the inclusive fitness it gains through relatives that share genes with it).

Unrelated individuals may also act altruistically to each other; this seems to defy the "selfish gene" explanation. An example of this is observed in many monkey species where a monkey will present its back to an unrelated monkey to have that individual pick the parasites from its fur. After a certain amount of time, the roles are reversed and the first monkey now grooms the second monkey. Thus, there is reciprocity in the behavior. Both benefit from the interaction and their fitness is raised more than if neither cooperated or if one cooperated and the other did not. This behavior is still not necessarily altruism, as the "giving" behavior of the actor is based on the expectation that it will be the "receiver" of the behavior in the future; a concept termed reciprocal altruism. Reciprocal altruism requires that individuals repeatedly encounter each other, often the result of living in the same social group, and that cheaters (those that never "give back") are punished.

Evolutionary Game Theory and Altruism

According to evolutionary game theory, a modification of classical game theory in mathematics, many of these so-called "altruistic behaviors" are not altruistic at all. The definition of "pure" altruism, based on human behavior, is an action that benefits another without any direct benefit to oneself. Most of the behaviors previously described do not seem to satisfy this definition; game theorists are good at finding "selfish" components in them. Others have argued that the terms "selfish" and "altruistic" should be dropped completely when discussing animal behavior, as they describe human behavior and may not be directly applicable to instinctual animal activity. What is clear, though, is that heritable behaviors that improve the chances of passing on one's genes or a portion of one's genes are favored by natural selection and will be retained in future generations as long as those behaviors convey a fitness advantage.

Key Points

- Behaviors that lower the fitness of the individual, but increase the fitness of another individual are termed altruistic; why altruistic behaviors exist has been the topic of some debate.
- One explanation for altruistic-type behaviors is found in the genetics of natural selection and the "selfish gene " theory: although a gene cannot be selfish in the human sense, it may appear that way if the sacrifice of an individual benefits related individuals that share genes that are identical.
- Even less-related individuals, those with less genetic identity than that shared by parent and offspring, benefit from seemingly-altruistic behavior, such as sterile worker bees protecting the queen.
- Unrelated individuals may also act altruistically to each other, which seems to defy the "selfish gene" explanation; however, this altruism is typically reciprocal, in that both benefit from the interaction.
- Most of the behaviors described when speaking of altruism do not seem to satisfy the definition of "pure" altruism; some evolutionary game theorists suggest that we get rid of the terms "altruistic" and "selfish" altogether since they describe human behavior.

Key Terms

- **kin selection**: an evolutionary mechanism by which an organism's behavior benefits the reproductive success of its relatives, including at the expense of its own survival or reproduction
- **altruism**: devotion to the interests of others; brotherly kindness; opposed to egoism or selfishness
- **game theory**: a branch of applied mathematics that studies strategic situations in which individuals or organizations choose various actions in an attempt to maximize their returns

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45.6E: Mating Systems and Sexual Selection

Learning Objectives

- Differentiate among monogamous, polygynous, and polyandrous mating systems, and distinguish between intersexual and intrasexual mate selection

Finding Sexual Partners

Not all animals reproduce sexually, but many that do have the same challenge: they need to find a suitable mate and often have to compete with other individuals to obtain one. Significant energy is spent in the process of locating, attracting, and mating with a sex partner.

Types of Mate Selection

Two types of selection that occur during the process of choosing a mate may be involved in the evolution of reproductive traits called secondary sexual characteristics. These types are: intersexual selection (the choice of a mate where individuals of one sex choose mates of the other sex) and intrasexual selection (the competition for mates between species members of the same sex). Intersexual selection is often complex because choosing a mate may be based on a variety of visual, aural, tactile, and chemical cues. An example of intersexual selection is when female peacocks choose to mate with the male with the brightest plumage. This type of selection often leads to traits in the chosen sex that do not enhance survival, but are those traits most attractive to the opposite sex (often at the expense of survival). Intrasexual selection involves mating displays and aggressive mating rituals such as rams butting heads; the winner of these battles is the one that is able to mate. Many of these rituals use up considerable energy, but result in the selection of the healthiest, strongest, and/or most dominant individuals for mating.

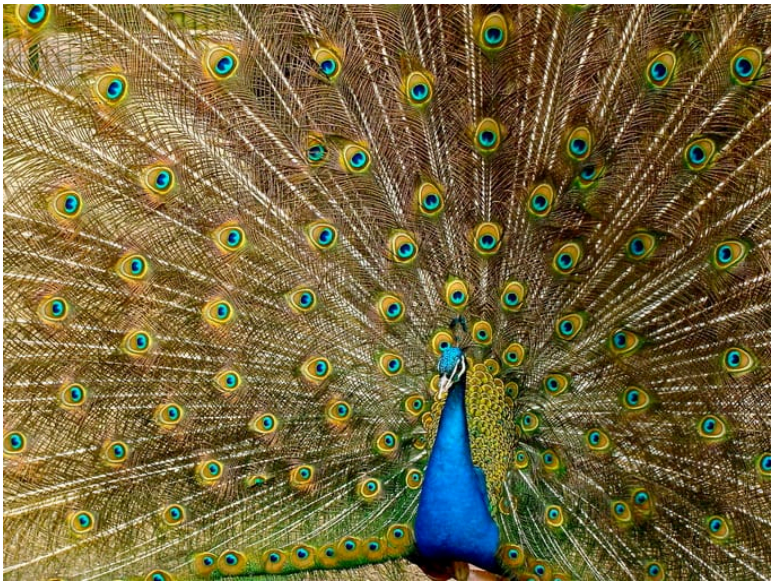


Figure $45.6E.1$: Courtship display of the male peacock: This male peacock's courtship display—his intricate, colorful tail feathers—is designed to attract potential mates.

Mating Systems

Three general mating systems, all involving innate as opposed to learned behaviors, are seen in animal populations: monogamous (monogamy), polygynous (polygyny), and polyandrous (polyandry).

In monogamous systems, one male and one female are paired for at least one breeding season. In some animals, such as the gray wolf, these associations can last much longer, even a lifetime. Several explanations have been proposed for this type of mating system. The “mate-guarding hypothesis” states that males stay with the female to prevent other males from mating with her. This behavior is advantageous in such situations where mates are scarce and difficult to find. Another explanation is the “male-assistance hypothesis,” where males that remain with a female to help guard and rear their young will have more and healthier offspring. Monogamy is observed in many bird populations where, in addition to the parental care from the female, the male is also a major provider of parental care for the chicks. A third explanation for the evolutionary advantages of monogamy is the “female-enforcement hypothesis.” In this scenario, the female ensures that the male does not have other offspring that might compete with her own, so she actively interferes with the male’s signaling to attract other mates.

Polygynous mating refers to one male mating with multiple females. In these situations, the female must be responsible for most of the parental care as the single male is not capable of providing care to that many offspring. In resourced-based polygyny, males compete for territories with the best resources. They then mate with females that enter the territory, drawn to its resource richness. The female benefits by mating with a dominant, genetically-fit male; however, it is at the cost of having no male help in caring for the offspring. An example is seen in the yellow-rumped honeyguide, a bird whose males defend beehives because the females feed on the wax. As the females approach, the male defending the nest will mate with them. Harem mating structures are a type of polygynous system where certain males dominate mating while controlling a territory with resources. Elephant seals, where the alpha male dominates the mating within the group, are an example. A third type of polygyny is a lek system. Here there is a communal courting area where several males perform elaborate displays for females; the females choose their mate from this group. This behavior is observed in several bird species.

In polyandrous mating systems, one female mates with many males. These types of systems are much rarer than monogamous and polygynous mating systems. In pipefishes and seahorses, males receive the eggs from the female, fertilize them, protect them within a pouch, and give birth to the offspring. Therefore, the female is able to provide eggs to several males without the burden of carrying the fertilized eggs.



Figure $45.6E.1$: Polyandry: Seahorses are a good example of a polyandrous mating system, in which one female mates with several males. In seahorse reproduction, the male receives the eggs from the female, fertilizes them, protects them within a pouch, and gives birth to the offspring.

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Key Points

- Two types of mate selection occur: intersexual selection (the choice of a mate where individuals of one sex choose mates of the other sex) and intrasexual selection (the competition for mates between species members of the same sex).
- Three general mating systems, all involving innate as opposed to learned behaviors, are seen in animal populations: monogamous (monogamy), polygynous (polygyny), and polyandrous (polyandry).
- In monogamous systems, one male and one female are paired for at least one breeding season; although in some animals, these partnerships can last even longer, sometimes an entire lifetime; males provide substantial parental care.
- Polygynous mating refers to one male mating with multiple females; in these situations, the female must be responsible for most of the parental care as the single male is not capable of providing care to that many offspring.
- In polyandrous mating systems, one female mates with many males; these types of systems are much rarer than monogamous and polygynous mating systems.

Key Terms

- **polyandry**: the mating pattern whereby a female copulates with several males
- **polygyny**: the mating patterns whereby a male copulates with several females
- **monogamy**: a form of sexual bonding involving an exclusive pair bond between two individuals

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45.7: LEARNED ANIMAL BEHAVIOR

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- Topic hierarchy

45.7A: Simple Learned Behaviors
45.7B: Conditioned Behavior
45.7C: Cognitive Learning and Sociobiology

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45.7A: Simple Learned Behaviors

Learning Objectives

- Distinguish between the simple learned behaviors of habituation and imprinting

Simple Learned Behaviors

The majority of the behaviors discussed in previous sections are innate or at least have an innate component. In other words, variations on the innate behaviors may be learned. Innate behaviors are inherited and do not change in response to signals from the environment. Conversely, learned behaviors, even though they may have instinctive components, allow an organism to adapt to changes in the environment and are modified by previous experiences. Simple learned behaviors include habituation and imprinting, both of which are important to the maturation process of young animals.

Habituation

Habituation is a simple form of learning in which an animal stops responding to a stimulus after a period of repeated exposure. This is a form of non-associative learning as the stimulus is not associated with any punishment or reward. Prairie dogs typically sound an alarm call when threatened by a predator, but they become habituated to the sound of human footsteps when no harm is associated with this sound; therefore, they no longer respond to them with an alarm call. In this example, habituation is specific to the sound of human footsteps, as the animals still respond to the sounds of potential predators.

Imprinting

Imprinting is a type of learning that occurs at a particular age or a life stage that is rapid and independent of the species involved. Hatchling ducks recognize the first adult they see, their mother, and make a bond with her. A familiar sight is ducklings walking or swimming after their mothers. This type of non-associative learning is very important in the maturation process of these animals as it encourages them to stay near their mother in order to be be protected, greatly increasing their chances of survival. However, if newborn ducks see a human before they see their mother, they will imprint on the human and follow it in just the same manner as they would follow their real mother.



Figure 45.7A.1: Imprinting: The attachment of ducklings to their mother is an example of imprinting.

Key Points

- Learned behaviors stand in opposition to innate behaviors: while learned behaviors may have an innate component, they allow the organism to modify its behavior according to environmental factors or previous experiences.
- Habituation is a simple form of learning in which an animal stops responding to a stimulus after a period of repeated exposure; it is a form of non-associative learning, as the stimulus is not associated with any punishment or reward.
- Imprinting is a type of learning that occurs at a particular age or a life stage that is rapid and independent of the species involved.

Key Terms

- **imprinting**: any kind of phase-sensitive learning (learning occurring at a particular age or a particular life stage) that is rapid and apparently independent of the consequences of behavior
- **habituation**: a learned behavior involving modifying behavior according to the environment or previous expriences
- **innate**: inborn; native; natural

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45.7B: Conditioned Behavior

Learning Objectives

- Distinguish between classical and operant conditioning techniques

Conditioned behaviors are types of associative learning where a stimulus becomes associated with a consequence. Two types of conditioning techniques include classical and operant conditioning.

Classical Conditioning

In classical conditioning, a response called the conditioned response is associated with a stimulus that it had previously not been associated with, the conditioned stimulus. The response to the original, unconditioned stimulus is called the unconditioned response. The most cited example of classical conditioning is Ivan Pavlov's experiments with dogs. In Pavlov's experiments, the unconditioned response was the salivation of dogs in response to the unconditioned stimulus of seeing or smelling their food. The conditioning stimulus that researchers associated with the unconditioned response was the ringing of a bell. During conditioning, every time the animal was given food, the bell was rung. This was repeated during several trials. After some time, the dog learned to associate the ringing of the bell with food and to respond by salivating. After the conditioning period was finished, the dog would respond by salivating when the bell was rung, even when the unconditioned stimulus (the food) was absent. Thus, the ringing of the bell became the conditioned stimulus and the salivation became the conditioned response. Although it is thought by some scientists that the unconditioned and conditioned responses are identical, Pavlov discovered that the saliva in the conditioned dogs had characteristic differences when compared to the unconditioned dog.

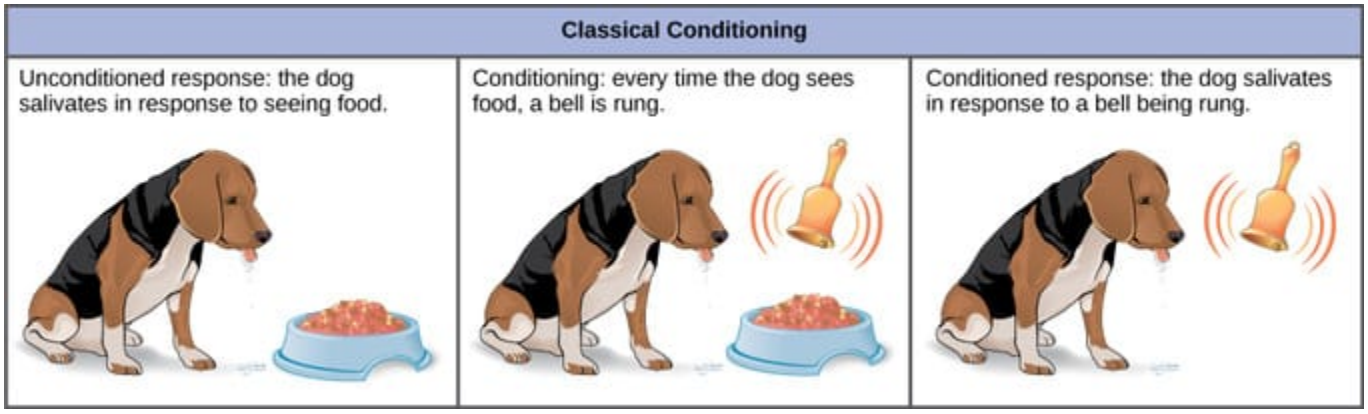


Figure $45.7B.1$: Classical conditioning: In the classic Pavlovian response, the dog becomes conditioned to associate the ringing of the bell with food.

Some believe that this type of conditioning requires multiple exposures to the paired stimulus and response, but it is now known that this is not necessary in all cases; some conditioning can be learned in a single pairing experiment. Classical conditioning is a major tenet of behaviorism, a branch of psychological philosophy that proposes that all actions, thoughts, and emotions of living things are behaviors that can be treated by behavior modification and changes in the environment.

Operant Conditioning

In operant conditioning, the conditioned behavior is gradually modified by its consequences as the animal responds to the stimulus. A major proponent of such conditioning was psychologist B.F. Skinner, the inventor of the Skinner box. Skinner put rats in his boxes that contained a lever that would dispense food to the rat when depressed. While initially the rat would push the lever a few times by accident, it eventually associated pushing the lever with getting the food. This type of learning is an example of operant conditioning. Operant learning is the basis of most animal training: the conditioned behavior is continually modified by positive or negative reinforcement (such as being given a reward or having a negative stimulus removed) or by positive or negative punishment (such as being given a punishment or having a pleasing stimulus removed). In this way, the animal is conditioned to

associate a type of behavior with the punishment or reward. Over time, the animal can be induced to perform behaviors that they would not have done in the wild, such as the “tricks” dolphins perform at marine amusement park shows.

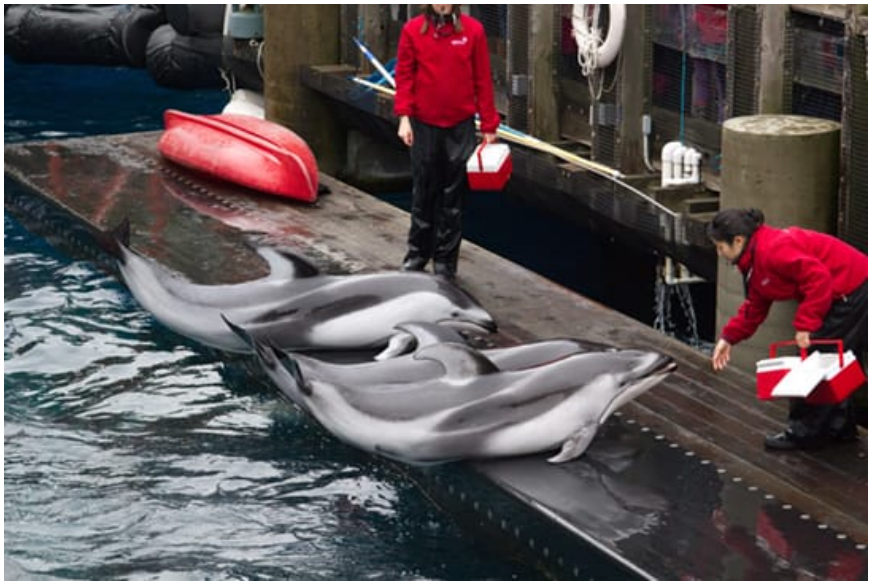


Figure $45.7B.1$: Operant conditioning: The training of dolphins by rewarding them with food is an example of positive reinforcement operant conditioning.

Key Points

- In classical conditioning, a response called the conditioned response is associated with a stimulus that it had previously not been associated with, the conditioned stimulus; the response to the original, unconditioned stimulus is called the unconditioned response.
- Classical conditioning is a major tenet of behaviorism, a branch of psychological philosophy that proposes that all actions, thoughts, and emotions of living things are behaviors that can be treated by behavior modification and changes in the environment.
- In operant conditioning, the conditioned behavior is gradually modified by its consequences as the animal responds to the stimulus.
- Operant conditioning relies on the use of reinforcement (i.e. a reward) and/or punishment to modify a conditioned behavior; in this way, the animal is conditioned to associate a type of behavior with the punishment or reward.

Key Terms

- **classical conditioning**: the use of a neutral stimulus, originally paired with one that invokes a response, to generate a conditioned response
- **operant conditioning**: a technique of behavior modification through positive and negative reinforcement and positive and negative punishment

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45.7C: Cognitive Learning and Sociobiology

Learning Objectives

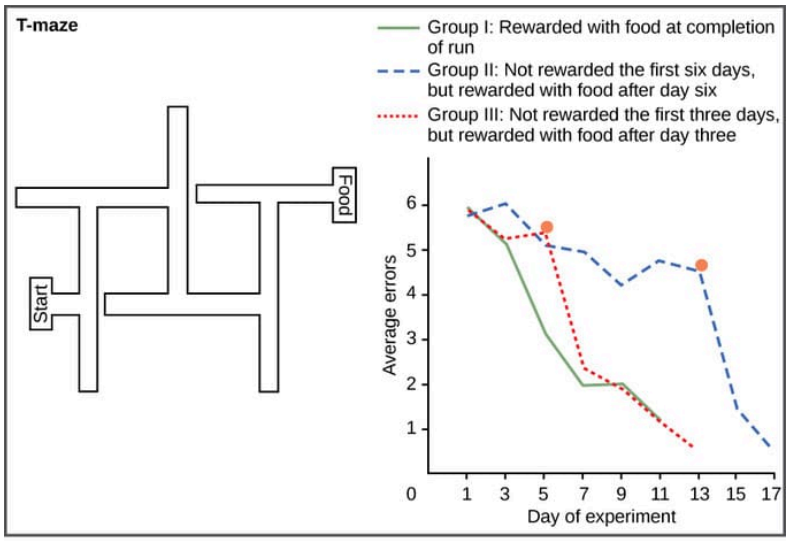
- Describe research models that indicate the presence of cognitive learning in animals

Cognitive Learning

Classical and operant conditioning are inefficient ways for humans and other intelligent animals to learn. Some primates, including humans, are able to learn by imitating the behavior of others and by taking instructions. The development of complex language by humans has made cognitive learning, or the manipulation of information using the mind, the most prominent method of human learning. In fact, that is how you are learning right now by reading this information. As students read, they can make mental images of objects or organisms, imagining changes to them or behaviors by them as they anticipate the consequences. In addition to visual processing, cognitive learning is also enhanced by remembering past experiences, touching physical objects, hearing sounds, tasting food, and a variety of other sensory-based inputs. Cognitive learning is so powerful that it can be used to understand conditioning (discussed in the previous concept) in detail. In the reverse scenario, conditioning cannot help someone learn about cognition.

Classic work on cognitive learning was done by Wolfgang Köhler with chimpanzees. He demonstrated that these animals were capable of abstract thought by showing that they could learn how to solve a puzzle. When a banana was hung in their cage too high for them to reach along with several boxes placed randomly on the floor, some of the chimps were able to stack the boxes one on top of the other, climb on top of them, and get the banana. This implies that they could visualize the result of stacking the boxes even before they had performed the action. This type of learning is much more powerful and versatile than conditioning.

Cognitive learning is not limited to primates, although they are the most efficient in using it. Maze-running experiments done with rats in the 1920s were the first to show cognitive skills in a simple mammal. The motivation for the animals to work their way through the maze was the presence of a piece of food at its end. In these studies, the animals in Group I were run in one trial per day and had food available to them each day on completion of the run. Group II rats were not fed in the maze for the first six days and then subsequent runs were done with food for several days after. Group III rats had food available on the third day and every day thereafter. The results were that the control rats, Group I, learned quickly, figuring out how to run the maze in seven days. Group III did not learn much during the three days without food, but rapidly caught up to the control group when given the food reward. Group II learned very slowly for the six days with no reward to motivate them. They did not begin to catch up to the control group until the day food was given; it then took two days longer to learn the maze.



Redrawn after H. C. Blodgett, The effect of the introduction of reward upon the maze performance of rats. Univ. Calif. Publ. Psychol., 1929, 4, No. 8, pages 117 and 120.

Figure 45.7C.1: Cognitive learning: Group I (the green solid line) found food at the end of each trial; group II (the blue dashed line) did not find food for the first 6 days; and group III (the red dotted line) did not find food during runs on the first three days. Notice that rats given food earlier learned faster and eventually caught up to the control group. The orange dots on the group II and III lines show the days when food rewards were added to the mazes.

It may not be immediately obvious that this type of learning is different from conditioning. Although one might be tempted to believe that the rats simply learned how to find their way through a conditioned series of right and left turns, E.C. Tolman proved a decade later that the rats were making a representation of the maze in their minds, which he called a "cognitive map." This was an early demonstration of the power of cognitive learning and how these abilities were not limited just to humans.

Sociobiology

Sociobiology is an interdisciplinary science originally popularized by social insect researcher E.O. Wilson in the 1970s. Wilson defined the science as "the extension of population biology and evolutionary theory to social organization." The main thrust of sociobiology is that animal and human behavior, including aggressiveness and other social interactions, can be explained almost solely in terms of genetics and natural selection. This science is controversial; some have criticized the approach for ignoring the environmental effects on behavior. This is another example of the "nature versus nurture" debate of the role of genetics versus the role of environment in determining an organism's characteristics.

Sociobiology also links genes with behaviors and has been associated with "biological determinism," the belief that all behaviors are hardwired into our genes. No one disputes that certain behaviors can be inherited and that natural selection plays a role retaining them. It is the application of such principles to human behavior that sparks this controversy, which remains active today.

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Key Points

- Cognitive learning involves the manipulation of information using the mind; it is a great deal more powerful than either operant or classical conditioning.
- The development of complex language by humans has made cognitive learning the most prominent method of human learning.
- Cognitive learning is not limited to primates; rats have demonstrated the ability to build cognitive maps, as well, which are mental representations used to acquire, code, store, recall, and decode information about the environment.
- Sociobiology argues that all animal and human behavior, including aggressiveness and other social interactions, can be explained almost solely in terms of genetics and natural selection.
- Sociobiology is controversial: some have criticized the approach for ignoring the environmental effects on behavior and for being similar to “biological determinism,” or the belief that all behaviors are hardwired into our genes.

Key Terms

- **cognitive map**: a mental epresentation which serves an organism to acquire, code, store, recall, and decode information about the relative locations and attributes of phenomena in their everyday environment
- **cognitive learning**: the process by which one acquires knowledge or skill in cognitive processes, which include reasoning, abstract thinking, and problem solving
- **sociobiology**: the science that applies the principles of evolutionary biology to the study of social behaviour in both humans and animals

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46: ECOSYSTEMS

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46.1: ECOLOGY OF ECOSYSTEMS

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46.1A: Ecosystem Dynamics

Learning Objectives

- Explain ecosystem dynamics

An ecosystem is a community of living organisms (plants, animals, and microbes) existing in conjunction with the nonliving components of their environment (air, water, and mineral soil), interacting as a system. These biotic and abiotic components are linked together through nutrient cycles and energy flows. As ecosystems are defined by the network of interactions among organisms, or between organisms and their environment, they can be of any size, but usually encompass specific, limited spaces.

Internal and External Factors

Ecosystems are dynamic entities controlled both by external and internal factors. External factors, such as climate and the parent material that forms the soil, control the overall structure of an ecosystem and the way things work within it, but are not themselves influenced by the ecosystem. While the resource inputs are generally controlled by external processes, the availability of these resources within the ecosystem is controlled by internal factors such as decomposition, root competition, or shading. Other internal factors include disturbance, succession, and the types of species present. From one year to another, ecosystems experience variation in their biotic and abiotic environments. A drought, an especially cold winter, and a pest outbreak all constitute short-term variability in environmental conditions. Animal populations vary from year to year, building up during resource-rich periods, but crashing as the food supply becomes scarce.

Equilibrium is the steady state of an ecosystem where all organisms are in balance with their environment and with each other. In equilibrium, any small changes to the system will be balanced by negative feedback, allowing the system to return to its original state.

Resistance and Resilience

In ecology, two parameters are used to measure changes in ecosystems: resistance and resilience. Resistance is the ability of an ecosystem to remain at equilibrium despite disturbances. Resilience is the speed at which an ecosystem recovers to equilibrium after being disturbed. Humans may impact the nature of an ecosystem to such a degree that the ecosystem can lose its resilience entirely. In these cases, external human influences can lead to the complete destruction or irreversible altering of the ecosystem equilibrium.



Figure 46.1A.1: Human intervention in ecosystem equilibrium: The Australian Aboriginal practice of “Fire-stick farming” has fundamentally modified Australian ecosystems. The legacy of this practice over long periods has resulted in forests being converted to grasslands. In this example, the forests became less and less resilient over time until the fundamental system equilibrium had changed.

The Sin Nombre Virus: Ecosystem Dynamics in a Human Population

In 1993, a change in ecosystem dynamics caused a disease outbreak in a human population. In May of 1993, an unexplained pulmonary illness struck inhabitants of the southwestern United States in an area shared by Arizona, New Mexico, Colorado and Utah known as “The Four Corners. ” A young, physically fit Navajo man suffering from shortness of breath was rushed to a hospital in New Mexico and died rapidly. After further investigation, state officials located another five young, healthy people who had all died after acute respiratory failure.

When laboratory tests failed to identify the disease causing the deaths, New Mexico state health officials notified the Centers for Disease Control (CDC), the United States government agency responsible for managing potential epidemics. As additional cases of the disease were reported in the following weeks, physicians and scientists worked intensively to narrow down the list of possible causes. Virologists at the CDC linked the pulmonary syndrome with a virus – a previously unknown type of hantavirus. The hantavirus became known as *Sin Nombre*, the virus “with no name. ”

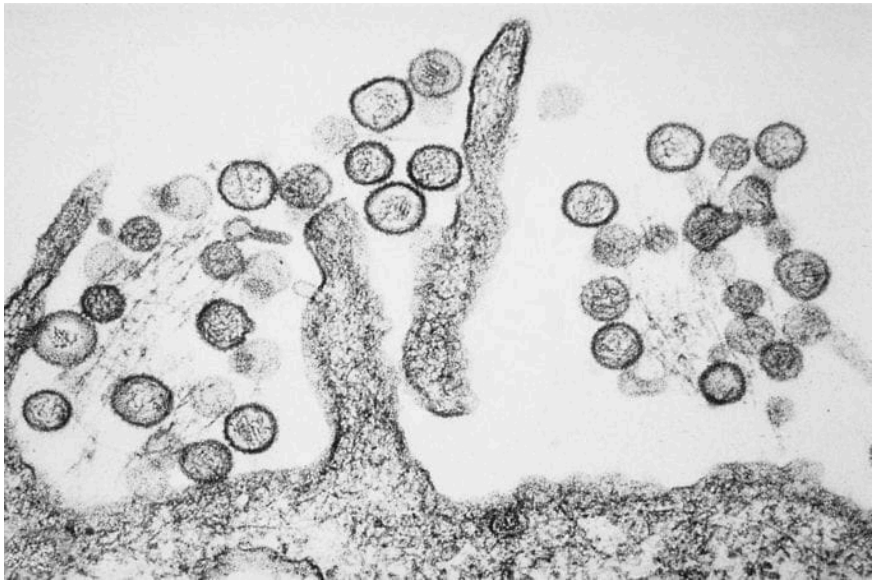


Figure 46.1A.1: Sin Nombre hantavirus: After a series of sudden deaths in 1993, scientists in the Four Corners area of the Southwestern United States rushed to determine the cause. They isolated a previously unknown hantavirus that caused pulmonary failure or Hantavirus Pulmonary Syndrome (HPS). The new virus was named Sin Nombre, or virus with “no name. “

Although they identified the virus as the cause of the disease, researchers did not understand how it was transmitted. The researchers trapped and examined rodents that lived in and around the homes of the victims, and found that almost 30% of the deer mice were infected with the Sin Nombre hantavirus. The virus had been transmitted to humans via aerosolized mouse droppings, and a dramatic increase in the deer mouse population increased human infection rates.

The Four Corners area had experienced a drought until early 1993, when there were heavy snows and rainfall. The end of the drought caused an increase in vegetation, and particularly pinon nut production. With the sudden increase in food supply, the local deer mice population exploded and reproduced so rapidly that there were ten times more mice in May 1993 than there had been in May of 1992. The higher population of deer mice meant more mouse droppings and more opportunities to transmit hantavirus to humans.



Figure 46.1A.1: Ecosystem dynamics can affect human populations: The Four Corners area had been in a drought for several years. In early 1993, the rainfall caused an increase in vegetation, which caused an increase the local deer mice population. Hantavirus infected the high deer mouse population and was quickly transmitted to humans via aerosolized mouse droppings.

As part of the effort to locate the source of the virus, researchers located and examined stored samples of lung tissue from people who had died of unexplained lung disease. Some of these samples showed evidence of previous infection with Sin Nombre virus, indicating that the earlier cases of the disease had not been recognized. The Navajo Native Americans recognize a similar disease in their medical traditions, and associate its occurrence with mice.

Key Points

- Biotic and abiotic factors interact through nutrient cycles and energy flows.
- External factors control resource inputs and are not influenced by the ecosystem itself.
- Internal factors are processes that exist within the ecosystem, such as decomposition, succession, and the types of species present.
- While in equilibrium, an ecosystem can recover from small changes through negative feedback, returning to its original state.
- Resistance describes an ecosystem's ability to resist disturbances to the ecosystems dynamics.
- Human disturbances to ecosystems can overwhelm the ecosystem's resilience, crippling its ability to return to equilibrium.

Key Terms

- **resilience**: the speed with which an ecosystem returns to its initial state after a disturbance
- **equilibrium**: the condition of a system in which competing influences are balanced, resulting in no net change
- **resistance**: the tendency of a system to remain close to its equilibrium state, despite disturbances

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46.1B: Food Chains and Food Webs

Learning Objectives

- Distinguish between food chains and food webs as models of energy flow in ecosystems

In ecology, a food web describes the feeding connections between organisms in a biotic community. Both energy and nutrients flow through a food web, moving through organisms as they are consumed by an organism above them in the food web. A single path of energy through a food web is called a food chain.

Trophic Levels

Each organism within a food web can be classified by trophic level according to their position within the web. Depending on an organism's location in a food web, it may be grouped into more than one of these categories. Energy and nutrients move up trophic levels in the following order:

1. Primary producers
2. Primary consumers
3. Secondary consumers
4. Tertiary and other high-level consumers

In both food webs and food chains, arrows point from an organism that is consumed to the organism that consumes it. In many ecosystems, the bottom of the food chain consists of photosynthetic organisms, such as plants or phytoplankton, known as primary producers. The organisms that consume the primary producers are herbivores: the primary consumers. Secondary consumers are usually carnivores that eat the primary consumers, while 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, which are called the apex consumers. Some lines within a food web may point to more than one organism; those organisms may occupy different trophic levels depending on their position in each food chain within the web.

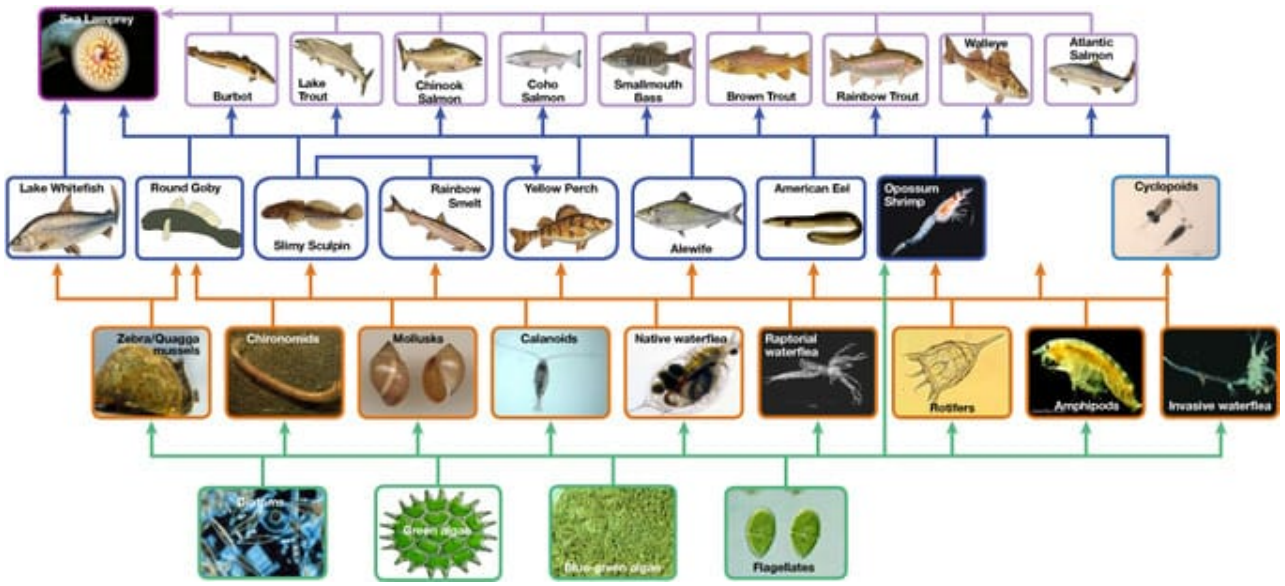


Figure 46.1B.1: Food web: This food web shows the interactions between organisms across trophic levels in the Lake Ontario ecosystem. Primary producers are outlined in green, primary consumers in orange, secondary consumers in blue, and tertiary (apex) consumers in purple. The opossum shrimp eats both primary producers and primary consumers; it is, therefore, both a primary consumer and a secondary consumer.

The Loss of Energy in Tropic Levels

It is rare to find food chains that have more than four or five links because the loss of energy limits the length of food chains. At each trophic level, most of the energy is lost through biological processes such as respiration or finding food. Only the energy that is directly assimilated into an animal's consumable mass will be transferred to the next level when that animal is eaten. Therefore, after a limited number of trophic energy transfers, the amount of energy remaining in the food chain cannot support a higher trophic level. Although energy is lost, nutrients are recycled through waste or decomposition.

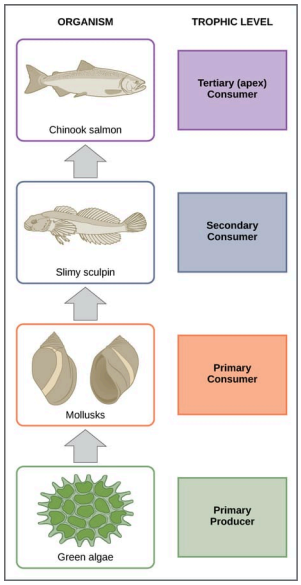


Figure $46.1B.1$: Food chain: These are the trophic levels of a food chain in Lake Ontario. Energy and nutrients flow from photosynthetic green algae at the bottom to the salmon at the top of the food chain. There are only four links in this chain because significant energy is lost between each successive trophic level.

A scientist named Howard T. Odum demonstrated the loss of energy in each trophic level in the Silver Springs, Florida, ecosystem in the 1940s. He found that the primary producers generated 20,819 kcal/m^2/yr (kilocalories per square meter per year), the primary consumers generated 3368 kcal/m^2/yr, the secondary consumers generated 383 kcal/m^2/yr, and the tertiary consumers only generated 21 kcal/m^2/yr. In each successive trophic level, the energy available to the next level decreased significantly.

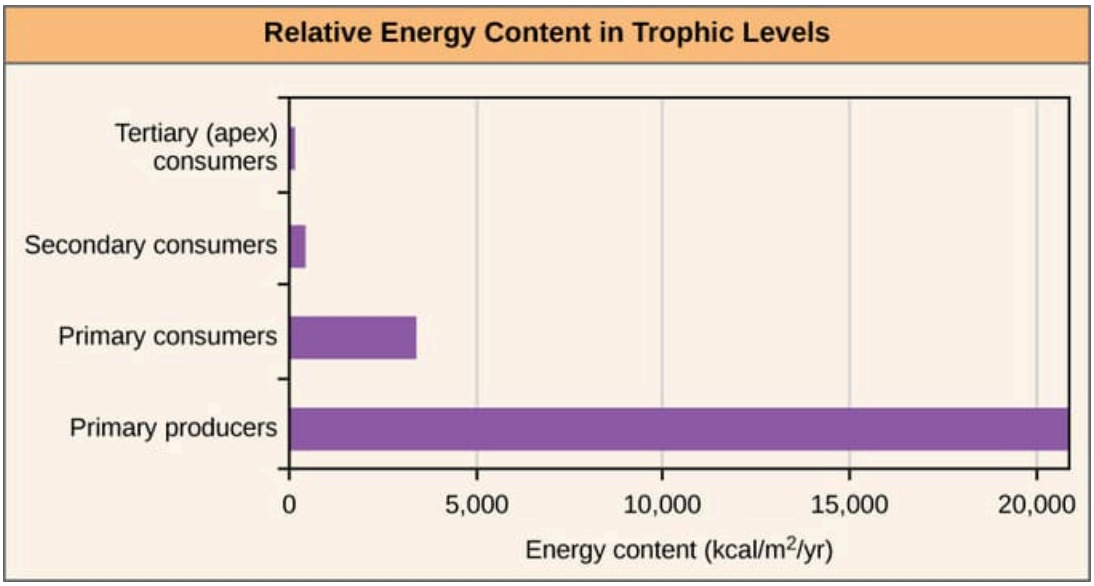


Figure $46.1B.1$: Energy decreases per trophic level: The relative energy in trophic levels in a Silver Springs, Florida, ecosystem is shown. Each trophic level has less energy available and supports fewer organisms at the next level.

Types of Food Webs

Two general types of food webs are often shown interacting within a single ecosystem. As an example, 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), called decomposers or detritivores. These organisms are usually bacteria or fungi that recycle organic material back into the biotic part of the ecosystem as they themselves are consumed by other organisms. As all ecosystems require a method to recycle material from dead organisms, most 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, fungi, and detrivorous invertebrates feeding off dead plants and animals.

Key Points

- Organisms can be organized into trophic levels: primary producer, primary consumer, secondary consumer, and tertiary or higher-order consumer.
- Energy decreases in each successive trophic level, preventing more than four or five levels in a food chain.
- An ecosystem usually has two different types of food webs: a grazing food web based on photosynthetic plants or algae, along with a detrital food web based on decomposers (such as fungi).
- There are different types of food webs including grazing food webs based on photosynthetic plants (such as algae) or detrital food webs based on decomposers (such as fungi).

Key Terms

- **detritivore**: an organism that feeds on detritus; a decomposer
- **food chain**: the feeding relationships between species in a biotic community; a linear path through a food web
- **trophic level**: a particular position occupied by a group of organisms in a food chain (primary producer, primary consumer, secondary consumer, or tertiary consumer)

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46.1C: Studying Ecosystem Dynamics

Learning Objectives

- Differentiate between conceptual, analytical, and simulation models of ecosystem dynamics, and mesocosm and microcosm research studies

Ecosystem dynamics is the study of the changes in ecosystem structure caused by environmental disturbances or by internal forces. Various research methodologies measure ecosystem dynamics. Some ecologists study ecosystems using controlled experimental systems, while some study entire ecosystems in their natural state; others use both approaches.

Holistic Ecosystem Model

A holistic ecosystem model attempts to quantify the composition, interaction, and dynamics of entire ecosystems. A food web is an example of a holistic ecosystem model, which is the most representative of the ecosystem in its natural state. However, this type of study is limited by time and expense, as well as its limited feasibility to conduct experiments on large natural ecosystems.

Experimental Systems

For these reasons, scientists study ecosystems under more controlled conditions. Experimental systems usually involve either partitioning a part of a natural ecosystem that can be used for experiments, termed a mesocosm, or by re-creating an ecosystem entirely in an indoor or outdoor laboratory environment, which is referred to as a microcosm. A major limitation to these approaches is that removing individual organisms from their natural ecosystem or altering a natural ecosystem through partitioning may change the dynamics of the ecosystem. These changes are often due to differences in species numbers and diversity, but also to environment alterations caused by partitioning (mesocosm) or re-creating (microcosm) the natural habitat. Thus, these types of experiments are not totally predictive of changes that would occur in the ecosystem from which they were gathered.



Figure $46.1C.1$: Mesocosm: Greenhouses contribute to mesocosm studies because they allow us to control the environment and, thus, the experiment. The mesocosms in this example, tomato plants, have been placed in a greenhouse to control the air, temperature, water, and light distribution in order to observe the effects when exposed to different amounts of each factor.

As both of these approaches have their limitations, some ecologists suggest that results from these experimental systems should be used only in conjunction with holistic ecosystem studies to obtain the most representative data about ecosystem structure,

function, and dynamics.

Ecosystem Models

Scientists use the data generated by these experimental studies to develop ecosystem models that demonstrate the structure and dynamics of ecosystems. Three basic types of ecosystem modeling are routinely used in research and ecosystem management: conceptual models, analytical models, and simulation models.

A conceptual model consists of flow charts to show interactions of different compartments of the living and nonliving components of the ecosystem. A conceptual model describes ecosystem structure and dynamics and shows how environmental disturbances affect the ecosystem, although its ability to predict the effects of these disturbances is limited.

Analytical and simulation models are mathematical methods of describing ecosystems that are capable of predicting the effects of potential environmental changes without direct experimentation, although with limitations in accuracy. An analytical model is created using simple mathematical formulas to predict the effects of environmental disturbances on ecosystem structure and dynamics.

A simulation model is created using complex computer algorithms to holistically model ecosystems and to predict the effects of environmental disturbances on ecosystem structure and dynamics. Ideally, these models are accurate enough to determine which components of the ecosystem are particularly sensitive to disturbances. They can serve as a guide to ecosystem managers (such as conservation ecologists or fisheries biologists) in the practical maintenance of ecosystem health.

Key Points

- A holistic ecosystem model quantifies the dynamics of an entire ecosystem.
- Scientists can use experimental systems, such as a microcosms or mesocosms, to study ecosystems under controlled laboratory conditions.
- A conceptual model uses flow charts to show the interactions between living and nonliving components of the ecosystem.
- An analytical model uses simple mathematical formulas to predict the effects of environmental disturbances on an ecosystem's structure and dynamics.
- A simulation model predicts the effects of environmental disturbances using complex computer algorithms; they are usually fairly-reliable predictors.

Key Terms

- **mesocosm**: a small portion of the natural environment that is brought under controlled conditions for experimental purposes
- **microcosm**: an artificial, simplified ecosystem that is used to simulate and predict the behaviour of natural ecosystems under controlled conditions

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46.1D: Modeling Ecosystem Dynamics

Learning Objectives

- Compare and contrast conceptual, analytical, and simulation models of ecosystem dynamics

Conceptual models

Conceptual models are useful for describing ecosystem structure and dynamics and for demonstrating the relationships between different organisms in a community and their environment. Conceptual models are usually depicted graphically as flow charts. The organisms and their resources are grouped into specific compartments with arrows showing the relationship and transfer of energy or nutrients between them. These diagrams are sometimes called compartment models.

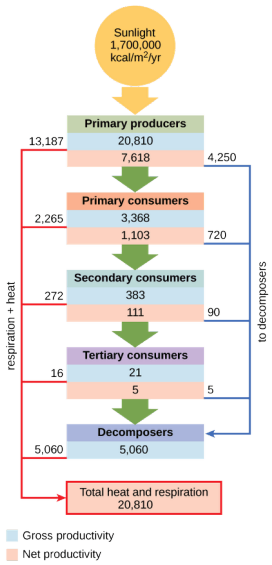


Figure $46.1D.1$: Conceptual model of energy: This conceptual model shows the flow of energy through a spring ecosystem in Silver Springs, Florida. Notice that the energy decreases with each increase in trophic level. Conceptual models are useful for describing ecosystem structure, but are limited by their poor prediction of ecosystem changes.

To model the cycling of mineral nutrients, organic and inorganic nutrients are subdivided into those that are bioavailable (ready to be incorporated into biological macromolecules) and those that are not. For example, in a terrestrial ecosystem near a deposit of coal, carbon will be available to the plants of this ecosystem as carbon dioxide gas in a short-term period, not from the carbon-rich coal itself. However, over a longer period, microorganisms capable of digesting coal will incorporate its carbon or release it as natural gas (methane, CH_4), changing this unavailable organic source into an available one.

Human combustion of fossil fuels accelerates this conversion by releasing large amounts of carbon dioxide into the atmosphere, which may be a large contributor to the rise of the atmospheric carbon dioxide levels in the industrial age. The carbon dioxide released from burning fossil fuels is produced faster than photosynthetic organisms can use it, while the number of photosynthetic trees have decreased because of worldwide deforestation. Most scientists agree that high atmospheric carbon dioxide is a major cause of global climate change.

Analytical and simulation models

Conceptual models are limited; they poorly predict the consequences of changes in ecosystem species and/or environment. Ecosystems are dynamic entities that are subject to a variety of abiotic and biotic disturbances. In these cases, scientists often use analytical or simulation models. These models predict how ecosystems recover from disturbances, returning to a state of

equilibrium. As most ecosystems are subject to periodic disturbances and are often in a state of change, they are usually either moving toward or away from multiple equilibrium states. Since human impact can greatly and rapidly alter the species content and habitat of an ecosystem, it is crucial for scientists to develop models that predict how ecosystems respond to these changes.

Analytical models

Analytical models generally work best when dealing with relatively-simple, linear systems; specifically, those that can be accurately described by a set of mathematical equations whose behavior is well known. They are mathematically complex models that are good at predicting components of ecosystems such as food chains. However, their accuracy is limited by their simplification of complex ecosystems.

Simulation models

Like analytical models, simulation models use complex algorithms to predict ecosystem dynamics. However, sophisticated computer programs have enabled simulation models to predict responses in complex ecosystems. Simulation models use numerical techniques to solve problems for which analytic solutions are impractical or impossible. These kinds of models tend to be more widely used. They are generally considered more ecologically realistic, while analytic models are valued for their mathematical elegance and explanatory power. These simulations are considered to be the most accurate and predictive of ecosystem dynamics.

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Key Points

- Conceptual models are often flow charts that demonstrate the relationships between different organisms in a community and their environment, including the transfer of energy and nutrients.
- Analytical models use mathematical equations to predict and describe simple, linear components of ecosystems, such as food chains.
- Simulation models use computer algorithms to predict ecosystem dynamics; they are considered the most ecologically-realistic and accurate.

Key Terms

- **conceptual model**: a model that is represented by conceptual representations of the relationships between different organisms in a community and their environment
- **analytical model**: a model that works best when dealing with relatively simple (often linear) systems, specifically those that can be accurately described by a set of mathematical equations whose behavior is well known
- **simulation model**: a model that utilizes mathematical algorithms to predict complex responses in ecosystem dynamics

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46.2: ENERGY FLOW THROUGH ECOSYSTEMS



- Topic hierarchy

46.2A: Strategies for Acquiring Energy

46.2B: Productivity within Trophic Levels

46.2C: Transfer of Energy between Trophic Levels

46.2D: Ecological Pyramids

46.2E: Biological Magnification

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46.2A: Strategies for Acquiring Energy

Learning Objectives

- Distinguish between photoautotrophs and chemoautotrophs and the ways in which they acquire energy

How Organisms Acquire Energy in a Food Web

All living things require energy in one form or another since energy is required by most, complex, metabolic pathways (often in the form of ATP); life itself is an energy-driven process. Living organisms would not be able to assemble macromolecules (proteins, lipids, nucleic acids, and complex carbohydrates) from their monomeric subunits without a constant energy input.

It is important to understand how organisms acquire energy and how that energy is passed from one organism to another through food webs and their constituent food chains. Food webs illustrate how energy flows directionally through ecosystems, including how efficiently organisms acquire it, use it, and how much remains for use by other organisms of the food web. Energy is acquired by living things in three ways: photosynthesis, chemosynthesis, and the consumption and digestion of other living or previously-living organisms by heterotrophs.

Photosynthetic and chemosynthetic organisms are grouped into a category known as autotrophs: 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, whereas chemosynthetic autotrophs (chemoautotrophs) use inorganic molecules as an energy source. Autotrophs act as producers and are critical for all ecosystems. 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, serve as the energy source for a majority of the world's ecosystems. These ecosystems are often described by grazing food webs. Photoautotrophs harness the solar energy of the sun 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.

Chemoautotrophs are primarily bacteria that are found in rare ecosystems where sunlight is not available, such as in those associated with dark caves or hydrothermal vents at the bottom of the ocean. Many chemoautotrophs in hydrothermal vents use hydrogen sulfide (H_2S), which is released from the vents, as a source of chemical energy. This allows chemoautotrophs to synthesize complex organic molecules, such as glucose, for their own energy and in turn supplies energy to the rest of the ecosystem.

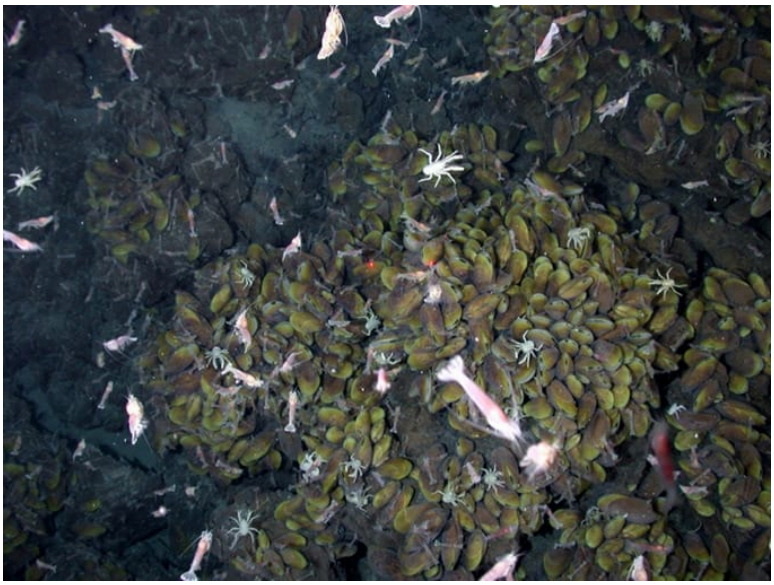


Figure 46.2A.1: Chemoautotrophs: Swimming shrimp, a few squat lobsters, and hundreds of vent mussels are seen at a hydrothermal vent at the bottom of the ocean. As no sunlight penetrates to this depth, the ecosystem is supported by chemoautotrophic bacteria and organic material that sinks from the ocean's surface.

Heterotrophs function as consumers in the food chain; they obtain energy in the form of organic carbon by eating autotrophs or other heterotrophs. They break down complex organic compounds produced by autotrophs into simpler compounds, releasing energy by oxidizing carbon and hydrogen atoms into carbon dioxide and water, respectively. Unlike autotrophs, heterotrophs are unable to synthesize their own food. If they cannot eat other organisms, they will die.

Key Points

- Food webs illustrate how energy flows through ecosystems, including how efficiently organisms acquire and use it.
- Autotrophs, producers in food webs, can be photosynthetic or chemosynthetic.
- Photoautotrophs use light energy to synthesize their own food, while chemoautotrophs use inorganic molecules.
- Chemoautotrophs are usually bacteria that live in ecosystems where sunlight is unavailable.
- Heterotrophs cannot synthesize their own energy, but must obtain it from autotrophs or other heterotrophs; they act as consumers in food webs.

Key Terms

- **photoautotroph**: an organism that can synthesize its own food by using light as a source of energy
- **chemoautotroph**: a simple organism, such as a protozoan, that derives its energy from chemical processes rather than photosynthesis
- **heterotroph**: an organism that requires an external supply of energy in the form of food, as it cannot synthesize its own

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46.2B: Productivity within Trophic Levels

Learning Objectives

- Explain the concept of primary production and distinguish between gross primary production and net primary production

Productivity within trophic levels

Productivity within an ecosystem can be defined as the percentage of energy entering the ecosystem incorporated into biomass in a particular trophic level. Biomass is the total mass in a unit area (at the time of measurement) of living or previously-living organisms within a trophic level. Ecosystems have characteristic amounts of biomass at each trophic level. For example, in the English Channel ecosystem, the primary producers account for a biomass of 4 g/m^2 (grams per meter squared), while the primary consumers exhibit a biomass of 21 g/m^2.

The productivity of the primary producers is especially important in any ecosystem because these organisms bring energy to other living organisms by photoautotrophy or chemoautotrophy. Photoautotrophy is the process by which an organism (such as a green plant) synthesizes its own food from inorganic material using light as a source of energy; chemoautotrophy, on the other hand, is the process by which simple organisms (such as bacteria or archaea) derive energy from chemical processes rather than photosynthesis. The rate at which photosynthetic primary producers incorporate energy from the sun is called gross primary productivity. An example of gross primary productivity is the compartment diagram of energy flow within the Silver Springs aquatic ecosystem. In this ecosystem, the total energy accumulated by the primary producers was shown to be 20,810 kcal/m^2/yr.

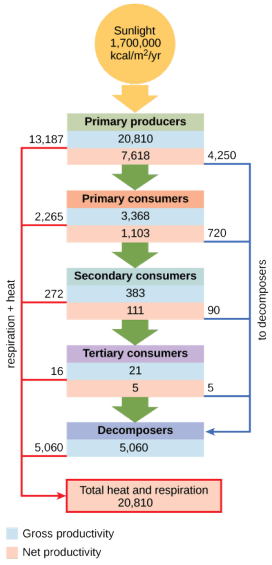


Figure $46.2B.1$: Energy flow in Silver Springs: This conceptual model shows the flow of energy through a spring ecosystem in Silver Springs, Florida. Notice that the energy decreases with each increase in trophic level.

Because all organisms need to use some of this energy for their own functions (such as respiration and resulting metabolic heat loss), scientists often refer to the net primary productivity of an ecosystem. Net primary productivity is the energy that remains in the primary producers after accounting for the organisms' respiration and heat loss. The net productivity is then available to the primary consumers at the next trophic level. In the Silver Spring example, 13,187 of the 20,810 kcal/m^2/yr were used for respiration or were lost as heat, leaving 7,632 kcal/m^2/yr of energy for use by the primary consumers.

Key Points

- A biomass is the total mass of living and previously-living organisms within a trophic level; ecosystems have characteristic amounts of biomass at each trophic level.
- The productivity of the primary producers (gross primary productivity) is important to ecosystems because these organisms bring energy to other living organisms.
- Net primary productivity (energy that remains in the primary producers after accounting for respiration and heat loss) is available to the primary consumers at the next trophic level.

Key Terms

- **biomass**: the total mass of all living things within a specific area, habitat, etc.
- **gross primary productivity**: rate at which photosynthetic primary producers incorporate energy from the sun
- **net primary productivity**: energy that remains in the primary producers after accounting for the organisms' respiration and heat loss
- **trophic level**: a particular position occupied by a group of organisms in a food chain (primary producer, primary consumer, secondary consumer, or tertiary consumer)

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46.2C: Transfer of Energy between Trophic Levels

Learning Objectives

- Illustrate the transfer of energy between trophic levels

Large amounts of energy are lost from the ecosystem between one trophic level and the next level as energy flows from the primary producers through the various trophic levels of consumers and decomposers. The main reason for this loss is the second law of thermodynamics, which states that whenever energy is converted from one form to another, there is a tendency toward disorder (entropy) in the system. In biologic systems, this means a great deal of energy is lost as metabolic heat when the organisms from one trophic level are consumed by the next level. The measurement of energy transfer efficiency between two successive trophic levels is termed the trophic level transfer efficiency (TLTE) and is defined by the formula:

TLTE=productionatpresenttrophiclevelproductionatprevioustrophiclevelx100TLTE=productionatpresenttrophiclevelproductionatpr

In Silver Springs, the TLTE between the first two trophic levels was approximately 14.8 percent. The low efficiency of energy transfer between trophic levels is usually the major factor that limits the length of food chains observed in a food web. The fact is, after four to six energy transfers, there is not enough energy left to support another trophic level. In the Lake Ontario ecosystem food web, only three energy transfers occurred between the primary producer (green algae) and the tertiary, or apex, consumer (Chinook salmon).

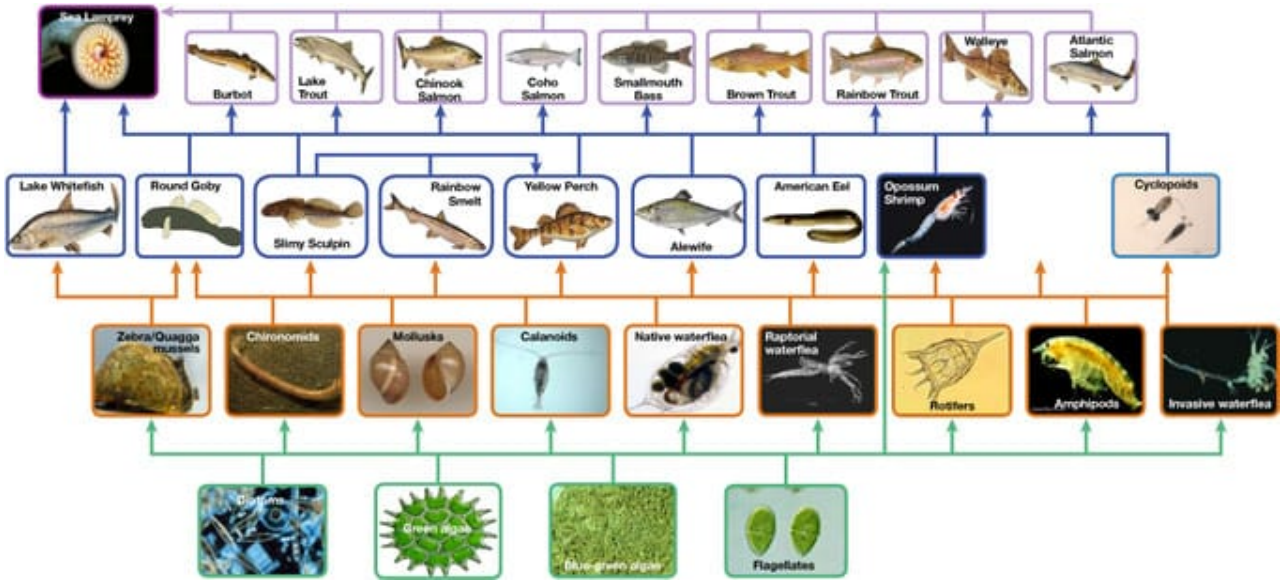


Figure 46.2C.1: Food web of Lake Ontario: This food web shows the interactions between organisms across trophic levels in the Lake Ontario ecosystem. Primary producers are outlined in green, primary consumers in orange, secondary consumers in blue, and tertiary (apex) consumers in purple. Arrows point from an organism that is consumed to the organism that consumes it. Notice how some lines point to more than one trophic level. For example, the opossum shrimp eats both primary producers and primary consumers.

Ecologists have many different methods of measuring energy transfers within ecosystems. Some transfers are easier or more difficult to measure depending on the complexity of the ecosystem and how much access scientists have to observe the ecosystem. In other words, some ecosystems are more difficult to study than others; sometimes the quantification of energy transfers has to be estimated.

Net production efficiency

Another main parameter that is important in characterizing energy flow within an ecosystem is the net production efficiency. Net production efficiency (NPE) allows ecologists to quantify how efficiently organisms of a particular trophic level incorporate the

energy they receive into biomass. It is calculated using the following formula:

NPE=netconsumerproductivityassimilationx100NPE=netconsumerproductivityassimilationx100

Net consumer productivity is the energy content available to the organisms of the next trophic level. Assimilation is the biomass (energy content generated per unit area) of the present trophic level after accounting for the energy lost due to incomplete ingestion of food, energy used for respiration, and energy lost as waste. Incomplete ingestion refers to the fact that some consumers eat only a part of their food. For example, when a lion kills an antelope, it will eat everything except the hide and bones. The lion is missing the energy-rich bone marrow inside the bone, so the lion does not make use of all the calories its prey could provide.

Thus, NPE measures how efficiently each trophic level uses and incorporates the energy from its food into biomass to fuel the next trophic level. In general, cold-blooded animals (ectotherms), such as invertebrates, fish, amphibians, and reptiles, use less of the energy they obtain for respiration and heat than warm-blooded animals (endotherms), such as birds and mammals. The extra heat generated in endotherms, although an advantage in terms of the activity of these organisms in colder environments, is a major disadvantage in terms of NPE. Therefore, many endotherms have to eat more often than ectotherms to obtain the energy they need for survival. In general, NPE for ectotherms is an order of magnitude (10x) higher than for endotherms. For example, the NPE for a caterpillar eating leaves has been measured at 18 percent, whereas the NPE for a squirrel eating acorns may be as low as 1.6 percent.

The inefficiency of energy use by warm-blooded animals has broad implications for the world's food supply. It is widely accepted that the meat industry uses large amounts of crops to feed livestock. Because the NPE is low, much of the energy from animal feed is lost. For example, it costs about $0.01 to produce 1000 dietary calories (kcal) of corn or soybeans, but approximately $0.19 to produce a similar number of calories growing cattle for beef consumption. The same energy content of milk from cattle is also costly, at approximately $0.16 per 1000 kcal. Much of this difference is due to the low NPE of cattle. Thus, there has been a growing movement worldwide to promote the consumption of non-meat and non-dairy foods so that less energy is wasted feeding animals for the meat industry.

Key Points

- Energy decreases as it moves up trophic levels because energy is lost as metabolic heat when the organisms from one trophic level are consumed by organisms from the next level.
- Trophic level transfer efficiency (TLTE) measures the amount of energy that is transferred between trophic levels.
- A food chain can usually sustain no more than six energy transfers before all the energy is used up.
- Net production efficiency (NPE) measures how efficiently each trophic level uses and incorporates the energy from its food into biomass to fuel the next trophic level.
- Endotherms have a low NPE and use more energy for heat and respiration than ectotherms, so most endotherms have to eat more often than ectotherms to get the energy they need for survival.
- Since cattle and other livestock have low NPEs, it is more costly to produce energy content in the form of meat and other animal products than in the form of corn, soybeans, and other crops.

Key Terms

- **assimilation**: the biomass of the present trophic level after accounting for the energy lost due to incomplete ingestion of food, energy used for respiration, and energy lost as waste
- **net consumer productivity**: energy content available to the organisms of the next trophic level
- **net production efficiency (NPE)**: measure of the ability of a trophic level to convert the energy it receives from the previous trophic level into biomass
- **trophic level transfer efficiency (TLTE)**: energy transfer efficiency between two successive trophic levels

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46.2D: Ecological Pyramids

Learning Objectives

- Explain the shape and structure of the ecological pyramid

Modeling ecosystems energy flow: ecological pyramids

The structure of ecosystems can be visualized with ecological pyramids, which were first described by the pioneering studies of Charles Elton in the 1920s. Ecological pyramids show the relative amounts of various parameters (such as number of organisms, energy, and biomass) across trophic levels. Ecological pyramids can also be called trophic pyramids or energy pyramids.

Pyramids of numbers can be either upright or inverted, depending on the ecosystem. A typical grassland during the summer has an upright shape since it has a base of many plants, with the numbers of organisms decreasing at each trophic level. However, during the summer in a temperate forest, the base of the pyramid consists of few trees compared with the number of primary consumers, mostly insects. Because trees are large, they have great photosynthetic capability and dominate other plants in this ecosystem to obtain sunlight. Even in smaller numbers, primary producers in forests are still capable of supporting other trophic levels.

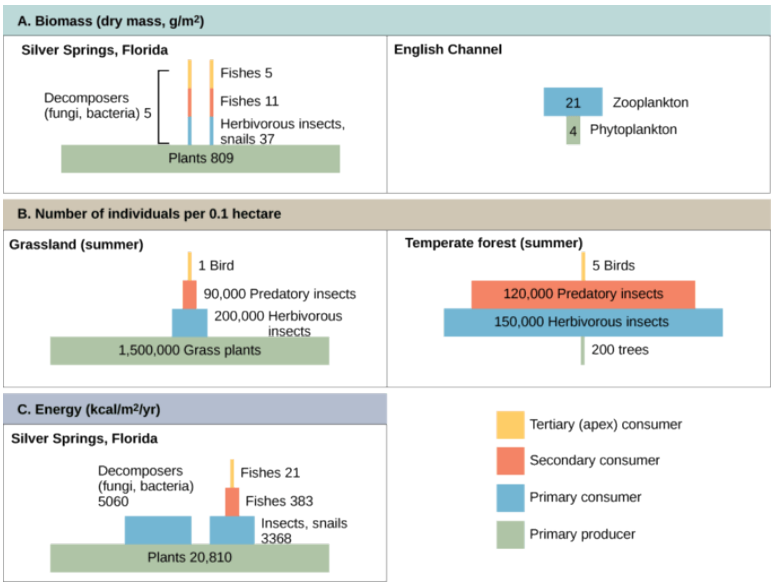


Figure $46.2D.1$: Ecological pyramids: Ecological pyramids depict the (a) biomass, (b) number of organisms, and (c) energy in each trophic level.

Another way to visualize ecosystem structure is with pyramids of biomass. This pyramid measures the amount of energy converted into living tissue at the different trophic levels. Using the Silver Springs ecosystem example, this data exhibits an upright biomass pyramid, whereas the pyramid from the English Channel example is inverted. The plants (primary producers) of the Silver Springs ecosystem make up a large percentage of the biomass found there. However, the phytoplankton in the English Channel example make up less biomass than the primary consumers, the zooplankton. As with inverted pyramids of numbers, the inverted biomass pyramid is not due to a lack of productivity from the primary producers, but results from the high turnover rate of the phytoplankton. The phytoplankton are consumed rapidly by the primary consumers, which minimizes their biomass at any particular point in time. However, since phytoplankton reproduce quickly, they are able to support the rest of the ecosystem.

Pyramid ecosystem modeling can also be used to show energy flow through the trophic levels. Pyramids of energy are always upright, since energy is lost at each trophic level; an ecosystem without sufficient primary productivity cannot be supported. All types of ecological pyramids are useful for characterizing ecosystem structure. However, in the study of energy flow through the ecosystem, pyramids of energy are the most consistent and representative models of ecosystem structure.

Key Points

- Pyramids of numbers can be either upright or inverted, depending on the ecosystem.
- Pyramids of biomass measure the amount of energy converted into living tissue at the different trophic levels.
- The English Channel ecosystem exhibits an inverted biomass pyramid since the primary producers make up less biomass than the primary consumers.
- Pyramid ecosystem modeling can also be used to show energy flow through the trophic levels; pyramids of energy are always upright since energy decreases at each trophic level.
- All types of ecological pyramids are useful for characterizing ecosystem structure; however, in the study of energy flow through the ecosystem, pyramids of energy are the most consistent and representative models of ecosystem structure.

Key Terms

- **ecological pyramid**: diagram that shows the relative amounts of energy or matter or numbers of organisms within each trophic level in a food chain or food web

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46.2E: Biological Magnification

Learning Objectives

- Describe the consequences of biomagnification between trophic levels

Consequences of Food Webs: Biological Magnification

One of the most important environmental consequences of ecosystem dynamics is biomagnification: the increasing concentration of persistent, toxic substances in organisms at each trophic level, from the primary producers to the apex consumers. Many substances have been shown to bioaccumulate, including classical studies with the pesticide dichlorodiphenyltrichloroethane (DDT), which was published in the 1960s bestseller, *Silent Spring*, by Rachel Carson. DDT was a commonly-used pesticide before its dangers became known. In some aquatic ecosystems, organisms from each trophic level consumed many organisms of 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, which was shown to have adverse 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 (PCBs), which were used in coolant liquids in the United States until their use was banned in 1979, and heavy metals, such as mercury, lead, and cadmium. These substances were best studied in aquatic ecosystems where fish species at different trophic levels accumulate toxic substances brought through the ecosystem by the primary producers. In a study performed by the National Oceanic and Atmospheric Administration (NOAA) in the Saginaw Bay of Lake Huron, PCB concentrations increased from the ecosystem's primary producers (phytoplankton) through the different trophic levels of fish species. The apex consumer (walleye) had 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.

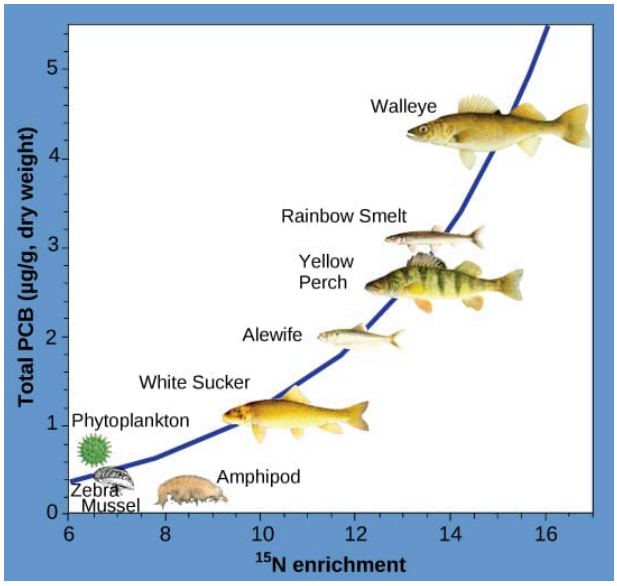


Figure 46.2E.1: PCB concentration in Lake Huron: This chart shows the PCB concentrations found at the various trophic levels in the Saginaw Bay ecosystem of Lake Huron. Numbers on the x-axis reflect enrichment with heavy isotopes of nitrogen (15N), which is a marker for increasing trophic levels. Notice that the fish in the higher trophic levels accumulate more PCBs than those in lower trophic levels.

Other concerns have been raised by the accumulation of heavy metals, such as mercury and cadmium, in certain types of seafood. The United States Environmental Protection Agency (EPA) 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, sardines, tilapia, shrimp, pollock, and catfish. Biomagnification is a good example of how

ecosystem dynamics can affect our everyday lives, even influencing the food we eat.

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Key Points

- Biomagnification increases the concentration of toxic substances in organisms at higher trophic levels.
- DDT is an example of a substance that biomagnifies; birds accumulate sufficient amounts of DDT from eating fish to cause adverse effects on bird populations.
- The presence of polychlorinated biphenyls (PCB) in phytoplankton causes increased PCB concentrations in walleyes and birds.
- Heavy metals, such as mercury and cadmium, found in certain types of seafood can also biomagnify.

Key Terms

- **biomagnification**: the process, in an ecosystem, in which a higher concentration of a substance in an organism is obtained higher up the food chain
- **dichlorodiphenyltrichloroethane**: a chlorinated hydrocarbon which is mainly used as an insecticide (DDT)
- **apex consumer**: consumers with few to no predators of their own, residing at the top of their food chain

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46.3: BIOGEOCHEMICAL CYCLES

- Topic hierarchy

46.3A: Biogeochemical Cycles

46.3B: The Water (Hydrologic) Cycle

46.3C: The Carbon Cycle

46.3D: The Nitrogen Cycle

46.3E: The Phosphorus Cycle

46.3E: The Sulfur Cycle

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46.3A: Biogeochemical Cycles

Learning Objectives

- Summarize the concept of biogeochemical cycles

Biogeochemocal Cycles: Introduction

Energy flows directionally through ecosystems, entering as sunlight (or inorganic molecules for chemoautotrophs) and leaving as heat during the many transfers between trophic levels. However, the matter that makes up living organisms is conserved and recycled. The six most common elements associated with organic molecules (carbon, nitrogen, hydrogen, oxygen, phosphorus, and sulfur) take a variety of chemical forms and may exist for long periods in the atmosphere, on land, in water, or beneath the earth's surface. Geologic processes, such as weathering, erosion, water drainage, and the movement of the continental plates, all play a role in this recycling of materials. Because geology and chemistry have major roles in the study of this process, the recycling of inorganic matter between living organisms and their environment is called a biogeochemical cycle.

The components of organic molecules are constantly being stored and recycled as part of their biogeochemical cycle. Water, which contains hydrogen and oxygen, is essential to all living processes. The hydrosphere is the area of the earth where water movement and storage occurs. Water can be liquid on the surface and beneath the surface or frozen (rivers, lakes, oceans, groundwater, polar ice caps, and glaciers) or exist as water vapor in the atmosphere. Carbon, found in all organic macromolecules, is an important constituent of fossil fuels. Nitrogen, a major component of our nucleic acids and proteins, is critical to human agriculture. Phosphorus, a major component of nucleic acid (along with nitrogen), is one of the main ingredients in artificial fertilizers used in agriculture and their associated environmental impacts on our surface water. Sulfur, critical to the 3–D folding of proteins (as in disulfide binding), is released into the atmosphere by the burning of fossil fuels, such as coal.

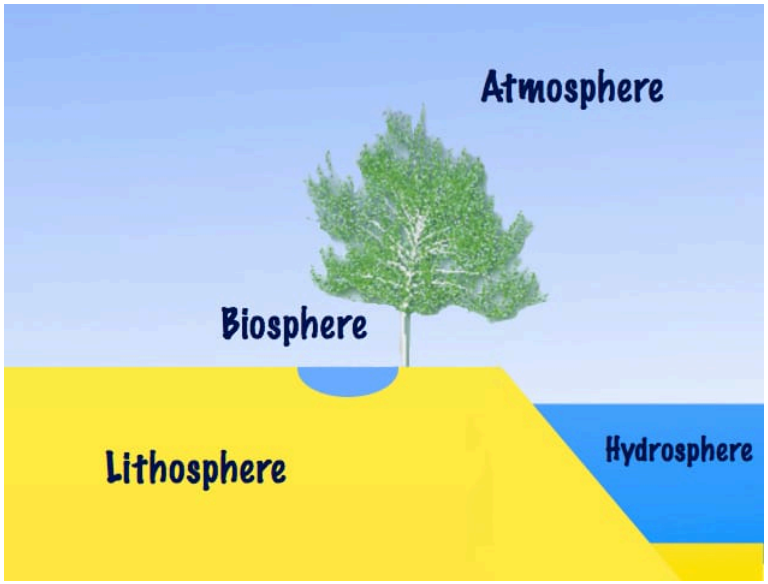


Figure 46.3A.1: Importance of the hydrosphere: Earth has a hydrosphere, where water movement and storage occurs. It is important for leaching certain components of organic matter into rivers, lakes, and oceans, and is a reservoir for carbon.

The cycling of all of these elements is interconnected. For example, the movement of water is critical for the leaching of nitrogen and phosphate into rivers, lakes, and oceans. Furthermore, the ocean itself is a major reservoir for carbon. Thus, mineral nutrients are cycled, either rapidly or slowly, through the entire biosphere, from one living organism to another, and between the biotic and abiotic world.

Key Points

- Carbon, nitrogen, hydrogen, oxygen, phosphorus, and sulfur are conserved and recycled in the atmosphere, on land, in water, or beneath the earth's surface.
- Materials are recycled via erosion, weathering, water drainage, and the movement of tectonic plates.
- Water is essential to all living processes, while carbon is found in all organic macromolecules.
- Nitrogen and phosphorus are major components of nucleic acids and play major roles in agriculture.
- Sulfur plays a role in the three-dimensional folding of proteins and is released into the atmosphere by the burning of fossil fuels.

Key Terms

- **hydrosphere**: combined mass of water found on, under, and over the surface of a planet
- **biogeochemical cycle**: cycling of mineral nutrients through ecosystems and through the non-living world

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46.3B: The Water (Hydrologic) Cycle

Learning Objectives

- Explain the path of the hydrologic cycle and its importance

Water is the basis of all living processes. More than half of the human body is made up of water, while human cells are more than 70 percent water. Thus, most land animals need a supply of fresh water to survive. However, when examining the stores of water on earth, 97.5 percent of it is non-potable salt water. Of the remaining water, 99 percent is locked underground as water or as ice. Thus, less than 1 percent of fresh water is easily accessible from lakes and rivers. Many living things, such as plants, animals, and fungi, are dependent on the small amount of fresh surface water supply, a lack of which can have massive effects on ecosystem dynamics. Humans, of course, have developed technologies to increase water availability, such as digging wells to harvest groundwater, storing rainwater, and using desalination to obtain drinkable water from the ocean. Although this pursuit of drinkable water has been ongoing throughout human history, the supply of fresh water is still a major issue in modern times.

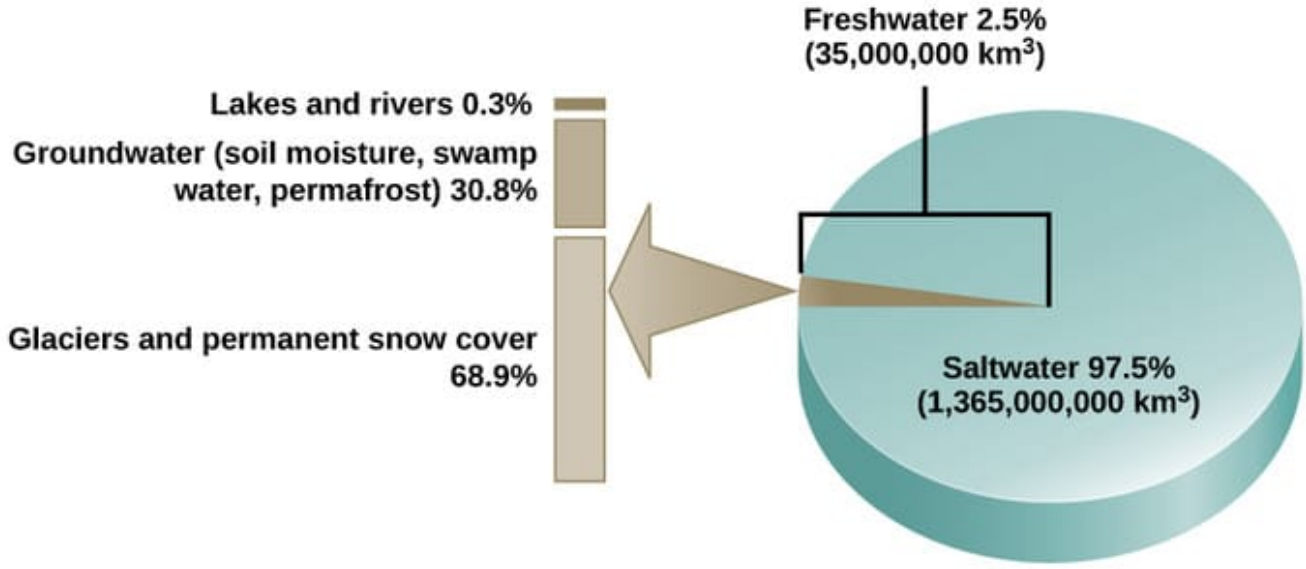


Figure $46.3B.1$: Water availability: Only 2.5 percent of water on earth is fresh water. Less than 1 percent of fresh water is easily accessible to living things.

Water cycling is extremely important to ecosystem dynamics as it has a major influence on climate and, thus, on the environments of ecosystems. For example, when water evaporates, it takes up energy from its surroundings, cooling the environment. When it condenses, it releases energy, warming the environment. The evaporation phase of the cycle purifies water, which then replenishes the land with fresh water. The flow of liquid water and ice transports minerals across the globe. It is also involved in reshaping the geological features of the earth through processes including erosion and sedimentation. The water cycle is also essential for the maintenance of most life and ecosystems on the planet. Most of the water on earth is stored for long periods in the oceans, underground, and as ice. Residence time is a measure of the average time an individual water molecule stays in a particular reservoir. A large amount of the earth's water is locked in place in these reservoirs as ice, beneath the ground, and in the ocean, and, thus, is unavailable for short-term cycling (only surface water can evaporate).

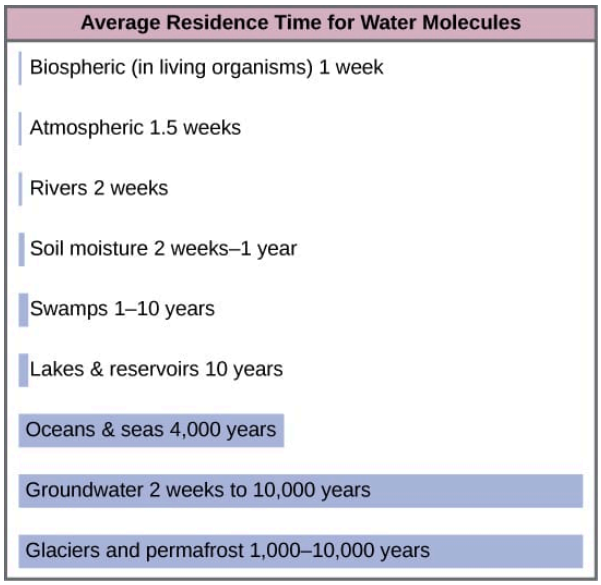


Figure $46.3B.1$: Residence time of water: This graph shows the average residence time for water molecules in the earth's water reservoirs. Most of the earth's water is unavailable for use because it is locked in ice, beneath the ground, or in the oceans.

There are various processes that occur during the cycling of water, which include the following:

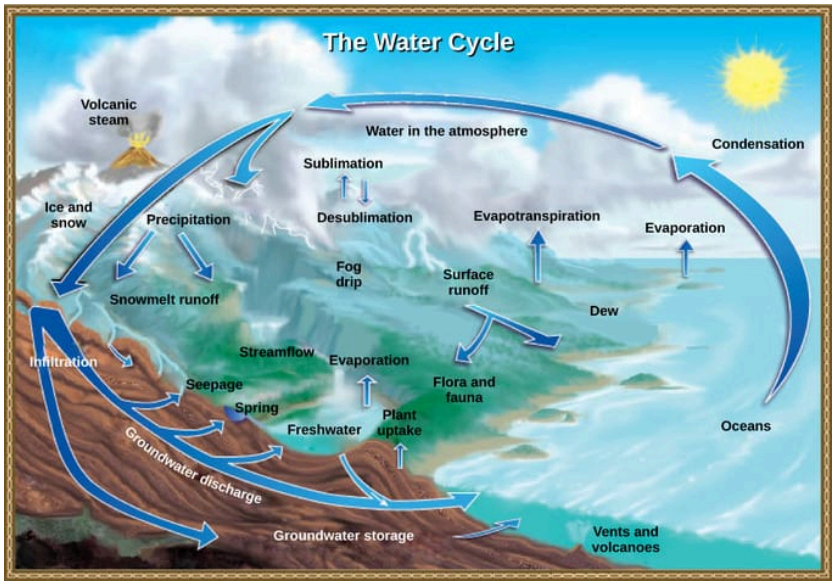


Figure $46.3B.1$: Cycling of water: Water from the land and oceans enters the atmosphere by evaporation or sublimation, where it condenses into clouds and falls as rain or snow. Precipitated water may enter freshwater bodies or infiltrate the soil. The cycle is complete when surface or groundwater reenters the ocean.

- evaporation/ sublimation
- condensation/precipitation
- subsurface water flow
- surface runoff/snowmelt
- streamflow

The water cycle is driven by the sun's energy as it warms the oceans and other surface waters. This leads to the evaporation (water to water vapor) of liquid surface water and the sublimation (ice to water vapor) of frozen water, which deposits large amounts of water vapor into the atmosphere. Over time, this water vapor condenses into clouds as liquid or frozen droplets, which is eventually followed by precipitation (rain or snow), returning water to the earth's surface. Rain eventually percolates into the ground, where it may evaporate again (if it is near the surface), flow beneath the surface, or be stored for long periods. More easily observed is surface runoff: the flow of fresh water either from rain or melting ice. Runoff can then make its way through streams and lakes to

the oceans or flow directly to the oceans themselves. Rain and surface runoff are major ways in which minerals, including carbon, nitrogen, phosphorus, and sulfur, are cycled from land to water.

Key Points

- Water cycling affects the climate, transports minerals, purifies water, and replenishes the land with fresh water.
- Water with a longer residence time, such as water in oceans and glaciers, is not available for short-term cycling, which occurs via evaporation.
- Surface water evaporates (water to water vapor) or sublimates (ice to water vapor), which deposits large amounts of water vapor into the atmosphere.
- Water vapor in the atmosphere condenses into clouds and is eventually followed by precipitation, which returns water to the earth's surface.
- Rain percolates into the ground, where it may evaporate or enter bodies of water.
- Surface runoff enters oceans directly or via streams and lakes.

Key Terms

- **residence time**: the average time a particular molecule of water will remain in a body of water
- **condensation**: the conversion of a gas to a liquid; the condensate so formed
- **surface runoff**: overland flow of excess water (with or without accumulated contaminants) that cannot be absorbed by the ground as infiltration
- **Evaporation**: the process of a liquid converting to the gaseous state
- **sublimation**: the transition of a substance from the solid phase directly to the vapor state such that it does not pass through the intermediate liquid phase

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46.3C: The Carbon Cycle

Learning Objectives

- Distinguish between the biological and biogeochemical cycles of carbon

Carbon, the second most abundant element in living organisms, is present in all organic molecules. Its role in the structure of macromolecules is of primary importance to living organisms. Carbon compounds contain especially- high forms of energy, which humans use as fuel. Since the 1800s (the beginning of the Industrial Revolution), the number of countries using massive amounts of fossil fuels increased, which raised the levels of carbon dioxide in the atmosphere. This increase in carbon dioxide has been associated with climate change and other disturbances of the earth's ecosystems. It is a major environmental concern worldwide.

The carbon cycle is most easily studied as two interconnected sub-cycles: one dealing with rapid carbon exchange among living organisms and the other dealing with the long-term cycling of carbon through geologic processes.

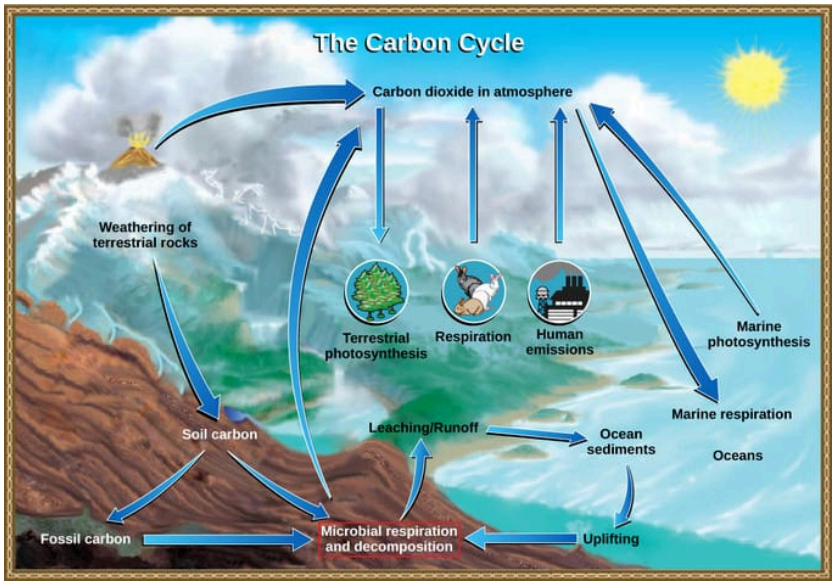


Figure $46.3C.1$: Carbon cycle: Carbon dioxide gas exists in the atmosphere and is dissolved in water. Photosynthesis converts carbon dioxide gas to organic carbon, while respiration cycles the organic carbon back into carbon dioxide gas. Long-term storage of organic carbon occurs when matter from living organisms is buried deep underground and becomes fossilized. Volcanic activity and human emissions bring this stored carbon back into the carbon cycle.

The Biological Carbon Cycle

Living organisms are connected in many ways, even between ecosystems. A good example of this connection is the exchange of carbon between autotrophs and heterotrophs. Carbon dioxide is the basic building block that most autotrophs use to build multi-carbon, high-energy compounds, such as glucose. The energy harnessed from the sun is used by these organisms to form the covalent bonds that link carbon atoms together. These chemical bonds store this energy for later use in the process of respiration. Most terrestrial autotrophs obtain their carbon dioxide directly from the atmosphere, while marine autotrophs acquire it in the dissolved form (carbonic acid, $H_2CO_3^-$). However carbon dioxide is acquired, a by-product of the process is oxygen. The photosynthetic organisms are responsible for depositing approximately 21 percent of the oxygen content in the atmosphere that we observe today.

Heterotrophs acquire the high-energy carbon compounds from the autotrophs by consuming them and breaking them down by respiration to obtain cellular energy, such as ATP. The most efficient type of respiration, aerobic respiration, requires oxygen obtained from the atmosphere or dissolved in water. Thus, there is a constant exchange of oxygen and carbon dioxide between the autotrophs (which need the carbon) and the heterotrophs (which need the oxygen). Gas exchange through the atmosphere

and water is one way that the carbon cycle connects all living organisms on Earth.

The Biogeochemical Carbon Cycle

The movement of carbon through the land, water, and air is complex and, in many cases, it occurs much more slowly than the biological carbon cycle. Carbon is stored for long periods in what are known as carbon reservoirs, which include the atmosphere, bodies of liquid water (mostly oceans), ocean sediment, soil, land sediments (including fossil fuels), and the earth's interior.

As stated, the atmosphere, a major reservoir of carbon in the form of carbon dioxide, is essential to the process of photosynthesis. The level of carbon dioxide in the atmosphere is greatly influenced by the reservoir of carbon in the oceans. The exchange of carbon between the atmosphere and water reservoirs influences how much carbon is found in each location; each affects the other reciprocally. Carbon dioxide (CO_2) from the atmosphere dissolves in water, combining with water molecules to form carbonic acid. It then ionizes to carbonate and bicarbonate ions.

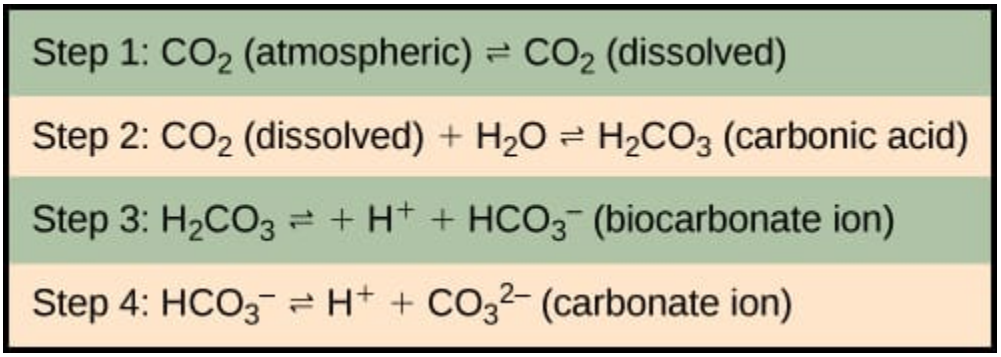


Figure $46.3C.1$: Formation of bicarbonate: Carbon dioxide reacts with water to form bicarbonate and carbonate ions.

More than 90 percent of the carbon in the ocean is found as bicarbonate ions. Some of these ions combine with seawater calcium to form calcium carbonate ($CaCO_3$), a major component of marine organism shells. These organisms eventually form sediments on the ocean floor. Over geologic time, the calcium carbonate forms limestone, which comprises the largest carbon reservoir on earth.

On land, carbon is stored in soil as a result of the decomposition of living organisms or the weathering of terrestrial rock and minerals. This carbon can be leached into the water reservoirs by surface runoff. Deeper underground, on land and at sea, are fossil fuels: the anaerobically-decomposed remains of plants that take millions of years to form. Fossil fuels are considered a non-renewable resource because their use far exceeds their rate of formation. A non-renewable resource is either regenerated very slowly or not at all. Another way for carbon to enter the atmosphere is from land by the eruption of volcanoes and other geothermal systems. Carbon sediments from the ocean floor are taken deep within the earth by the process of subduction: the movement of one tectonic plate beneath another. Carbon is released as carbon dioxide when a volcano erupts or from volcanic hydrothermal vents.

Carbon dioxide is also added to the atmosphere by the breeding and raising of livestock. The large numbers of land animals raised to feed the earth's growing population results in increased carbon dioxide levels in the atmosphere due to farming practices, respiration, and methane production. This is another example of how human activity indirectly affects biogeochemical cycles in a significant way. Although much of the debate about the future effects of increasing atmospheric carbon on climate change focuses on fossils fuels, scientists take natural processes, such as volcanoes and respiration, into account as they model and predict the future impact of this increase.

Key Points

- Carbon is present in all organic molecules; carbon compounds contain large amounts of energy, which humans use as fuel.
- The biological carbon cycle is the rapid exchange of carbon among living things; autotrophs use carbon dioxide produced by heterotrophs to produce glucose and oxygen, which are then utilized by heterotrophs.
- The biogeochemical cycle occurs at a much slower rate than the biological cycle since carbon is stored in carbon reservoirs for long periods of time.
- Carbon dioxide from the atmosphere dissolves in water, combining with water molecules to form carbonic acid, which then

ionizes to carbonate and bicarbonate ions.
- Most of the carbon in the ocean is in the form of bicarbonate ions, which can combine with seawater calcium to form calcium carbonate ($CaCO_3$), a major component of marine organism shells.
- Carbon can enter the soil as a result of the decomposition of living organisms, the weathering of rocks, the eruption of volcanoes, and other geothermal systems.

Key Terms

- **subduction**: movement of one tectonic plate beneath another
- **non-renewable resource**: resource, such as fossil fuel, that is either regenerated very slowly or not at all
- **autotroph**: Any organism that can synthesize its food from inorganic substances, using heat or light as a source of energy
- **heterotroph**: an organism that requires an external supply of energy in the form of food, as it cannot synthesize its own

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46.3D: The Nitrogen Cycle

Learning Objectives

- Describe the nitrogen cycle

Getting nitrogen into the living world is difficult. Plants and phytoplankton are not equipped to incorporate nitrogen from the atmosphere (which exists as tightly-bonded, triple-covalent N_2), even though this molecule comprises approximately 78 percent of the atmosphere. Nitrogen enters the living world via free-living and symbiotic bacteria, which incorporate nitrogen into their macromolecules through nitrogen fixation (conversion of N_2). Cyanobacteria live in most aquatic ecosystems where sunlight is present; they play a key role in nitrogen fixation. Cyanobacteria are able to use inorganic sources of nitrogen to "fix" nitrogen. *Rhizobium*bacteria live symbiotically in the root nodules of legumes (such as peas, beans, and peanuts), providing them with the organic nitrogen they need. Free-living bacteria, such as *Azotobacter*, are also important nitrogen fixers.

Organic nitrogen is especially important to the study of ecosystem dynamics as many ecosystem processes, such as primary production and decomposition, are limited by the available supply of nitrogen. The nitrogen that enters living systems by nitrogen fixation is successively converted from organic nitrogen back into nitrogen gas by bacteria. This process occurs in three steps in terrestrial systems: ammonification, nitrification, and denitrification. First, the ammonification process converts nitrogenous waste from living animals or from the remains of dead animals into ammonium (NH_4^+) by certain bacteria and fungi. Second, the ammonium is converted to nitrites (NO_2^-) by nitrifying bacteria, such as *Nitrosomonas*, through nitrification. Subsequently, nitrites are converted to nitrates (NO_3^-) by similar organisms. Third, the process of denitrification occurs, whereby bacteria, such as *Pseudomonas* and *Clostridium*, convert the nitrates into nitrogen gas, allowing it to re-enter the atmosphere.

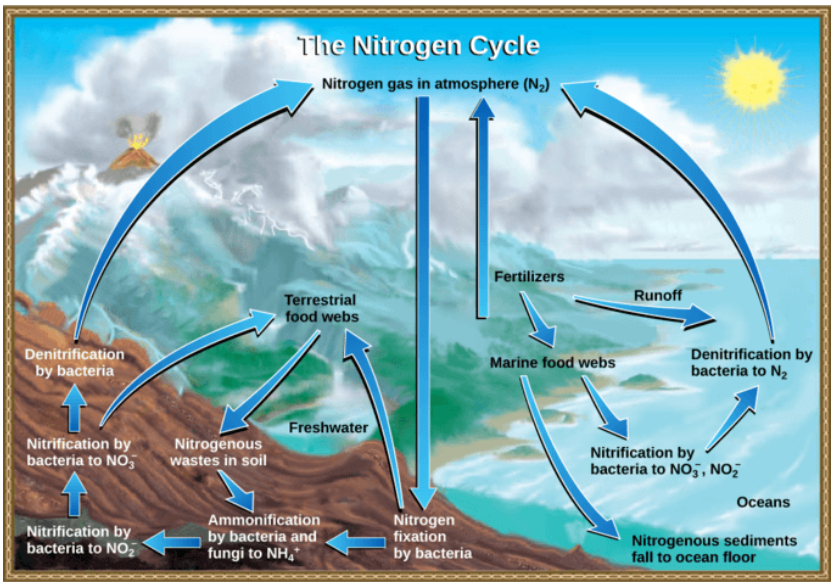


Figure $46.3D.1$: Nitrogen fixation: Nitrogen enters the living world from the atmosphere via nitrogen-fixing bacteria. This nitrogen and nitrogenous waste from animals is then processed back into gaseous nitrogen by soil bacteria, which also supply terrestrial food webs with the organic nitrogen they need.

Human activity can release nitrogen into the environment by two primary means: the combustion of fossil fuels, which releases different nitrogen oxides, and the use of artificial fertilizers in agriculture, which are then washed into lakes, streams, and rivers by surface runoff. Atmospheric nitrogen is associated with several effects on earth's ecosystems, including the production of acid rain (as nitric acid, HNO_3) and greenhouse gas (as nitrous oxide, N_2O), potentially causing climate change. A major effect from fertilizer runoff is saltwater and freshwater eutrophication: a process whereby nutrient runoff causes the excess growth of microorganisms, depleting dissolved oxygen levels and killing ecosystem fauna.

A similar process occurs in the marine nitrogen cycle, where the ammonification, nitrification, and denitrification processes are

performed by marine bacteria. Some of this nitrogen falls to the ocean floor as sediment, which can then be moved to land in geologic time by uplift of the earth's surface, becoming incorporated into terrestrial rock. Although the movement of nitrogen from rock directly into living systems has been traditionally seen as insignificant compared with nitrogen fixed from the atmosphere, a recent study showed that this process may indeed be significant and should be included in any study of the global nitrogen cycle.

Key Points

- Bacteria, such as cyanobacteria, convert nitrogen into nitrogen gas via nitrogen fixation.
- Nitrogen fixation occurs in three steps: ammonification, nitrification, and denitrification.
- Human activity can release nitrogen into the environment by the combustion of fossil fuels and by the use of artificial fertilizers in agriculture.
- Atmospheric nitrogen is responsible for acid rain, the release of greenhouse gasses, and eutrophication.
- Nitrogen fixation can be performed by marine bacteria; nitrogen falls to the ocean floor as sediment and is then moved to land, becoming incorporated into terrestrial rock.

Key Terms

- **denitrification**: process of converting nitrates into nitrogen gas, especially by the action of bacteria
- **nitrification**: the conversion of ammonium into nitrites (NO_2^-) by nitrifying bacteria
- **ammonification**: the formation of ammonia or its compounds from nitrogenous compounds, especially as a result of bacterial decomposition

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46.3E: The Phosphorus Cycle

Learning Objectives

- Describe the phosphorus cycle and the effects of phosphorus on the environment

Phosphorus is an essential nutrient for living processes. It is a major component of nucleic acid, both DNA and RNA; of phospholipids, the major component of cell membranes; and, as calcium phosphate, makes up the supportive components of our bones. Phosphorus is often the limiting nutrient (necessary for growth) in aquatic ecosystems.

Phosphorus occurs in nature as the phosphate ion (PO_4^{3-}). In addition to phosphate runoff as a result of human activity, natural surface runoff occurs when it is leached from phosphate-containing rock by weathering, thus sending phosphates into rivers, lakes, and the ocean. This rock has its origins in the ocean. Phosphate-containing ocean sediments form primarily from the bodies of ocean organisms and from their excretions. However, in remote regions, volcanic ash, aerosols, and mineral dust may also be significant phosphate sources. This sediment then is moved to land over geologic time by the uplifting of areas of the earth's surface.

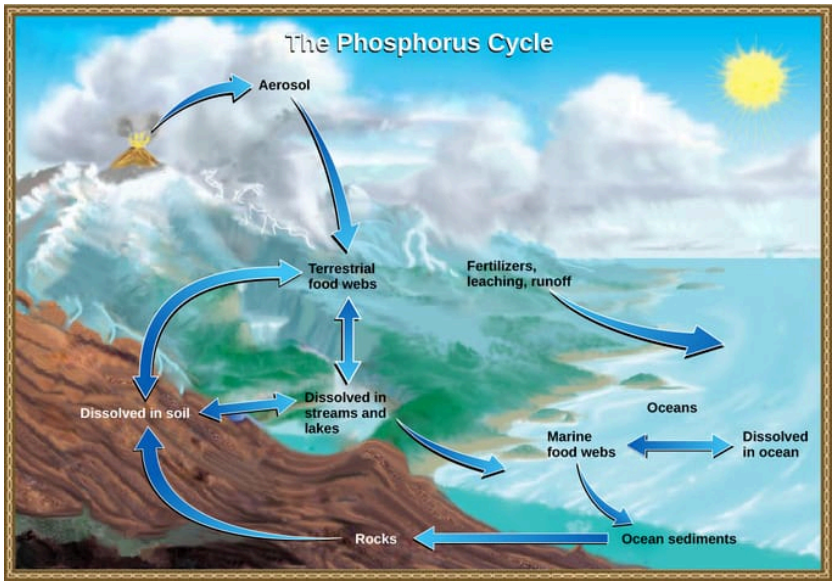


Figure $46.3E.1$: Phosphorus cycle: In nature, phosphorus exists as the phosphate ion (PO43–). Weathering of rocks and volcanic activity releases phosphate into the soil, water, and air, where it becomes available to terrestrial food webs. Phosphate enters the oceans via surface runoff, groundwater flow, and river flow. Phosphate dissolved in ocean water cycles into marine food webs. Some phosphate from the marine food webs falls to the ocean floor, where it forms sediment.

Phosphorus is also reciprocally exchanged between phosphate dissolved in the ocean and marine ecosystems. The movement of phosphate from the ocean to the land and through the soil is extremely slow, with the average phosphate ion having an oceanic residence time between 20,000 and 100,000 years.

Excess phosphorus and nitrogen that enters these ecosystems from fertilizer runoff and from sewage causes excessive growth of microorganisms and depletes the dissolved oxygen, which leads to the death of many ecosystem fauna, such as shellfish and finfish. This process is responsible for dead zones in lakes and at the mouths of many major rivers.

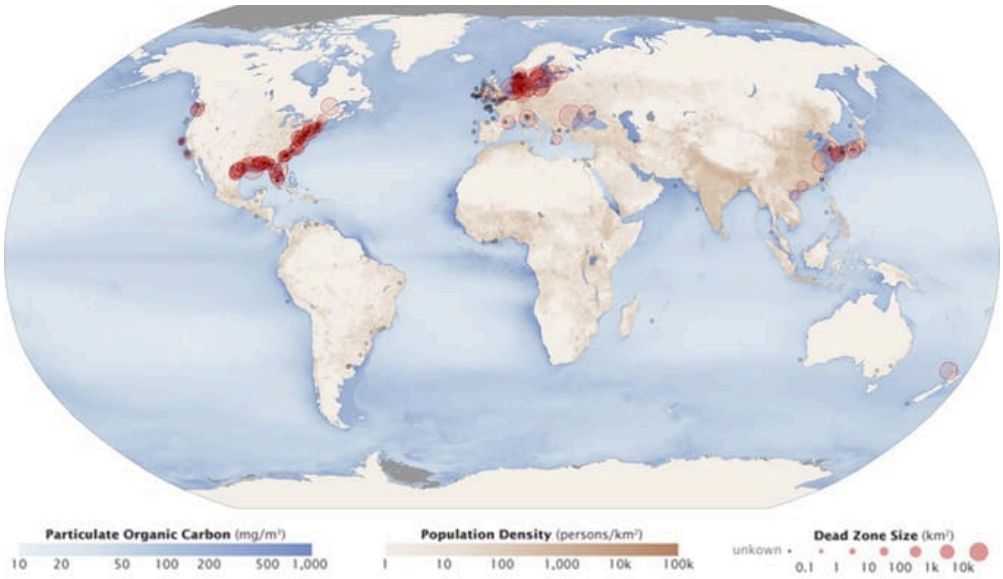


Figure $46.3E.1$: Dead zones: Dead zones occur when phosphorus and nitrogen from fertilizers cause excessive growth of microorganisms, which depletes oxygen, killing flora and fauna. Worldwide, large dead zones are found in coastal areas of high population density.

A dead zone is an area within a freshwater or marine ecosystem where large areas are depleted of their normal flora and fauna. These zones can be caused by eutrophication, oil spills, dumping of toxic chemicals, and other human activities. The number of dead zones has been increasing for several years; more than 400 of these zones were present as of 2008. One of the worst dead zones is off the coast of the United States in the Gulf of Mexico, where fertilizer runoff from the Mississippi River basin has created a dead zone of over 8,463 square miles. Phosphate and nitrate runoff from fertilizers also negatively affect several lake and bay ecosystems, including the Chesapeake Bay in the eastern United States, which was one of the first ecosystems to have identified dead zones.

Key Points

- Phosphorus, a major component of nucleic acid and phospholipids, also makes up the supportive components of our bones; it is often necessary for growth in aquatic ecosystems.
- Phosphates (PO_4^{3-}) are sent into rivers, lakes, and the ocean by leaching and natural surface runoff.
- Phosphate-containing ocean sediments slowly move to land by the uplifting of areas of the earth's surface.
- Excess phosphorus and nitrogen in the ecosystem leads to the death of many organisms, causing dead zones.
- Dead zones are caused by by eutrophication, oil spills, dumping of toxic chemicals, and other human activities.

Key Terms

- **eutrophication**: process whereby excess levels of nitrogen or phosphorus cause excessive growth of microorganisms, depleting dissolved oxygen levels and kill ecosystem fauna
- **dead zone**: an area within a freshwater or marine ecosystem where large areas are depleted of their normal flora and fauna; caused by excessive nutrient pollution

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46.3E: The Sulfur Cycle

Learning Objectives

- Describe the sulfur cycle

Sulfur is an essential element for the macromolecules of living things. As a part of the amino acid cysteine, it is involved in the formation of disulfide bonds within proteins, which help to determine their 3-D folding patterns and, hence, their functions. Sulfur cycles exist between the oceans, land, and atmosphere.

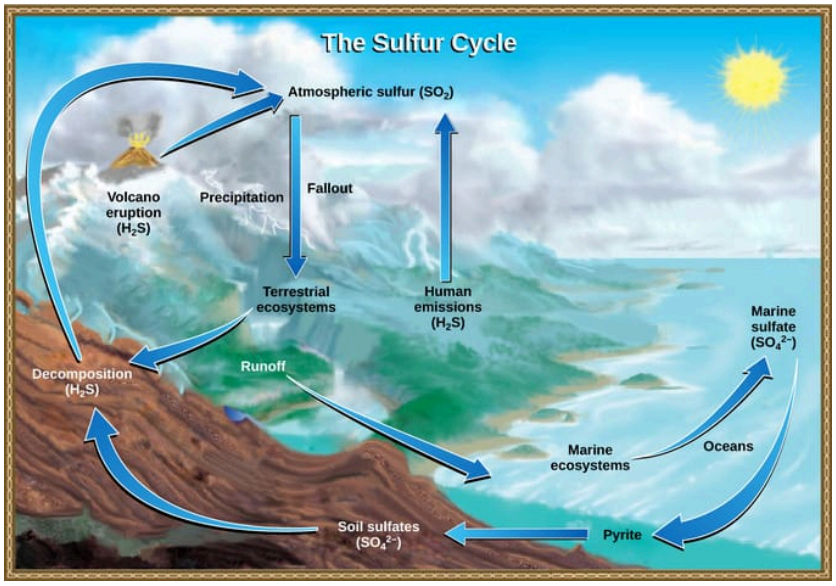


Figure $46.3E.1$: Sulfur cycle: Sulfur dioxide from the atmosphere becomes available to terrestrial and marine ecosystems when it is dissolved in precipitation as weak sulfuric acid or when it falls directly to the earth as fallout. Weathering of rocks also makes sulfates available to terrestrial ecosystems. Decomposition of living organisms returns sulfates to the ocean, soil, and atmosphere.

On land, sulfur is deposited in four major ways: precipitation, direct fallout from the atmosphere, rock weathering, and decomposition of organic materials. Atmospheric sulfur is found in the form of sulfur dioxide (SO_2). As rain falls through the atmosphere, sulfur is dissolved in the form of weak sulfuric acid (H_2SO_4), creating acid rain. Sulfur can also fall directly from the atmosphere in a process called fallout. The weathering of sulfur-containing rocks also releases sulfur into the soil. These rocks originate from ocean sediments that are moved to land by the geologic uplift. Terrestrial ecosystems can then make use of these soil sulfates (SO_4^{2-}). Upon the death and decomposition of these organisms, sulfur is released back into the atmosphere as hydrogen sulfide (H_2S) gas. Sulfur may also enter the atmosphere through geothermal vents.



Figure $46.3E.1$: Sulfur vents: At this sulfur vent in Lassen Volcanic National Park in northeastern California, the yellowish sulfur deposits are visible near the mouth of the vent.

Sulfur enters the ocean via runoff from land, fallout, and underwater geothermal vents. Some marine ecosystems rely on chemoautotrophs, using sulfur as a biological energy source. This sulfur then supports marine ecosystems in the form of sulfates.

Human activities have played a major role in altering the balance of the global sulfur cycle. The burning of large quantities of fossil fuels, especially from coal, releases large amounts of hydrogen sulfide gas into the atmosphere, creating acid rain. Acid rain is corrosive rain that causes damage to aquatic ecosystems and the natural environment by lowering the pH of lakes, which kills many of the resident fauna; it also affects the human-made environment through the chemical degradation of buildings. For example, many marble monuments, such as the Lincoln Memorial in Washington, DC, have suffered significant damage from acid rain over the years. These examples show the wide-ranging effects of human activities on our environment and the challenges that remain for our future.

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Key Points

- Sulfur is an essential element for the macromolecules of living things since it determines the 3-D folding patterns of proteins.
- On land, sulfur enters the atmosphere via acid rain, fallout, the weathering of rocks, decompostion of organic materials, and geothermal vents.
- Sulfur enters the ocean via runoff, fallout, and underwater geothermal vents; some marine ecosystems also rely on chemoautotrophs as a sulfur source.

- The burning of fossil fuels increases the amount of sulfide in the atmosphere and causes acid rain.
- Acid rain is corrosive rain that causes damage to aquatic ecosystems by lowering the pH of lakes, killing many of the resident fauna; it also degrades buildings and human-made structures.

Key Terms

- **chemoautotroph**: a simple organism, such as a protozoan, that derives its energy from chemical processes rather than photosynthesis
- **fallout**: direct deposit of solid minerals on land or in the ocean from the atmosphere
- **acid rain**: corrosive rain caused by rainwater falling to the ground through sulfur dioxide gas, turning it into weak sulfuric acid; can damage structures and ecosystems

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47: CONSERVATION BIOLOGY AND BIODIVERSITY

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47.1: THE BIODIVERSITY CRISIS

47.1A: Loss of Biodiversity

47.1B: Types of Biodiversity

47.1C: Biodiversity Change through Geological Time

47.1D: The Pleistocene Extinction

47.1E: Present-Time Extinctions

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47.1A: Loss of Biodiversity

Learning Objectives

- Explain the biodiversity crisis

The Biodiversity Crisis

Traditionally, ecologists have measured biodiversity, a general term for the variety of species present in the biosphere, by taking into account both the number of species and their commonness. Biodiversity can be estimated at a number of levels of organization of living things. These estimation indexes, which came from information theory, are most useful as a first step in quantifying biodiversity between and within ecosystems, yet they are less useful when the main concern among conservation biologists is simply the loss of biodiversity. However, biologists recognize that measures of biodiversity, in terms of species diversity, may help focus efforts to preserve the biologically or technologically important elements of biodiversity.

Cichlids in Lake Victoria

The Lake Victoria cichlids provide an example through which we can begin to understand biodiversity. The biologists studying cichlids in the 1980s discovered hundreds of cichlid species representing a variety of specializations to particular habitat types and specific feeding strategies: eating plankton floating in the water, scraping and then eating algae from rocks, eating insect larvae from the bottom, and eating the eggs of other species of cichlid. The cichlids of Lake Victoria are the product of an adaptive radiation. An adaptive radiation is a rapid (less than three million years in the case of the Lake Victoria cichlids) branching through speciation of a phylogenetic tree into many closely-related species; typically, the species “radiate” into different habitats and niches. The Galápagos finches are an example of a modest adaptive radiation with 15 species. The cichlids of Lake Victoria are an example of a spectacular adaptive radiation that includes about 500 species.

At the time biologists were making this discovery, some species began to quickly disappear. A culprit in these declines was a species of large fish that was introduced to Lake Victoria by fisheries to feed the people living around the lake. The Nile perch was introduced in 1963, but was not a problem until the 1980s when its population began to surge by consuming cichlids, driving species after species to the point of extinction (the disappearance of a species). In fact, there were several factors that played a role in the extinction of perhaps 200 cichlid species in Lake Victoria. These factors included not only the Nile perch, but also the declining lake water quality due to agriculture and land clearing on the shores of Lake Victoria, and increased fishing pressure. Scientists had not even cataloged all of the species present, so many were lost that they were never named. The diversity is now a shadow of what it once was.



Figure 47.1A.1: Lake Victoria and biodiversity loss: Lake Victoria in Africa, shown in this satellite image, was the site of one of the most extraordinary evolutionary findings on the planet, as well as a casualty of devastating biodiversity loss.

Causes of Biodiversity

The cichlids of Lake Victoria are a thumbnail sketch of contemporary rapid species loss caused by human activity occurring all over earth. Extinction, a natural process of macroevolution, occurs at the rate of about one out of 1 million species becoming extinct per year. The fossil record reveals that there have been five periods of mass extinction in history with much higher rates of species loss. The rate of species loss today is comparable to those periods of mass extinction. However, there is a major difference between the previous mass extinctions and the current extinction we are experiencing: human activity. Specifically, three human activities have a major impact: destruction of habitat, introduction of exotic invasive species, and over-harvesting. Predictions of species loss within the next century, a tiny amount of time on geological timescales, range from 10 percent to 50 percent. The five previous extinctions on this scale were caused by cataclysmic events that changed the course of the history of life in each instance. Earth is now in one of those times.

Key Points

- Biodiversity is the variety of species present in the biosphere; the main goal of conservationists is to preserve biodiversity.
- An example of biodiversity loss was the extinction of over 200 species of cichlids in Lake Victoria; this was caused by the introduction of the Nile Perch as well as increased agriculture and fishing.
- Unlike the five previous mass extinctions, the current one is a result of detrimental human activities.
- Current human-caused biodiversity loss is the result activities such as habitat destruction, the introduction of exotic invasive species, and the over-harvesting of species.

Key Terms

- **biodiversity**: the diversity (number and variety of species) of plant and animal life within a region
- **adaptive radiation**: the diversification of species into separate forms that each adapt to occupy a specific environmental niche
- **invasive species**: any species that has been introduced to an environment where it is not native and has since become a nuisance through rapid spread and increase in numbers, often to the detriment of native species
- **extinction**: disappearance of a species from earth; local extinction is the disappearance of a species from a region

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47.1B: Types of Biodiversity

Learning Objectives

- Differentiate among the types of biodiversity

Types of Biodiversity

Scientists generally accept that the term biodiversity describes the number and kinds of species in a location or on the planet. Species can be difficult to define, but most biologists still feel comfortable with the concept and are able to identify and count eukaryotic species in most contexts. Biologists have also identified alternate measures of biodiversity, some of which are important for planning how to preserve biodiversity.

Genetic diversity is one of those alternate concepts. 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. If there were a choice between one of these genera of species being preserved, the one with the greatest potential for subsequent evolution is the most genetically-diverse one. It would be ideal not to have to make such choices, but, increasingly, this may be the norm.

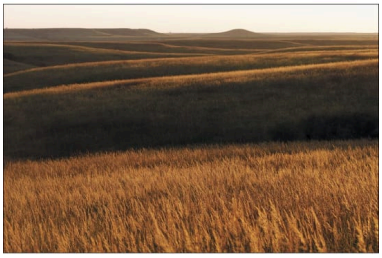
Many genes code for proteins, which in turn carry out the metabolic processes that keep organisms alive and reproducing. Genetic diversity can be measured as chemical diversity in that different species produce a variety of chemicals in their cells, both the proteins as well as the products and by-products of metabolism. This chemical diversity has potential benefit for humans as a source of pharmaceuticals, so it provides one way to measure diversity that is important to human health and welfare.

Humans have generated diversity in domestic animals, plants, and fungi. This diversity is also suffering losses because of migration, market forces, and increasing globalism in agriculture, especially in heavily-populated regions such as China, India, and Japan. The human population directly depends on this diversity as a stable food source; its decline is troubling to biologists and agricultural scientists.

It is also useful to define ecosystem diversity: the number of different ecosystems on the planet or in a given geographic 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 interactions between species, the loss of unique features of co-adaptation, 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. Prairies once spanned central North America from the boreal forest in northern Canada down into Mexico. Now, they have mostly disappeared, replaced by crop fields, pasture lands, and suburban sprawl. Many of the species survive, but the hugely-productive ecosystem that was responsible for creating the most productive agricultural soils is now gone. As a consequence, soils are disappearing or must be maintained at greater expense.



(a)



(b)

Figure 47.1B.1: Ecosystem diversity: The variety of ecosystems on earth, from (a) coral reef to (b) prairie, enables a great diversity of species to exist.

Current Species Diversity

Despite considerable effort, knowledge of the species that inhabit the planet is limited. A recent estimate suggests that the number of identified eukaryote species, 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 begun to catalog their diversity. Even with what is known, there is no central repository of names or samples of the described species; therefore, there is no way to be sure that 1.5 million is an accurate number. It is a best guess based on the opinions of experts in different taxonomic groups. Given that earth is losing species at an accelerating pace, science knows little about what is being lost.

Estimates of the Numbers of Described and Predicted Species by Taxonomic Group						
	Mora et al. 2011[1]		Chapman 2009[2]		Groombridge & Jenkins 2002[3]	
	Described	Predicted	Described	Predicted	Described	Predicted
Animalia	1,124,516	9,920,000	1,424,153	6,836,330	1,225,500	10,820,000
Chromista	17,892	34,900	25,044	200,500	—	—
Fungi	44,368	616,320	98,998	1,500,000	72,000	1,500,000
Plantae	224,244	314,600	310,129	390,800	270,000	320,000
Protozoa	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

Figure 47.1B.1: Estimates of species diversity: Scientists have only been able to account for less than 20 percent of eukaryotic species that live on the planet. This table depicts the estimates based on taxonomic group.

There are various initiatives to catalog described species in accessible ways; the internet is facilitating that effort. Nevertheless, it has been pointed out that at the current rate of species description, which according to the State of Observed Species Report is 17,000 to 20,000 new species per year, it will take close to 500 years to finish describing life on this planet.

Naming and counting species may seem an unimportant pursuit given the other needs of humanity, but it is not as simple as counting. 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, which allows them to follow up on questions about its biology. In addition, the unique characteristics of each species make it potentially valuable to humans or other species on which humans depend. Understanding these characteristics is the value of finding and naming species.

Key Points

- A genus with a high variety of species will have more genetic diversity; the most genetically-diverse species will have the greatest potential for evolution and preservation.
- The loss of ecosystem diversity results in the loss of interactions between species, unique features of co- adaptation, and biological productivity.
- Human-generated species diversity has decreased due to migration, market forces, and agriculture.
- Humans have only been able to estimate the number of species that inhabit earth; this estimate accounts for about 20 percent of predicted species on the planet.
- Humans have only been able to estimate the number of species that inhabit Earth; this estimate only accounts for 20 percent of predicted species on the planet.

Key Terms

- **genetic diversity**: variety of genes in a species or other taxonomic group or ecosystem; can refer to allelic diversity or genome-wide diversity
- **ecosystem diversity**: variety of ecosystems in a biosphere or the variety of species and ecological processes that occur in different physical settings
- **chemical diversity**: variety of metabolic compounds in an ecosystem

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47.1C: Biodiversity Change through Geological Time

Learning Objectives

- Describe how biodiversity has changed through geological time as a result of mass extinctions

Biodiversity Change through Geological 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 number of species will decrease when extinction rates begin to overtake speciation rates. Throughout earth's history, these two processes have fluctuated, sometimes leading to dramatic changes in the number of species on earth.

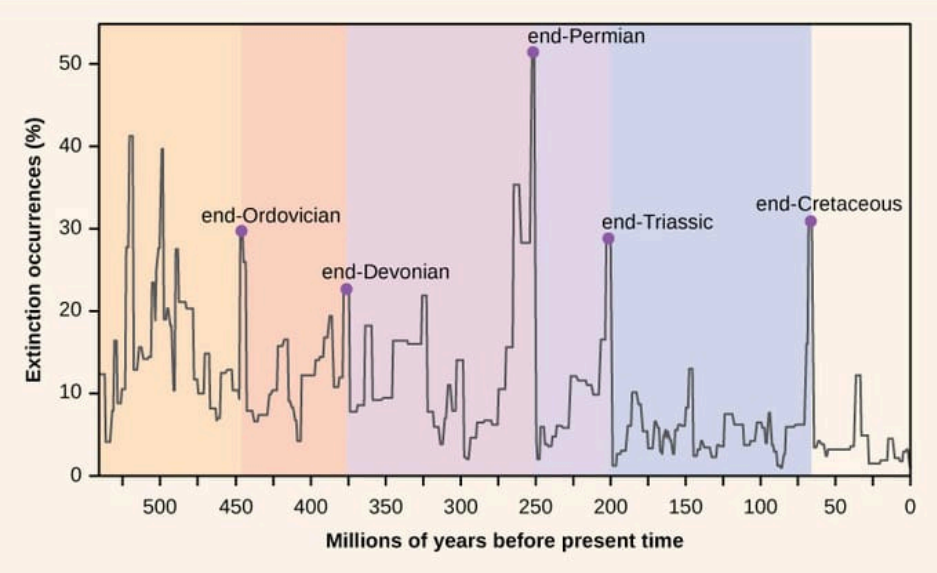


Figure $47.1C.1$: Fossil record: Extinction occurrences, as reflected in the fossil record, have fluctuated throughout earth's history. Sudden and dramatic losses of biodiversity, called mass extinctions, have occurred five times.

Paleontologists have identified five strata in the fossil record that appear to show sudden and dramatic losses in biodiversity known as mass extinctions. There are many lesser, yet still dramatic, extinction events, but the five mass extinctions have attracted the most research. 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 Phanerozoic (since 542 million years ago). In most cases, the hypothesized causes are still controversial.

The Five Mass Extinctions

The fossil record of the mass extinctions was the basis for defining periods of geological history, so they typically occur at the transition point between geological periods. The transition in fossils from one period to another reflects the dramatic loss of species and the gradual origin of new species.

Mass Extinctions		
Geological Period	**Mass Extinction Name**	**Time (millions of years ago)**
Ordovician–Silurian	end-Ordovician O–S	450–440
Late Devonian	end-Devonian	375–360
Permian–Triassic	end-Permian	251
Triassic–Jurassic	end-Triassic	205
Cretaceous–Paleogene	end-Cretaceous K–Pg (K–T)	65.5

Figure $47.1C.1$: Five mass extinctions: The transitions between the five main mass extinctions can be seen in the rock strata. The table shows the time that elapsed between each period.

The Ordovician-Silurian extinction event is the first-recorded mass extinction and the second largest. During this period, about 85 percent of marine species (few species lived outside the oceans) became extinct. The main hypothesis for its cause was a period of glaciation followed by warming. These two extinction events, cooling and warming, were separated by about 1 million years; the climate changes affected temperatures and sea levels. Some researchers have suggested that a gamma-ray burst caused by a nearby supernova is a possible cause of the Ordovician-Silurian extinction. The gamma-ray burst would have stripped away the earth's ozone layer, causing intense ultraviolet radiation from the sun. It may account for climate changes observed at the time.

The late Devonian extinction may have occurred over a relatively long period of time. Its causes are poorly-understood and it appears to have have affected only marine species.

The end-Permian extinction was the largest in the history of life. Estimates predict that 96 percent of all marine species and 70 percent of all terrestrial species were lost.The causes for this mass extinction are not clear, but the leading suspect is extended and widespread volcanic activity that led to a runaway global-warming event. The oceans became largely anoxic, suffocating marine life. Terrestrial tetrapod diversity took 30 million years to recover after the end-Permian extinction. The Permian extinction dramatically altered earth's biodiversity composition and the course of evolution.

The causes of the Triassic–Jurassic extinction event are not clear. Hypotheses of climate change, asteroid impact, and volcanic eruptions have been argued. The extinction event occurred just before the breakup of the supercontinent Pangaea; although, recent scholarship suggests that the extinctions may have occurred more gradually throughout the Triassic.

The causes of the end-Cretaceous extinction event are the ones that are best understood. It was during this extinction event, about 65 million years ago, that the dinosaurs, the dominant vertebrate group for millions of years, disappeared from the planet (with the exception of a theropod clade that gave rise to birds). Indeed, every land animal that weighed more then 25 kg became extinct. The cause of this extinction is now understood to be the result of a cataclysmic impact of a large meteorite or asteroid off the coast of what is now the Yucatán Peninsula. This hypothesis, proposed first in 1980, was a radical explanation based on a sharp spike in the levels of iridium (which rains down from space in meteors at a fairly constant rate, but is otherwise absent on earth's surface) at the rock stratum that marks the boundary between the Cretaceous and Paleogene periods. The Cretaceous-Paleogene (K-Pg) boundary marked the disappearance of the dinosaurs in fossils, as well as many other taxa. The researchers who discovered the iridium spike interpreted it as a rapid influx of iridium from space to the atmosphere (in the form of a large asteroid), rather than a slowing in the deposition of sediments during that period. It was a radical explanation, but the report of an appropriately aged and sized impact crater in 1991 made the hypothesis more credible. Now, an abundance of geological evidence supports the hypothesis. Recovery times for biodiversity after the end-Cretaceous extinction were shorter, in geological time, than for the end-Permian extinction: on the order of 10 million years.



Figure 47.1C.1: K-Pg mass extinction: In 1980, Luis and Walter Alvarez, Frank Asaro, and Helen Michels discovered, across the world, a spike in the concentration of iridium within the sedimentary layer at the K–Pg boundary. These researchers hypothesized that this iridium spike was caused by an asteroid impact that resulted in the K–Pg mass extinction. In the photo, the iridium layer is the light band.

Key Points

- Fossil records have been instrumental in differentiating between five periods that appear to show sudden and dramatic losses in biodiversity.
- Although there have been smaller periods of extinction, the five mass extinction periods demonstrate a continuous series of large extinction events.
- The Ordovician-Silurian extinction event was caused by glaciation followed by warming; it led to the extinction of 85 percent of marine species.
- The late Devonian extinction affected only marine species; the end- Permian extinction, the largest in history, may have been caused by volcanic activity, leading to a global-warming type event.
- The Triassic–Jurassic extinction event may have been caused by climate change, asteroid impact, or volcanic eruptions; however, the main cause is still unclear.
- The end- Cretaceous extinction event, in which the extinction of the dinosaurs occurred, is believed to have been caused by the impact of a large asteroid.

Key Terms

- **macroevolution**: large-scale patterns or processes in the history of life, including the origins of novel organism designs, evolutionary trends, adaptive radiations and extinctions
- **theropod**: any large, bipedal dinosaur, of the suborder Theropoda, from the Jurassic and Cretaceous periods
- **anoxic**: suffering from a reduced supply of oxygen

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47.1D: The Pleistocene Extinction

Learning Objectives

- Describe the biodiversity loss associated with the Pleistocene extinction

The Pleistocene Extinction is one of the lesser extinctions and a relatively-recent one. It is well known that the North American, and to some degree Eurasian, megafauna disappeared toward the end of the last glaciation period. The extinction appears to have happened in a relatively-restricted time period between 10,000–12,000 years ago. In North America, the losses were quite dramatic and included the woolly mammoths (last dated about 4,000 years ago in an isolated population), mastodons, giant beavers, giant ground sloths, saber-toothed cats, and the North American camel, to name just a few. The possibility that the rapid extinction of these large animals was caused by over-hunting was first suggested in the 1900s; research into this hypothesis continues today. It seems probable that over-hunting was a factor in extinctions in many regions of the world.



Figure $47.1D.1$: Giant ground sloth: Giant ground sloths, relatives of the living South American tree sloths, lived across much of North America. The giant sloths disappeared, along with the mammoths, mastodons, and many other large animals, at the end of the Pleistocene Epoch.

In general, the timing of the Pleistocene extinctions correlated with the arrival of humans and not with climate -change events, which is the main competing hypothesis for these extinctions. The extinctions began in Australia about 40,000 to 50,000 years ago, 10,000 to 20,000 years after the arrival of humans in the area. A marsupial lion, a giant one-ton wombat, and several giant kangaroo species disappeared. In North America, the extinctions of almost all of the large mammals occurred 10,000 to 12,000 years ago, several thousand years after the first evidence of humans in North America. All that are left are the smaller mammals such as bears, elk, moose, and cougars. Finally, on many remote oceanic islands, the extinctions of many species occurred with the coincidence of human arrivals. Not all of the islands had large animals, but when there were large animals, they were lost. Madagascar was colonized about 2,000 years ago; the large mammals (prosimians) that lived there became extinct. Eurasia and Africa do not show this pattern, but they also did not experience a recent arrival of humans. Humans arrived in Eurasia hundreds of thousands to over one million years ago, after the origin of the species in Africa. This topic remains an area of active research and hypothesizing. It seems clear that even if climate played a role, human hunting was an additional factor in the extinctions.

Key Points

- The Pleistocene extinction in North America appears to have happened 10,000–12,000 years ago; this is several thousand years after the arrival of humans, who may have contributed to the extinction through hunting.
- Regions that experienced relatively-recent human arrivals show patterns of dramatic extinctions of megafauna hundreds to thousands of years after humans arrived; the same patterns are not observed in Eurasia and Africa as they did not experience

a relatively-recent arrival of humans.
- To date, over-hunting by humans is one probable factor for the extinction of large mammals in the Pleistocene period.

Key Terms

- **Pleistocene**: of a geologic epoch within the Neogene period from about 2.6 million to 11,000 years ago; marked by the evolution of humans and the extinction of the large mammals
- **megafauna**: the large animals of a given region or time, considered as a group

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47.1E: Present-Time Extinctions

Learning Objectives

- Describe the biodiversity loss during the Holocene extinction

Present-Time Extinctions

The sixth, or Holocene, mass extinction appears to have begun earlier than previously believed and is mostly due to the activities of *Homo sapiens*. Since the beginning of the Holocene period, there have been numerous recent extinctions of individual species that are recorded in human writings. Most of these coincide with the expansion of the European colonies in the 1500s.

One of the earlier and popularly-known examples of extinction in this period is the dodo bird. The dodo bird lived in the forests of Mauritius, an island in the Indian Ocean, but became extinct around 1662. It was hunted for its meat by sailors as it 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.

Another example, Steller's sea cows, became extinct in 1768.The sea cow, first discovered by Europeans in 1741, was hunted for meat and oil. The last of the species was killed in 1768, which amounts to 27 years between the species' first contact with Europeans and its extinction. In addition, the last living passenger pigeon died in a zoo in Cincinnati, Ohio in 1914. This species was hunted and suffered from habitat loss through the clearing of forests for farmland. Furthermore, in 1918, the last living Carolina parakeet died in captivity. This species, once common in the eastern United States, was a victim of habitat loss and hunting as well. Adding to the extinction list, the Japanese sea lion, which inhabited a broad area around Japan and the coast of Korea, became extinct in the 1950s due to overfishing. The Caribbean monk seal, found in the Caribbean Sea, was driven to extinction through hunting by 1952.

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 extinct species of vertebrates after 1500 AD, 86 of which were made extinct by over-hunting or overfishing.

Estimates of Present-Time Extinction Rates

Estimates of extinction rates are hampered by the fact that most extinctions are probably happening without observation since there are many organisms that are of less interest to humans and many that are undescribed.

The background extinction rate is estimated to be about one per million species per year (E/MSY). For example, assuming there are about ten million species in existence, the expectation is that ten species would become extinct each year.

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. However, this value may be underestimated for three reasons. First, many species would not have been described until much later in the time period, so their loss would have gone unnoticed. Secondly, the number of recently-extinct species is increasing because extinct species now are being described from skeletal remains. Lastly, 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 closer to 100 E/MSY. The predicted rate by the end of the century is 1500 E/MSY.

A second approach to estimating present-day extinction rates is to correlate species loss with habitat loss by 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. Studies have shown that the number of species present increases as the size of the island increases. This phenomenon has also been shown to hold true in other habitats as well. Turning this relationship around, if the habitat area is reduced, the number of species living there will also decline. Estimates of extinction rates based on habitat loss and species-area relationships have suggested that with about 90 percent habitat loss an expected 50 percent of species would become extinct. Species-area estimates have led to species extinction rate calculations of about 1000 E/MSY and higher. In general, actual observations do not show this amount of loss, suggesting that there is a delay in extinction. 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. A better relationship to use may be the endemics-area relationship. Using this 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.

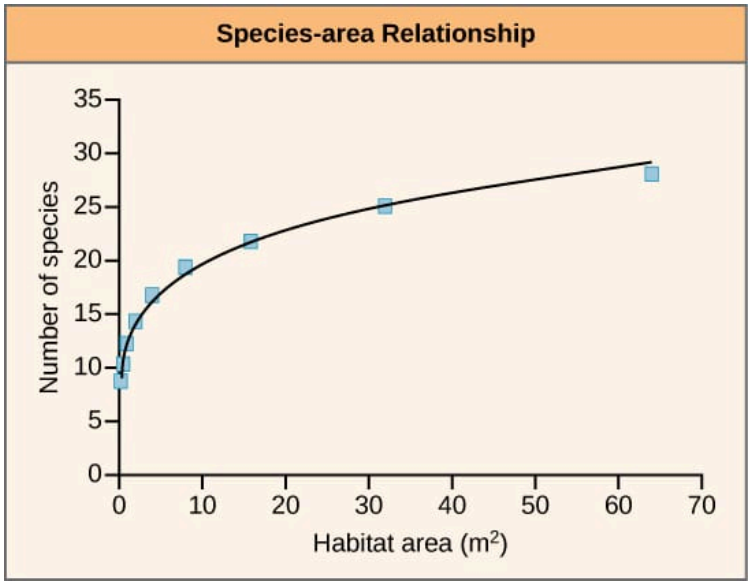


Figure 47.1E.1: Species-area extinction estimates: Studies have shown that the number of species that are present increases with the size of the habitat. As habitat is lost, the number of species present will decrease.

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Key Points

- The dodo was one of the first-known examples of a species that went extinct (in the 1600s) during the Holocene period.
- Steller's sea cows, passenger pigeons, Carolina parakeets, Japanese sea lions, and Caribbean monk seals are examples of species that went extinct from the 1700s-1900s.
- Major reasons for species extinctions during the Holocene period are due to overhunting, overfishing, and other human-related activities.
- Extinction rates can be estimated by comparing extinction events since the 1500s, but this method may underestimate the actual extinction rate value.
- Extinction rates can be estimated by observing species-area relationships and correlating species loss with habitat loss; however, this method may lead to overestimation.

Key Terms

- **species-area relationship**: 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
- **Holocene**: of a geologic epoch within the Neogene period from about 11,000 years ago to the present
- **extinction rate**: number of species becoming extinct over time, sometimes defined as extinctions per million species–years to make numbers manageable (E/MSY)

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47.2: THE IMPORTANCE OF BIODIVERSITY TO HUMAN LIFE

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- Topic hierarchy

47.2A: Human Health and Biodiversity
47.2B: Agricultural Diversity
47.2C: Managing Fisheries

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47.2A: Human Health and Biodiversity

Learning Objectives

- Describe the benefits to human health of maintaining biodiversity

Human Health

Contemporary societies that live close to the land often have a broad knowledge of the medicinal uses of plants growing in their area. Most plants produce secondary plant compounds, which are toxins used to protect the plants from insects and other animals that eat them, but some of which also work as medicines. For centuries in Europe, older knowledge about the medicinal uses of plants was compiled in herbals: books that identified plants and their uses. Humans are not the only species to use plants for medicinal reasons: the 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. Many medicines 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. Antibiotics, which are responsible for extraordinary improvements in health and lifespans in developed countries, are compounds largely derived from fungi and bacteria.



Figure $47.2A.1$: Medicinal uses of plants: 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.

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. 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 medicines improve people's lives. Pharmaceutical companies are actively looking for new compounds synthesized by living organisms that can function as medicine. It is estimated that one-third of pharmaceutical research and development is spent on natural compounds. About 35 percent of new drugs brought to market between 1981 and 2002 were from natural compounds. The opportunities for new medications will be reduced in direct proportion to the disappearance of species. It is beneficial to humans, therefore, for medicinal purposes and many others, to

maintain biodiversity.

Key Points

- Most plants produce secondary plant compounds, which are toxins used to protect the plant from insects and other animals that eat them, but some of which also work as medication.
- Antibiotics, which are responsible for extraordinary improvements in health and lifespans in developed countries, are compounds largely derived from fungi and bacteria.
- In recent years, animal venoms and poisons have excited intense research for their medicinal potential; at least five of these drugs have been FDA approved since 2007.

Key Terms

- **atropine**: an alkaloid extracted from the plant deadly nightshade (Atropa belladonna); used as a drug in medicine for its paralytic effects (in surgery to relax muscles, in dentistry to dry the mouth, etc.)
- **vincristine**: a particular drug used in chemotherapy
- **antibiotic**: any substance that can destroy or inhibit the growth of bacteria and similar microorganisms

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47.2B: Agricultural Diversity

Learning Objectives

- Assess the interactions of biodiversity with agricultural diversity

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 potatoes grown in that region belong to seven species, while the number of varieties is probably in the thousands. Each variety has been bred to thrive at particular elevations and soil and climate conditions. The diversity is driven by the demands of the topography, the limited movement of people, and the demands created by crop rotation for different varieties that will do well in different fields and microclimates.

Potatoes are only one example of human-generated 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. The tragic, Irish potato famine occurred when the single 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; 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.



Figure $47.2B.1$: Svalbard Global Seed Vault: The Svalbard Global Seed Vault is a protected storage facility in the arctic for seeds of earth's diverse crops.

The ability to create new crop varieties relies on the diversity of varieties available and the accessibility 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 food supply.

Since the 1920s, government agriculture departments have maintained seed banks of crop varieties as a way to maintain crop diversity. Sometimes, however, seed banks are lost through accidents; there is no way to replace them. In 2008, the Svalbard Global Seed Vault 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 those stored here. The seed vault is located deep into the

rock of an 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.

Key Points

- Agricultural diversity is driven by the demands of the topography, the limited movement of people, and the needs for crop rotation of varieties that do well in different fields.
- Resistance to disease is a chief benefit to maintaining crop biodiversity; lack of diversity in crop species risks an entire crop being wiped out by a disease to which it is susceptible.
- The ability to create new crop varieties relies on the diversity of varieties available and the accessibility of wild forms related to the crop plant that can be bred with existing varieties.
- Seed companies must continually breed new varieties to keep up with evolving pest organisms.

Key Terms

- **blight**: any of many plant diseases causing damage to, or the death of, leaves, fruit or other parts

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47.2C: Managing Fisheries

Learning Objectives

- Explain the impact that the collapse of marine fisheries will have on human diet and health

Managing Wild Food Resources

In addition to growing crops and raising animals for food, humans obtain food resources from wild populations, primarily fish populations. For approximately 1 billion people, aquatic resources provide the main source of animal protein. But since 1990, global fish production has declined dramatically. Despite considerable effort, few fisheries on the planet are managed for sustainability.

Overfishing

Overfishing is the harvest of an aquatic population to a level that is too low for that population to replenish itself. Resource depletion, low biological growth rates, and critically low biomass levels result from overfishing. For example, overfishing of sharks has disrupted entire marine ecosystems.



Figure $47.2C.1$: Overfishing: When a fish stock is reduced to a level that is too low to allow that stock to replenish itself, overfishing has occurred. In addition to eliminating major food sources, overfishing is a threat to aquatic biodiversity.

The ability of a fishery to recover from overfishing depends on the species' natural ability to replenish itself as well as the ecosystem's conditions. Dramatic changes in species composition can result in an ecosystem shift, where other equilibrium energy flows involve species compositions different from those that had been present before overfishing occurred. For example, once trout have been overfished, carp might take over in a way that makes it impossible for the trout to re-establish a breeding population.

Sustainable Ecosystem Management

Fishery extinctions rarely lead to complete extinction of the harvested species, but rather to a radical restructuring of the marine ecosystem in which an abundant species is so over-harvested that it becomes a minor player, ecologically. In general, the fish taken from fisheries have shifted to smaller species as larger species are fished to extinction. 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 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 as larger species are fished to extinction. 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 populations that work in the fishery, not only the fishermen who depend directly on the fish stocks but all of the workers who are part of the industry, such as chefs, fish mongers, truck drivers, boat mechanics, and many more. In addition, the loss of an inexpensive protein source to populations that cannot afford to replace it can increase the cost of living and limit societies in other ways. The ultimate outcomes of overfishing and the commercial extinctions of fish stocks could include the loss of aquatic systems as food sources and economic crises for societies that depend on them.

Sustainable seafood is a movement that has gained momentum as more people become aware of overfishing and environmentally-destructive fishing methods. Sustainable seafood is seafood from either fished or farmed sources that can maintain or increase production in the future without jeopardizing the ecosystems from which it was acquired. In general, slow-growing fish that reproduce late in life, such as orange roughy, are vulnerable to overfishing and are considered unsustainable seafood. Seafood species that grow quickly and breed young, such as anchovies and sardines, are much more resistant to overfishing and are therefore labeled “sustainable” and promoted as good alternatives.

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Key Points

- Dramatic changes in species composition can result in an ecosystem shift, where species compositions differ from those that had been present before the depletion of the original fish stock.
- In general, the fish taken from fisheries have shifted to smaller species as larger species are fished to extinction; if such trends continue, aquatic ecosystems could become unavailable as food sources.
- Sustainable seafood is seafood from either fished or farmed sources that can maintain or increase production in the future without affecting the ecosystem in which it lives.

Key Terms

- **sustainability**: configuring society so that each can meet his own needs and greatest potential, while preserving biodiversity and natural ecosystems, and planning for future generations to maintain this potential.
- **overfishing**: fishing that reduces an aquatic population, or stock, to a level that is inadequate for the stock to replenish itself

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47.3: THREATS TO BIODIVERSITY



- Topic hierarchy

47.3A: Habitat Loss and Sustainability

47.3B: Overharvesting

47.3C: Exotic Species

47.3D: Climate Change and Biodiversity

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47.3A: Habitat Loss and Sustainability

Learning Objectives

- Describe the effects of habitat loss to biodiversity and concept of sustainability

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 ecosystem – whether it is a forest, a desert, a grassland, a freshwater estuary, or a marine environment – will kill the individuals within most 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.

Effects of Habitat Loss on Biodiversity

Habitat loss is a process of environmental change in which a natural habitat is rendered functionally unable to support the species present. This process may be natural or unnatural, and may be caused by habitat fragmentation, geological processes, climate change, or human activities such as the introduction of invasive species or ecosystem nutrient depletion. In the process of habitat destruction, the organisms that previously used the site are displaced or destroyed, reducing biodiversity.

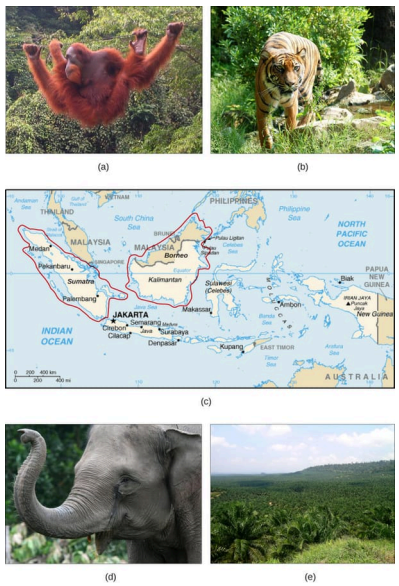


Figure 47.3A.1: Biodiversity loss in Sumatra: (a) One sub-species of orangutan is found only in the rain forests of Borneo, while the other sub-species of orangutan is found only in the rain forests of Sumatra. These animals are examples of the exceptional biodiversity of (c) the islands of Sumatra and Borneo. Other species include the (b) Sumatran tiger and the (d) Sumatran elephant, both of which are critically endangered. Rainforest habitat is being removed to make way for (e) oil palm plantations such as this one in Borneo's Sabah Province.

Human destruction of habitats has accelerated greatly in the latter half of the twentieth century. Natural habitats are often destroyed through human activity for the purpose of harvesting natural resources for industry production and urbanization. Clearing habitats for agriculture, for example, is the principal cause of habitat destruction. Other important causes of habitat destruction include mining, logging, and urban sprawl. Habitat destruction is currently ranked as the primary cause of species extinction worldwide.

Consider the exceptional biodiversity of Sumatra. It is home to one sub-species of orangutan, a species of critically endangered elephant, and the Sumatran tiger; however half of Sumatra's forest is now gone. The neighboring island of Borneo, home to the other sub-species of orangutan, has lost a similar area of forest, and forest loss continues in protected areas. 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 being removed for their timber, and to clear space for plantations of palm oil, an oil used in Europe for many items including food products, cosmetics, and biodiesel.

A five-year estimate of global forest cover loss for the years 2000–2005 was 3.1 percent. In the humid tropics where forest loss is primarily from timber extraction, 272,000 km^2 was lost out of a global total of 11,564,000 km^2 (or 2.4 percent). In the tropics, these losses also represent the extinction of species because of high levels of endemism.

Since the Neolithic Revolution, about 47% of the world's forests have been lost to human use. Present-day forests occupy about a quarter of the world's ice-free land, with about half of these occurring in the tropics. In temperate and boreal regions, forest area is gradually increasing (with the exception of Siberia), but deforestation in the tropics is of major concern.

Feeding more than seven billion human bodies takes a heavy toll on the earth's resources. This begins with the appropriation of about 38 percent of the earth's land surface and about 20 percent of its net primary productivity. Added to this are the resource-hungry activities of industrial agribusiness: everything from crops' need for irrigation water, synthetic fertilizers, and pesticides, to the resource costs of food packaging, transport (now a major part of global trade), and retail.



Figure 47.3A.1: Sustainability and deforestation: Since the Neolithic Revolution, nearly half of the world's forests have been destroyed for human use. Sustainable practices, which preserve environments for long-term maintenance and well-being, can help preserve habitats and ecosystems for greater biodiversity.

Sustainability

Sustainability is a concept that describes how biological systems remain diverse and productive over time. Long-lived and healthy wetlands and forests are examples of sustainable biological systems. For humans, sustainability is the potential for long-term maintenance of well-being, which has ecological, economic, political, and cultural dimensions. Sustainability requires the reconciliation of environmental, social, and economic demands, which are also referred to as the "three pillars" of sustainability.

Healthy ecosystems and environments are necessary for the survival and flourishing of humans and other organisms, and there are a number of ways to reduce humans' negative impact on the environment. One approach is environmental management, which is based largely on information gained from earth science, environmental science, and conservation biology. A second approach is management of human consumption of resources, which is based largely on information gained from economics. A third, more recent, approach adds cultural and political concerns into the sustainability matrix.

Loss of biodiversity stems largely from the habitat loss and fragmentation produced by human appropriation of land for development, forestry and agriculture as natural capital is progressively converted to human-made capital. At the local human scale, sustainability benefits accrue from the creation of green cities and sustainable parks and gardens. Similarly, environmental problems associated with industrial agriculture and agribusiness are now being addressed through such movements as

sustainable agriculture, organic farming, and more-sustainable business practices.

Key Points

- Habitat destruction renders entire habitats functionally unable to support the species present; biodiversity is reduced in this process when existing organisms in the habitat are displaced or destroyed.
- Clearing areas for agricultural purposes is the main cause of habitat destruction; other principal causes include mining, logging, and urban sprawl.
- The primary cause of species extinction worldwide is habitat destruction.
- Sustainability is a term that describes how biological systems remain diverse and productive over time, creating the potential for long-term maintenance of human well-being.
- Reducing negative human impact requires three concepts: environmental management, management of human consumption of resources, and awareness of cultural and political concerns to increase sustainability.

Key Terms

- **sustainability**: Configuring society so that each person can meet their own needs and greatest potential, while preserving biodiversity and natural ecosystems, and planning for future generations to maintain this potential.
- **endemism**: The ecological state of a species being unique to a defined geographic location, such as an island, nation, country or other defined zone, or habitat type; organisms that are indigenous to a place are not endemic to it if they are also found elsewhere.
- **biodiversity**: The diversity (number and variety of species) of plant and animal life within a region.

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47.3B: Overharvesting

Learning Objectives

- Explain why overharvesting is a threat to biodiversity

Overharvesting

Overharvesting, also called overexploitation, refers to harvesting a renewable resource to the point of diminishing returns. Ecologists use the term to describe populations that are harvested at a rate that is unsustainable, given their natural rates of mortality and capacities for reproduction. The term applies to natural resources such as wild medicinal plants, grazing pastures, game animals, fish stocks, forests, and water aquifers. Sustained overharvesting can lead to the destruction of the resource, and is one of the five main activities – along with pollution, introduced species, habitat fragmentation, and habitat destruction – that threaten global biodiversity today.

All living organisms require resources to survive. Overharvesting these resources for extended periods of time can deplete natural resources to the point where they are unable to recover within a short time frame. Humans have always harvested food and other resources they have needed to survive; however, human populations, historically, were small and methods of collection limited to small quantities. Exponential increase in human population, expanding markets, and increasing demand, combined with improved access and techniques for capture, are causing the exploitation of many species beyond sustainable levels.

Effects of overharvesting

As mentioned above, sustained overharvesting is one of the primary threats to biodiversity. Overharvesting can lead to resource destruction, including extinction at the population level and even extinction of whole species. Depleting the numbers or amount of certain resources can also change their quality; for example, the overharvesting of footstool palm (a wild palm tree found in Southeast Asia, the leaves of which are used for thatching and food wrapping) has resulted in its leaf size becoming smaller.

Overharvesting not only threatens the resource being harvested, but can directly impact humans as well – for example by decreasing the biodiversity necessary for medicinal resources. A significant proportion of drugs and medicines are natural products which are derived, directly or indirectly, from biological sources. However, unregulated and inappropriate harvesting could potentially lead to overexploitation, ecosystem degradation, and loss of biodiversity; further, it can negatively impact the rights of the communities and states from which the resources are taken.

Tragedy of the commons

Overharvesting is a serious threat to many species, especially aquatic ones. Common resources – or resources that are shared, such as fisheries – are subject to an economic pressure known as “the tragedy of the commons,” in which essentially no harvester has a motivation to exercise restraint in harvesting from a certain area, because that area is not owned by that harvester. The natural outcome of harvesting common resources is their overexploitation.

For example, most fisheries are managed as a common resource even when the fishing territory lies within a country’s territorial waters; because of this, fishers have very little motivation to limit their harvesting, and in fact 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 (for example, whales) economic forces will always drive toward fishing the population to extinction.



Figure $47.3B.1$: Cod trawler and net: Overharvesting fisheries is an especially salient problem because of a situation termed the tragedy of the commons. In this situation, fishers have no real incentive to practice restraint when harvesting fish because they do not own the fisheries.

Cascade Effects

Overexploitation of species can also result in cascade effects, particularly if a habitat loses its apex predator. Because of the loss of the top predator, a dramatic increase in their prey species can occur. In turn, the unchecked prey can then overexploit their own food resources until population numbers dwindle, possibly to the point of extinction.

Key Points

- Until recently, human populations harvested resources in limited quantities. Today, new methods of harvest and capture contribute to overharvesting and overexploitation.
- Overharvesting stems from several factors, including an exponential increase in the human population, expanding markets, increasing demand, and improved access and techniques for capture.
- Overharvesting natural resources for extended periods of time depletes these resources until they cannot recover within a short period of time; some may never recover.
- Overharvesting is one of five primary activities threatening global biodiversity; others include pollution, introduced species, habitat fragmentation, and habitat destruction.
- Aquatic species are especially threatened by overharvesting, due to a situation known as the tragedy of the commons.

Key Terms

- **overexploitation**: Excessive and damaging use of natural resources, including plants and animals.
- **trawler**: A fishing boat that uses a dragnet, or “trawl net,” to catch fish.
- **apex predator**: An animal at the top of the food chain, preying on other species but not prey itself.

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47.3C: Exotic Species

Learning Objectives

- Describe the impact of exotic and invasive species on native species

Exotic species are those that have been intentionally or unintentionally introduced by humans into an ecosystem in which they did not evolve. Such introductions probably occur frequently as natural phenomena. For example, Kudzu (*Pueraria lobata*), which is native to Japan, was introduced in the United States in 1876. It was later planted for soil conservation. Problematically, it grows too well in the southeastern United States: up to one foot each day. It is now a pest species, covering over seven million acres in the southeastern United States. If an introduced species is able to survive in its new habitat, that introduction is now reflected in the observed range of the species. Human transportation of people and goods, including the intentional transport of organisms for trade, has dramatically increased the introduction of species into new ecosystems, 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.



Figure $47.3C.1$: Exotic threats: 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.

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, possess preadaptations that can make them especially successful in a new ecosystem. These exotic species often undergo dramatic population increases in their new habitat, resetting the ecological conditions in the new environment, while threatening the species that exist there. For this reason, exotic species, also called invasive species, can threaten other species through competition for resources, predation, or disease.

Exotic Species Threaten Native Species

Invasive species can change the functions of ecosystems. For example, invasive plants can alter the fire regimen, nutrient cycling, and hydrology in native ecosystems. Invasive species that are closely related to rare native species have the potential to hybridize with the native species. Harmful effects of hybridization have led to a decline and even extinction of native species. For example, hybridization with introduced cordgrass, *Spartina alterniflora*, threatens the existence of California cordgrass in San Francisco Bay. Invasive species cause competition for native species. Four hundred of the 958 endangered species under the Endangered Species Act are at risk due to this competition.



Figure $47.3C.1$: Global decline in amphibian species: 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.

Lakes and islands are particularly vulnerable to extinction threats from introduced species. In Lake Victoria, as mentioned earlier, 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 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.

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. There is evidence that the fungus, native to Africa, may have been spread throughout the world by transport of a commonly-used laboratory and pet species: the African clawed toad (*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 Batrachochytriumdendrobatidis and can act as a reservoir for the disease.

Key Points

- Exotic species introduced to new environments often reset the ecological conditions in that new habitat, threatening the species that exist there; this is the reason that they are also termed invasive species.
- Invasive species that are closely related to rare native species have the potential to hybridize with the native species; harmful effects of hybridization have led to a decline and even extinction of native species.
- Biologists studying frogs and toads may be inadvertently responsible for the worldwide spread of a fungus deadly to amphibians.

Key Terms

- **invasive species**: any species that has been introduced to an environment where it is not native and has since become a nuisance through rapid spread and increase in numbers, often to the detriment of native species

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47.3D: Climate Change and Biodiversity

Learning Objectives

- Evaluate climate change and its impact on biodiversity

Climate Change

Climate change, specifically, the anthropogenic (caused by humans) warming trend presently underway, is recognized as a major extinction threat, particularly when combined with other threats such as habitat loss. Scientists disagree about the probable magnitude of the effects, with extinction rate estimates ranging from 15 percent to 40 percent of species by 2050. Scientists do agree, however, that climate change will alter regional climates, including rainfall and snowfall patterns, making habitats less hospitable to the species living in them.

Impact of Climate Change on Biodiversity



Figure $47.3D.1$: Grizzly-polar bear hybrid: Since 2008, grizzly bears (Ursus arctos horribilis) have been spotted farther north than their historic range, a possible consequence of climate change. As a result, grizzly bear habitat now overlaps polar bear (Ursus maritimus) habitat. The two kinds of bears, which are capable of mating and producing viable offspring, are considered separate species as historically they lived in different habitats and never met. However, in 2006 a hunter shot a wild grizzly-polar bear hybrid known as a grolar bear, the first wild hybrid ever found.

The warming trend will shift colder climates toward the north and south poles, forcing species to move with their adapted climate norms while facing 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, with their ranges are overlapping, there are documented cases of these two species mating and producing viable offspring. Changing climates also throw off species' delicate timing adaptations to seasonal food resources and breeding times. Many contemporary mismatches to shifts in resource availability and timing have recently been documented.

Range shifts are already being observed. For example, some European bird species' ranges have moved 91 km northward. The same study suggests 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, 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.

Finally, global warming will raise ocean levels due to glacial melt and the greater volume of warmer water. Shorelines will be inundated, reducing island size, which will have an effect on many species; 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 also be jeopardized. This could result in an overabundance of salt water and a shortage of fresh water.

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Key Points

- This warming trend is persistently shifting colder climates further toward the north and south poles, forcing species to move with their own adapted climate norms, while also facing habitat gaps along the way.
- Climate shifts will move up mountains, resulting in the crowding of species higher in altitude and eliminating the habitat for those species adapted to those high elevations; indeed, some climates will completely disappear.
- Global warming will also raise ocean water levels due to melted water from glaciers and the greater volume of warmer water; shorelines will be flooded, affecting many species; many islands will disappear altogether.

Key Terms

- **anthropogenic**: having its origin in the influence of human activity on nature
- **biodiversity**: the diversity (number and variety of species) of plant and animal life within a region

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47.4: PRESERVING BIODIVERSITY



- Topic hierarchy

47.4A: Measuring Biodiversity

47.4B: Changing Human Behavior in Response to Biodiversity Loss

47.4C: Ecological Restoration

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47.4A: Measuring Biodiversity

Learning Objectives

- Explain how DNA barcoding aids in measuring biodiversity

Measuring Biodiversity

The technologies of molecular genetics, data processing, and data storage are maturing to the point where cataloging the planet's species in an accessible way is close to feasible. DNA barcoding is one molecular genetic method, which takes advantage of the rapid evolution in a mitochondrial gene present in eukaryotes, to identify species using the sequence of portions of the gene. Plants may be barcoded using a combination of chloroplast genes.

DNA Barcoding

DNA barcoding is a taxonomic method that uses a short genetic marker in an organism's DNA to identify it as belonging to a particular species. It differs from molecular phylogeny in that the main goal is not to determine patterns of relationship, but to identify an unknown sample in terms of a preexisting classification. The most commonly-used barcode region for animals, at least, is a segment of approximately 600 base pairs of the mitochondrial gene cytochrome oxidase I (COI).

Applications include, for example, identifying plant leaves (even when flowers or fruit are not available), identifying insect larvae (which may have fewer diagnostic characters than adults and are frequently less well-known), identifying the diet of an animal (based on its stomach contents or feces), and identifying products in commerce (for example, herbal supplements or wood).

Rapid, mass-sequencing machines make the molecular genetics portion of the work relatively inexpensive and quick. Computer resources store and make available the large volumes of data. Projects are currently underway to use DNA barcoding to catalog museum specimens, which have already been named and studied, as well as testing the method on less studied groups. As of mid-2012, close to 150,000 named species had been barcoded. Early studies suggest there are significant numbers of undescribed species that looked too much like sibling species to previously be recognized as different. These now can be identified with DNA barcoding.

Numerous computer databases now provide information about named species and a framework for adding new species. However, as already noted, at the present rate of description of new species, it will take close to 500 years before the complete catalog of life is known. Many, perhaps most, species on the planet do not have that much time.

There is also the problem of understanding which species known to science are threatened and to what degree they are threatened. This task is carried out by the non-profit IUCN (International Union for Conservation of Nature) which maintains the Red List: an online listing of endangered species categorized by taxonomy, type of threat, and other criteria. The Red List is supported by scientific research. In 2011, the list contained 61,000 species, all with supporting documentation.

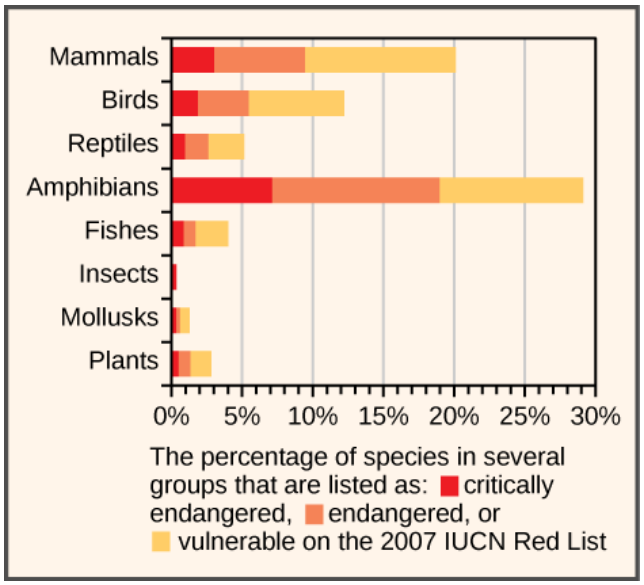


Figure 47.4A.1: IUCN Red List: This chart shows the percentage of various animal species, by group, on the IUCN Red List as of 2007. The Red List is an online listing of endangered species categorized by taxonomy, type of threat, and other criteria.

Key Points

- DNA barcoding is a taxonomic method that uses a short genetic marker in an organism's DNA to identify it as belonging to a particular species.
- Barcoding allows us to classify organisms that would otherwise be difficult to identify, such as in situations where only part of an organism is available, or is too immature to identify by conventional methods.
- At the present rate of description of new species, it will take close to 500 years before the complete catalog of life is known; however, most species will be extinct before this time.
- Even with barcoding, it is difficult to know which species are threatened and to what degree they are threatened, a task carried out by the non-profit IUCN (International Union for Conservation of Nature).

Key Terms

- **barcoding**: a taxonomic method that uses a short genetic marker in an organism's DNA to identify it as belonging to a particular species
- **phylogeny**: the evolutionary history of an organism
- **taxonomy**: the science of finding, describing, classifying and naming organisms

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47.4B: Changing Human Behavior in Response to Biodiversity Loss

Learning Objectives

- Detail the benefits and limitations of different human responses to climate change and species loss, such as using preserves to conserve species

Human Responses to Climate Change and Species Loss

Legislation throughout the world has been enacted to protect species and include 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 approximately 33,000 listed species from being transported across nations' borders, thus protecting them from being caught or killed when international trade is involved. 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 worth hundreds of millions of dollars. Illegal wildlife trade is monitored by another non-profit, the Trade Records Analysis of Flora and Fauna in Commerce (TRAFFIC).

Within many countries there are laws that protect endangered species and regulate hunting and fishing. In the United States, the Endangered Species Act (ESA) was enacted in 1973. The U.S. Fish & Wildlife Service is required by law to develop management plans that protect the species listed as at risk in the Act in order to bring them 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 it 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 is inefficient as it focuses efforts on a few highly-visible and often charismatic species, perhaps at the expense of other species that go unprotected. At the same time, the Act has a critical habitat provision outlined in the recovery mechanism that may benefit species other than the one targeted for management.

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).

In relation to global warming, 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 important countries in terms of their potential impact that did not ratify the Kyoto Protocol were the United States and China. The United States rejected it as a result of a powerful fossil fuel industry, while China did so because of a concern that it would stifle the nation's growth. 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, climate scientists predict the resulting costs to human societies and biodiversity will be high.

Using Preserves to Conserve Species

The private, non-profit sector plays a large role in the conservation effort both in North America and around the world. The approaches range from species-specific organizations to the broadly-focused groups mentioned above.

Many nations have laws that protect endangered species: for example, forbidding hunting, restricting land development, or creating preserves. Preserves are purchased land for the explicit purpose of attempting to protect species and ecosystems. They also protect biodiversity in many ways, such as through captive breeding and private farming.

Captive breeding is the process of breeding rare or endangered species in human-controlled environments with restricted settings, such as wildlife preserves and conservation facilities. Captive breeding is meant to prevent species extinction and to stabilize the population of the species so that it will not disappear. This technique has worked for many species for some time, such as for Pere David's deer. However, captive breeding techniques are usually difficult to implement for such highly-mobile species as some migratory birds (e.g. cranes) and fish (e.g. hilsa). Additionally, if the captive-breeding population is too small, then inbreeding may occur due to a reduced gene pool, which may also reduce immunity.



Figure $47.4B.1$: Captive breeding: Père David's deer is a species of deer that is currently extinct in the wild: all known specimens are found only in captivity. This species was successfully saved through captive breeding programs after almost being hunted to extinction in China.

Key Points

- Legislation throughout the world has been enacted to protect species; the legislation includes international treaties as well as national and state laws.
- The international response to global warming has been mixed; the Kyoto Protocol, an international agreement that came out of the United Nations climate change convention that committed countries to reducing greenhouse gas emissions, was ratified by some countries, but spurned by others.
- Many nations have laws that protect endangered species: for example, forbidding hunting, restricting land development, or creating preserves (purchased land for the explicit purpose of attempting to protect species and ecosystems).
- Preserves protect biodiversity in many ways, two of which are captive breeding and private farming.

Key Terms

- **endangered species**: a species which is in danger of becoming extinct

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47.4C: Ecological Restoration

Learning Objectives

- Explain the purpose of ecological restoration projects

Conservation in Preserves

Establishment of wildlife and ecosystem preserves is one of the key tools in conservation efforts. 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 in the short term for protecting both species and ecosystems, but they face challenges that scientists are still exploring in order to strengthen their viability as long-term solutions.

Due to the way protected lands are allocated (they tend to contain less economically-valuable resources rather than being set aside specifically for at-risk species or ecosystems) and the way biodiversity is distributed, determining a target percentage of land or marine habitat that should be protected to maintain biodiversity levels is challenging. The IUCN (International Union for Conservation of Nature) World Parks Congress estimated that 11.5 percent of earth's land surface was covered by preserves of various kinds in 2003. This area is greater than previous goals; however, it only represents 9 out of 14 recognized major biomes. Research has shown that 12 percent of all species live solely outside preserves; these percentages are much higher when only threatened species and high-quality preserves are considered.

Limitations on Preserves

Some of the limitations on preserves as conservation tools stem from preserve designs. Additionally, political and economic pressures typically make preserves smaller, never larger, so setting aside areas that are large enough is difficult. Climate change will create inevitable problems with the location of preserves. The species within them will migrate to higher latitudes as the habitat of the preserve becomes less favorable. Scientists are planning for the effects of global warming on future preserves and striving to predict the need for new preserves to accommodate anticipated changes to habitats. Some argue 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.

Habitat Restoration

Habitat restoration holds considerable promise as a mechanism for restoring and maintaining biodiversity. Restoration ecology aims to return ecosystems to a more natural, pre-disturbance state. 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, which function to suppress elk and coyote populations, provide more-abundant resources to the guild of carrion (flesh) eaters. Reducing elk populations has allowed re-vegetation of riparian areas, which has increased the diversity of species in that habitat. Decreasing the coyote population increased the populations of species that were 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: it is a species that is instrumental in maintaining diversity in an ecosystem. Removing a keystone species from an ecological community may cause a collapse in diversity. Similarly, restoring a keystone species can have dramatic effects. The results from the Yellowstone experiment suggest that restoring a keystone species 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 those species. It also makes sense to attempt to return them to their ecosystem if they have been removed.

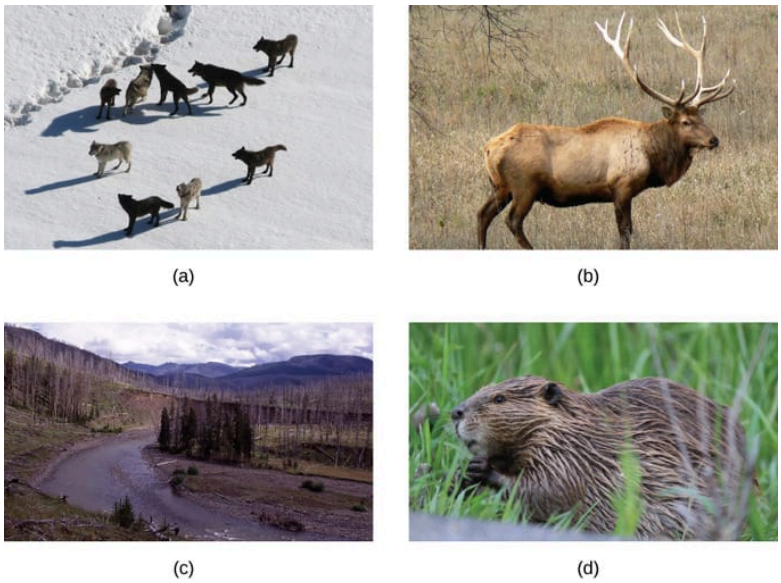


Figure 47.4C.1: Yellowstone National Park restoration efforts: (a) The Gibbon wolf pack in Yellowstone National Park represents a keystone species. The reintroduction of wolves into Yellowstone National Park in 1995 led to a change in the grazing behavior of (b) elk. To avoid predation, the elk no longer grazed exposed stream and riverbeds, such as (c) the Lamar Riverbed in Yellowstone. This allowed willow and cottonwood seedlings to grow. The seedlings decreased erosion and provided shading to the creek, which improved fish habitat. A new colony of (d) beaver may also have benefited from the habitat change.

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 and because many dams no longer provide the benefit and functions that they did when they were first built. The measured benefits of dam removal include restoration of naturally-fluctuating water levels (the purpose of dams is frequently 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 key nutrients to inland ecosystems during its annual spawning migrations. In other regions, such as the Atlantic coast, dam removal has allowed the return of 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.

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Key Points

- Ecological preserves, while effective in the short term, are not yet viable, long-term solutions.
- Some of the limitations on preserves as conservation tools include preserve designs, political and economic pressures, and climate change.
- Habitat restoration is a promising tool for restoring and maintaining biodiversity; restoration can improve the biodiversity of degraded ecosystems.

Key Terms

- **biodiversity**: the diversity (number and variety of species) of plant and animal life within a region
- **keystone species**: a species that exerts a large, stabilizing influence throughout an ecological community, despite its relatively small numerical abundance
- **carrion**: dead flesh; carcasses

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