CLACKAMAS BIOLOGY 112 OER TEXTBOOK (OPENSTAX)



Jennifer Bown
Clackamas Community College

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Clackamas Biology 112 OER Textbook (OpenStax)

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Preface

Welcome to *Concepts of Biology*, an OpenStax resource. This textbook has been created with several goals in mind: accessibility, customization, and student engagement—all while encouraging students toward high levels of academic scholarship. Instructors and students alike will find that this textbook offers a strong introduction to biology in an accessible format.

About OpenStax

OpenStax is a non-profit organization committed to improving student access to quality learning materials. Our free textbooks are developed and peer-reviewed by educators to ensure they are readable, accurate, and meet the scope and sequence requirements of today's college courses. Unlike traditional textbooks, OpenStax resources live online and are owned by the community of educators using them. Through our partnerships with companies and foundations committed to reducing costs for students, OpenStax is working to improve access to higher education for all. OpenStax is an initiative of Rice University and is made possible through the generous support of several philanthropic foundations.

About OpenStax's Resources

OpenStax resources provide quality academic instruction. Three key features set our materials apart from others: they can be customized by instructors for each class, they are a "living" resource that grows online through contributions from science educators, and they are available free or for minimal cost.

Customization

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Instructors also have the option of creating a customized version of their OpenStax book. The custom version can be made available to students in low-cost print or digital form through their campus bookstore. Visit your book page on openstax.org for more information.

Curation

To broaden access and encourage community curation, *Concepts of Biology* is "open source" licensed under a Creative Commons Attribution (CC-BY) license. The scientific community is invited to submit examples, emerging research, and other feedback to enhance and strengthen the material and keep it current and relevant for today's students. You can submit your suggestions to Support@OpenStax.org.

Cost

Our textbooks are available for free online, and in low-cost print and e-book editions.

About *Concepts of Biology*

Concepts of Biology is designed for the single-semester introduction to biology course for non-science majors, which for many students is their only college-level science course. As such, this course represents an important opportunity for students to develop the necessary knowledge, tools, and skills to make informed decisions as they continue with their lives. Rather than being mired down with facts and vocabulary, the typical non-science major student needs information presented in a way that is easy to read and understand. Even more importantly, the content should be meaningful. Students do much better when they understand why biology is relevant to their everyday lives. For these reasons, *Concepts of Biology* is grounded on an evolutionary basis and includes exciting features that highlight careers in the biological sciences and everyday applications of the concepts at hand. We also strive to show the interconnectedness of topics within this extremely broad discipline. In order to meet the needs of today's instructors and students, we maintain the overall organization and coverage found in most syllabi for this course. A strength of *Concepts of Biology* is that instructors can customize the book, adapting it to the approach that works best in their classroom. Concepts of

Biology also includes an innovative art program that incorporates critical thinking and clicker questions to help students understand —and apply—key concepts.

Coverage and Scope

Our *Concepts of Biology* textbook adheres to the scope and sequence of most one-semester non-majors courses nationwide. We also strive to make biology, as a discipline, interesting and accessible to students. In addition to a comprehensive coverage of core concepts and foundational research, we have incorporated features that draw learners into the discipline in meaningful ways. Our scope of content was developed after surveying over a hundred biology professors and listening to their coverage needs. We provide a thorough treatment of biology's fundamental concepts with a scope that is manageable for instructors and students alike.

- Unit 1: **The Cellular Foundation of Life** (Ch. 1-5). Our opening unit introduces students to the sciences, including the process of science and the underlying concepts from the physical sciences that provide a framework within which learners comprehend biological processes. Additionally, students will gain solid understanding of the structures, functions, and processes of the most basic unit of life: the cell.
- Unit 2: **Cell Division and Genetics** (Ch. 6-8). Our genetics unit takes learners from the foundations of cellular reproduction to the experiments that revealed the basis of genetics and laws of inheritance.
- Unit 3: **Molecular Biology and Biotechnology** (Ch. 9-10). Students will learn the intricacies of DNA, protein synthesis, and gene regulation and current applications of biotechnology and genomics.
- Unit 4: **Evolution and the Diversity of Life** (Ch. 11-15). The core concepts of evolution are discussed in this unit with examples illustrating evolutionary processes. Additionally, the evolutionary basis of biology reappears throughout the textbook in general discussion and is reinforced through special call-out features highlighting specific evolution-based topics. The diversity of life is explored with detailed study of various organisms and discussion of emerging phylogenetic relationships between and among bacteria, protist kingdoms, fungi, plants, and animals.
- Unit 5: **Animal Structure and Function** (Ch. 16-18). An introduction to the form and function of the animal body is followed by chapters on the immune system and animal development. This unit touches on the biology of all organisms while maintaining an engaging focus on human anatomy and physiology that helps students connect to the topics.
- Unit 6: **Ecology** (Ch. 19-21). Ecological concepts are broadly covered in this unit, with features highlighting localized, real-world issues of conservation and biodiversity.

Pedagogical Foundation and Features

Because of the impact science has on students and society, an important goal of science education is to achieve a scientifically literate population that consistently makes informed decisions. Scientific literacy transcends a basic understanding of scientific principles and processes to include the ability to make sense of the myriad instances where people encounter science in day-to-day life. Thus, a scientifically literate person is one who uses science content knowledge to make informed decisions, either personally or socially, about topics or issues that have a connection with science. Concepts of Biology is grounded on a solid scientific base and designed to promote scientific literacy. Throughout the text, you will find features that engage the students in scientific inquiry by taking selected topics a step further.

- **Evolution in Action** features uphold the importance of evolution to all biological study through discussions like "Global Decline of Coral Reefs" and "The Red Queen Hypothesis."
- **Career in Action** features present information on a variety of careers in the biological sciences, introducing students to the educational requirements and day-to-day work life of a variety of professions, such as forensic scientists, registered dietitians, and biogeographers.
- **Biology in Action** features tie biological concepts to emerging issues and discuss science in terms of everyday life. Topics include "Invasive Species" and "Photosynthesis at the Grocery Store."

Art and Animations that Engage

Our art program takes a straightforward approach designed to help students learn the concepts of biology through simple, effective illustrations, photos, and micrographs. Concepts of Biology also incorporates links to relevant animations and interactive exercises that help bring biology to life for students.

- **Art Connection** features call out core figures in each chapter for student attention. Questions about key figures, including clicker questions that can be used in the classroom, engage students' critical thinking and analytical abilities to ensure their genuine understanding of the concept at hand.
- **Concept in Action** features direct students to online interactive exercises and animations to add a fuller context and examples to core content.

About Our Team

Concepts of Biology would not be possible if not for the tremendous contributions of the authors and community reviewing team.

Senior Contributing Authors

Samantha Fowler, Clayton State University
Rebecca Roush, Sandhills Community College
James Wise, Hampton University

Contributing Authors and Reviewers

Mark Belk, Brigham Young University
Lisa Boggs, Southwestern Oklahoma State University
Sherryl Broverman, Duke University
David Byres, Florida State College at Jacksonville
Aaron Cassill, The University of Texas at San Antonio
Karen Champ, College of Central Florida
Sue Chaplin, University of St. Thomas
Diane Day, Clayton State University
Jean DeSaix, University of North Carolina at Chapel Hill
David Hunnicutt, St. Norbert College
Barbara Kuehner, Hawaii Community College
Brenda Leady, University of Toledo
Bernie Marcus, Genesee Community College
Flora Mhlanga, Lipscomb University
Madeline Mignone, Dominican College
Elizabeth Nash, Long Beach City College
Mark Newton, San Jose City College
Diana Oliveras, University of Colorado Boulder
Ann Paterson, Williams Baptist College
Joel Piperberg, Millersville University
Nick Reeves, Mt. San Jacinto College
Ann Reisenauer, San Jose State University
Lynn Rumfelt, Gordon College
Michael Rutledge, Middle Tennessee State University
Edward Saiff, Ramapo College of New Jersey
Brian Shmaefsky, Kingwood College
Gary Shultz, Marshall University
Donald Slish, SUNY Plattsburgh
Anh-Hue Tu, Georgia Southwestern State University
Elena Zoubina, Bridgewater State University

Learning Resources

Wiley Plus for Biology-Fall 2013 Pilot

WileyPLUS provides an engaging online environment for effective teaching and learning. WileyPLUS builds students' confidence because it takes the guesswork out of studying by providing a clear roadmap; what to do, how to do it, and if they did it right. With

WileyPLUS, students take more initiative. Therefore, the course has a greater impact on their learning experience. Adaptive tools provide students with a personal, adaptive learning experience so they can build their proficiency on topics and use their study time most effectively. Please let us know if you would like to participate in a Fall 2013 Pilot.

Concepts of Biology Powerpoint Slides (faculty only)

The PowerPoint slides are based on the extensive illustrations from College Physics. They can be edited, incorporated into lecture notes, and you are free to share with anyone in the community. This is a restricted item requiring faculty registration. NOTE: This file is very large and may take some time to download.

SimBio (Laboratory)

SimBio's interactive modules (virtual labs and interactive tutorials and chapters) provide engaging, discovery-based learning tools that complement many of the chapters of Concepts of Biology. SimBio is best known for their EcoBeaker® and EvoBeaker® suites of simulated ecology and evolution laboratories that guide students through the "discovery" of important concepts via a mix of structured and open-ended experimentation on simulated systems. In response to popular demand, SimBio has begun applying the same powerful approaches to topics in cell biology, genetics, and neurobiology. All of SimBio's modules include instant-feedback questions that enhance student comprehension and auto-graded questions that facilitate implementation.



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CHAPTER OVERVIEW

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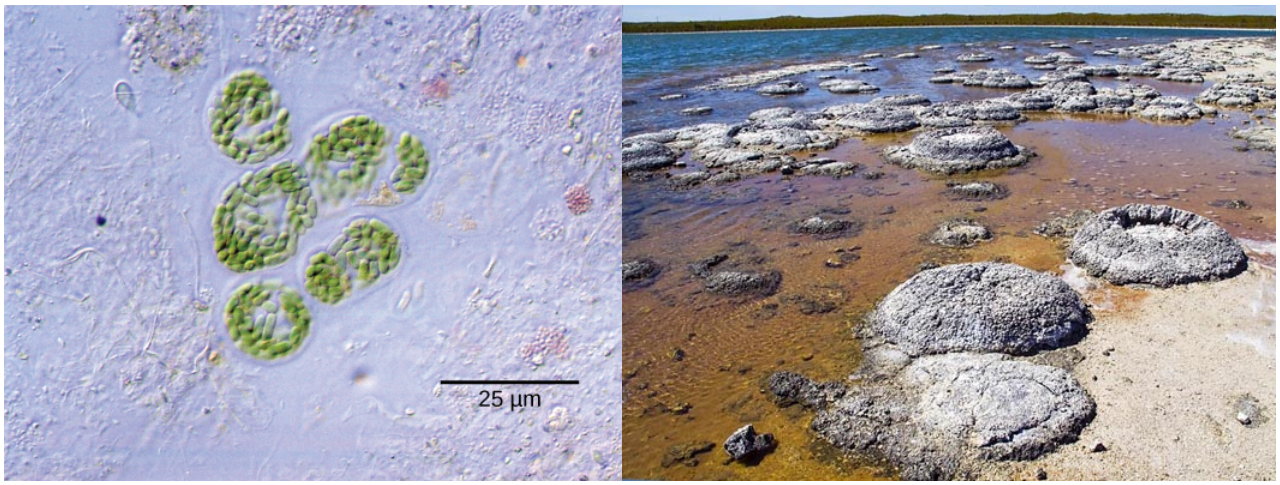
1.1: The Science of Biology

Introduction

What is biology? In simple terms, biology is the study of living organisms and their interactions with one another and their environments. This is a very broad definition because the scope of biology is vast.

Learning Objectives

- Identify the shared characteristics of the natural sciences
- Summarize the steps of the scientific method
- Compare inductive reasoning with deductive reasoning
- Describe the goals of basic science and applied science
- Describe the structure of an atoms
- Describe how several bonds arise from the interaction of atomic particles and resulting charges on elements
- Describe the properties of water that are critical to maintaining life
- Describe the pH scale and compare its values



(a) (b)

Figure 1.1.1: Formerly called blue-green algae, these (a) cyanobacteria, shown here at 300x magnification under a light microscope, are some of Earth's oldest life forms. These (b) stromatolites along the shores of Lake Thetis in Western Australia are ancient structures formed by the layering of cyanobacteria in shallow waters. (credit a: modification of work by NASA; credit b: modification of work by Ruth Ellison; scale-bar data from Matt Russell)

Biologists may study anything from the microscopic or submicroscopic view of a cell to ecosystems and the whole living planet (Figure 1.1.1). Listening to the daily news, you will quickly realize how many aspects of biology are discussed every day. For example, recent news topics include *Escherichia coli* (Figure 1.1.2) outbreaks in spinach and *Salmonella* contamination in peanut butter. Other subjects include efforts toward finding a cure for AIDS, Alzheimer's disease, and cancer. On a global scale, many researchers are committed to finding ways to protect the planet, solve environmental issues, and reduce the effects of climate change. All of these diverse endeavors are related to different facets of the discipline of biology.

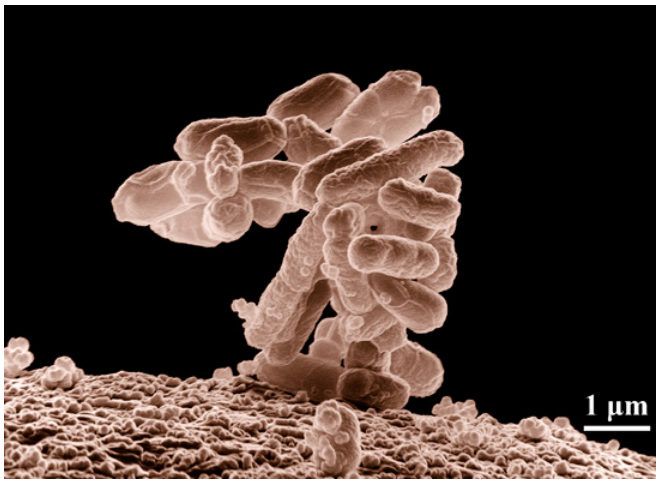


Figure 1.1.2: Escherichia coli (*E. coli*) bacteria, seen in this scanning electron micrograph, are normal residents of our digestive tracts that aid in the absorption of vitamin K and other nutrients. However, virulent strains are sometimes responsible for disease outbreaks. (credit: Eric Erbe, digital colorization by Christopher Pooley, both of USDA, ARS, EMU)

The Process of Science

Biology is a science, but what exactly is science? What does the study of biology share with other scientific disciplines? Science (from the Latin *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. It becomes clear from this definition that the application of the scientific method plays a major role in science. The scientific method is a method of research with defined steps that include experiments and careful observation.

The steps of the scientific method will be examined in detail later, but one of the most important aspects of this method is the testing of hypotheses by means of repeatable experiments. A hypothesis is a suggested explanation for an event, which can be tested. 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, 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 archeology—even though one cannot perform repeatable experiments, hypotheses may still be supported. For instance, an archeologist 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, and these hypotheses may be found to be correct or false through continued support or contradictions from other findings. A hypothesis may become a verified theory. A theory is a tested and confirmed explanation for observations or phenomena. Science may be better defined as fields of study that attempt to comprehend the nature of the universe.

Natural Sciences

What would you expect to see in a museum of natural sciences? Frogs? Plants? Dinosaur skeletons? Exhibits about how the brain functions? A planetarium? Gems and minerals? Or, maybe all of the above? Science includes such diverse fields as astronomy, biology, computer sciences, geology, logic, physics, chemistry, and mathematics (Figure 1.1.3). However, those fields of science related to the physical world and its phenomena and processes are considered natural sciences. Thus, a museum of natural sciences might contain any of the items listed above.

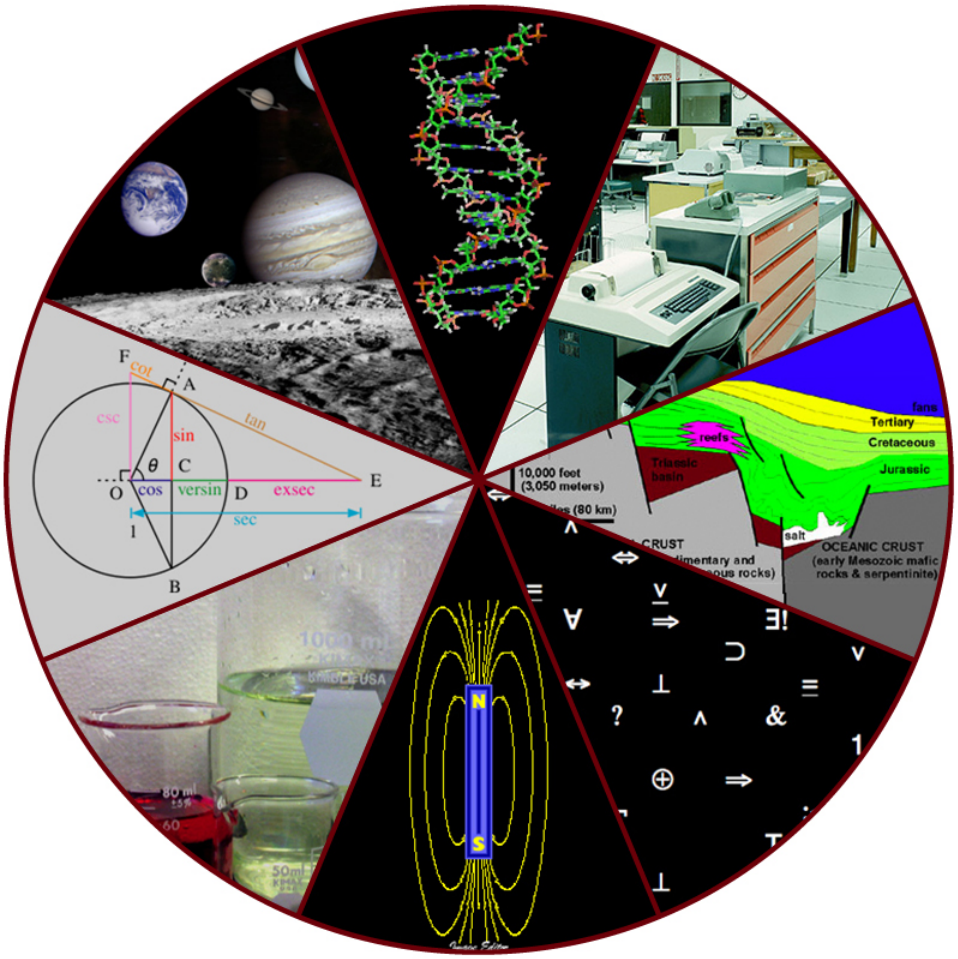


Figure 1.1.3: The diversity of scientific fields includes astronomy, biology, computer science, geology, logic, physics, chemistry, mathematics, and many other fields. (credit: "Image Editor"/Flickr)

There is no complete agreement when it comes to defining what the natural sciences include, however. For some experts, the natural sciences are astronomy, biology, chemistry, earth science, and physics. Other scholars choose to divide natural sciences into life sciences, which study living things and include biology, and physical sciences, which study nonliving matter and include astronomy, geology, physics, and chemistry. Some disciplines such as biophysics and biochemistry build on both life and physical sciences and are interdisciplinary. Natural sciences are sometimes referred to as "hard science" because they rely on the use of quantitative data; social sciences that study society and human behavior are more likely to use qualitative assessments to drive investigations and findings.

Not surprisingly, the natural science of biology has many branches or subdisciplines. Cell biologists study cell structure and function, while biologists who study anatomy investigate the structure of an entire organism. Those biologists studying physiology, however, focus on the internal functioning of an organism. Some areas of biology focus on only particular types of living things. For example, botanists explore plants, while zoologists specialize in animals.

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.

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 made and tested, and many such changes have been found, such as the modification of arable areas for agriculture, with change based on temperature averages.

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. On 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.

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) (Figure 1.1.4), who set up inductive methods for scientific inquiry. The scientific method is not exclusively used by biologists but can be applied to almost all fields of study as a logical, rational problem-solving method.



Figure 1.1.4: Sir Francis Bacon (1561–1626) is credited with being the first to define the scientific method. (credit: Paul van Somer)

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

Proposing a Hypothesis

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

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

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 about. Therefore, 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. Look for the variables and controls in the examples that follow. To test the first hypothesis, the student would find out if the air conditioning is on. If the air conditioning is turned on but does not work, there should be another reason, and this hypothesis should be rejected. To test the second hypothesis, the student could check if the lights in the classroom are functional. If so, there is no power failure and this hypothesis should be rejected. 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 (Figure 1.1.5). Using the scientific method, the hypotheses that are inconsistent with experimental data are rejected.

While this “warm classroom” 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 observation to explain this occurrence might be, “When I eat breakfast before class, I am better able to pay attention.” The student could then design an experiment with a control to test this hypothesis.

In hypothesis-based science, specific results are predicted from a general premise. This type of reasoning is called deductive reasoning: deduction proceeds from the general to the particular. But the reverse of the process is also possible: sometimes, scientists reach a general conclusion from a number of specific observations. This type of reasoning is called inductive reasoning, and it proceeds from the particular to the general. Inductive and deductive reasoning are often used in tandem to advance scientific knowledge (Figure 1.1.6).

Art Connection

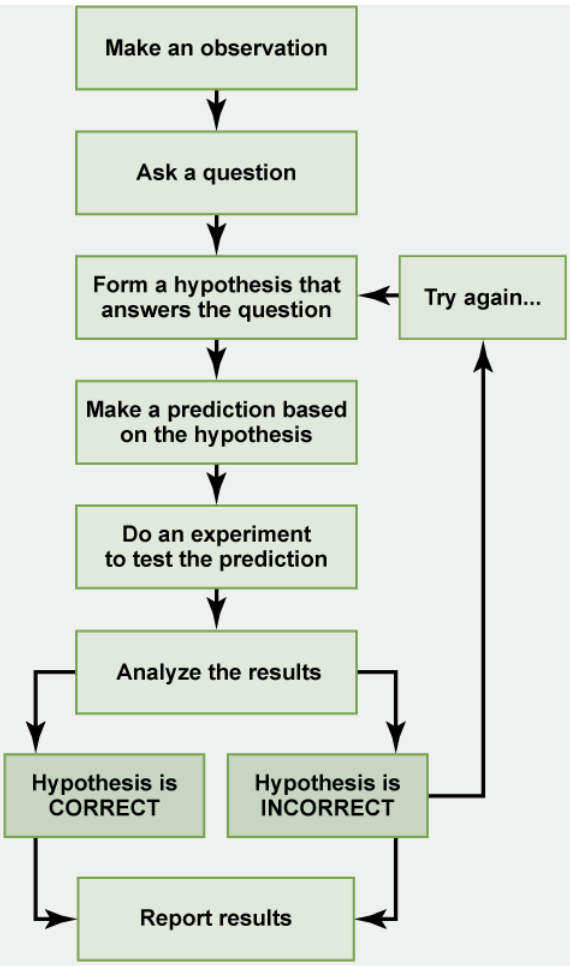


Figure 1.1.5: The scientific method consists of a series of well-defined steps. If a hypothesis is not supported by experimental data, a new hypothesis can be proposed.

In the example below, the scientific method is used to solve an everyday problem. Order the scientific method steps (numbered items) with the process of solving the everyday problem (lettered items). Based on the results of the experiment, is the hypothesis correct? If it is incorrect, propose some alternative hypotheses.

1. Observation
2. Question
3. Hypothesis (answer)
4. Prediction
5. Experiment
6. Result

A. There is something wrong with the electrical outlet.
B. If something is wrong with the outlet, my coffeemaker also won't work when plugged into it.
C. My toaster doesn't toast my bread.
D. I plug my coffee maker into the outlet.
E. My coffeemaker works.
F. Why doesn't my toaster work?

Art Connection

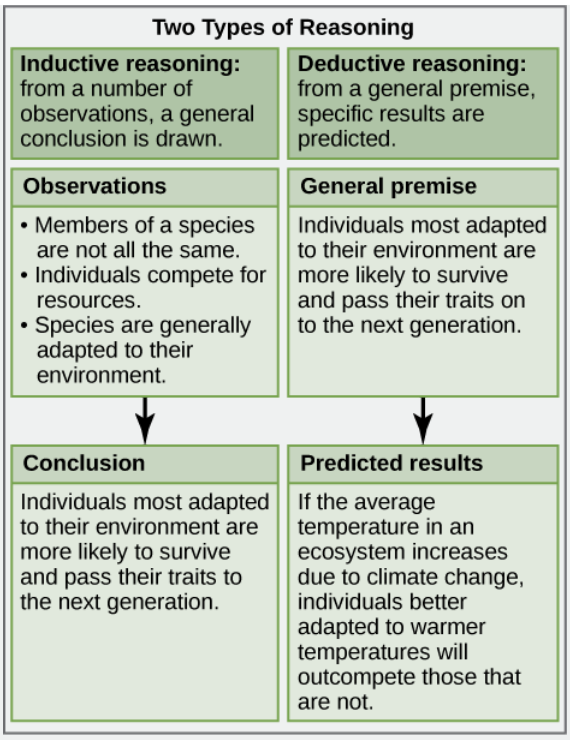


Figure 1.1.6: Scientists use two types of reasoning, inductive and deductive reasoning, to advance scientific knowledge. As is the case in this example, the conclusion from inductive reasoning can often become the premise for inductive reasoning.

Decide if each of the following is an example of inductive or deductive reasoning.

1. All flying birds and insects have wings. Birds and insects flap their wings as they move through the air. Therefore, wings enable flight.
2. Insects generally survive mild winters better than harsh ones. Therefore, insect pests will become more problematic if global temperatures increase.
3. Chromosomes, the carriers of DNA, separate into daughter cells during cell division. Therefore, DNA is the genetic material.
4. Animals as diverse as humans, insects, and wolves all exhibit social behavior. Therefore, social behavior must have an evolutionary advantage.

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. Sometimes an experiment leads to conclusions that favor a change in approach; often, an experiment brings entirely new scientific questions to the puzzle. Many times, science does not operate in a linear fashion; instead, scientists continually draw inferences and make generalizations, finding patterns as their research proceeds. Scientific reasoning is more complex than the scientific method alone suggests. Notice, too, that the scientific method can be applied to solving problems that aren't necessarily scientific in nature.

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 immediate goal of basic science is knowledge for knowledge's sake, though this does not mean that, in the end, it may not result in a practical application.

In contrast, applied science or “technology,” aims to use science to solve real-world problems, making it possible, for example, to improve a crop yield, find a cure for a particular disease, or save animals threatened by a natural disaster (Figure 1.1.7). In applied science, the problem is usually defined for the researcher.



Figure 1.1.7: 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. (credit: FEMA)

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.

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 (Figure 1.1.8) 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, seeking cures and early diagnoses for genetically related diseases.

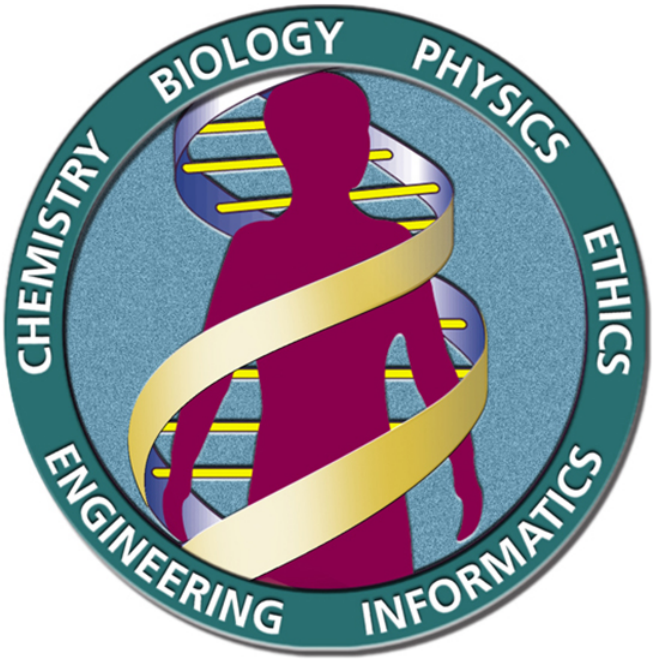


Figure 1.1.8: The Human Genome Project was a 13-year collaborative effort among researchers working in several different fields of science. The project, which sequenced the entire human genome, was completed in 2003. (credit: the U.S. Department of Energy Genome Programs (http://genomics.energy.gov))

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.

Reporting Scientific Work

Whether scientific research is basic science or applied science, 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, important aspects of a scientist's work are 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.

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. First, scientific writing must be brief, concise, and accurate. A scientific paper 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 of the work; it justifies the work carried out and also briefly mentions the end of the paper, where the hypothesis

or research question driving the research will be presented. 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 used, and the method and techniques used by the researchers to gather data. The description should be thorough enough to allow another researcher to repeat the experiment and obtain similar results, but it does not have to be verbose. 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.

Some journals require a results section followed by a discussion section, but it is more common to combine both. 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. Therefore, a well-done 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 and typically include extensive reference sections.

Summary

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

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

Two types of logical reasoning are used in science. Inductive reasoning uses particular results to produce general scientific principles. Deductive reasoning is a form of logical thinking that predicts results by applying general principles. The common thread throughout scientific research is the use of the scientific method, a step-based process that consists of making observations, defining a problem, posing hypotheses, testing these hypotheses, and drawing one or more conclusions. The testing uses proper controls. Scientists present their results in peer-reviewed scientific papers published in scientific journals. A scientific research paper consists of several well-defined sections: introduction, materials and methods, results, and, finally, a concluding discussion. Review papers summarize the research done in a particular field over a period of time.

Art Connections

Figure 1.1.5: In the example below, the scientific method is used to solve an everyday problem. Order the scientific method steps (numbered items) with the process of solving the everyday problem (lettered items). Based on the results of the experiment, is the hypothesis correct? If it is incorrect, propose some alternative hypotheses.

1. Observation
2. Question
3. Hypothesis (answer)
4. Prediction
5. Experiment
6. Result

A. There is something wrong with the electrical outlet.
B. If something is wrong with the outlet, my coffeemaker also won't work when plugged into it.

C. My toaster doesn’t toast my bread.
D. I plug my coffee maker into the outlet.
E. My coffeemaker works.
F. Why doesn’t my toaster work?

Answer

1: C; 2: F; 3: A; 4: B; 5: D; 6: E. The original hypothesis is incorrect, as the coffeemaker works when plugged into the outlet. Alternative hypotheses include that the toaster might be broken or that the toaster wasn't turned on.

Figure 1.1.6: Decide if each of the following is an example of inductive or deductive reasoning.

1. All flying birds and insects have wings. Birds and insects flap their wings as they move through the air. Therefore, wings enable flight.
2. Insects generally survive mild winters better than harsh ones. Therefore, insect pests will become more problematic if global temperatures increase.
3. Chromosomes, the carriers of DNA, separate into daughter cells during cell division. Therefore, DNA is the genetic material.
4. Animals as diverse as humans, insects, and wolves all exhibit social behavior. Therefore, social behavior must have an evolutionary advantage.

Answer

1: inductive; 2: deductive; 3: deductive; 4: inductive.

Glossary

abstract
opening section of a scientific paper that summarizes the research and conclusions

applied science
form of science that aims to solve real-world problems

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

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

conclusion
section of a scientific paper that summarizes the importance of the experimental findings

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

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

descriptive science
(also, discovery science) form of science that aims to observe, explore, and investigate

discussion
section of a scientific paper in which the author interprets experimental results, describes how variables may be related, and attempts to explain the phenomenon in question

falsifiable
able to be disproven by experimental results

hypothesis
suggested explanation for an observation, which can be tested

hypothesis-based science
form of science that begins with a specific question and potential testable answers

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

introduction
opening section of a scientific paper, which provides background information about what was known in the field prior to the research reported in the paper

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

materials and methods
section of a scientific paper that includes a complete description of the substances, methods, and techniques used by the researchers to gather data

natural science
field of science that is related to the physical world and its phenomena and processes

peer-reviewed manuscript
scientific paper that is reviewed by a scientist's colleagues who are experts in the field of study

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

plagiarism
using other people's work or ideas without proper citation, creating the false impression that those are the author's original ideas

results
section of a scientific paper in which the author narrates the experimental findings and presents relevant figures, pictures, diagrams, graphs, and tables, without any further interpretation

review article
paper that summarizes and comments on findings that were published as primary literature

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

scientific method
method of research with defined steps that include observation, formulation of a hypothesis, testing, and confirming or falsifying the hypothesis

serendipity
fortunate accident or a lucky surprise

theory

tested and confirmed explanation for observations or phenomena

variable

part of an experiment that the experimenter can vary or change

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1.2: Themes and Concepts of Biology

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

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

Properties of Life

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

Order

Organisms are highly organized structures that consist of one or more cells. Even very simple, single-celled organisms are remarkably complex. Inside each cell, atoms make up molecules. These in turn make up cell components or organelles. Multicellular organisms, which may consist of millions of individual cells, have an advantage over single-celled organisms in that their cells can be specialized to perform specific functions, and even sacrificed in certain situations for the good of the organism as a whole. How these specialized cells come together to form organs such as the heart, lung, or skin in organisms like the toad shown in Figure 1.2.1 will be discussed later.



Figure 1.2.1: A toad represents a highly organized structure consisting of cells, tissues, organs, and organ systems. (credit: "Ivengo(RUS)"/Wikimedia Commons)

Sensitivity or Response to Stimuli

Organisms respond to diverse stimuli. For example, plants can bend toward a source of light or respond to touch (Figure 1.2.2). Even tiny bacteria can move toward or away from chemicals (a process called chemotaxis) or light (phototaxis). Movement toward a stimulus is considered a positive response, while movement away from a stimulus is considered a negative response.



Figure 1.2.2: The leaves of this sensitive plant (Mimosa pudica) will instantly droop and fold when touched. After a few minutes, the plant returns to its normal state. (credit: Alex Lomas)

CONCEPT IN ACTION

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

Reproduction

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

Adaptation

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

Growth and Development

Organisms grow and develop according to specific instructions coded for by their genes. These genes provide instructions that will direct cellular growth and development, ensuring that a species' young (Figure 1.2.3) will grow up to exhibit many of the same characteristics as its parents.



Figure 1.2.3: Although no two look alike, these kittens have inherited genes from both parents and share many of the same characteristics. (credit: Pieter & Renée Lanser)

Regulation

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

Homeostasis

To function properly, cells require appropriate conditions such as proper temperature, pH, and concentrations of diverse chemicals. These conditions may, however, change from one moment to the next. Organisms are able to maintain internal conditions within a narrow range almost constantly, despite environmental changes, through a process called homeostasis or “steady state”—the ability of an organism to maintain constant internal conditions. For example, many organisms regulate their body temperature in a process known as thermoregulation. Organisms that live in cold climates, such as the polar bear (Figure 1.2.4), have body structures that help them withstand low temperatures and conserve body heat. In hot climates, organisms have methods (such as perspiration in humans or panting in dogs) that help them to shed excess body heat.



Figure 1.2.4: Polar bears and other mammals living in ice-covered regions maintain their body temperature by generating heat and reducing heat loss through thick fur and a dense layer of fat under their skin. (credit: "longhorndave"/Flickr)

Energy Processing

All organisms (such as the California condor shown in Figure 1.2.5) use a source of energy for their metabolic activities. Some organisms capture energy from the Sun and convert it into chemical energy in food; others use chemical energy from molecules they take in.



Figure 1.2.5: A lot of energy is required for a California condor to fly. Chemical energy derived from food is used to power flight. California condors are an endangered species; scientists have strived to place a wing tag on each bird to help them identify and locate each individual bird. (credit: Pacific Southwest Region U.S. Fish and Wildlife)

Levels of Organization of Living Things

Living things are highly organized and structured, following a hierarchy on a scale from small to large. The atom is the smallest and most fundamental unit of matter. It consists of a nucleus surrounded by electrons. Atoms form molecules. A molecule is a chemical structure consisting of at least two atoms held together by a chemical bond. Many molecules that are biologically important are macromolecules, large molecules that are typically formed by combining smaller units called monomers. An example of a macromolecule is deoxyribonucleic acid (DNA) (Figure 1.2.6), which contains the instructions for the functioning of the organism that contains it.

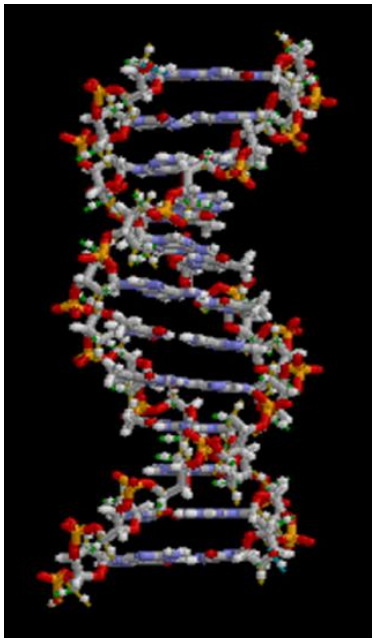


Figure 1.2.6: A molecule, like this large DNA molecule, is composed of atoms. (credit: "Brian0918"/Wikimedia Commons)

CONCEPT IN ACTION

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

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

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

ART CONNECTION

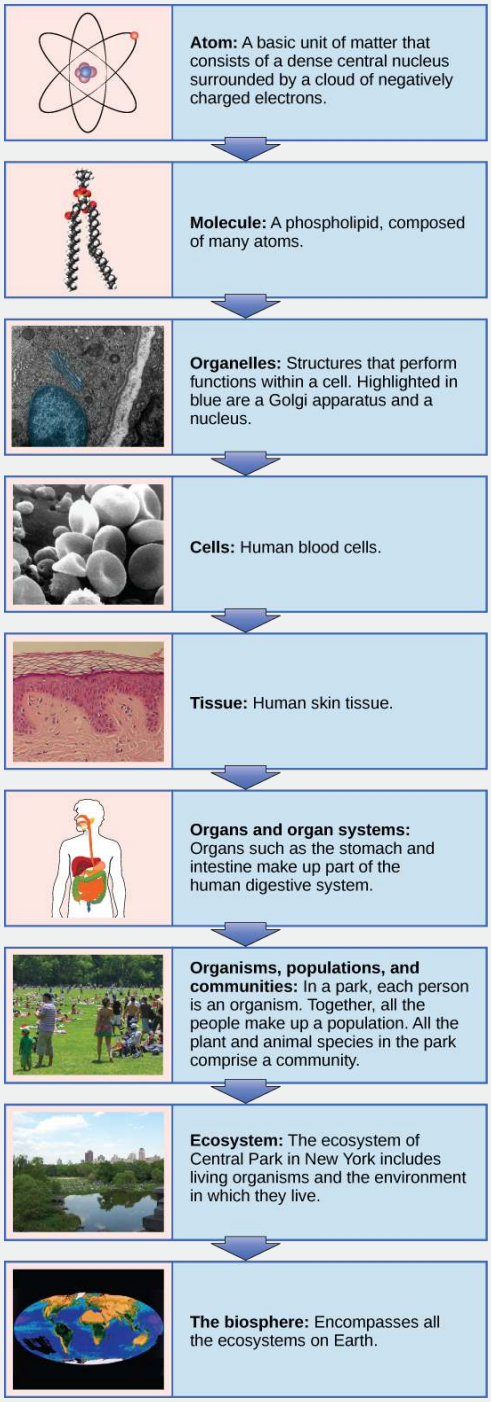


Figure 1.2.7: From an atom to the entire Earth, biology examines all aspects of life. (credit "molecule": modification of work by Jane Whitney; credit "organelles": modification of work by Louisa Howard; credit "cells": modification of work by Bruce Wetzel, Harry Schaefer, National Cancer Institute; credit "tissue": modification of work by "Kilbad"/Wikimedia Commons; credit "organs": modification of work by Mariana Ruiz Villareal, Joaquim Alves Gaspar; credit "organisms": modification of work by Peter Dutton; credit "ecosystem": modification of work by "gigi4791"/Flickr; credit "biosphere": modification of work by NASA)

Which of the following statements is false?

A. Tissues exist within organs which exist within organ systems.

B. Communities exist within populations which exist within ecosystems.

C. Organelles exist within cells which exist within tissues.

D. Communities exist within ecosystems which exist in the biosphere.

Answer

B

All the individuals of a species living within a specific area are collectively called a population. For example, a forest may include many white pine trees. All of these pine trees represent the population of white pine trees in this forest. Different populations may live in the same specific area. For example, the forest with the pine trees includes populations of flowering plants and also insects and microbial populations. A community is the set of populations inhabiting a particular area. For instance, all of the trees, flowers, insects, and other populations in a forest form the forest's community. The forest itself is an ecosystem. An ecosystem consists of all the living things in a particular area together with the abiotic, or non-living, parts of that environment such as nitrogen in the soil or rainwater. At the highest level of organization (Figure 1.2.7), the biosphere is the collection of all ecosystems, and it represents the zones of life on Earth. It includes land, water, and portions of the atmosphere.

The Diversity of Life

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

In the 18th century, a scientist named Carl Linnaeus first proposed organizing the known species of organisms into a hierarchical taxonomy. In this system, species that are most similar to each other are put together within a grouping known as a genus. Furthermore, similar genera (the plural of genus) are put together within a family. This grouping continues until all organisms are collected together into groups at the highest level. The current taxonomic system now has eight levels in its hierarchy, from lowest to highest, they are: species, genus, family, order, class, phylum, kingdom, domain. Thus species are grouped within genera, genera are grouped within families, families are grouped within orders, and so on (Figure 1.2.8).

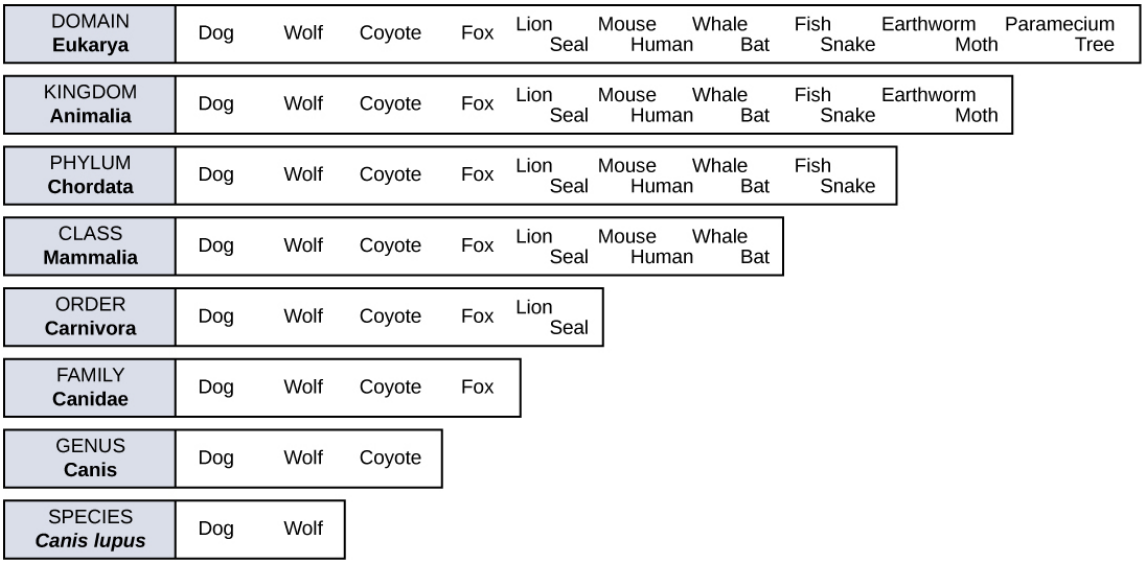


Figure 1.2.8: This diagram shows the levels of taxonomic hierarchy for a dog, from the broadest category—domain—to the most specific—species.

The highest level, domain, is a relatively new addition to the system since the 1990s. Scientists now recognize three domains of life, the Eukarya, the Archaea, and the Bacteria. The domain Eukarya contains organisms that have cells with nuclei. It includes the kingdoms of fungi, plants, animals, and several kingdoms of protists. The Archaea, are single-celled organisms without nuclei and include many extremophiles that live in harsh environments like hot springs. The Bacteria are another quite different group of single-celled organisms without nuclei (Figure 1.2.9). Both the Archaea and the Bacteria are prokaryotes, an informal name for cells without nuclei. The recognition in the 1990s that certain "bacteria," now known as the Archaea, were as different genetically and biochemically from other bacterial cells as they were from eukaryotes, motivated the recommendation to divide life into three

domains. This dramatic change in our knowledge of the tree of life demonstrates that classifications are not permanent and will change when new information becomes available.

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



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

Figure 1.2.9: These images represent different domains. The scanning electron micrograph shows (a) bacterial cells belong to the domain Bacteria, while the (b) extremophiles, seen all together as colored mats in this hot spring, belong to domain Archaea. Both the (c) sunflower and (d) lion are part of domain Eukarya. (credit a: modification of work by Rocky Mountain Laboratories, NIAID, NIH; credit b: modification of work by Steve Jurvetson; credit c: modification of work by Michael Arrighi; credit d: modification of work by Frank Vassen)

EVOLUTION IN ACTION: Carl Woese and the Phylogenetic Tree

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

In the past, biologists grouped living organisms into five kingdoms: animals, plants, fungi, protists, and bacteria. The pioneering work of American microbiologist Carl Woese in the early 1970s has shown, however, that life on Earth has evolved along three lineages, now called domains—Bacteria, Archaea, and Eukarya. Woese proposed the domain as a new taxonomic level and Archaea as a new domain, to reflect the new phylogenetic tree (Figure 1.2.10). Many organisms belonging to the Archaea domain live under extreme conditions and are called extremophiles. To construct his tree, Woese used genetic relationships rather than similarities based on morphology (shape). Various genes were used in phylogenetic studies. Woese's tree was constructed from comparative sequencing of the genes that are universally distributed, found in some slightly altered form in every organism, conserved (meaning that these genes have remained only slightly changed throughout evolution), and of an appropriate length.

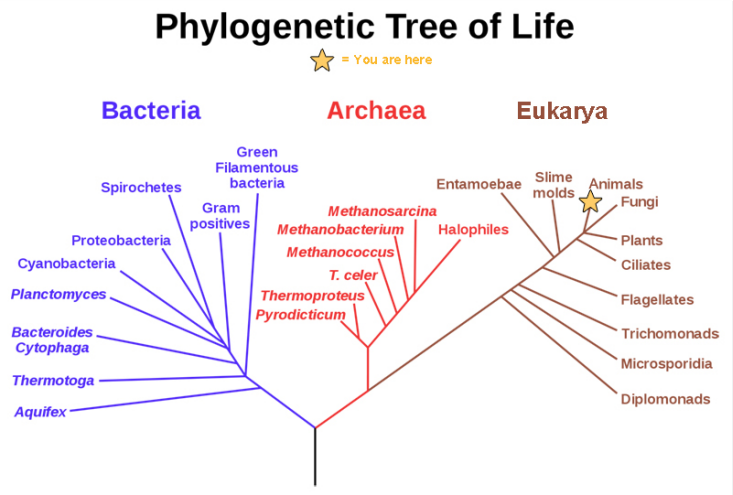


Figure 1.2.10: This phylogenetic tree was constructed by microbiologist Carl Woese using genetic relationships. The tree shows the separation of living organisms into three domains: Bacteria, Archaea, and Eukarya. Bacteria and Archaea are organisms without a nucleus or other organelles surrounded by a membrane and, therefore, are prokaryotes. (credit: modification of work by Eric Gaba)

Branches of Biological Study

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

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



Figure 1.2.11: Researchers work on excavating dinosaur fossils at a site in Castellón, Spain. (credit: Mario Modesto)

Paleontology, another branch of biology, uses fossils to study life's history (Figure 1.2.11). Zoology and botany are the study of animals and plants, respectively. Biologists can also specialize as biotechnologists, ecologists, or physiologists, to name just a few areas. Biotechnologists apply the knowledge of biology to create useful products. Ecologists study the interactions of organisms in their environments. Physiologists study the workings of cells, tissues and organs. This is just a small sample of the many fields that biologists can pursue. From our own bodies to the world we live in, discoveries in biology can affect us in very direct and important ways. We depend on these discoveries for our health, our food sources, and the benefits provided by our ecosystem. Because of this, knowledge of biology can benefit us in making decisions in our day-to-day lives.

The development of technology in the twentieth century that continues today, particularly the technology to describe and manipulate the genetic material, DNA, has transformed biology. This transformation will allow biologists to continue to understand

the history of life in greater detail, how the human body works, our human origins, and how humans can survive as a species on this planet despite the stresses caused by our increasing numbers. Biologists continue to decipher huge mysteries about life suggesting that we have only begun to understand life on the planet, its history, and our relationship to it. For this and other reasons, the knowledge of biology gained through this textbook and other printed and electronic media should be a benefit in whichever field you enter.

CAREERS IN ACTION: Forensic Scientist

Forensic science is the application of science to answer questions related to the law. Biologists as well as chemists and biochemists can be forensic scientists. Forensic scientists provide scientific evidence for use in courts, and their job involves examining trace material associated with crimes. Interest in forensic science has increased in the last few years, possibly because of popular television shows that feature forensic scientists on the job. Also, the development of molecular techniques and the establishment of DNA databases have updated the types of work that forensic scientists can do. Their job activities are primarily related to crimes against people such as murder, rape, and assault. Their work involves analyzing samples such as hair, blood, and other body fluids and also processing DNA (Figure 1.2.12) found in many different environments and materials. Forensic scientists also analyze other biological evidence left at crime scenes, such as insect parts or pollen grains. Students who want to pursue careers in forensic science will most likely be required to take chemistry and biology courses as well as some intensive math courses.



Figure 1.2.12: This forensic scientist works in a DNA extraction room at the U.S. Army Criminal Investigation Laboratory. (credit: U.S. Army CID Command Public Affairs)

Summary

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

Glossary

atom

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

biology

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

biosphere

a collection of all ecosystems on Earth

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

community
a set of populations inhabiting a particular area

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

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

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

homeostasis
the ability of an organism to maintain constant internal conditions

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

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

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

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

organelle
a membrane-bound compartment or sac within a cell

organism
an individual living entity

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

population
all individuals within a species living within a specific area

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

tissue
a group of similar cells carrying out the same function

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1.3: The Process of Science

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



Figure 1.3.1: Formerly called blue-green algae, the (a) cyanobacteria seen through a light microscope are some of Earth's oldest life forms. These (b) stromatolites along the shores of Lake Thetis in Western Australia are ancient structures formed by the layering of cyanobacteria in shallow waters. (credit a: modification of work by NASA; scale-bar data from Matt Russell; credit b: modification of work by Ruth Ellison)

The methods of science include careful observation, record keeping, logical and mathematical reasoning, experimentation, and submitting conclusions to the scrutiny of others. Science also requires considerable imagination and creativity; a well-designed experiment is commonly described as elegant, or beautiful. Like politics, science has considerable practical implications and some science is dedicated to practical applications, such as the prevention of disease (Figure 1.3.2). Other science proceeds largely motivated by curiosity. Whatever its goal, there is no doubt that science, including biology, has transformed human existence and will continue to do so.

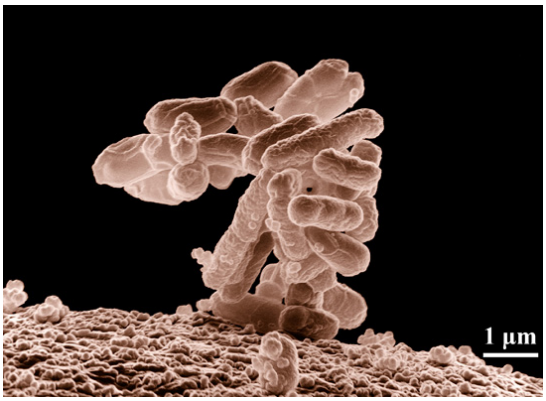


Figure 1.3.2: Biologists may choose to study *Escherichia coli* (*E. coli*), a bacterium that is a normal resident of our digestive tracts but which is also sometimes responsible for disease outbreaks. In this micrograph, the bacterium is visualized using a scanning electron microscope and digital colorization. (credit: Eric Erbe; digital colorization by Christopher Pooley, USDA-ARS)

The Nature of Science

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

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

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

Natural Sciences

What would you expect to see in a museum of natural sciences? Frogs? Plants? Dinosaur skeletons? Exhibits about how the brain functions? A planetarium? Gems and minerals? Or maybe all of the above? Science includes such diverse fields as astronomy, biology, computer sciences, geology, logic, physics, chemistry, and mathematics (Figure 1.3.3). However, those fields of science related to the physical world and its phenomena and processes are considered natural sciences. Thus, a museum of natural sciences might contain any of the items listed above.

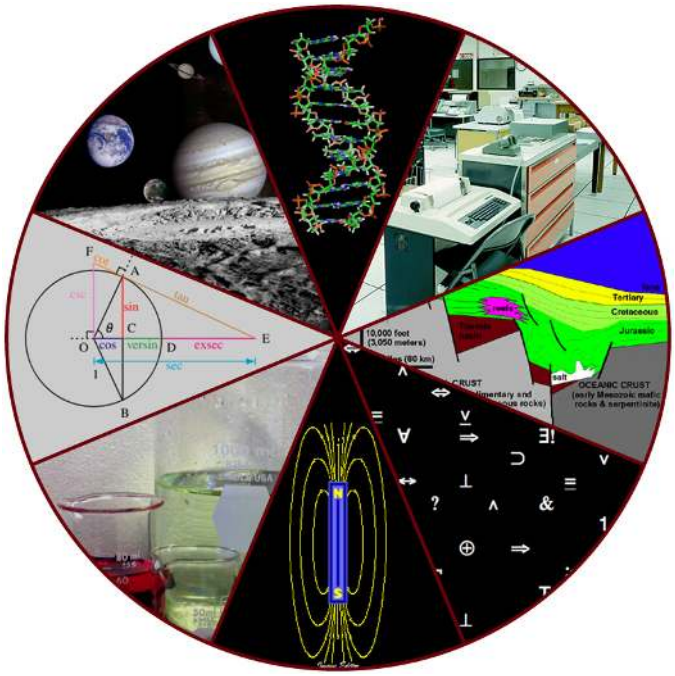


Figure 1.3.3: Some fields of science include astronomy, biology, computer science, geology, logic, physics, chemistry, and mathematics. (credit: "Image Editor"/Flickr)

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

Scientific Inquiry

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

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

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

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

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

Hypothesis Testing

Biologists study the living world by posing questions about it and seeking science-based responses. This approach is common to other sciences as well and is often referred to as the scientific method. The scientific method was used even in ancient times, but it was first documented by England's Sir Francis Bacon (1561–1626) (Figure 1.3.4), who set up inductive methods for scientific inquiry. The scientific method is not exclusively used by biologists but can be applied to almost anything as a logical problem-solving method.



Figure 1.3.4: Sir Francis Bacon is credited with being the first to document the scientific method.

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

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

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

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

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

Each experiment will have one or more variables and one or more controls. A variable is any part of the experiment that can vary or change during the experiment. A control is a part of the experiment that does not change. Look for the variables and controls in the example that follows. As a simple example, an experiment might be conducted to test the hypothesis that phosphate limits the growth of algae in freshwater ponds. A series of artificial ponds are filled with water and half of them are treated by adding phosphate each week, while the other half are treated by adding a salt that is known not to be used by algae. The variable here is the phosphate (or lack of phosphate), the experimental or treatment cases are the ponds with added phosphate and the control ponds are those with something inert added, such as the salt. Just adding something is also a control against the possibility that adding extra matter to the pond has an effect. If the treated ponds show lesser growth of algae, then we have found support for our hypothesis. If they do not, then we reject our hypothesis. Be aware that rejecting one hypothesis does not determine whether or not the other hypotheses can be accepted; it simply eliminates one hypothesis that is not valid (Figure 1.3.5). Using the scientific method, the hypotheses that are inconsistent with experimental data are rejected.

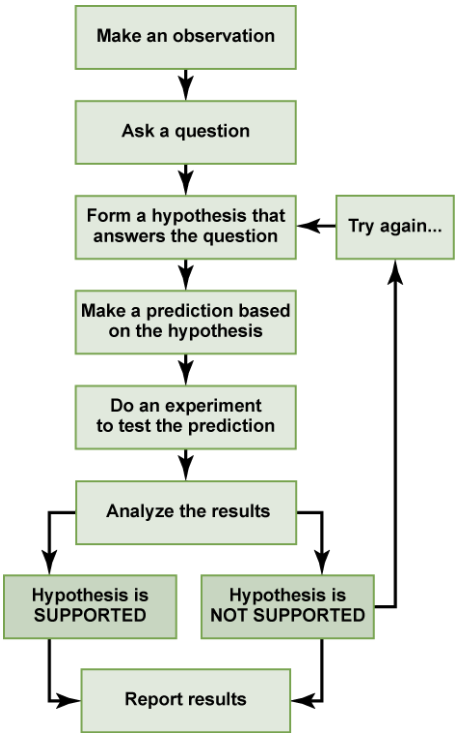


Figure 1.3.5: The scientific method is a series of defined steps that include experiments and careful observation. If a hypothesis is not supported by data, a new hypothesis can be proposed.

Example 1.3.1

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

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

Solution

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

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

Basic and Applied Science

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

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

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

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

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

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

Another example of the link between basic and applied research is the Human Genome Project, a study in which each human chromosome was analyzed and mapped to determine the precise sequence of DNA subunits and the exact location of each gene. (The gene is the basic unit of heredity; an individual’s complete collection of genes is his or her genome.) Other organisms have also been studied as part of this project to gain a better understanding of human chromosomes. The Human Genome Project (Figure 1.3.6) relied on basic research carried out with non-human organisms and, later, with the human genome. An important end goal eventually became using the data for applied research seeking cures for genetically related diseases.

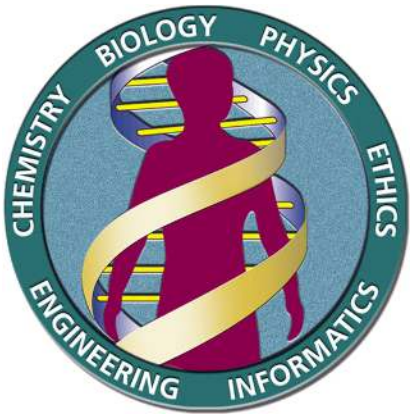


Figure 1.3.6: The Human Genome Project was a 13-year collaborative effort among researchers working in several different fields of science. The project was completed in 2003. (credit: the U.S. Department of Energy Genome Programs)

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

Reporting Scientific Work

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

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

Summary

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

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

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

Glossary

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

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

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

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

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

falsifiable
: able to be disproven by experimental results

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

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

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

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

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

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

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

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

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

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

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

variable
a part of an experiment that can vary or change

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1.4: The Building Blocks of Molecules

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

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

Atoms

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

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

All atoms contain protons, electrons, and neutrons (Figure 1.4.1). The only exception is hydrogen (H), which is made of one proton and one electron. A proton is a positively charged particle that resides in the nucleus (the core of the atom) of an atom and has a mass of 1 and a charge of +1. An electron is a negatively charged particle that travels in the space around the nucleus. In other words, it resides outside of the nucleus. It has a negligible mass and has a charge of –1.

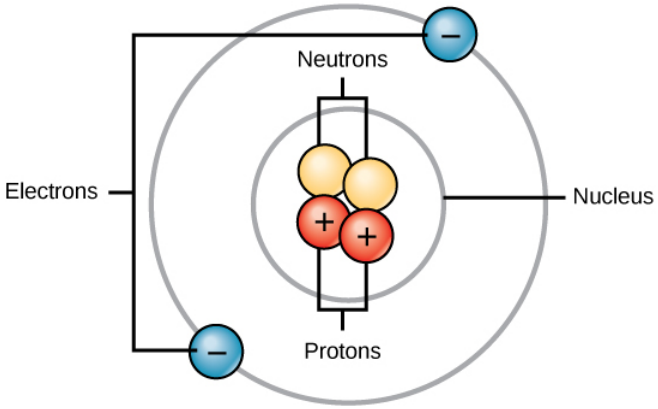


Figure 1.4.1**:** Atoms are made up of protons and neutrons located within the nucleus, and electrons surrounding the nucleus.

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

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

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

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

Because of these characteristics, the elements are arranged into the periodic table of elements, a chart of the elements that includes the atomic number and relative atomic mass of each element. The periodic table also provides key information about the properties of elements (Figure 1.4.2)—often indicated by color-coding. The arrangement of the table also shows how the electrons in each element are organized and provides important details about how atoms will react with each other to form molecules.

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

ART CONNECTION

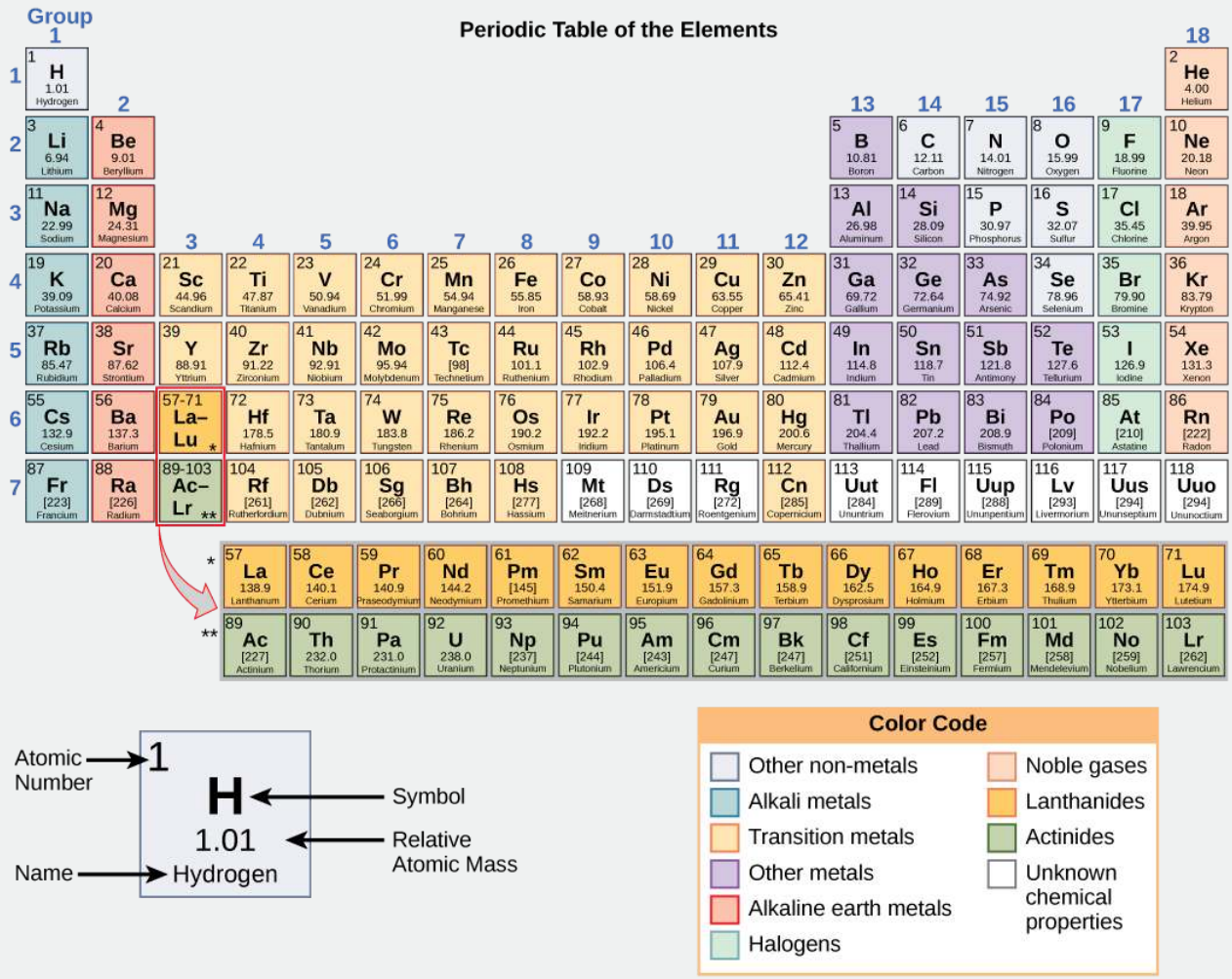


Figure 1.4.2**:** Arranged in columns and rows based on the characteristics of the elements, the periodic table provides key information about the elements and how they might interact with each other to form molecules. Most periodic tables provide a key or legend to the information they contain.

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

EVOLUTION IN ACTION: Carbon Dating

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

After approximately 5,730 years, only one-half of the starting concentration of ^{14}C will have been converted to ^{14}N. The time it takes for half of the original concentration of an isotope to decay to its more stable form is called its half-life. Because the half-life of ^{14}C is long, it is used to age formerly living objects, such as fossils. Using the ratio of the ^{14}C concentration found in an object to the amount of ^{14}C detected in the atmosphere, the amount of the isotope that has not yet decayed can be determined. Based on this amount, the age of the fossil can be calculated to about 50,000 years (Figure 1.4.3). Isotopes with longer half-lives, such as potassium-40, are used to calculate the ages of older fossils. Through the use of carbon dating, scientists can reconstruct the ecology and biogeography of organisms living within the past 50,000 years.



Figure 1.4.3**:** The age of remains that contain carbon and are less than about 50,000 years old, such as this pygmy mammoth, can be determined using carbon dating. (credit: Bill Faulkner/NPS)

CONCEPT IN ACTION

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

Chemical Bonds

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

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

Looking at the periodic table again (Figure 1.4.2), you will notice that there are seven rows. These rows correspond to the number of shells that the elements within that row have. The elements within a particular row have increasing numbers of electrons as the columns proceed from left to right. Although each element has the same number of shells, not all of the shells are completely filled with electrons. If you look at the second row of the periodic table, you will find lithium (Li), beryllium (Be), boron (B), carbon (C), nitrogen (N), oxygen (O), fluorine (F), and neon (Ne). These all have electrons that occupy only the first and second shells. Lithium

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

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

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

For example, sodium only has one electron in its outermost 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. If sodium loses an electron, it now has 11 protons and only 10 electrons, leaving it with an overall charge of +1. It is now called a sodium ion.

The chlorine atom 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 and 18 electrons, giving it a net negative (–1) charge. It is now called a chloride ion. This movement of electrons from one element to another is referred to as electron transfer. As Figure 1.4.4 illustrates, a sodium atom (Na) only has one electron in its outermost shell, whereas a chlorine atom (Cl) has seven electrons in its outermost shell. A sodium atom will donate its one electron to empty its shell, and a chlorine atom will accept that electron to fill its shell, becoming chloride. Both ions now satisfy the octet rule and have complete outermost shells. Because the number of electrons is no longer equal to the number of protons, each is now an ion and has a +1 (sodium) or –1 (chloride) charge.

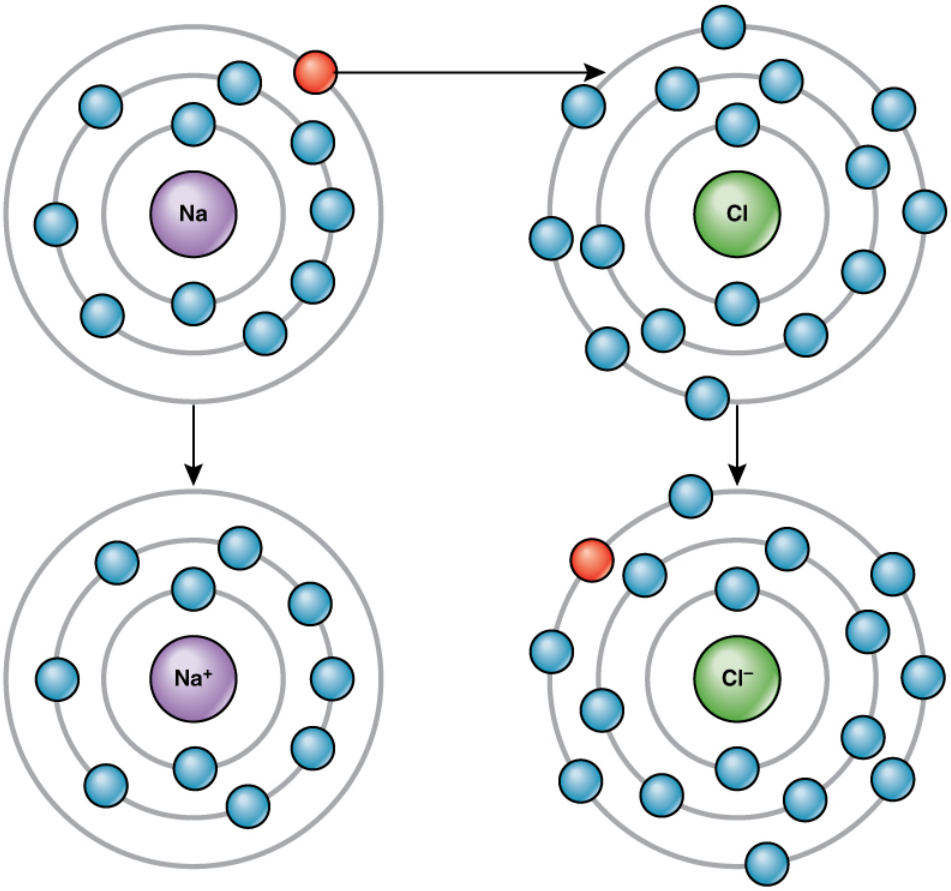


Figure 1.4.4**:** Elements tend to fill their outermost shells with electrons. To do this, they can either donate or accept electrons from other elements.

Ionic Bonds

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

Covalent Bonds

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

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

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

covalent bonds form between the two oxygen atoms because oxygen requires two shared electrons to fill its outermost shell. Nitrogen atoms will form three covalent bonds (also called triple covalent) between two atoms of nitrogen because each nitrogen atom needs three electrons to fill its outermost shell. Another example of a nonpolar covalent bond is found in the methane (CH_4) molecule. The carbon atom has four electrons in its outermost shell and needs four more to fill it. It gets these four from four hydrogen atoms, each atom providing one. These elements all share the electrons equally, creating four nonpolar covalent bonds (Figure 1.4.5).

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

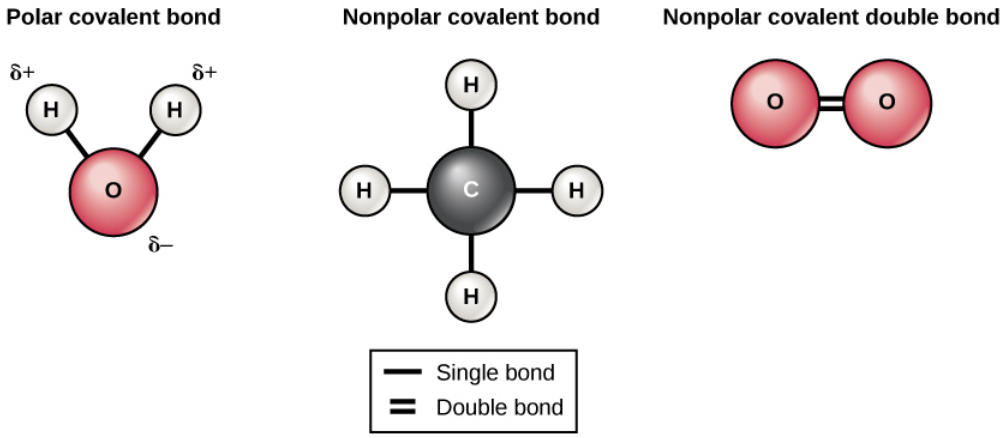


Figure 1.4.5**:** The water molecule (left) depicts a polar bond with a slightly positive charge on the hydrogen atoms and a slightly negative charge on the oxygen. Examples of nonpolar bonds include methane (middle) and oxygen (right).

Hydrogen Bonds

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

When polar covalent bonds containing a hydrogen atom form, the hydrogen atom in that bond has a slightly positive charge. This is because the shared electron is pulled more strongly toward the other element and away from the hydrogen nucleus. Because the hydrogen atom is slightly positive (δ+), it will be attracted to neighboring negative partial charges (δ–). When this happens, a weak interaction occurs between the δ+ charge of the hydrogen atom of one molecule and the δ– charge of the other molecule. This interaction is called a hydrogen bond. This type of bond is common; for example, the liquid nature of water is caused by the hydrogen bonds between water molecules (Figure 1.4.6). Hydrogen bonds give water the unique properties that sustain life. If it were not for hydrogen bonding, water would be a gas rather than a liquid at room temperature.

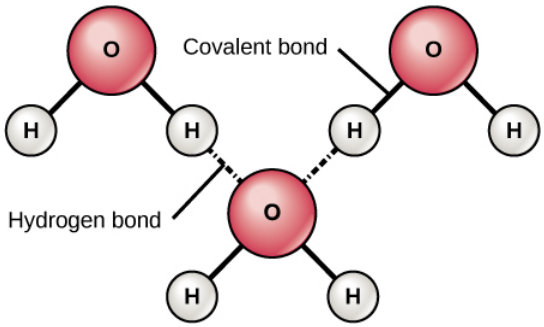


Figure 1.4.6**:** Hydrogen bonds form between slightly positive (δ+) and slightly negative (δ–) charges of polar covalent molecules, such as water.

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

van der Waals Interactions

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

CAREERS IN ACTION: Radiography Technician

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

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

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

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

Summary

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

Art Connections

Figure 1.4.2: How many neutrons do (K) potassium-39 and potassium-40 have, respectively?

Answer

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

Glossary

anion
a negative ion formed by gaining electrons

atomic number
the number of protons in an atom

cation
a positive ion formed by losing electrons

chemical bond

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

covalent bond

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

electron

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

electron transfer

the movement of electrons from one element to another

element

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

hydrogen bond

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

ion

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

ionic bond

a chemical bond that forms between ions of opposite charges

isotope

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

mass number

the number of protons plus neutrons in an atom

matter

anything that has mass and occupies space

neutron

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

nonpolar covalent bond

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

nucleus

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

octet rule

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

periodic table of elements

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

polar covalent bond

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

proton

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

radioactive isotope

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

van der Waals interaction

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

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1.5: Water

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

Water Is Polar

The hydrogen and oxygen atoms within water molecules form polar covalent bonds. The shared electrons spend more time associated with the oxygen atom than they do with hydrogen atoms. There is no overall charge to a water molecule, but there is a slight positive charge on each hydrogen atom and a slight negative charge on the oxygen atom. Because of these charges, the slightly positive hydrogen atoms repel each other and form the unique shape seen in Figure 2.1.6. Each water molecule attracts other water molecules because of the positive and negative charges in the different parts of the molecule. Water also attracts other polar molecules (such as sugars), forming hydrogen bonds. When a substance readily forms hydrogen bonds with water, it can dissolve in water and is referred to as hydrophilic ("water-loving"). Hydrogen bonds are not readily formed with nonpolar substances like oils and fats (Figure 1.5.1). These nonpolar compounds are hydrophobic ("water-fearing") and will not dissolve in water.



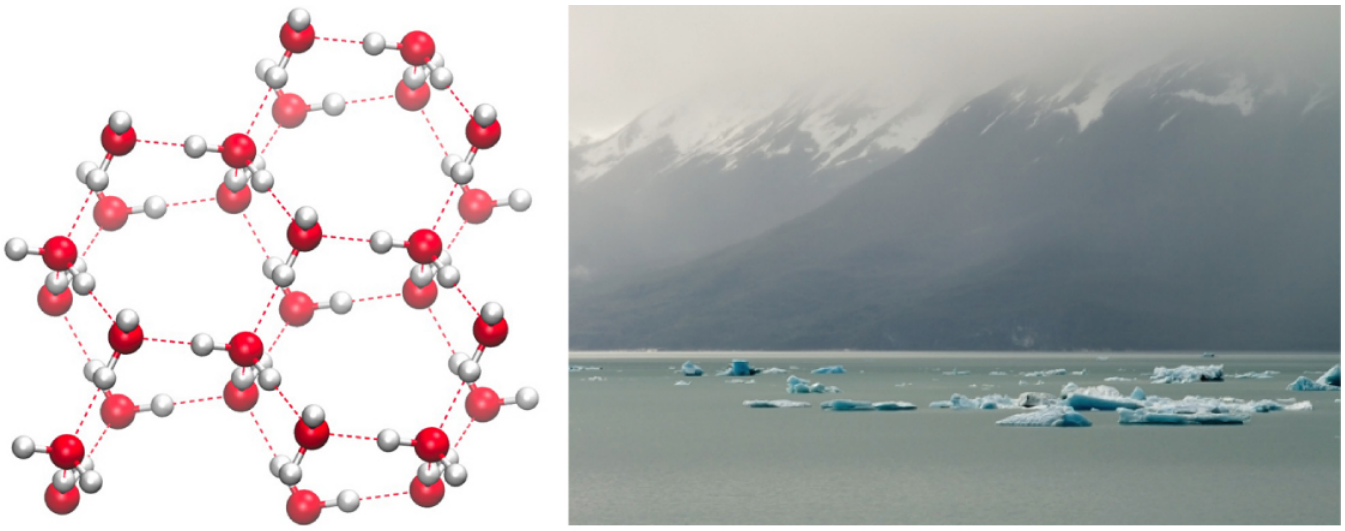
Figure 1.5.1: As this macroscopic image of oil and water show, oil is a nonpolar compound and, hence, will not dissolve in water. Oil and water do not mix. (credit: Gautam Dogra)

Water Stabilizes Temperature

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

Conversely, as molecular motion decreases and temperatures drop, less energy is present to break the hydrogen bonds between water molecules. These bonds remain intact and begin to form a rigid, lattice-like structure (e.g., ice) (Figure 1.5.2**a**). When frozen,

ice is less dense than liquid water (the molecules are farther apart). This means that ice floats on the surface of a body of water (Figure 1.5.2**b**). In lakes, ponds, and oceans, ice will form on the surface of the water, creating an insulating barrier to protect the animal and plant life beneath from freezing in the water. If this did not happen, plants and animals living in water would freeze in a block of ice and could not move freely, making life in cold temperatures difficult or impossible.



(a) (b)

Figure 1.5.2**:** (a) The lattice structure of ice makes it less dense than the freely flowing molecules of liquid water. Ice's lower density enables it to (b) float on water. (credit a: modification of work by Jane Whitney; credit b: modification of work by Carlos Ponte)

CONCEPTS IN ACTION

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

Water Is an Excellent Solvent

Because water is polar, with slight positive and negative charges, ionic compounds and polar molecules can readily dissolve in it. Water is, therefore, what is referred to as a solvent—a substance capable of dissolving another substance. The charged particles will form hydrogen bonds with a surrounding layer of water molecules. This is referred to as a sphere of hydration and serves to keep the particles separated or dispersed in the water. In the case of table salt (NaCl) mixed in water (Figure 1.5.3), the sodium and chloride ions separate, or dissociate, in the water, and spheres of hydration are formed around the ions. A positively charged sodium ion is surrounded by the partially negative charges of oxygen atoms in water molecules. A negatively charged chloride ion is surrounded by the partially positive charges of hydrogen atoms in water molecules. These spheres of hydration are also referred to as hydration shells. The polarity of the water molecule makes it an effective solvent and is important in its many roles in living systems.

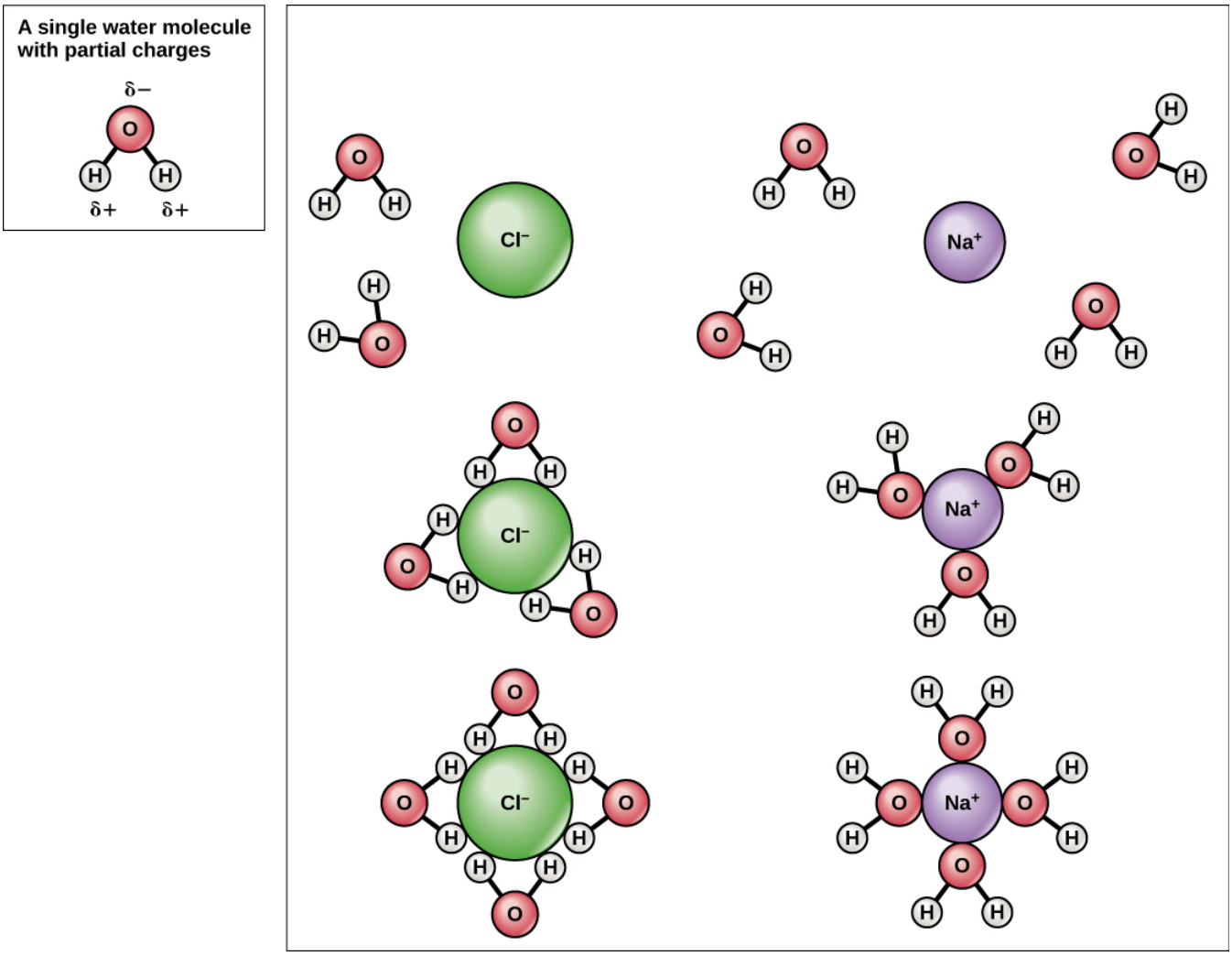


Figure 1.5.3**:** When table salt (NaCl) is mixed in water, spheres of hydration form around the ions.

Water Is Cohesive

Have you ever filled up a glass of water to the very top and then slowly added a few more drops? Before it overflows, the water actually 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-air (gas) interface, although there is no more room in the glass. Cohesion gives rise to surface tension, the capacity of a substance to withstand rupture when placed under tension or stress. When you drop a small scrap of paper onto a droplet of water, the paper floats on top of the water droplet, although the object is denser (heavier) than the water. This occurs because of the surface tension that is created by the water molecules. Cohesion and surface tension keep the water molecules intact and the item floating on the top. It is even possible to "float" a steel needle on top of a glass of water if you place it gently, without breaking the surface tension (Figure 1.5.4).



Figure 1.5.4**:** The weight of a needle on top of water pulls the surface tension downward; at the same time, the surface tension of the water is pulling it up, suspending the needle on the surface of the water and keeping it from sinking. Notice the indentation in the water around the needle. (credit: Cory Zanker)

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

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

CONCEPT IN ACTION

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

Buffers, pH, Acids, and Bases

The pH of a solution is a measure of its acidity or alkalinity. You have probably used litmus paper, paper that has been treated with a natural water-soluble dye so it can be used as a pH indicator, to test how much acid or base (alkalinity) exists in a solution. You might have even used some to make sure the water in an outdoor swimming pool is properly treated. In both cases, this pH test measures the amount of hydrogen ions that exists in a given solution. High concentrations of hydrogen ions yield a low pH, whereas low levels of hydrogen ions result in a high pH. The overall concentration of hydrogen ions is inversely related to its pH and can be measured on the pH scale (Figure 1.5.5). Therefore, the more hydrogen ions present, the lower the pH; conversely, the fewer hydrogen ions, the higher the pH.

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

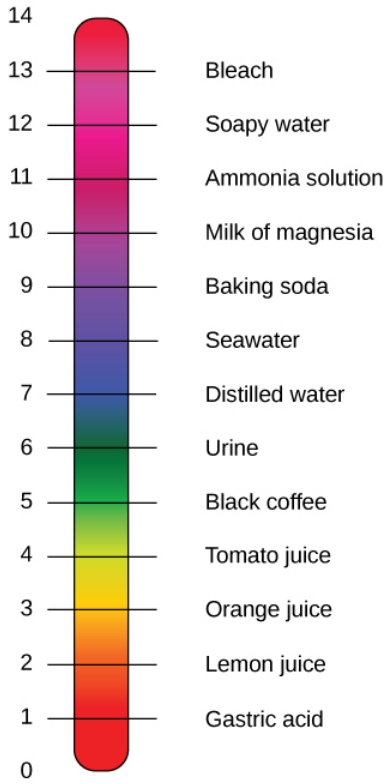


Figure 1.5.5**:** The pH scale measures the amount of hydrogen ions (H^+) in a substance. (credit: modification of work by Edward Stevens)

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

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

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

Summary

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

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

Footnotes

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

Glossary

acid
a substance that donates hydrogen ions and therefore lowers pH

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

base
a substance that absorbs hydrogen ions and therefore raises pH

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

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

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

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

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

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

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

solvent
a substance capable of dissolving another substance

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

temperature
a measure of molecular motion

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1.A: Introduction to Biology (Exercises)

1.1: Themes and Concepts of Biology

Multiple Choice

The smallest unit of biological structure that meets the functional requirements of “living” is the _____.

A. organ
B. organelle
C. cell
D. macromolecule

Answer

C

Which of the following sequences represents the hierarchy of biological organization from the most complex to the least complex level?

A. organelle, tissue, biosphere, ecosystem, population
B. organ, organism, tissue, organelle, molecule
C. organism, community, biosphere, molecule, tissue, organ
D. biosphere, ecosystem, community, population, organism

Answer

D

Free Response

Using examples, explain how biology can be studied from a microscopic approach to a global approach.

Answer

Researchers can approach biology from the smallest to the largest, and everything in between. For instance, an ecologist may study a population of individuals, the population’s community, the community’s ecosystem, and the ecosystem’s part in the biosphere. When studying an individual organism, a biologist could examine the cell and its organelles, the tissues that the cells make up, the organs and their respective organ systems, and the sum total—the organism itself.

1.2: The Process of Science

Multiple Choice

A suggested and testable explanation for an event is called a _____.

A. hypothesis
B. variable
C. theory
D. control

Answer

A

The type of logical thinking that uses related observations to arrive at a general conclusion is called _____.

A. deductive reasoning
B. the scientific method

C. hypothesis-based science
D. inductive reasoning

Answer

D

Free Response

Give an example of how applied science has had a direct effect on your daily life.

Answer

Answers will vary. One example of how applied science has had a direct effect on daily life is the presence of vaccines. Vaccines to prevent diseases such polio, measles, tetanus, and even the influenza affect daily life by contributing to individual and societal health.

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1.B: Chemistry of Life (Exercises)

1.4: The Building Blocks of Molecules

At its most fundamental level, life is made up of matter. Matter occupies space and has mass. All matter is composed of elements, substances that cannot be broken down or transformed chemically into other substances. Each element is made of atoms, each with a constant number of protons and unique properties. Each element is designated by its chemical symbol and possesses unique properties. These unique properties allow elements to combine and to bond with each other in specific ways.

Multiple Choice

Magnesium has an atomic number of 12. Which of the following statements is true of a neutral magnesium atom?

A. It has 12 protons, 12 electrons, and 12 neutrons.
B. It has 12 protons, 12 electrons, and six neutrons.
C. It has six protons, six electrons, and no neutrons.
D. It has six protons, six electrons, and six neutrons.

Answer

A

Which type of bond represents a weak chemical bond?

A. hydrogen bond
B. ionic bond
C. covalent bond
D. polar covalent bond

Answer

A

Free Response

Why are hydrogen bonds and van der Waals interactions necessary for cells?

Answer

Hydrogen bonds and van der Waals interactions form weak associations between different molecules. They provide the structure and shape necessary for proteins and DNA within cells so that they function properly. Hydrogen bonds also give water its unique properties, which are necessary for life.

1.5: Water

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

Multiple Choice

Which of the following statements is not true?

A. Water is polar.
B. Water stabilizes temperature.
C. Water is essential for life.
D. Water is the most abundant atom in Earth’s atmosphere.

Answer

D

Using a pH meter, you find the pH of an unknown solution to be 8.0. How would you describe this solution?

A. weakly acidic
B. strongly acidic
C. weakly basic
D. strongly basic

Answer

C

The pH of lemon juice is about 2.0, whereas tomato juice's pH is about 4.0. Approximately how much of an increase in hydrogen ion concentration is there between tomato juice and lemon juice?

A. 2 times
B. 10 times
C. 100 times
D. 1000 times

Answer

C

Free Response

Describe the structure of a single water molecule, including all bonds that occur within and between a water molecule and dissolved substance such as NaCl.

Answer

One oxygen atom is covalently bonded to two hydrogen atoms resulting in polarity in the water molecule. The oxygen has a a partially negative charge due to it electromagnetic pull on the electrons and the two hydrogen atoms are partially negative. Due to this polarity, both hydrogen and ionic bonds are readily formed between Na and Cl when salt is dissolved in water.

Why can some insects walk on water?

Answer

Some insects can walk on water, although they are heavier (denser) than water, because of the surface tension of water. Surface tension results from cohesion, or the attraction between water molecules at the surface of the body of water [the liquid-air (gas) interface].

Explain why water is an excellent solvent.

Answer

Water molecules are polar, meaning they have separated partial positive and negative charges. Because of these charges, water molecules are able to surround charged particles created when a substance dissociates. The surrounding layer of water molecules stabilizes the ion and keeps differently charged ions from reassociating, so the substance stays dissolved.

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CHAPTER OVERVIEW

2: The Chemical Basis of Life

2.1: Biological Molecules
2.A: Biological Molecules (Exercises)

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2.1: Biological Molecules

The large molecules necessary for life that are built from smaller organic molecules are called biological macromolecules. There are four major classes of biological macromolecules (carbohydrates, lipids, proteins, and nucleic acids), and each is an important component of the cell and performs a wide array of functions. Combined, these molecules make up the majority of a cell's mass. Biological macromolecules are organic, meaning that they contain carbon (with some exceptions, like carbon dioxide). In addition, they may contain hydrogen, oxygen, nitrogen, phosphorus, sulfur, and additional minor elements

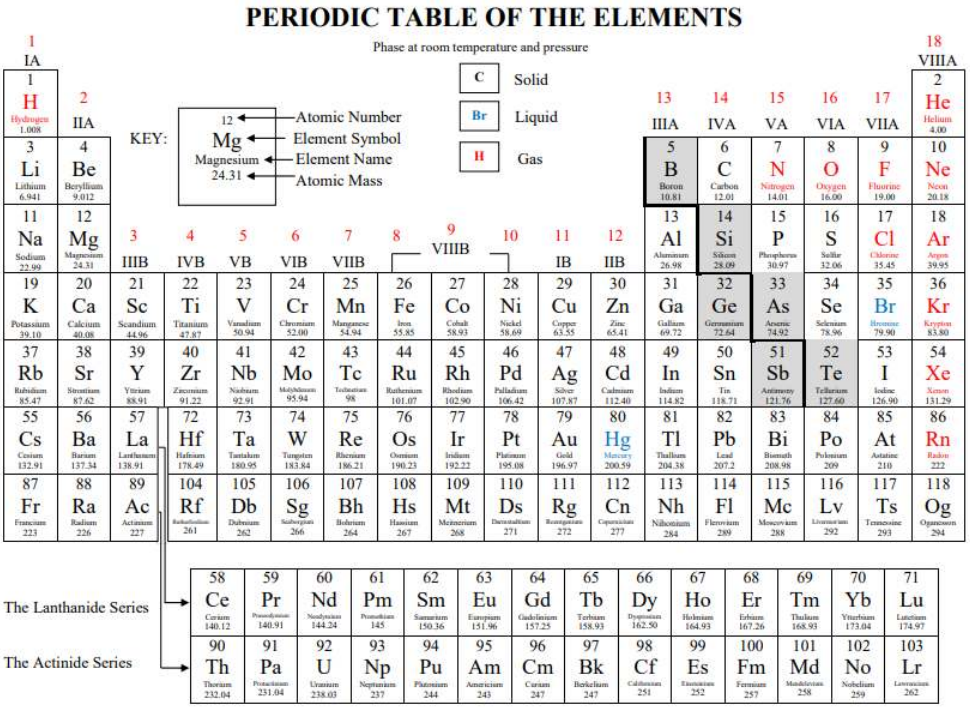


Figure 2.1.1: Periodic Table of Chemicals. (Copyright; Tom Neils)

Carbon

It is often said that life is "carbon-based." This means that carbon atoms, bonded to other carbon atoms or other elements, form the fundamental components of many, if not most, of the molecules found uniquely in living things. Other elements play important roles in biological molecules, but carbon certainly qualifies as the "foundation" element for molecules in living things. It is the bonding properties of carbon atoms that are responsible for its important role.

Carbon Bonding

Carbon contains four electrons in its outer shell. Therefore, it can form four covalent bonds with other atoms or molecules. The simplest organic carbon molecule is methane (CH_4), in which four hydrogen atoms bind to a carbon atom (Figure 2.1.1).

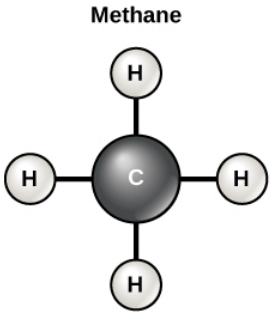
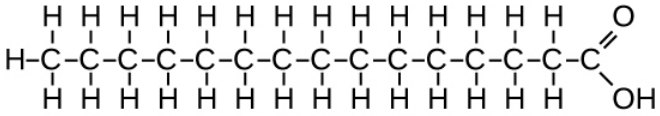
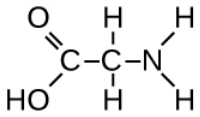


Figure 2.1.2: Carbon can form four covalent bonds to create an organic molecule. The simplest carbon molecule is methane (CH_4), depicted here.

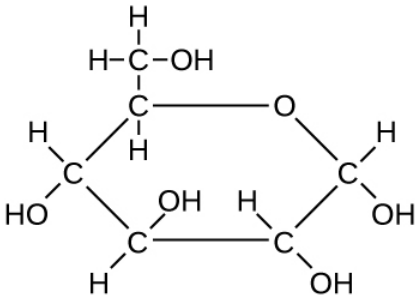
However, structures that are more complex are made using carbon. Any of the hydrogen atoms can be replaced with another carbon atom covalently bonded to the first carbon atom. In this way, long and branching chains of carbon compounds can be made (Figure 2.1.2**a**). The carbon atoms may bond with atoms of other elements, such as nitrogen, oxygen, and phosphorus (Figure 2.1.2**b**). The molecules may also form rings, which themselves can link with other rings (Figure 2.1.2**c**). This diversity of molecular forms accounts for the diversity of functions of the biological macromolecules and is based to a large degree on the ability of carbon to form multiple bonds with itself and other atoms.



(a)



(b)



(c)

Figure 2.1.3: These examples show three molecules (found in living organisms) that contain carbon atoms bonded in various ways to other carbon atoms and the atoms of other elements. (a) This molecule of stearic acid has a long chain of carbon atoms. (b) Glycine, a component of proteins, contains carbon, nitrogen, oxygen, and hydrogen atoms. (c) Glucose, a sugar, has a ring of carbon atoms and one oxygen atom.

Carbohydrates

Carbohydrates are macromolecules with which most consumers are somewhat familiar. To lose weight, some individuals adhere to “low-carb” diets. Athletes, in contrast, often “carb-load” before important competitions to ensure that they have sufficient energy to compete at a high level. Carbohydrates are, in fact, an essential part of our diet; grains, fruits, and vegetables are all natural sources of carbohydrates. Carbohydrates provide energy to the body, particularly through glucose, a simple sugar. Carbohydrates also have other important functions in humans, animals, and plants.

Carbohydrates can be represented by the formula $(CH_2O)_n$, where n is the number of carbon atoms in the molecule. In other words, the ratio of carbon to hydrogen to oxygen is 1:2:1 in carbohydrate molecules. Carbohydrates are classified into three subtypes: monosaccharides, disaccharides, and polysaccharides.

Monosaccharides (mono- = “one”; sacchar- = “sweet”) are simple sugars, the most common of which is glucose. In monosaccharides, the number of carbon atoms usually ranges from three to six. Most monosaccharide names end with the suffix -ose. Depending on the number of carbon atoms in the sugar, they may be known as trioses (three carbon atoms), pentoses (five carbon atoms), and hexoses (six carbon atoms).

Monosaccharides may exist as a linear chain or as ring-shaped molecules; in aqueous solutions, they are usually found in the ring form.

The chemical formula for glucose is $C_6H_{12}O_6$. In most living species, glucose is 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 by the process of photosynthesis, and the glucose, in turn, is used for the energy requirements of the plant. The excess synthesized glucose is often stored as starch that is broken down by other organisms that feed on plants.

Galactose (part of lactose, or 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 chemically (and are known as isomers) because of differing arrangements of atoms in the carbon chain (Figure 2.1.3).

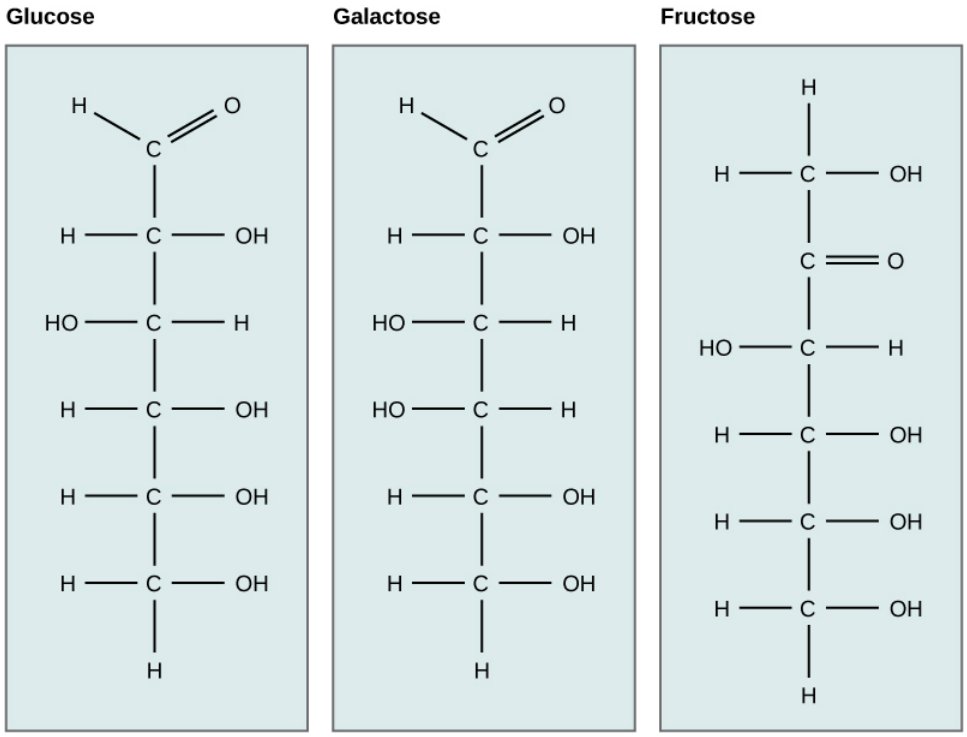


Figure 2.1.4: Glucose, galactose, and fructose are isomeric monosaccharides, meaning that they have the same chemical formula but slightly different structures.

Disaccharides (di- = “two”) form when two monosaccharides undergo a dehydration reaction (a reaction in which the removal of a water molecule occurs). During this process, the hydroxyl group (–OH) of one monosaccharide combines with a hydrogen atom of another monosaccharide, releasing a molecule of water (H_2O) and forming a covalent bond between atoms in the two sugar molecules.

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 from 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.

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

Starch is the stored form of sugars in plants and is made up of amylose and amylopectin (both polymers of glucose). Plants are able to synthesize glucose, and the excess glucose is stored as starch in different plant parts, including roots and seeds. The starch that is consumed by animals is broken down into smaller molecules, such as glucose. The cells can then absorb the glucose.

Glycogen is the storage form of glucose in humans and other vertebrates, and 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 glucose levels decrease, glycogen is broken down to release glucose.

Cellulose is one of the most abundant natural biopolymers. The cell walls of plants are mostly made of cellulose, which provides structural support to the cell. Wood and paper are mostly cellulosic in nature. Cellulose is made up of glucose monomers that are linked by bonds between particular carbon atoms in the glucose molecule.

Every other glucose monomer in cellulose is flipped over and packed tightly as extended long chains. This gives cellulose its rigidity and high tensile strength—which is so important to plant cells. Cellulose passing through our digestive system is called dietary fiber. While the glucose-glucose bonds in cellulose cannot be broken down by human digestive enzymes, herbivores such as cows, buffalos, and horses are able to digest grass that is rich in cellulose and use it as a food source. In these animals, certain species of bacteria reside in the rumen (part of the digestive system of herbivores) and secrete the enzyme cellulase. The appendix also contains bacteria that break down cellulose, giving it an important role in the digestive systems of ruminants. Cellulases can break down cellulose into glucose monomers that can be used as an energy source by the animal.

Carbohydrates serve other functions in different animals. Arthropods, such as insects, spiders, and crabs, have an outer skeleton, called the exoskeleton, which protects their internal body parts. This exoskeleton is made of the biological macromolecule chitin, which is a nitrogenous carbohydrate. It is made of repeating units of a modified sugar containing nitrogen.

Thus, through differences in molecular structure, carbohydrates are able to serve the very different functions of energy storage (starch and glycogen) and structural support and protection (cellulose and chitin) (Figure 2.1.4).

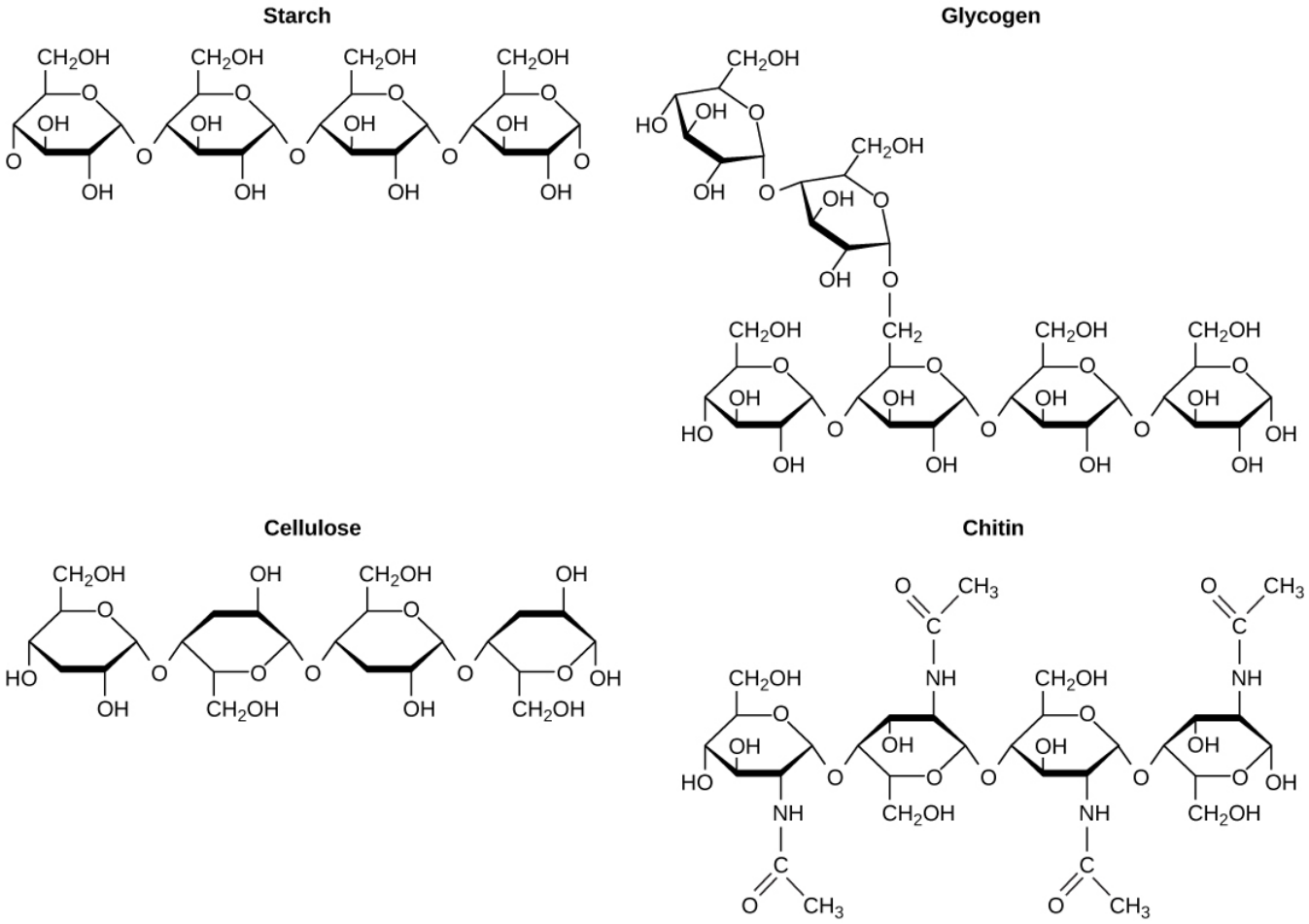


Figure 2.1.5: Although their structures and functions differ, all polysaccharide carbohydrates are made up of monosaccharides and have the chemical formula $(CH_2O)n$.

CAREERS IN ACTION: Registered Dietitian

Obesity is a worldwide health concern, and many diseases, such as diabetes and heart disease, are becoming more prevalent because of obesity. This is one of the reasons why registered dietitians are increasingly sought after for advice. Registered dietitians help plan food and nutrition programs for individuals in various settings. They often work with patients in health-care facilities, designing nutrition plans to prevent and treat diseases. For example, dietitians may teach a patient with diabetes how to manage blood-sugar levels by eating the correct types and amounts of carbohydrates. Dietitians may also work in nursing homes, schools, and private practices.

To become a registered dietitian, one needs to earn at least a bachelor's degree in dietetics, nutrition, food technology, or a related field. In addition, registered dietitians must complete a supervised internship program and pass a national exam. Those who pursue careers in dietetics take courses in nutrition, chemistry, biochemistry, biology, microbiology, and human physiology. Dietitians must become experts in the chemistry and functions of food (proteins, carbohydrates, and fats).

Lipids

Lipids include a diverse group of compounds that are united by a common feature. Lipids are hydrophobic ("water-fearing"), or insoluble in water, because they are nonpolar molecules. This is because they are hydrocarbons that include only nonpolar carbon-carbon or carbon-hydrogen bonds. Lipids perform many different functions in a cell. Cells store energy for long-term use in the form of lipids called fats. Lipids also provide insulation from the environment for plants and animals (Figure 2.1.5). For example, they help keep aquatic birds and mammals dry because of their water-repelling nature. Lipids are also the building blocks of many hormones and are an important constituent of the plasma membrane. Lipids include fats, oils, waxes, phospholipids, and steroids.



Figure 2.1.6: Hydrophobic lipids in the fur of aquatic mammals, such as this river otter, protect them from the elements. (credit: Ken Bosma)

A fat molecule, such as a triglyceride, consists of two main components—glycerol and fatty acids. Glycerol is an organic compound with three carbon atoms, five hydrogen atoms, and three hydroxyl (–OH) groups. Fatty acids have a long chain of hydrocarbons to which an acidic carboxyl group is attached, hence the name “fatty acid.” The number of carbons in the fatty acid may range from 4 to 36; most common are those containing 12–18 carbons. In a fat molecule, a fatty acid is attached to each of the three oxygen atoms in the –OH groups of the glycerol molecule with a covalent bond (Figure 2.1.6).

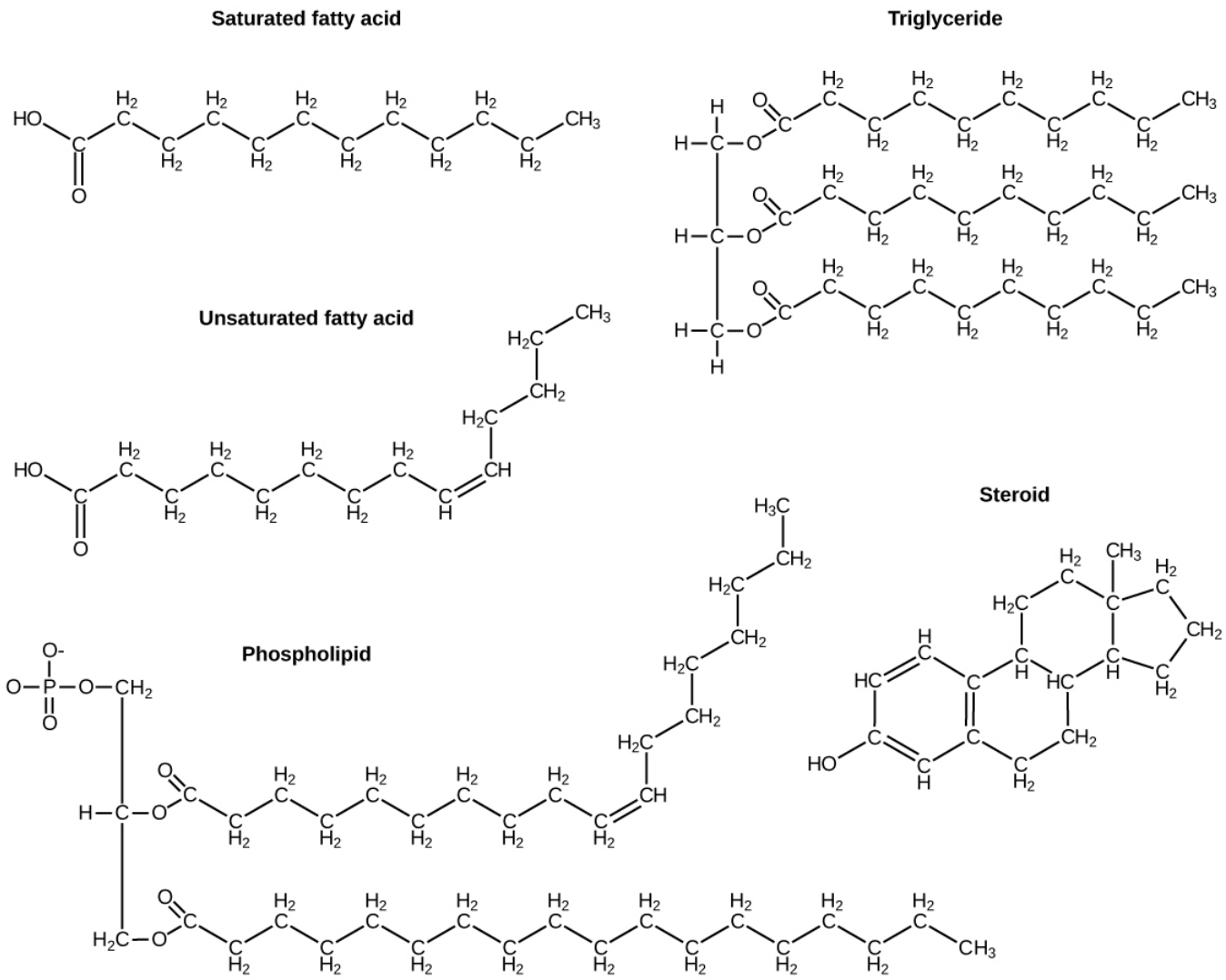


Figure 2.1.7: Lipids include fats, such as triglycerides, which are made up of fatty acids and glycerol, phospholipids, and steroids.

During this covalent bond formation, three water molecules are released. The three fatty acids in the fat may be similar or dissimilar. These fats are also called triglycerides because they have three fatty acids. Some fatty acids have common names that specify their origin. For example, palmitic acid, a saturated fatty acid, is derived from the palm tree. Arachidic acid is derived from *Arachis hypogaea*, the scientific name for peanuts.

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 saturated. Saturated fatty acids are saturated with hydrogen; in other words, the number of hydrogen atoms attached to the carbon skeleton is maximized.

When the hydrocarbon chain contains a double bond, the fatty acid is an unsaturated fatty acid.

Most unsaturated fats are liquid at room temperature and are called oils. If there is one double bond in the molecule, then it is known as a monounsaturated fat (e.g., olive oil), and if there is more than one double bond, then it is known as a polyunsaturated fat (e.g., canola oil).

Saturated fats tend to get packed tightly and are solid at room temperature. Animal fats with stearic acid and palmitic acid contained in meat, and the fat with butyric acid contained in butter, are examples of saturated fats. Mammals store fats in specialized cells called adipocytes, where globules of fat occupy most of the cell. In plants, fat or oil is stored in seeds and is used as a source of energy during embryonic development.

Unsaturated fats or oils are usually of plant origin and contain unsaturated fatty acids. The double bond causes a bend or a “kink” that prevents the fatty acids from packing tightly, keeping them liquid at room temperature. Olive oil, corn oil, canola oil, and cod liver oil are examples of unsaturated fats. Unsaturated fats help to improve blood cholesterol levels, whereas saturated fats contribute to plaque formation in the arteries, which increases the risk of a heart attack.

In the food industry, oils are artificially hydrogenated to make them semi-solid, leading to less spoilage and increased shelf life. Simply speaking, hydrogen gas is bubbled through oils to solidify them. During this hydrogenation process, double bonds of the *cis*-conformation in the hydrocarbon chain may be converted to double bonds in the *trans*-conformation. This forms a *trans*-fat from a *cis*-fat. The orientation of the double bonds affects the chemical properties of the fat (Figure 2.1.7).

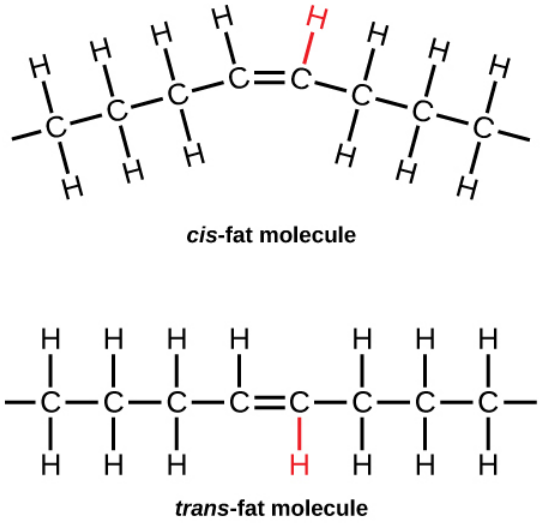


Figure 2.1.8: During the hydrogenation process, the orientation around the double bonds is changed, making a trans-fat from a cis-fat. This changes the chemical properties of the molecule.

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 lipoprotein (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 eliminated the use of *trans*-fats, and U.S. food labels are now required to list their *trans*-fat content.

Essential fatty acids are fatty acids that are required but not synthesized by the human body. Consequently, they must be supplemented through the diet. Omega-3 fatty acids fall into this category and are one of only two known essential fatty acids for humans (the other being omega-6 fatty acids). They are a type of polyunsaturated fat and are called omega-3 fatty acids because the third carbon from the end of the fatty acid participates in a double bond.

Salmon, trout, and tuna are good sources of omega-3 fatty acids. Omega-3 fatty acids are important in brain function and normal growth and development. They may also prevent heart disease and reduce the risk of cancer.

Like carbohydrates, fats have received a lot of bad publicity. It is true that eating an excess of fried foods and other “fatty” foods leads to weight gain. However, fats do have important functions. Fats serve as long-term energy storage. They also provide insulation for the body. Therefore, “healthy” unsaturated fats in moderate amounts should be consumed on a regular basis.

Phospholipids are the major constituent of the plasma membrane. Like fats, they are composed of fatty acid chains attached to a glycerol or similar backbone. Instead of three fatty acids attached, however, there are two fatty acids and the third carbon of the glycerol backbone is bound to a phosphate group. The phosphate group is modified by the addition of an alcohol.

A phospholipid has both hydrophobic and hydrophilic regions. The fatty acid chains are hydrophobic and exclude themselves from water, whereas the phosphate is hydrophilic and interacts with water.

Cells are surrounded by a membrane, which has a bilayer of phospholipids. The fatty acids of phospholipids face inside, away from water, whereas the phosphate group can face either the outside environment or the inside of the cell, which are both aqueous.

Steroids and Waxes

Unlike the phospholipids and fats discussed earlier, steroids have a ring structure. Although they do not resemble other lipids, they are grouped with them because they are also hydrophobic. All steroids have four, linked carbon rings and several of them, like cholesterol, have a short tail.

Cholesterol is a steroid. Cholesterol is mainly synthesized in the liver and is the precursor of many steroid hormones, such as testosterone and estradiol. It is also the precursor of vitamins E and K. Cholesterol is the precursor of bile salts, which help in the breakdown of fats and their subsequent absorption by cells. Although cholesterol is often spoken of in negative terms, it is necessary for the proper functioning of the body. It is a key component of the plasma membranes of animal cells.

Waxes are made up of a hydrocarbon chain with an alcohol (–OH) group and a fatty acid. Examples of animal waxes include beeswax and lanolin. Plants also have waxes, such as the coating on their leaves, that helps prevent them from drying out.

CONCEPT IN ACTION

For an additional perspective on lipids, explore “Biomolecules: The Lipids” through this interactive animation.

Proteins

Proteins are one of the most abundant organic molecules in living systems and have the most diverse range of functions of all macromolecules. Proteins may be structural, regulatory, contractile, or protective; they may serve in transport, storage, or membranes; or they may be toxins or enzymes. Each cell in a living system may contain thousands of different proteins, each with a unique function. Their structures, like their functions, vary greatly. They are all, however, polymers of amino acids, arranged in a linear sequence.

The functions of proteins are very diverse because there are 20 different chemically distinct amino acids that form long chains, and the amino acids can be in any order. For example, proteins can function as enzymes or hormones. Enzymes, which are produced by living cells, are catalysts in biochemical reactions (like digestion) and are usually proteins. Each enzyme is specific for the substrate (a reactant that binds to an enzyme) upon which it acts. Enzymes can function to break molecular bonds, to rearrange bonds, or to form new bonds. An example of an enzyme is salivary amylase, which breaks down amylose, a component of starch.

Hormones are chemical signaling molecules, usually proteins or steroids, secreted by an endocrine gland or group of endocrine cells that act to control or regulate specific physiological processes, including growth, development, metabolism, and reproduction. For example, insulin is a protein hormone that maintains blood glucose levels.

Proteins have different shapes and molecular weights; some proteins are globular in shape whereas others are fibrous in nature. For example, hemoglobin is a globular protein, but collagen, found in our skin, is a fibrous protein. Protein shape is critical to its function. Changes in temperature, pH, and exposure to chemicals may lead to permanent changes in the shape of the protein, leading to a loss of function or denaturation (to be discussed in more detail later). All proteins are made up of different arrangements of the same 20 kinds of amino acids.

Amino acids are the monomers that make up proteins. Each amino acid has the same fundamental structure, which consists of a central carbon atom bonded to an amino group ($–NH_2$), a carboxyl group (–COOH), and a hydrogen atom. Every amino acid also has another variable atom or group of atoms bonded to the central carbon atom known as the R group. The R group is the only difference in structure between the 20 amino acids; otherwise, the amino acids are identical (Figure 2.1.8).

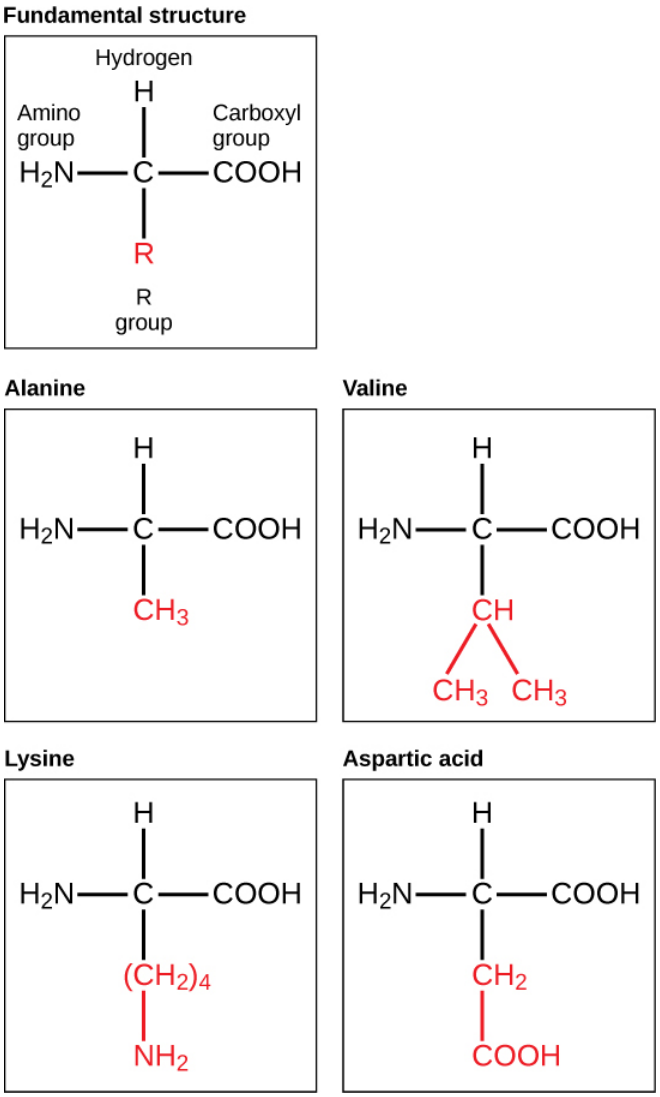


Figure 2.1.9: Amino acids are made up of a central carbon bonded to an amino group ($–NH_2$), a carboxyl group (–COOH), and a hydrogen atom. The central carbon's fourth bond varies among the different amino acids, as seen in these examples of alanine, valine, lysine, and aspartic acid.

The chemical nature of the R group determines the chemical nature of the amino acid within its protein (that is, whether it is acidic, basic, polar, or nonpolar).

The sequence and number of amino acids ultimately determine a protein's shape, size, and function. Each amino acid is attached to another amino acid by a covalent bond, known as a peptide bond, which is formed by a dehydration reaction. The carboxyl group of one amino acid and the amino group of a second amino acid combine, releasing a water molecule. The resulting bond is the peptide bond.

The products formed by such a linkage are called polypeptides. While the terms polypeptide and protein are sometimes used interchangeably, a polypeptide is technically a polymer of amino acids, whereas the term protein is used for a polypeptide or polypeptides that have combined together, have a distinct shape, and have a unique function.

EVOLUTION IN ACTION: The Evolutionary Significance of Cytochrome c

Cytochrome c is an important component of the molecular machinery that harvests energy from glucose. Because this protein's role in producing cellular energy is crucial, it has changed very little over millions of years. Protein sequencing has shown that there is a considerable amount of sequence similarity among cytochrome c molecules of different species; evolutionary relationships can be assessed by measuring the similarities or differences among various species' protein sequences.

For example, scientists have determined that human cytochrome c contains 104 amino acids. For each cytochrome c molecule that has been sequenced to date from different organisms, 37 of these amino acids appear in the same position in each cytochrome c. This indicates that all of these organisms are descended from a common ancestor. On comparing the human and chimpanzee protein sequences, no sequence difference was found. When human and rhesus monkey sequences were compared, a single difference was found in one amino acid. In contrast, human-to-yeast comparisons show a difference in 44 amino acids, suggesting that humans and chimpanzees have a more recent common ancestor than humans and the rhesus monkey, or humans and yeast.

Protein Structure

As discussed earlier, the shape of a protein is critical to its function. To understand how the protein gets its final shape or conformation, we need to understand the four levels of protein structure: primary, secondary, tertiary, and quaternary (Figure 2.1.9).

The unique sequence and number of amino acids in a polypeptide chain is its primary structure. The unique sequence for every protein is ultimately determined by the gene that encodes the protein. Any change in the gene sequence may lead to a different amino acid being added to the polypeptide chain, causing a change in protein structure and function. In sickle cell anemia, the hemoglobin β chain has a single amino acid substitution, causing a change in both the structure and function of the protein. What is most remarkable to consider is that a hemoglobin molecule is made up of two alpha chains and two beta chains that each consist of about 150 amino acids. The molecule, therefore, has about 600 amino acids. The structural difference between a normal hemoglobin molecule and a sickle cell molecule—that dramatically decreases life expectancy in the affected individuals—is a single amino acid of the 600.

Because of this change of one amino acid in the chain, the normally biconcave, or disc-shaped, red blood cells assume a crescent or “sickle” shape, which clogs arteries. This can lead to a myriad of serious health problems, such as breathlessness, dizziness, headaches, and abdominal pain for those who have this disease.

Folding patterns resulting from interactions between the non-R group portions of amino acids give rise to the secondary structure of the protein. The most common are the alpha (α)-helix and beta (β)-pleated sheet structures. Both structures are held in shape by hydrogen bonds. In the alpha helix, the bonds form between every fourth amino acid and cause a twist in the amino acid chain.

In the β-pleated sheet, the “pleats” are formed by hydrogen bonding between atoms on the backbone of the polypeptide chain. The R groups are attached to the carbons, and extend above and below the folds of the pleat. The pleated segments align parallel to each other, and hydrogen bonds form between the same pairs of atoms on each of the aligned amino acids. The α-helix and β-pleated sheet structures are found in many globular and fibrous proteins.

The unique three-dimensional structure of a polypeptide is known as its tertiary structure. This structure is caused by chemical interactions between various amino acids and regions of the polypeptide. Primarily, the interactions among R groups create the complex three-dimensional tertiary structure of a protein. There may be ionic bonds formed between R groups on different amino acids, or hydrogen bonding beyond that involved in the secondary structure. When protein folding takes place, the hydrophobic R groups of nonpolar amino acids lay in the interior of the protein, whereas the hydrophilic R groups lay on the outside. The former types of interactions are also known as hydrophobic interactions.

In nature, some proteins are formed from several polypeptides, also known as subunits, and the interaction of these subunits forms the quaternary structure. Weak interactions between the subunits help to stabilize the overall structure. For example, hemoglobin is a combination of four polypeptide subunits.

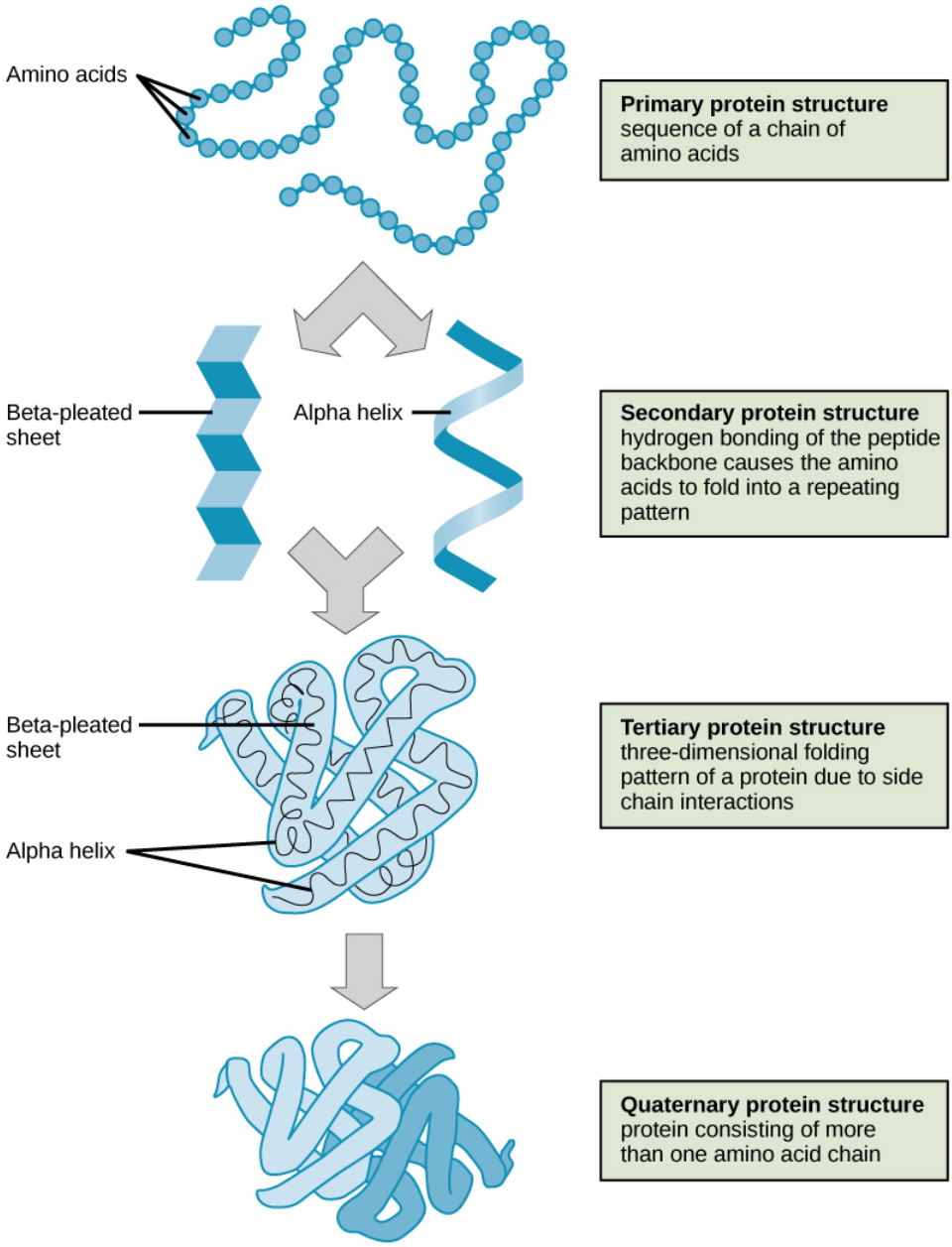


Figure 2.1.10: The four levels of protein structure can be observed in these illustrations. (credit: modification of work by National Human Genome Research Institute)

Each protein has its own unique sequence and shape held together by chemical interactions. If the protein is subject to changes in temperature, pH, or exposure to chemicals, the protein structure may change, losing its shape in what is known as denaturation as discussed earlier. Denaturation is often reversible because the primary structure is preserved if the denaturing agent is removed, allowing the protein to resume its function. Sometimes denaturation is irreversible, leading to a loss of function. One example of protein denaturation can be seen when an egg is fried or boiled. The albumin protein in the liquid egg white is denatured when placed in a hot pan, changing from a clear substance to an opaque white substance. Not all proteins are denatured at high temperatures; for instance, bacteria that survive in hot springs have proteins that are adapted to function at those temperatures.

CONCEPT IN ACTION

For an additional perspective on proteins, explore “Biomolecules: The Proteins” through this interactive animation.

Nucleic Acids

Nucleic acids are key macromolecules in the continuity of life. They carry the genetic blueprint of a cell and carry instructions for the functioning of the cell.

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.

The other type of nucleic acid, RNA, is mostly involved in protein synthesis. The DNA molecules never leave the nucleus, but instead use an RNA intermediary to communicate with the rest of the cell. Other types of RNA are also involved in protein synthesis and its regulation.

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: a nitrogenous base, a pentose (five-carbon) sugar, and a phosphate group (Figure 2.1.10). Each nitrogenous base in a nucleotide is attached to a sugar molecule, which is attached to a phosphate group.

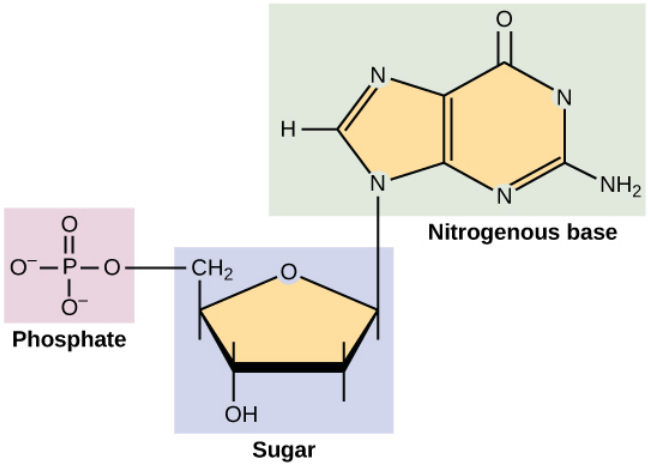


Figure 2.1.11: A nucleotide is made up of three components: a nitrogenous base, a pentose sugar, and a phosphate group.

DNA Double-Helical Structure

DNA has a double-helical structure (Figure 2.1.11). It is composed of two strands, or polymers, of nucleotides. The strands are formed with bonds between phosphate and sugar groups of adjacent nucleotides. The strands are bonded to each other at their bases with hydrogen bonds, and the strands coil about each other along their length, hence the “double helix” description, which means a double spiral.

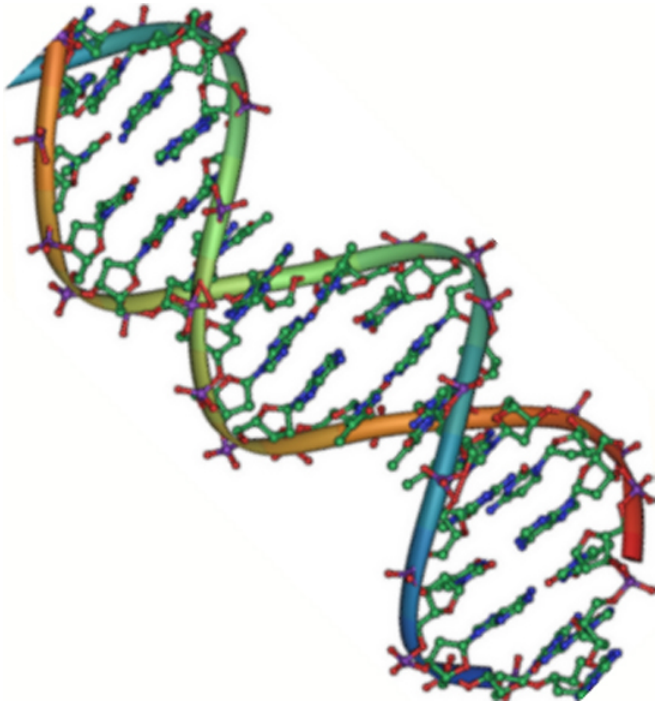


Figure 2.1.12: The double-helix model shows DNA as two parallel strands of intertwining molecules. (credit: Jerome Walker, Dennis Myts)

The alternating sugar and phosphate groups lie on the outside of each strand, forming the backbone of the DNA. The nitrogenous bases are stacked in the interior, like the steps of a staircase, and these bases pair; the pairs are bound to each other by hydrogen bonds. The bases pair in such a way that the distance between the backbones of the two strands is the same all along the molecule.

Summary

Living things are carbon-based because carbon plays such a prominent role in the chemistry of living things. The four covalent bonding positions of the carbon atom can give rise to a wide diversity of compounds with many functions, accounting for the importance of carbon in living things. Carbohydrates are a group of macromolecules that are a vital energy source for the cell, provide structural support to many organisms, and can be found on the surface of the cell as receptors or for cell recognition. Carbohydrates are classified as monosaccharides, disaccharides, and polysaccharides, depending on the number of monomers in the molecule.

Lipids are a class of macromolecules that are nonpolar and hydrophobic in nature. Major types include fats and oils, waxes, phospholipids, and steroids. Fats and oils are a stored form of energy and can include triglycerides. Fats and oils are usually made up of fatty acids and glycerol.

Proteins are a class of macromolecules that can perform a diverse range of functions for the cell. They help in metabolism by providing structural support and by acting as enzymes, carriers or as hormones. The building blocks of proteins are amino acids. Proteins are organized at four levels: primary, secondary, tertiary, and quaternary. Protein shape and function are intricately linked; any change in shape caused by changes in temperature, pH, or chemical exposure may lead to protein denaturation and a loss of function.

Nucleic acids are molecules made up of repeating units of nucleotides that direct cellular activities such as cell division and protein synthesis. Each nucleotide is made up of a pentose sugar, a nitrogenous base, and a phosphate group. There are two types of nucleic acids: DNA and RNA.

Glossary

amino acid

a monomer of a protein

carbohydrate

a biological macromolecule in which the ratio of carbon to hydrogen to oxygen is 1:2:1; carbohydrates serve as energy sources and structural support in cells

cellulose

a polysaccharide that makes up the cell walls of plants and provides structural support to the cell

chitin

a type of carbohydrate that forms the outer skeleton of arthropods, such as insects and crustaceans, and the cell walls of fungi

denaturation

the loss of shape in a protein as a result of changes in temperature, pH, or exposure to chemicals

deoxyribonucleic acid (DNA)

a double-stranded polymer of nucleotides that carries the hereditary information of the cell

disaccharide

two sugar monomers that are linked together by a peptide bond

enzyme

a catalyst in a biochemical reaction that is usually a complex or conjugated protein

fat

a lipid molecule composed of three fatty acids and a glycerol (triglyceride) that typically exists in a solid form at room temperature

glycogen

a storage carbohydrate in animals

hormone

a chemical signaling molecule, usually a protein or steroid, secreted by an endocrine gland or group of endocrine cells; acts to control or regulate specific physiological processes

lipids

a class of macromolecules that are nonpolar and insoluble in water

macromolecule

a large molecule, often formed by polymerization of smaller monomers

monosaccharide

a single unit or monomer of carbohydrates

nucleic acid

a biological macromolecule that carries the genetic information of a cell and carries instructions for the functioning of the cell

nucleotide

a monomer of nucleic acids; contains a pentose sugar, a phosphate group, and a nitrogenous base

oil

an unsaturated fat that is a liquid at room temperature

phospholipid

a major constituent of the membranes of cells; composed of two fatty acids and a phosphate group attached to the glycerol backbone

polypeptide
a long chain of amino acids linked by peptide bonds

polysaccharide
a long chain of monosaccharides; may be branched or unbranched

protein
a biological macromolecule composed of one or more chains of amino acids

ribonucleic acid (RNA)
a single-stranded polymer of nucleotides that is involved in protein synthesis

saturated fatty acid
a long-chain hydrocarbon with single covalent bonds in the carbon chain; the number of hydrogen atoms attached to the carbon skeleton is maximized

starch
a storage carbohydrate in plants

steroid
a type of lipid composed of four fused hydrocarbon rings

***trans*-fat**
a form of unsaturated fat with the hydrogen atoms neighboring the double bond across from each other rather than on the same side of the double bond

triglyceride
a fat molecule; consists of three fatty acids linked to a glycerol molecule

unsaturated fatty acid
a long-chain hydrocarbon that has one or more than one double bonds in the hydrocarbon chain

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2.A: Biological Molecules (Exercises)

Biological Molecules

There are four major classes of biological macromolecules (carbohydrates, lipids, proteins, and nucleic acids), and each is an important component of the cell and performs a wide array of functions. Combined, these molecules make up the majority of a cell's mass. Biological macromolecules are organic, meaning that they contain carbon (with some exceptions, like carbon dioxide).

Multiple Choice

An example of a monosaccharide is _____.

A. fructose
B. glucose
C. galactose
D. all of the above

Answer

D

Cellulose and starch are examples of _____.

A. monosaccharides
B. disaccharides
C. lipids
D. polysaccharides

Answer

D

Phospholipids are important components of _____.

A. the plasma membrane of cells
B. the ring structure of steroids
C. the waxy covering on leaves
D. the double bond in hydrocarbon chains

Answer

A

The monomers that make up proteins are called _____.

A. nucleotides
B. disaccharides
C. amino acids
D. chaperones

Answer

C

Free Response

Explain at least three functions that lipids serve in plants and/or animals.

Answer

Fat serves as a valuable way for animals to store energy. It can also provide insulation. Phospholipids and steroids are important components of cell membranes.

Explain what happens if even one amino acid is substituted for another in a polypeptide chain. Provide a specific example.

Answer

A change in gene sequence can lead to a different amino acid being added to a polypeptide chain instead of the normal one. This causes a change in protein structure and function. For example, in sickle cell anemia, the hemoglobin β chain has a single amino acid substitution. Because of this change, the disc-shaped red blood cells assume a crescent shape, which can result in serious health problems.

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CHAPTER OVERVIEW

3: Cell Structure and Function

3.1: How Cells Are Studied

3.2: Comparing Prokaryotic and Eukaryotic Cells

3.3: Eukaryotic Cells

3.4: The Cell Membrane

3.A: Cell Structure and Function (Exercises)

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3.1: How Cells Are Studied

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

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

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

Microscopy

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

Light Microscopes

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

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

Most student microscopes are classified as light microscopes (Figure 3.1.1**a**). Visible light both passes through and is bent by the lens system to enable the user to see the specimen. Light microscopes are advantageous for viewing living organisms, but since individual cells are generally transparent, their components are not distinguishable unless they are colored with special stains. Staining, however, usually kills the cells.

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

CONCEPT IN ACTION



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

A second type of microscope used in laboratories is the dissecting microscope (Figure 3.1.1**b**). These microscopes have a lower magnification (20 to 80 times the object size) than light microscopes and can provide a three-dimensional view of the specimen. Thick objects can be examined with many components in focus at the same time. These microscopes are designed to give a magnified and clear view of tissue structure as well as the anatomy of the whole organism. Like light microscopes, most modern dissecting microscopes are also binocular, meaning that they have two separate lens systems, one for each eye. The lens systems are separated by a certain distance, and therefore provide a sense of depth in the view of their subject to make manipulations by hand easier. Dissecting microscopes also have optics that correct the image so that it appears as if being seen by the naked eye and not as an inverted image. The light illuminating a sample under a dissecting microscope typically comes from above the sample, but may also be directed from below.

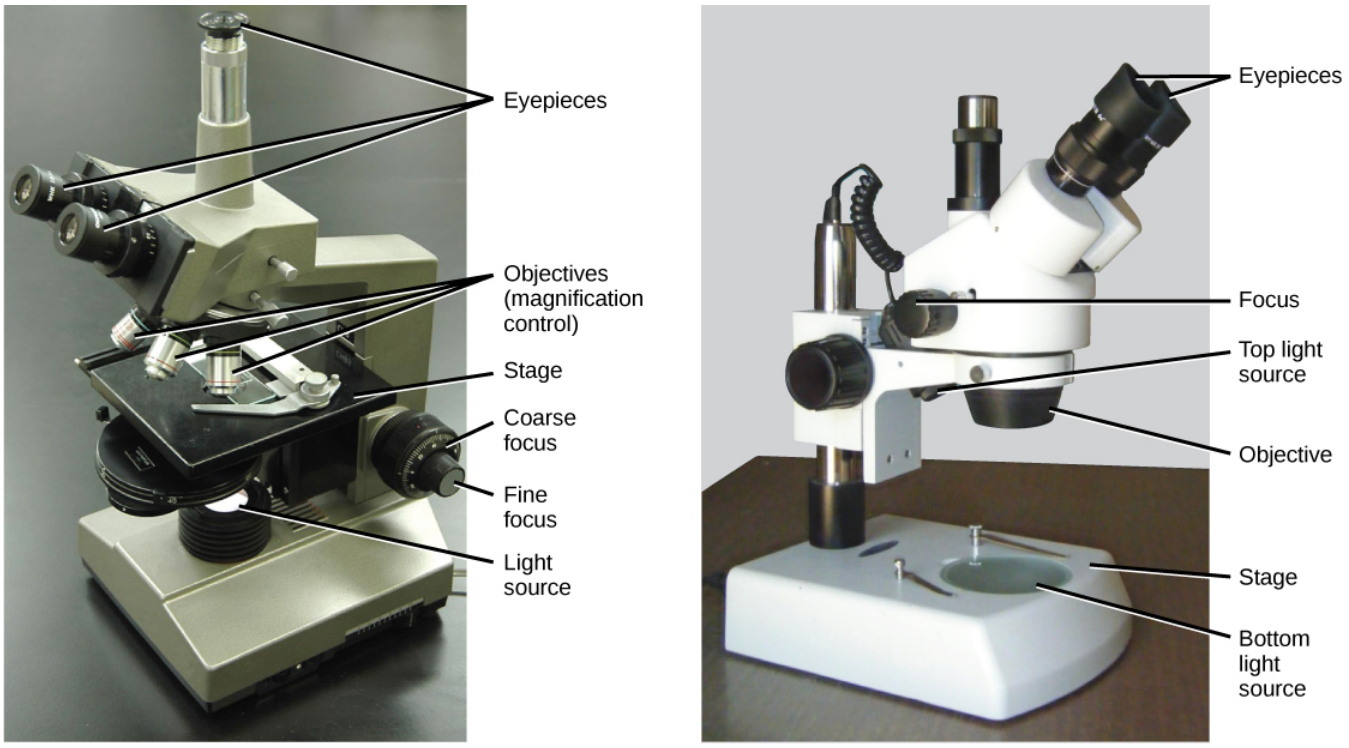


Figure 3.1.1**:** (a) Most light microscopes used in a college biology lab can magnify cells up to approximately 400 times. (b) Dissecting microscopes have a lower magnification than light microscopes and are used to examine larger objects, such as tissues.

Electron Microscopes

In contrast to light microscopes, electron microscopes use a beam of electrons instead of a beam of light. Not only does this allow for higher magnification and, thus, more detail (Figure 3.1.2), it also provides higher resolving power. Preparation of a specimen for viewing under an electron microscope will kill it; therefore, live cells cannot be viewed using this type of microscopy. In addition, the electron beam moves best in a vacuum, making it impossible to view living materials.

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

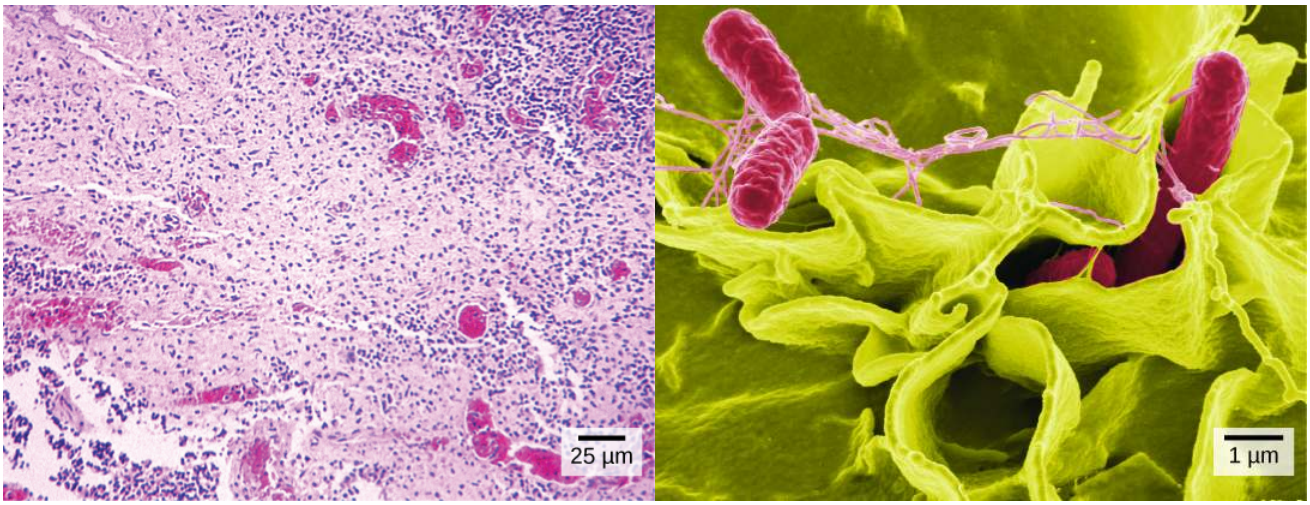


Figure 3.1.2**:** (a) *Salmonella* bacteria are viewed with a light microscope. (b) This scanning electron micrograph shows *Salmonella* bacteria (in red) invading human cells. (credit a: modification of work by CDC, Armed Forces Institute of Pathology, Charles N. Farmer; credit b: modification of work by Rocky Mountain Laboratories, NIAID, NIH; scale-bar data from Matt Russell)

CAREERS IN ACTION: Cytotechnologist

Have you ever heard of a medical test called a Pap smear (Figure 3.1.3)? In this test, a doctor takes a small sample of cells from the uterine cervix of a patient and sends it to a medical lab where a cytotechnologist stains the cells and examines them for any changes that could indicate cervical cancer or a microbial infection.

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

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

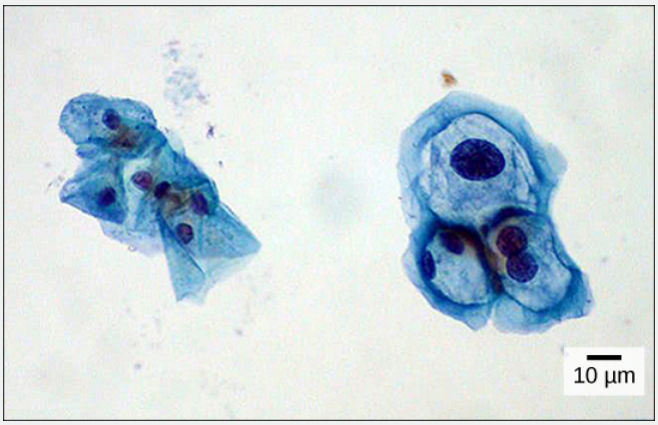


Figure 3.1.3**:** These uterine cervix cells, viewed through a light microscope, were obtained from a Pap smear. Normal cells are on the left. The cells on the right are infected with human papillomavirus. (credit: modification of work by Ed Uthman; scale-bar data from Matt Russell)

Cell Theory

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

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

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

Section Summary

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

Glossary

microscope
: the instrument that magnifies an object

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

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3.2: Comparing Prokaryotic and Eukaryotic Cells

Cells fall into one of two broad categories: prokaryotic and eukaryotic. The predominantly single-celled organisms of the domains Bacteria and Archaea are classified as prokaryotes (*pro-* = before; *-karyon-* = nucleus). Animal cells, plant cells, fungi, and protists are eukaryotes (*eu-* = true).

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, consisting of a jelly-like region within the cell in which other cellular components are found; 3) DNA, the genetic material of the cell; and 4) ribosomes, particles that synthesize proteins. However, prokaryotes differ from eukaryotic cells in several ways.

A prokaryotic cell is a simple, single-celled (unicellular) organism that lacks a 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 the central part of the cell: a darkened region called the nucleoid (Figure 3.2.1).

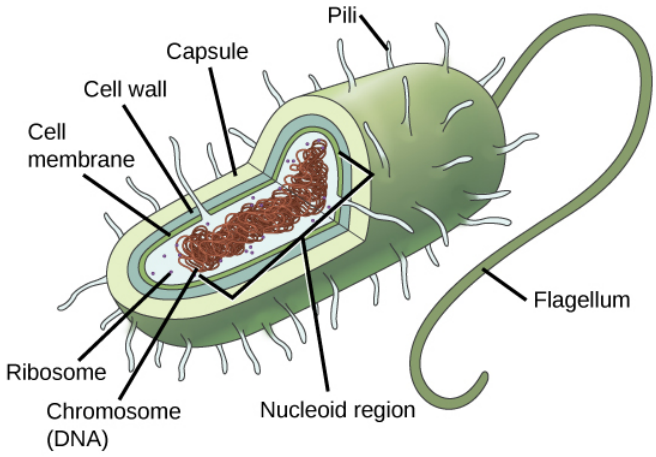


Figure 3.2.1: This figure shows the generalized structure of a prokaryotic cell.

Unlike Archaea and eukaryotes, bacteria have a cell wall made of peptidoglycan, comprised of sugars and amino acids, and many have a polysaccharide capsule (Figure 3.2.1). 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, while most pili are used to exchange genetic material during a type of reproduction called conjugation.

Eukaryotic Cells

In nature, the relationship between form and function is apparent at all levels, including the level of the cell, and this will become clear as we explore eukaryotic cells. The principle "form follows function" is found in many contexts. For example, birds and fish have streamlined bodies that allow them to move quickly through the medium in which they live, be it air or water. It means that, in general, one can deduce the function of a structure by looking at its form, because the two are matched.

A eukaryotic cell is a cell that has a membrane-bound nucleus and other membrane-bound compartments or sacs, called organelles, which have specialized functions. The word eukaryotic means "true kernel" or "true nucleus," alluding to the presence of the membrane-bound nucleus in these cells. The word "organelle" means "little organ," and, as already mentioned, organelles have specialized cellular functions, just as the organs of your body have specialized functions.

Cell Size

At 0.1–5.0 µm in diameter, prokaryotic cells are significantly smaller than eukaryotic cells, which have diameters ranging from 10–100 µm (Figure 3.2.2). The small size of prokaryotes allows ions and organic molecules that enter them to quickly spread to other parts of the cell. Similarly, any wastes produced within a prokaryotic cell can quickly move out. However, larger eukaryotic cells

have evolved different structural adaptations to enhance cellular transport. Indeed, the large size of these cells would not be possible without these adaptations. In general, cell size is limited because volume increases much more quickly than does cell surface area. As a cell becomes larger, it becomes more and more difficult for the cell to acquire sufficient materials to support the processes inside the cell, because the relative size of the surface area across which materials must be transported declines.

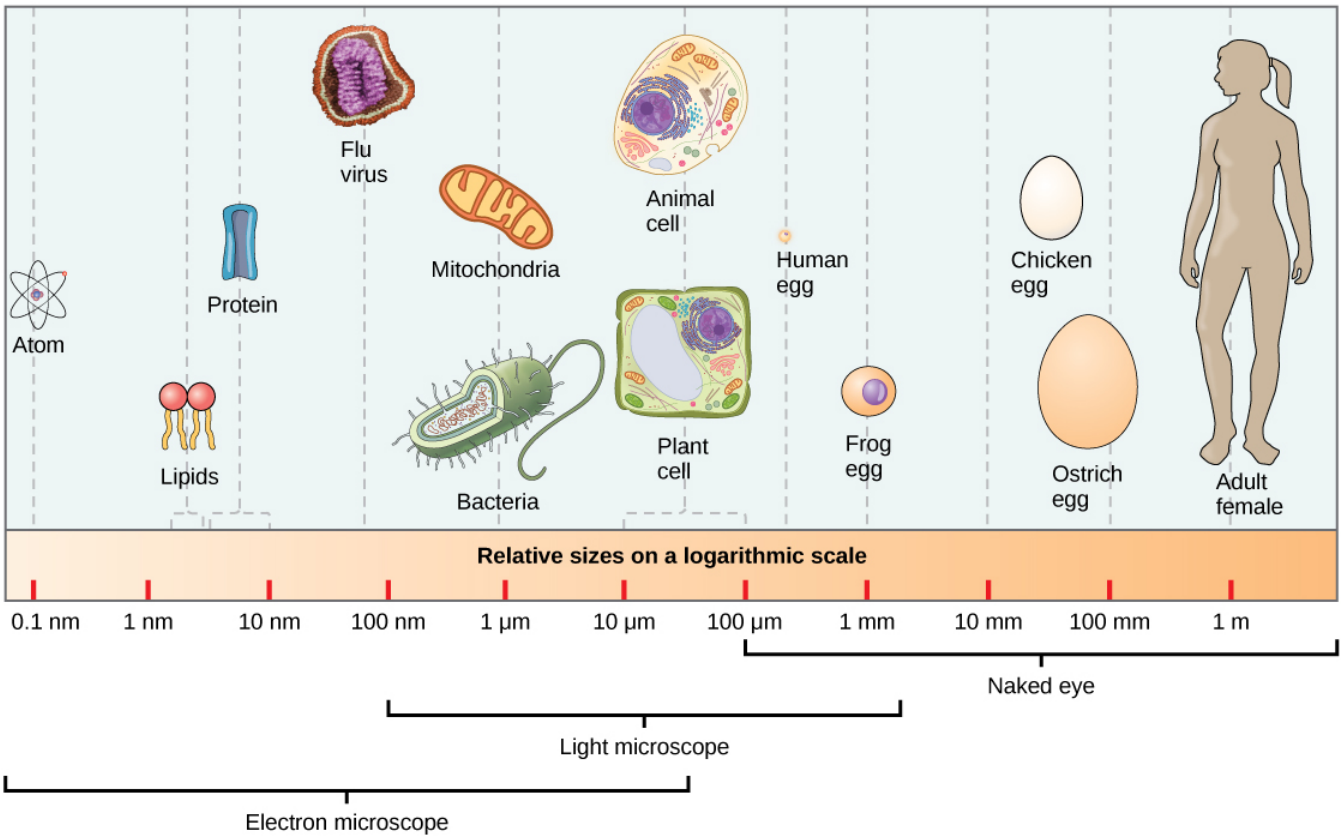


Figure 3.2.2**:** This figure shows the relative sizes of different kinds of cells and cellular components. An adult human is shown for comparison.

Section Summary

Prokaryotes are predominantly single-celled organisms of the domains Bacteria and Archaea. All prokaryotes have plasma membranes, cytoplasm, ribosomes, a cell wall, DNA, and lack membrane-bound organelles. Many also have polysaccharide capsules. Prokaryotic cells range in diameter from 0.1–5.0 µm.

Like a prokaryotic cell, a eukaryotic cell has a plasma membrane, cytoplasm, and ribosomes, but a eukaryotic cell is typically larger than a prokaryotic cell, has a true nucleus (meaning its DNA is surrounded by a membrane), and has other membrane-bound organelles that allow for compartmentalization of functions. Eukaryotic cells tend to be 10 to 100 times the size of prokaryotic cells.

Glossary

eukaryotic cell

a cell that has a membrane-bound nucleus and several other membrane-bound compartments or sacs

organelle

a membrane-bound compartment or sac within a cell

prokaryotic cell

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

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3.3: Eukaryotic Cells

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

ART CONNECTION

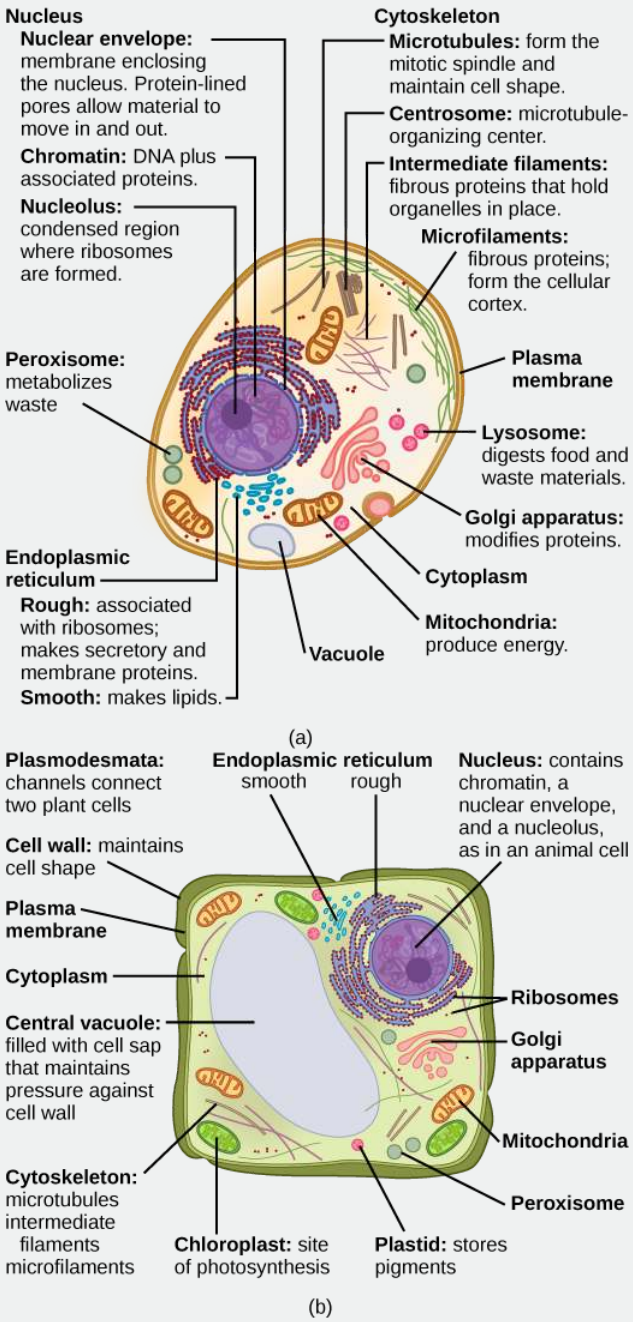


Figure 3.3.1**:** This figure shows (a) a typical animal cell and (b) a typical plant cell.

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

The Plasma Membrane

Like prokaryotes, eukaryotic cells have a plasma membrane (Figure 3.3.2) made up of a phospholipid bilayer with embedded proteins that separates the internal contents of the cell from its surrounding environment. A phospholipid is a lipid molecule composed of two fatty acid chains, a glycerol backbone, and a phosphate group. The plasma membrane regulates the passage of some substances, such as organic molecules, ions, and water, preventing the passage of some to maintain internal conditions, while actively bringing in or removing others. Other compounds move passively across the membrane.

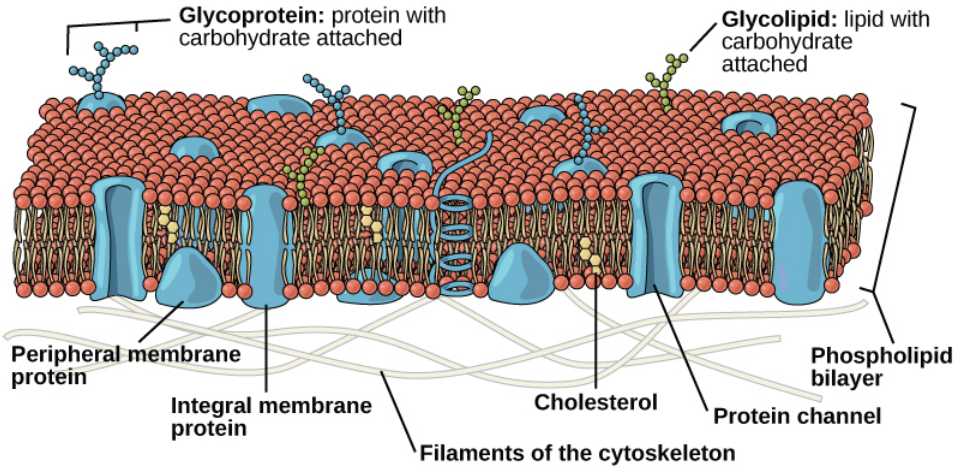


Figure 3.3.2: The plasma membrane is a phospholipid bilayer with embedded proteins. There are other components, such as cholesterol and carbohydrates, which can be found in the membrane in addition to phospholipids and protein.

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

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

The Cytoplasm

The cytoplasm comprises the contents of a cell between the plasma membrane and the nuclear envelope (a structure to be discussed shortly). It is made up of organelles suspended in the gel-like cytosol, the cytoskeleton, and various chemicals (Figure 3.3.1). Even though the cytoplasm consists of 70 to 80 percent water, it has a semi-solid consistency, which comes from the proteins within it. However, proteins are not the only organic molecules found in the cytoplasm. Glucose and other simple sugars, polysaccharides, amino acids, nucleic acids, fatty acids, and derivatives of glycerol are found there too. Ions of sodium, potassium, calcium, and many other elements are also dissolved in the cytoplasm. Many metabolic reactions, including protein synthesis, take place in the cytoplasm.

The Cytoskeleton

If you were to remove all the organelles from a cell, would the plasma membrane and the cytoplasm be the only components left? No. Within the cytoplasm, there would still be ions and organic molecules, plus a network of protein fibers that helps to maintain the shape of the cell, secures certain organelles in specific positions, allows cytoplasm and vesicles to move within the cell, and enables unicellular organisms to move independently. Collectively, this network of protein fibers is known as the cytoskeleton. There are three types of fibers within the cytoskeleton: microfilaments, also known as actin filaments, intermediate filaments, and microtubules (Figure 3.3.3).

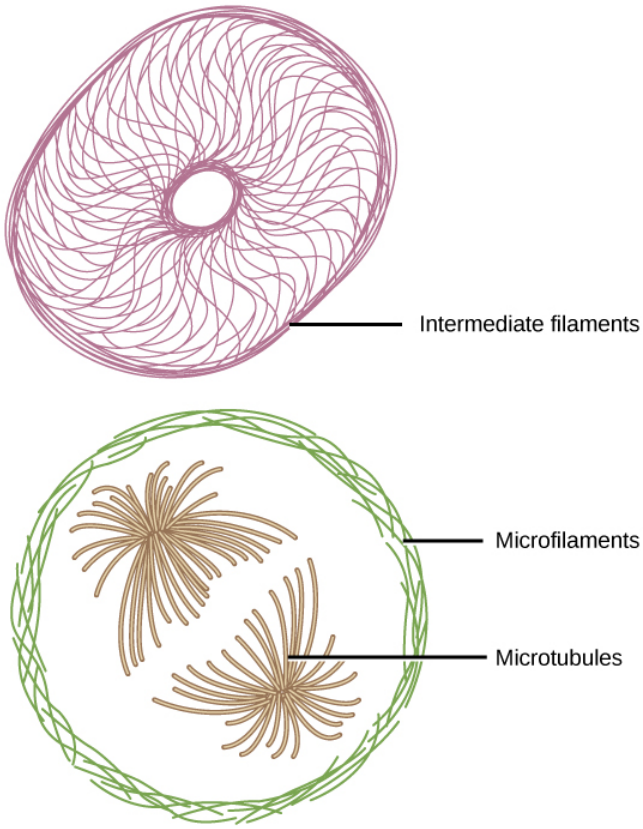


Figure 3.3.3**:** Microfilaments, intermediate filaments, and microtubules compose a cell's cytoskeleton.

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

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

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

Flagella and Cilia

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

The Endomembrane System

The endomembrane system (*endo* = within) is a group of membranes and organelles (Figure 3.3.3) in eukaryotic cells that work together to modify, package, and transport lipids and proteins. It includes the nuclear envelope, lysosomes, and vesicles, the endoplasmic reticulum and Golgi apparatus, which we will cover shortly. Although not technically *within* the cell, the plasma membrane is included in the endomembrane system because, as you will see, it interacts with the other endomembranous organelles.

The Nucleus

Typically, the nucleus is the most prominent organelle in a cell (Figure 3.3.1). The nucleus (plural = nuclei) houses the cell's DNA in the form of chromatin and directs the synthesis of ribosomes and proteins. Let us look at it in more detail (Figure 3.3.4).

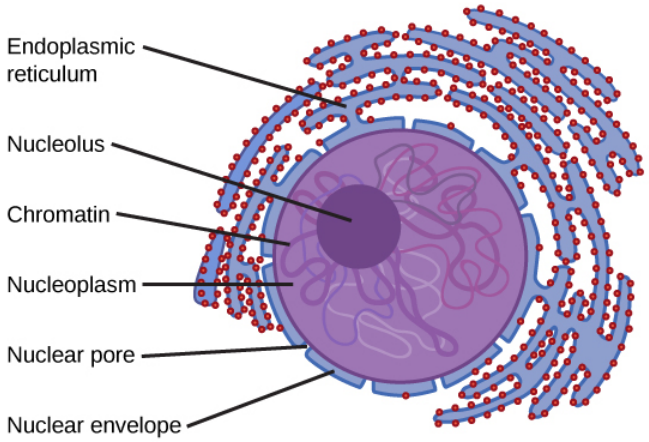


Figure 3.3.4: The outermost boundary of the nucleus is the nuclear envelope. Notice that the nuclear envelope consists of two phospholipid bilayers (membranes)—an outer membrane and an inner membrane—in contrast to the plasma membrane (Figure 3.3.2), which consists of only one phospholipid bilayer. (credit: modification of work by NIGMS, NIH)

The nuclear envelope is a double-membrane structure that constitutes the outermost portion of the nucleus (Figure 3.3.4). Both the inner and outer membranes of the nuclear envelope are phospholipid bilayers.

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

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

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

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

The Endoplasmic Reticulum

The endoplasmic reticulum (ER) (Figure 3.3.7) is a series of interconnected membranous tubules that collectively modify proteins and synthesize lipids. However, these two functions are performed in separate areas of the endoplasmic reticulum: the rough endoplasmic reticulum and the smooth endoplasmic reticulum, respectively.

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

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

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

If the phospholipids or modified proteins are not destined to stay in the RER, they will be packaged within vesicles and transported from the RER by budding from the membrane (Figure 3.3.7). Since the RER is engaged in modifying proteins that will be secreted from the cell, it is abundant in cells that secrete proteins, such as the liver.

The smooth endoplasmic reticulum (SER) is continuous with the RER but has few or no ribosomes on its cytoplasmic surface (see Figure 3.3.1). The SER's functions include synthesis of carbohydrates, lipids (including phospholipids), and steroid hormones; detoxification of medications and poisons; alcohol metabolism; and storage of calcium ions.

The Golgi Apparatus

We have already mentioned that vesicles can bud from the ER, but where do the vesicles go? Before reaching their final destination, the lipids or proteins within the transport vesicles need to be sorted, packaged, and tagged so that they wind up in the right place. The sorting, tagging, packaging, and distribution of lipids and proteins take place in the Golgi apparatus (also called the Golgi body), a series of flattened membranous sacs (Figure 3.3.5).

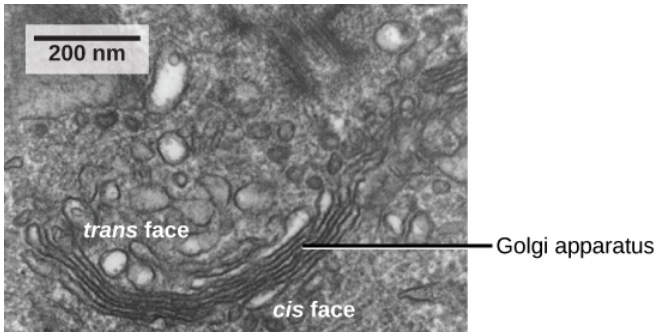


Figure 3.3.5: The Golgi apparatus in this transmission electron micrograph of a white blood cell is visible as a stack of semicircular flattened rings in the lower portion of this image. Several vesicles can be seen near the Golgi apparatus. (credit: modification of work by Louisa Howard; scale-bar data from Matt Russell)

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

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

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

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

Lysosomes

In animal cells, the lysosomes are the cell's "garbage disposal." Digestive enzymes within the lysosomes aid the breakdown of proteins, polysaccharides, lipids, nucleic acids, and even worn-out organelles. In single-celled eukaryotes, lysosomes are important for digestion of the food they ingest and the recycling of organelles. These enzymes are active at a much lower pH (more acidic)

than those located in the cytoplasm. Many reactions that take place in the cytoplasm could not occur at a low pH, thus the advantage of compartmentalizing the eukaryotic cell into organelles is apparent.

Lysosomes also use their hydrolytic enzymes to destroy disease-causing organisms that might enter the cell. A good example of this occurs in a group of white blood cells called macrophages, which are part of your body's immune system. In a process known as phagocytosis, a section of the plasma membrane of the macrophage invaginates (folds in) and engulfs a pathogen. The invaginated section, with the pathogen inside, then pinches itself off from the plasma membrane and becomes a vesicle. The vesicle fuses with a lysosome. The lysosome's hydrolytic enzymes then destroy the pathogen (Figure 3.3.6).

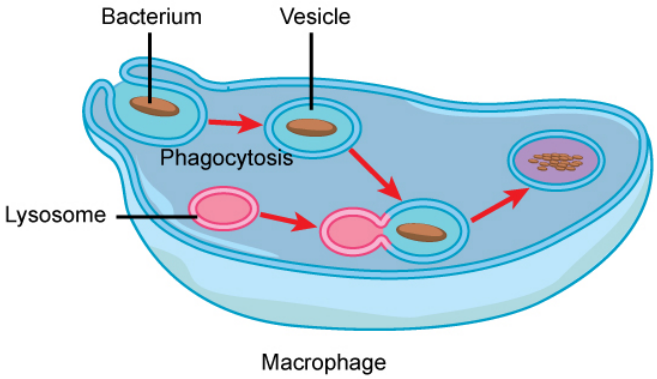


Figure 3.3.6**:** A macrophage has phagocytized a potentially pathogenic bacterium into a vesicle, which then fuses with a lysosome within the cell so that the pathogen can be destroyed. Other organelles are present in the cell, but for simplicity, are not shown.

Vesicles and Vacuoles

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

ART CONNECTION

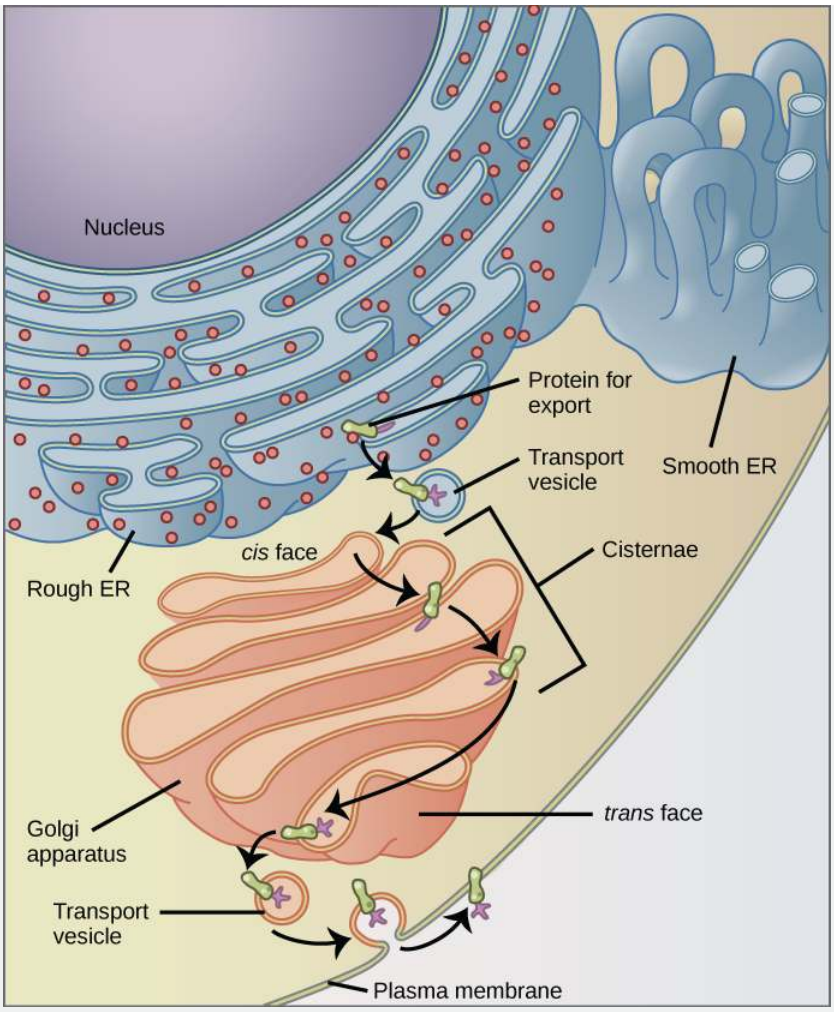


Figure 3.3.7**:** The endomembrane system works to modify, package, and transport lipids and proteins. (credit: modification of work by Magnus Manske)

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

Ribosomes

Ribosomes are the cellular structures responsible for protein synthesis. When viewed through an electron microscope, free ribosomes appear as either clusters or single tiny dots floating freely in the cytoplasm. Ribosomes may be attached to either the cytoplasmic side of the plasma membrane or the cytoplasmic side of the endoplasmic reticulum (Figure 3.3.7). Electron microscopy has shown that ribosomes consist of large and small subunits. Ribosomes are enzyme complexes that are responsible for protein synthesis.

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

Mitochondria

Mitochondria (singular = mitochondrion) are often called the “powerhouses” or “energy factories” of a cell because they are responsible for making adenosine triphosphate (ATP), the cell’s main energy-carrying molecule. The formation of ATP from the breakdown of glucose is known as cellular respiration. Mitochondria are oval-shaped, double-membrane organelles (Figure 3.3.8) that have their own ribosomes and DNA. Each membrane is a phospholipid bilayer embedded with proteins. The inner layer has folds called cristae, which increase the surface area of the inner membrane. The area surrounded by the folds is called the mitochondrial matrix. The cristae and the matrix have different roles in cellular respiration.

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

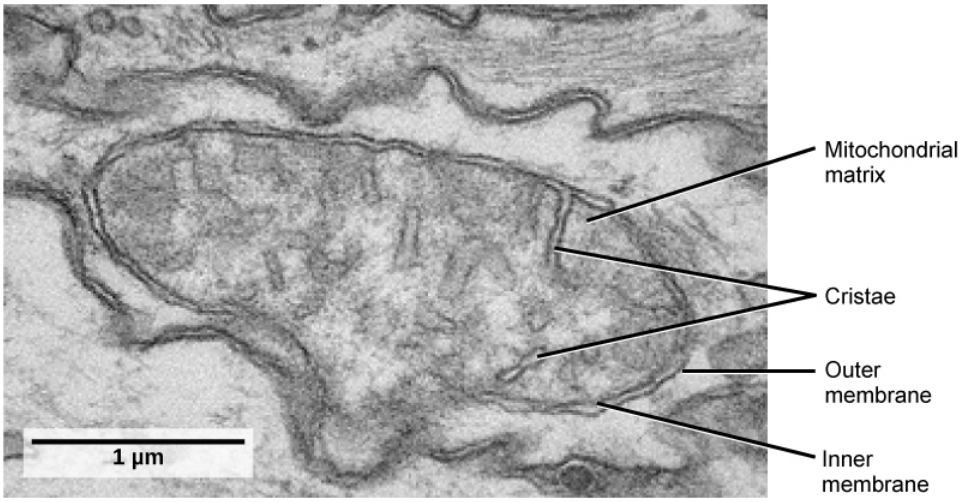


Figure 3.3.8**:** This transmission electron micrograph shows a mitochondrion as viewed with an electron microscope. Notice the inner and outer membranes, the cristae, and the mitochondrial matrix. (credit: modification of work by Matthew Britton; scale-bar data from Matt Russell)

Peroxisomes

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

Animal Cells versus Plant Cells

Despite their fundamental similarities, there are some striking differences between animal and plant cells (see Table 3.3.1). Animal cells have centrioles, centrosomes (discussed under the cytoskeleton), and lysosomes, whereas plant cells do not. Plant cells have a cell wall, chloroplasts, plasmodesmata, and plastids used for storage, and a large central vacuole, whereas animal cells do not.

The Cell Wall

In Figure 3.3.1**b**, the diagram of a plant cell, you see a structure external to the plasma membrane called the cell wall. The cell wall is a rigid covering that protects the cell, provides structural support, and gives shape to the cell. Fungal and protist cells also have cell walls.

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

Chloroplasts

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

Like mitochondria, chloroplasts have outer and inner membranes, but within the space enclosed by a chloroplast's inner membrane is a set of interconnected and stacked, fluid-filled membrane sacs called thylakoids (Figure 3.3.9). Each stack of thylakoids is called a granum (plural = grana). The fluid enclosed by the inner membrane and surrounding the grana is called the stroma.

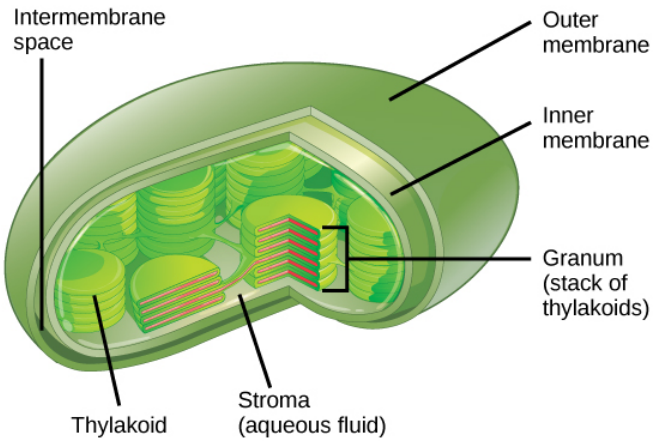


Figure 3.3.9**:** This simplified diagram of a chloroplast shows the outer membrane, inner membrane, thylakoids, grana, and stroma.

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

EVOLUTION IN ACTION: Endosymbiosis

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

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

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

The Central Vacuole

Previously, we mentioned vacuoles as essential components of plant cells. If you look at Figure 3.3.1, you will see that plant cells each have a large, central vacuole that occupies most of the cell. The central vacuole plays a key role in regulating the cell's concentration of water in changing environmental conditions. In plant cells, the liquid inside the central vacuole provides turgor pressure, which is the outward pressure caused by the fluid inside the cell. Have you ever noticed that if you forget to water a plant for a few days, it wilts? That is because as the water concentration in the soil becomes lower than the water concentration in the plant, water moves out of the central vacuoles and cytoplasm and into the soil. As the central vacuole shrinks, it leaves the cell wall unsupported. This loss of support to the cell walls of a plant results in the wilted appearance. Additionally, this fluid has a very bitter taste, which discourages consumption by insects and animals. The central vacuole also functions to store proteins in developing seed cells.

Extracellular Matrix of Animal Cells

Most animal cells release materials into the extracellular space. The primary components of these materials are glycoproteins and the protein collagen. Collectively, these materials are called the extracellular matrix (Figure 3.3.10). Not only does the extracellular matrix hold the cells together to form a tissue, but it also allows the cells within the tissue to communicate with each other.

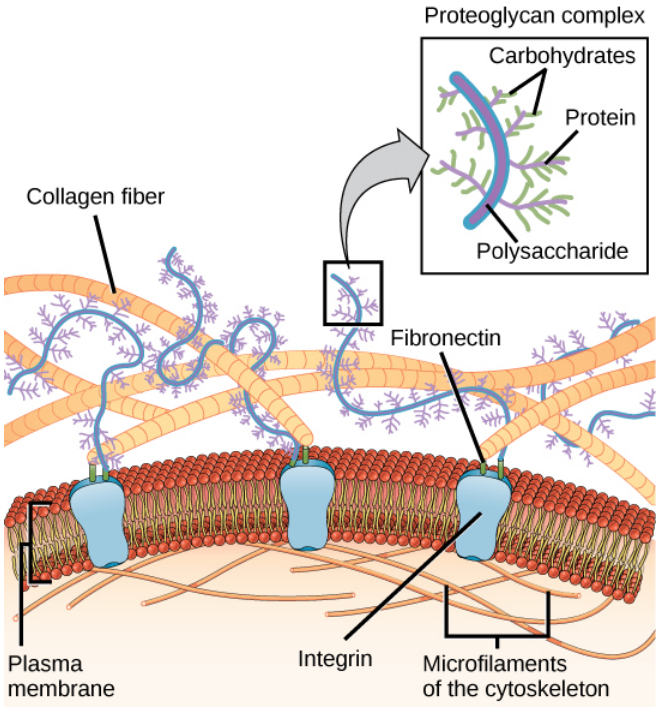


Figure 3.3.10**:** The extracellular matrix consists of a network of substances secreted by cells.

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

Intercellular Junctions

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

In general, long stretches of the plasma membranes of neighboring plant cells cannot touch one another because they are separated by the cell walls surrounding each cell. Plasmodesmata are numerous channels that pass between the cell walls of adjacent plant cells, connecting their cytoplasm and enabling signal molecules and nutrients to be transported from cell to cell (Figure 3.3.11**a**).

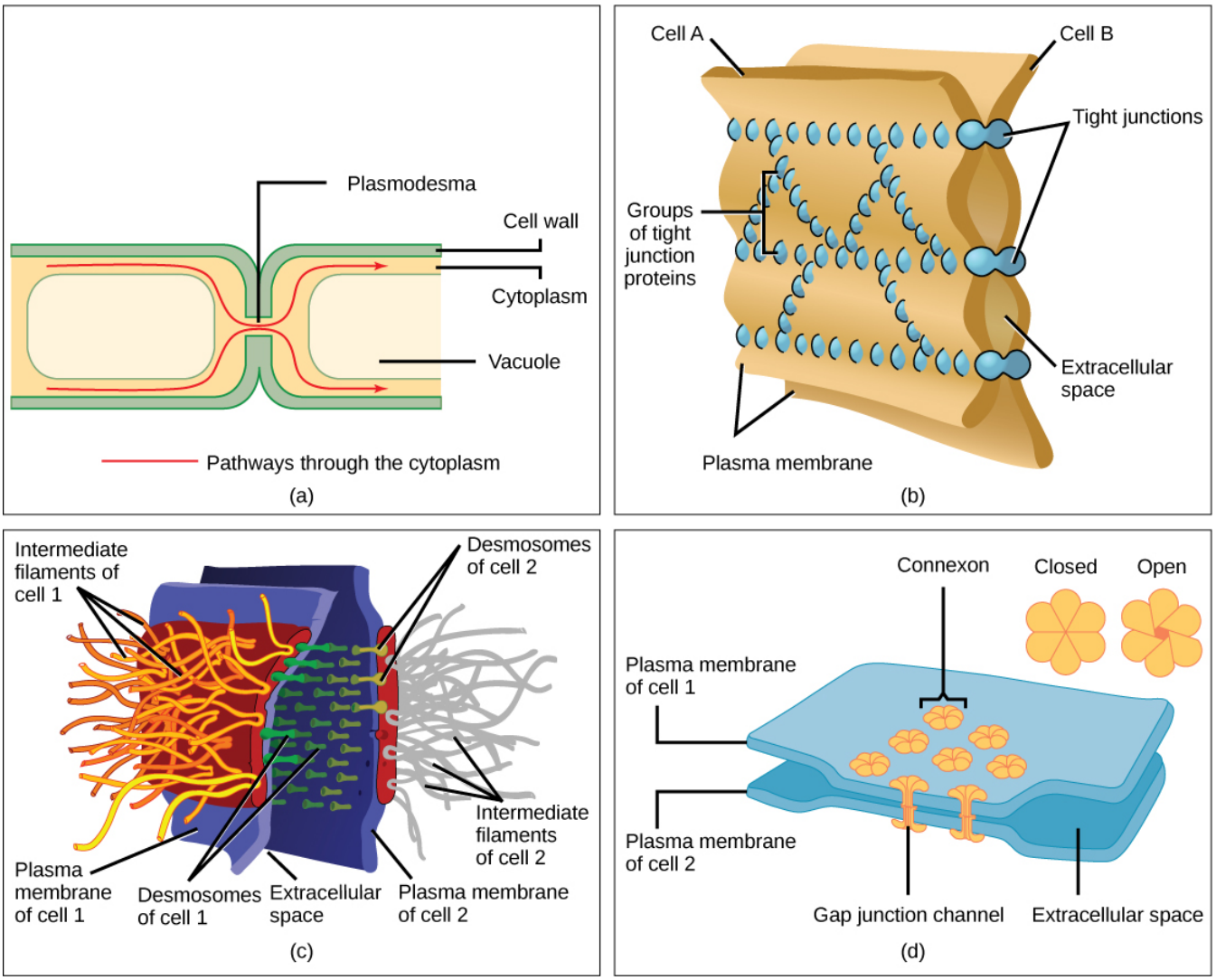


Figure 3.3.11**:** There are four kinds of connections between cells. (a) A plasmodesma is a channel between the cell walls of two adjacent plant cells. (b) Tight junctions join adjacent animal cells. (c) Desmosomes join two animal cells together. (d) Gap junctions act as channels between animal cells. (credit b, c, d: modification of work by Mariana Ruiz Villareal)

A tight junction is a watertight seal between two adjacent animal cells (Figure 3.3.11**b**). Proteins hold the cells tightly against each other. This tight adhesion prevents materials from leaking between the cells. Tight junctions are typically found in the epithelial tissue that lines internal organs and cavities, and composes most of the skin. For example, the tight junctions of the epithelial cells lining the urinary bladder prevent urine from leaking into the extracellular space.

Also found only in animal cells are desmosomes, which act like spot welds between adjacent epithelial cells (Figure 3.3.11**c**). They keep cells together in a sheet-like formation in organs and tissues that stretch, like the skin, heart, and muscles.

Gap junctions in animal cells are like plasmodesmata in plant cells in that they are channels between adjacent cells that allow for the transport of ions, nutrients, and other substances that enable cells to communicate (Figure 3.3.11**d**). Structurally, however, gap junctions and plasmodesmata differ.

Table 3.3.1**:** This table provides the components of prokaryotic and eukaryotic cells and their respective functions.

Cell Component	Function	Present in Prokaryotes?	Present in Animal Cells?	Present in Plant Cells?
Plasma membrane	Separates cell from external environment; controls passage of organic molecules, ions, water, oxygen, and wastes into and out of the cell	Yes	Yes	Yes
Cytoplasm	Provides structure to cell; site of many metabolic reactions; medium in which organelles are found	Yes	Yes	Yes
Nucleoid	Location of DNA	Yes	No	No
Nucleus	Cell organelle that houses DNA and directs synthesis of ribosomes and proteins	No	Yes	Yes
Ribosomes	Protein synthesis	Yes	Yes	Yes
Mitochondria	ATP production/cellular respiration	No	Yes	Yes
Peroxisomes	Oxidizes and breaks down fatty acids and amino acids, and detoxifies poisons	No	Yes	Yes
Vesicles and vacuoles	Storage and transport; digestive function in plant cells	No	Yes	Yes
Centrosome	Unspecified role in cell division in animal cells; organizing center of microtubules in animal cells	No	Yes	No
Lysosomes	Digestion of macromolecules; recycling of worn-out organelles	No	Yes	No
Cell wall	Protection, structural support and maintenance of cell shape	Yes, primarily peptidoglycan in bacteria but not Archaea	No	Yes, primarily cellulose
Chloroplasts	Photosynthesis	No	No	Yes
Endoplasmic reticulum	Modifies proteins and synthesizes lipids	No	Yes	Yes
Golgi apparatus	Modifies, sorts, tags,	No	Yes	Yes

Cell Component	Function	Present in Prokaryotes?	Present in Animal Cells?	Present in Plant Cells?
	packages, and distributes lipids and proteins			
Cytoskeleton	Maintains cell's shape, secures organelles in specific positions, allows cytoplasm and vesicles to move within the cell, and enables unicellular organisms to move independently	Yes	Yes	Yes
Flagella	Cellular locomotion	Some	Some	No, except for some plant sperm
Cilia	Cellular locomotion, movement of particles along extracellular surface of plasma membrane, and filtration	No	Some	No

Summary

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

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

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

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

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

Animal cells communicate through their extracellular matrices and are connected to each other by tight junctions, desmosomes, and gap junctions. Plant cells are connected and communicate with each other by plasmodesmata.

Art Connections

Figure 3.3.1: What structures does a plant cell have that an animal cell does not have? What structures does an animal cell have that a plant cell does not have?

Answer

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

Figure 3.3.7: Why does the *cis* face of the Golgi not face the plasma membrane?

Answer

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

Glossary

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

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

chloroplast
a plant cell organelle that carries out photosynthesis

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

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

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

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

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

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

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

extracellular matrix
the material, primarily collagen, glycoproteins, and proteoglycans, secreted from animal cells that holds cells together as a tissue, allows cells to communicate with each other, and provides mechanical protection and anchoring for cells in the tissue

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

gap junction

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

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

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

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

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

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

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

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

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

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

ribosome
a cellular structure that carries out protein synthesis

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

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

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

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

vesicle

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

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3.4: The Cell Membrane

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

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

Fluid Mosaic Model

In 1972, S. J. Singer and Garth L. Nicolson proposed a new model of the plasma membrane that, compared to earlier understanding, better explained both microscopic observations and the function of the plasma membrane. This was called the fluid mosaic model. The model has evolved somewhat over time, but still best accounts for the structure and functions of the plasma membrane as we now understand them. The fluid mosaic model describes the structure of the plasma membrane as a mosaic of components—including phospholipids, cholesterol, proteins, and carbohydrates—in which the components are able to flow and change position, while maintaining the basic integrity of the membrane. Both phospholipid molecules and embedded proteins are able to diffuse rapidly and laterally in the membrane. The fluidity of the plasma membrane is necessary for the activities of certain enzymes and transport molecules within the membrane. Plasma membranes range from 5–10 nm thick. As a comparison, human red blood cells, visible via light microscopy, are approximately 8 µm thick, or approximately 1,000 times thicker than a plasma membrane. (Figure 3.4.1)

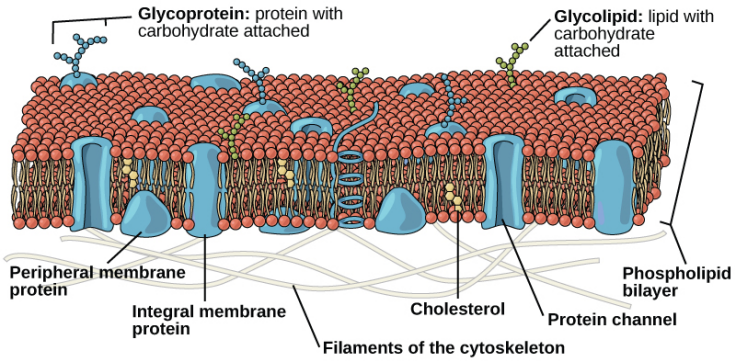


Figure 3.4.1**:** The fluid mosaic model of the plasma membrane structure describes the plasma membrane as a fluid combination of phospholipids, cholesterol, proteins, and carbohydrates.

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

The main fabric of the membrane is composed of two layers of phospholipid molecules, and the polar ends of these molecules (which look like a collection of balls in an artist's rendition of the model) (Figure 3.4.1) are in contact with aqueous fluid both

inside and outside the cell. Thus, both surfaces of the plasma membrane are hydrophilic. In contrast, the interior of the membrane, between its two surfaces, is a hydrophobic or nonpolar region because of the fatty acid tails. This region has no attraction for water or other polar molecules.

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

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

EVOLUTION IN ACTION: How Viruses Infect Specific Organs

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

These viruses are able to invade these cells, because the cells have binding sites on their surfaces that the viruses have exploited with equally specific glycoproteins in their coats (Figure 3.4.2). The cell is tricked by the mimicry of the virus coat molecules, and the virus is able to enter the cell. Other recognition sites on the virus's surface interact with the human immune system, prompting the body to produce antibodies. Antibodies are made in response to the antigens (or proteins associated with invasive pathogens). These same sites serve as places for antibodies to attach, and either destroy or inhibit the activity of the virus. Unfortunately, these sites on HIV are encoded by genes that change quickly, making the production of an effective vaccine against the virus very difficult. The virus population within an infected individual quickly evolves through mutation into different populations, or variants, distinguished by differences in these recognition sites. This rapid change of viral surface markers decreases the effectiveness of the person's immune system in attacking the virus, because the antibodies will not recognize the new variations of the surface patterns.

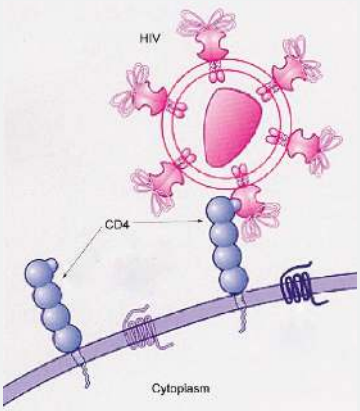


Figure 3.4.2: HIV docks at and binds to the CD4 receptor, a glycoprotein on the surface of T cells, before entering, or infecting, the cell. (credit: modification of work by US National Institutes of Health/National Institute of Allergy and Infectious Diseases).

Summary

The modern understanding of the plasma membrane is referred to as the fluid mosaic model. The plasma membrane is composed of a bilayer of phospholipids, with their hydrophobic, fatty acid tails in contact with each other. The landscape of the membrane is studded with proteins, some of which span the membrane. Some of these proteins serve to transport materials into or out of the cell. Carbohydrates are attached to some of the proteins and lipids on the outward-facing surface of the membrane. These form

complexes that function to identify the cell to other cells. The fluid nature of the membrane owes itself to the configuration of the fatty acid tails, the presence of cholesterol embedded in the membrane (in animal cells), and the mosaic nature of the proteins and protein-carbohydrate complexes, which are not firmly fixed in place. Plasma membranes enclose the borders of cells, but rather than being a static bag, they are dynamic and constantly in flux.

Glossary

fluid mosaic model

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

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3.A: Cell Structure and Function (Exercises)

How Cells Are Studied

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

Multiple Choice

When viewing a specimen through a light microscope, scientists use _____ to distinguish the individual components of cells.

A. a beam of electrons
B. radioactive isotopes
C. special stains
D. high temperatures

Answer

C

The _____ is the basic unit of life.

A. organism
B. cell
C. tissue
D. organ

Answer

B

Free Response

What are the advantages and disadvantages of light, transmission, and scanning electron microscopes?

Answer

The advantages of light microscopes are that they are easily obtained, and the light beam does not kill the cells. However, typical light microscopes are somewhat limited in the amount of detail that they can reveal. Electron microscopes are ideal because you can view intricate details, but they are bulky and costly, and preparation for the microscopic examination kills the specimen. Transmission electron microscopes are designed to examine the internal structures of a cell, whereas a scanning electron microscope only allows visualization of the surface of a structure.

Comparing Prokaryotic and Eukaryotic Cells

Cells fall into one of two broad categories: prokaryotic and eukaryotic. The predominantly single-celled organisms of the domains Bacteria and Archaea are classified as prokaryotes (pro- = before; -karyon- = nucleus). Animal cells, plant cells, fungi, and protists are eukaryotes (eu- = true).

Multiple Choice

Which of these do all prokaryotes and eukaryotes share?

A. nuclear envelope
B. cell walls
C. organelles
D. plasma membrane

Answer

Answer

D

A typical prokaryotic cell _____ compared to a eukaryotic cell.

A. is smaller in size by a factor of 100
B. is similar in size
C. is smaller in size by a factor of one million
D. is larger in size by a factor of 10

Answer

A

Free Response

Describe the structures that are characteristic of a prokaryote cell.

Answer

Prokaryotic cells are surrounded by a plasma membrane and have DNA, cytoplasm, and ribosomes, like eukaryotic cells. They also have cell walls and may have a cell capsule. Prokaryotes have a single large chromosome that is not surrounded by a nuclear membrane. Prokaryotes may have flagella or motility, pili for conjugation, and fimbriae for adhesion to surfaces.

Eukaryotic Cells

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

Multiple Choice

Which of the following is found both in eukaryotic and prokaryotic cells?

A. nucleus
B. mitochondrion
C. vacuole
D. ribosome

Answer

D

Which of the following is not a component of the endomembrane system?

A. mitochondrion
B. Golgi apparatus
C. endoplasmic reticulum
D. lysosome

Answer

A

Free Response

In the context of cell biology, what do we mean by form follows function? What are at least two examples of this concept?

Answer

“Form follows function” refers to the idea that the function of a body part dictates the form of that body part. As an example, organisms like birds or fish that fly or swim quickly through the air or water have streamlined bodies that reduce drag. At the level of the cell, in tissues involved in secretory functions, such as the salivary glands, the cells have abundant Golgi.

The Cell Membrane

The plasma membrane is referred to as the fluid mosaic model and is composed of a bilayer of phospholipids, with their hydrophobic, fatty acid tails in contact with each other. The landscape of the membrane is studded with proteins, some of which span the membrane. Some of these proteins serve to transport materials into or out of the cell. Carbohydrates are attached to some of the proteins and lipids on the outward-facing surface of the membrane. These function to identify other cells.

Multiple Choice

Which plasma membrane component can be either found on its surface or embedded in the membrane structure?

A. protein
B. cholesterol
C. carbohydrate
D. phospholipid

Answer

A

The tails of the phospholipids of the plasma membrane are composed of _____ and are _____?

A. phosphate groups; hydrophobic
B. fatty acid groups; hydrophilic
C. phosphate groups; hydrophilic
D. fatty acid groups; hydrophobic

Answer

D

Free Response

Why is it advantageous for the cell membrane to be fluid in nature?

Answer

The fluidity of the cell membrane is necessary for the operation of some enzymes and transport mechanisms within the membrane.

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CHAPTER OVERVIEW

4: The Working Cell

4.1: Passive Transport

4.2: Active Transport

4.3: Energy and Metabolism

4.A: Cell Structure and Function (Exercises)

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4.1: Passive Transport

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

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

Selective Permeability

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

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

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

Diffusion

Diffusion is a passive process of transport. A single substance tends to move from an area of high concentration to an area of low concentration until the concentration is equal across the space. You are familiar with diffusion of substances through the air. For example, think about someone opening a bottle of perfume in a room filled with people. The perfume is at its highest concentration in the bottle and is at its lowest at the edges of the room. The perfume vapor will diffuse, or spread away, from the bottle, and gradually, more and more people will smell the perfume as it spreads. Materials move within the cell’s cytosol by diffusion, and certain materials move through the plasma membrane by diffusion (Figure 4.1.1). Diffusion expends no energy. Rather the different concentrations of materials in different areas are a form of potential energy, and diffusion is the dissipation of that potential energy as materials move down their concentration gradients, from high to low.

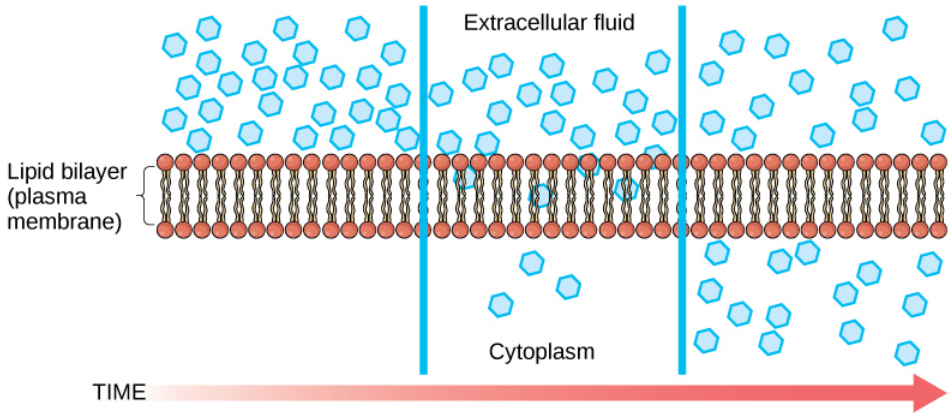


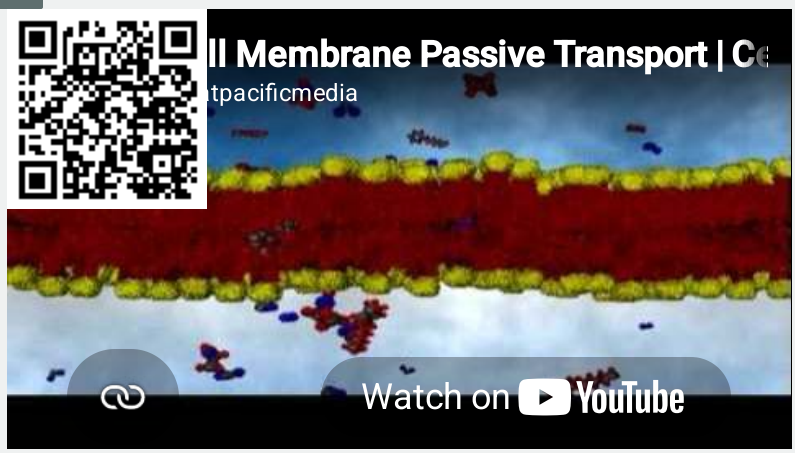
Figure 4.1.1: Diffusion through a permeable membrane follows the concentration gradient of a substance, moving the substance from an area of high concentration to one of low concentration. (credit: modification of work by Mariana Ruiz Villarreal)

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

Several factors affect the rate of diffusion.

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

CONCEPT IN ACTION



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

Facilitated transport

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

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

Osmosis

Osmosis is the diffusion of water through a semipermeable membrane according to the concentration gradient of water across the membrane. Whereas diffusion transports material across membranes and within cells, osmosis transports *only water* across a membrane and the membrane limits the diffusion of solutes in the water. Osmosis is a special case of diffusion. Water, like other substances, moves from an area of higher concentration to one of lower concentration. Imagine a beaker with a semipermeable membrane, separating the two sides or halves (Figure 4.1.2). On both sides of the membrane, the water level is the same, but there are different concentrations on each side of a dissolved substance, or solute, that cannot cross the membrane. If the volume of the water is the same, but the concentrations of solute are different, then there are also different concentrations of water, the solvent, on either side of the membrane.

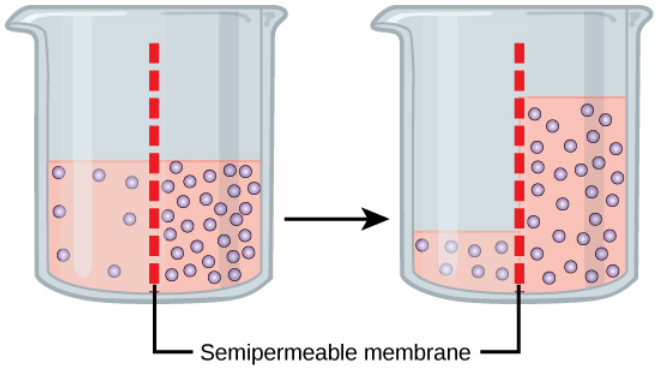


Figure 4.1.2: In osmosis, water always moves from an area of higher concentration (of water) to one of lower concentration (of water). In this system, the solute cannot pass through the selectively permeable membrane.

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

Tonicity

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

In a hypertonic solution (the prefix *hyper-* refers to the extracellular fluid having a higher concentration of solutes than the cell's cytoplasm), the fluid contains less water than the cell does, such as seawater. Because the cell has a lower concentration of solutes, the water will leave the cell. In effect, the solute is drawing the water out of the cell. This may cause an animal cell to shrivel, or crenate.

In an isotonic solution, the extracellular fluid has the same osmolarity as the cell. If the concentration of solutes of the cell matches that of the extracellular fluid, there will be no net movement of water into or out of the cell. Blood cells in hypertonic, isotonic, and hypotonic solutions take on characteristic appearances (Figure 4.1.3).

ART CONNECTION

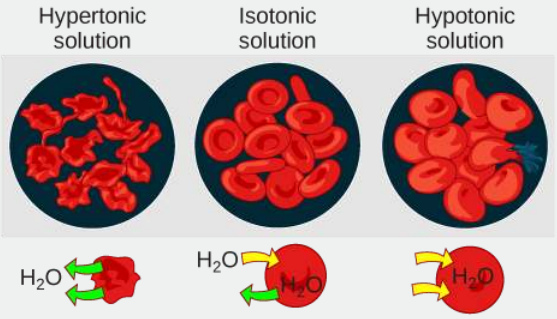


Figure 4.1.3: Osmotic pressure changes the shape of red blood cells in hypertonic, isotonic, and hypotonic solutions. (credit: modification of work by Mariana Ruiz Villarreal)

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

Some organisms, such as plants, fungi, bacteria, and some protists, have cell walls that surround the plasma membrane and prevent cell lysis. The plasma membrane can only expand to the limit of the cell wall, so the cell will not lyse. In fact, the cytoplasm in plants is always slightly hypertonic compared to the cellular environment, and water will always enter a cell if water is available. This influx of water produces turgor pressure, which stiffens the cell walls of the plant (Figure 4.1.4). In nonwoody plants, turgor pressure supports the plant. If the plant cells become hypertonic, as occurs in drought or if a plant is not watered adequately, water will leave the cell. Plants lose turgor pressure in this condition and wilt.

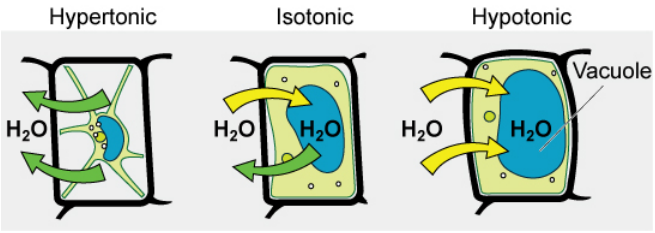


Figure 4.1.4: The turgor pressure within a plant cell depends on the tonicity of the solution that it is bathed in. (credit: modification of work by Mariana Ruiz Villarreal)

Section Summary

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

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

Art Connections

Figure 4.1.3: A doctor injects a patient with what he thinks is isotonic saline solution. The patient dies, and autopsy reveals that many red blood cells have been destroyed. Do you think the solution the doctor injected was really isotonic?

Answer

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

Glossary

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

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

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

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

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

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

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

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

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

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

solute
a substance dissolved in another to form a solution

tonicity
the amount of solute in a solution.

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4.2: Active Transport

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

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

Electrochemical Gradient

We have discussed simple concentration gradients—differential concentrations of a substance across a space or a membrane—but in living systems, gradients are more complex. Because cells contain proteins, most of which are negatively charged, and because ions move into and out of cells, there is an electrical gradient, a difference of charge, across the plasma membrane. The interior of living cells is electrically negative with respect to the extracellular fluid in which they are bathed; at the same time, cells have higher concentrations of potassium (K^+) and lower concentrations of sodium (Na^+) than does the extracellular fluid. Thus, in a living cell, the concentration gradient and electrical gradient of Na^+ promotes diffusion of the ion into the cell, and the electrical gradient of Na^+ (a positive ion) tends to drive it inward to the negatively charged interior. The situation is more complex, however, for other elements such as potassium. The electrical gradient of K^+ promotes diffusion of the ion *into* the cell, but the concentration gradient of K^+ promotes diffusion *out* of the cell (Figure 4.2.1). The combined gradient that affects an ion is called its electrochemical gradient, and it is especially important to muscle and nerve cells.

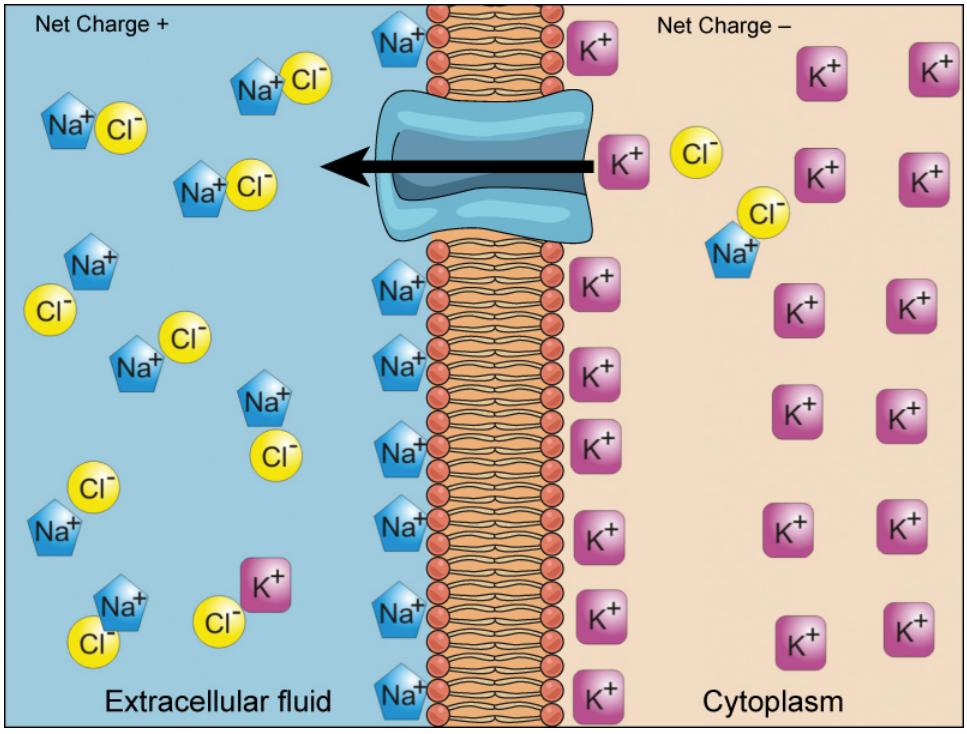


Figure 4.2.1**:** Electrochemical gradients arise from the combined effects of concentration gradients and electrical gradients. (credit: modification of work by "Synaptitude"/Wikimedia Commons)

Moving Against a Gradient

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

Active transport maintains concentrations of ions and other substances needed by living cells in the face of these passive changes. Much of a cell's supply of metabolic energy may be spent maintaining these processes. Because active transport mechanisms depend on cellular metabolism for energy, they are sensitive to many metabolic poisons that interfere with the supply of ATP.

Two mechanisms exist for the transport of small-molecular weight material and macromolecules. Primary active transport moves ions across a membrane and creates a difference in charge across that membrane. The primary active transport system uses ATP to move a substance, such as an ion, into the cell, and often at the same time, a second substance is moved out of the cell. The sodium-potassium pump, an important pump in animal cells, expends energy to move potassium ions into the cell and a different number of sodium ions out of the cell (Figure 4.2.2). The action of this pump results in a concentration and charge difference across the membrane.

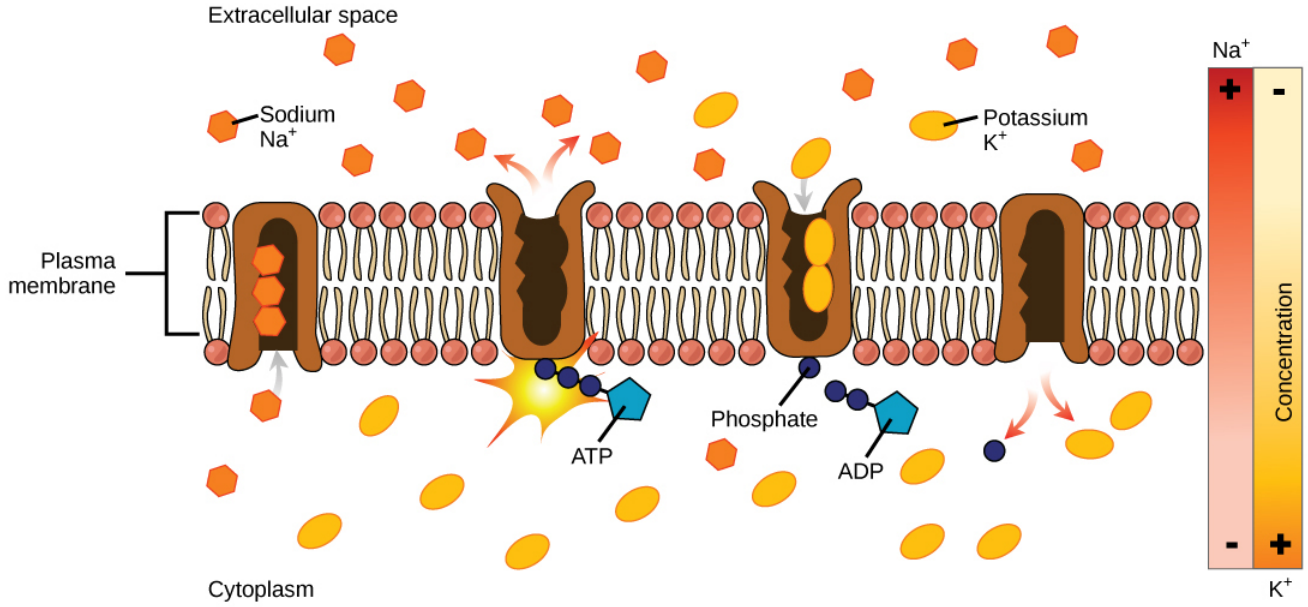


Figure 4.2.2**:** The sodium-potassium pump moves potassium and sodium ions across the plasma membrane. (credit: modification of work by Mariana Ruiz Villarreal)

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

Endocytosis

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

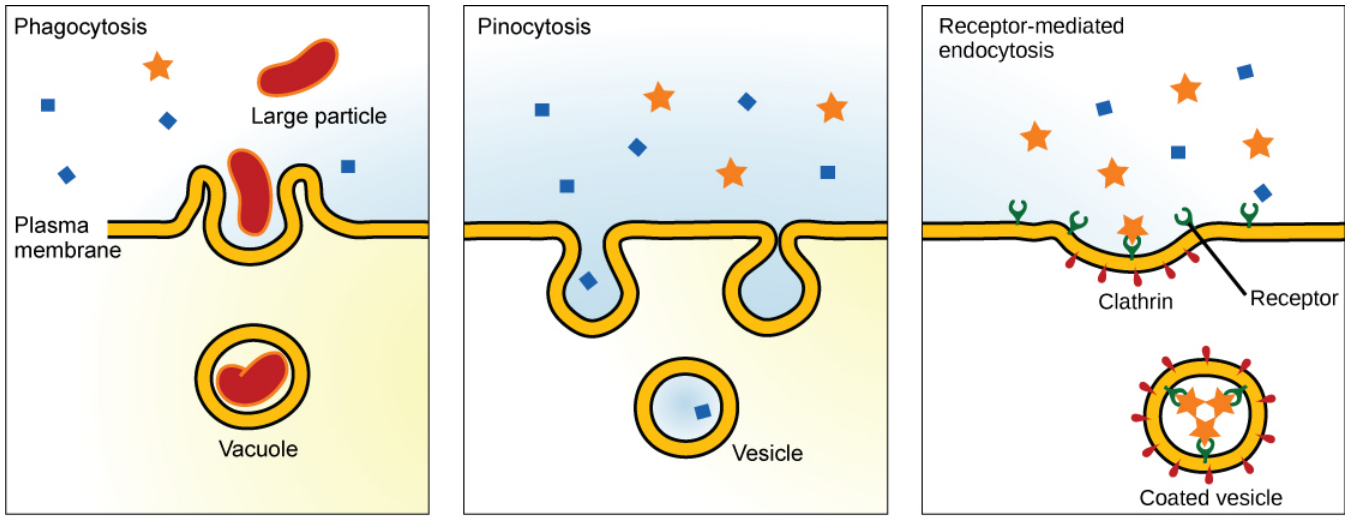


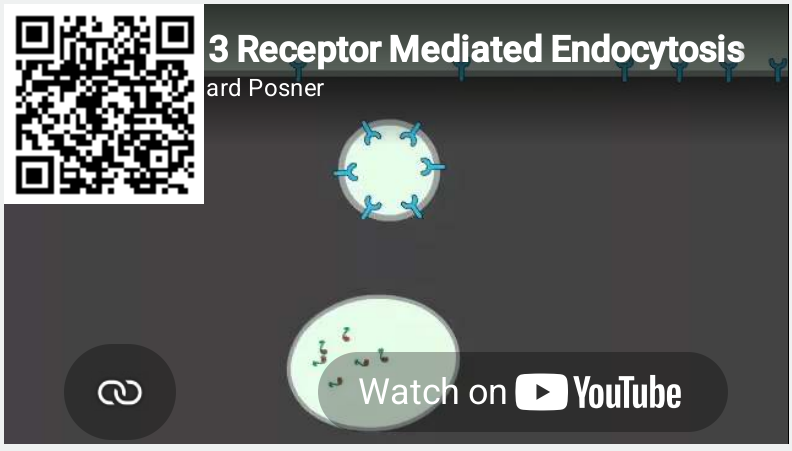
Figure 4.2.3**:** Three variations of endocytosis are shown. (a) In one form of endocytosis, phagocytosis, the cell membrane surrounds the particle and pinches off to form an intracellular vacuole. (b) In another type of endocytosis, pinocytosis, the cell membrane surrounds a small volume of fluid and pinches off, forming a vesicle. (c) In receptor-mediated endocytosis, uptake of substances by the cell is targeted to a single type of substance that binds at the receptor on the external cell membrane. (credit: modification of work by Mariana Ruiz Villarreal)

Phagocytosis is the process by which large particles, such as cells, are taken in by a cell. For example, when microorganisms invade the human body, a type of white blood cell called a neutrophil removes the invader through this process, surrounding and engulfing the microorganism, which is then destroyed by the neutrophil (Figure 4.2.3).

A variation of endocytosis is called pinocytosis. This literally means “cell drinking” and was named at a time when the assumption was that the cell was purposefully taking in extracellular fluid. In reality, this process takes in solutes that the cell needs from the extracellular fluid (Figure 4.2.3).

A targeted variation of endocytosis employs binding proteins in the plasma membrane that are specific for certain substances (Figure 4.2.3). The particles bind to the proteins and the plasma membrane invaginates, bringing the substance and the proteins into the cell. If passage across the membrane of the target of receptor-mediated endocytosis is ineffective, it will not be removed from the tissue fluids or blood. Instead, it will stay in those fluids and increase in concentration. Some human diseases are caused by a failure of receptor-mediated endocytosis. For example, the form of cholesterol termed low-density lipoprotein or LDL (also referred to as “bad” cholesterol) is removed from the blood by receptor-mediated endocytosis. In the human genetic disease familial hypercholesterolemia, the LDL receptors are defective or missing entirely. People with this condition have life-threatening levels of cholesterol in their blood, because their cells cannot clear the chemical from their blood.

CONCEPT IN ACTION



> See receptor-mediated endocytosis animation in action.

Exocytosis

In contrast to these methods of moving material into a cell is the process of exocytosis. Exocytosis is the opposite of the processes discussed above in that its purpose is to expel material from the cell into the extracellular fluid. A particle enveloped in membrane fuses with the interior of the plasma membrane. This fusion opens the membranous envelope to the exterior of the cell, and the particle is expelled into the extracellular space (Figure 4.2.4).

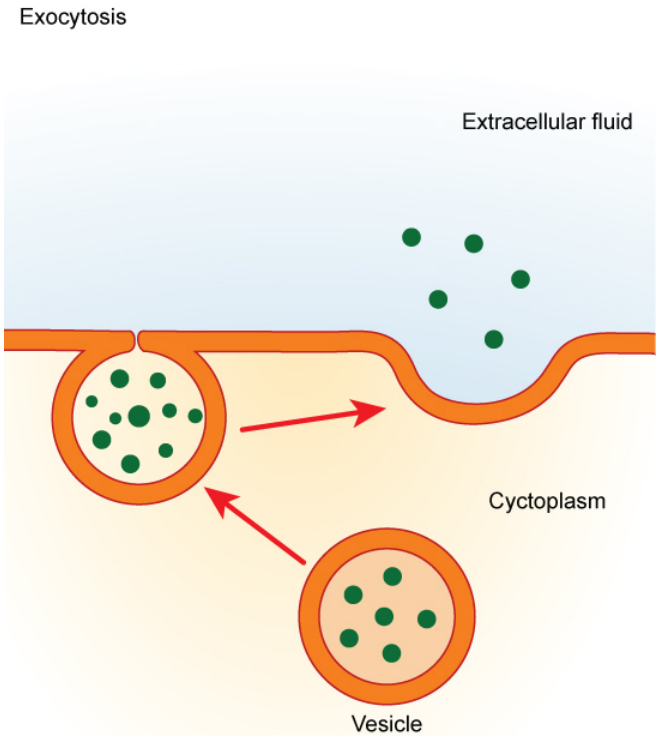


Figure 4.2.4: In exocytosis, a vesicle migrates to the plasma membrane, binds, and releases its contents to the outside of the cell. (credit: modification of work by Mariana Ruiz Villarreal)

Section Summary

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

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

Glossary

active transport

the method of transporting material that requires energy

electrochemical gradient

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

endocytosis

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

exocytosis

a process of passing material out of a cell

phagocytosis

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

pinocytosis

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

receptor-mediated endocytosis

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

Contributors and Attributions

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

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4.3: Energy and Metabolism

Scientists use the term bioenergetics to describe the concept of energy flow (Figure 4.3.1) through living systems, such as cells. Cellular processes such as the building and breaking down of complex molecules occur through stepwise chemical reactions. Some of these chemical reactions are spontaneous and release energy, whereas others require energy to proceed. Just as living things must continually consume food to replenish their energy supplies, cells must continually produce more energy to replenish that used by the many energy-requiring chemical reactions that constantly take place. Together, all of the chemical reactions that take place inside cells, including those that consume or generate energy, are referred to as the cell's metabolism.

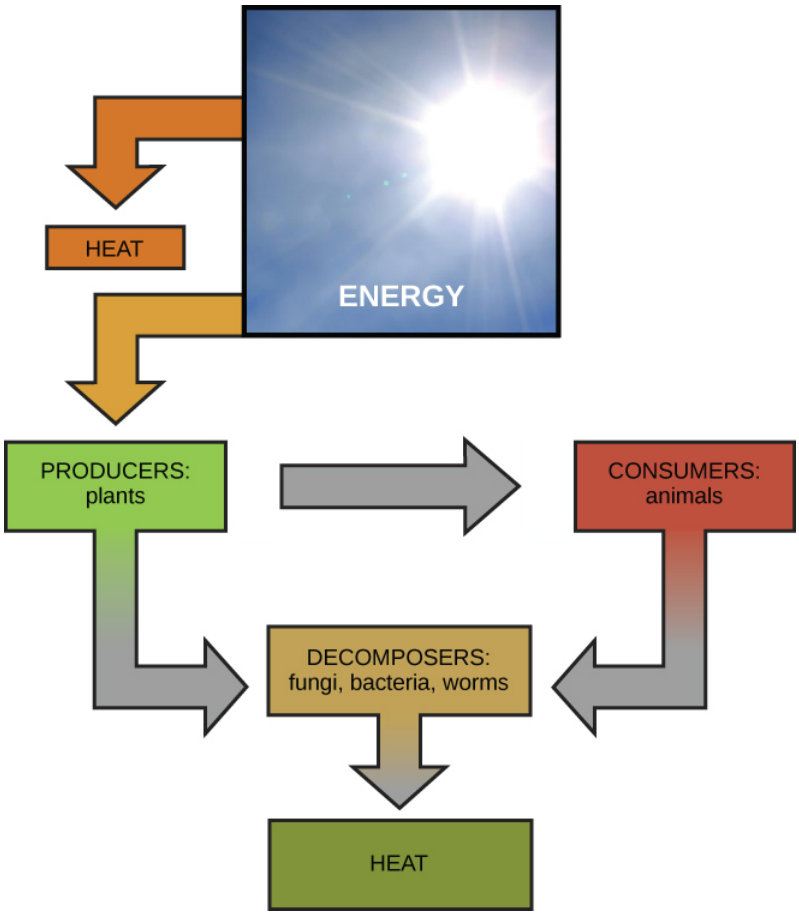


Figure 4.3.1: Ultimately, most life forms get their energy from the sun. Plants use photosynthesis to capture sunlight, and herbivores eat the plants to obtain energy. Carnivores eat the herbivores, and eventual decomposition of plant and animal material contributes to the nutrient pool.

Metabolic Pathways

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

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

Because this process involves synthesizing an energy-storing molecule, it requires energy input to proceed. During the light reactions of photosynthesis, energy is provided by a molecule called adenosine triphosphate (ATP), which is the primary energy currency of all cells. Just as the dollar is used as currency to buy goods, cells use molecules of ATP as energy currency to perform immediate work. In contrast, energy-storage molecules such as glucose are consumed only to be broken down to use their energy.

The reaction that harvests the energy of a sugar molecule in cells requiring oxygen to survive can be summarized by the reverse reaction to photosynthesis. In this reaction, oxygen is consumed and carbon dioxide is released as a waste product. The reaction is summarized as:

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

Both of these reactions involve many steps.

The processes of making and breaking down sugar molecules illustrate two examples of metabolic pathways. A metabolic pathway is a series of chemical reactions that takes a starting molecule and modifies it, step-by-step, through a series of metabolic intermediates, eventually yielding a final product. In the example of sugar metabolism, the first metabolic pathway synthesized sugar from smaller molecules, and the other pathway broke sugar down into smaller molecules. These two opposite processes—the first requiring energy and the second producing energy—are referred to as anabolic pathways (building polymers) and catabolic pathways (breaking down polymers into their monomers), respectively. Consequently, metabolism is composed of synthesis (anabolism) and degradation (catabolism) (Figure 4.3.2).

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

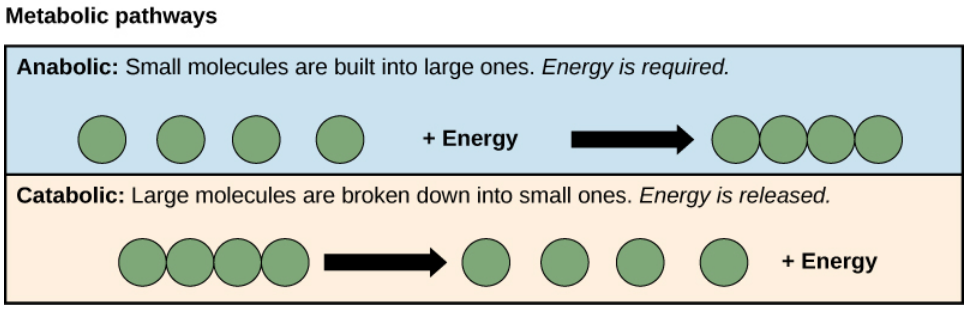


Figure 4.3.2: Catabolic pathways are those that generate energy by breaking down larger molecules. Anabolic pathways are those that require energy to synthesize larger molecules. Both types of pathways are required for maintaining the cell's energy balance.

Energy

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

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

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

Thermodynamics

The first law of thermodynamics states that the total amount of energy in the universe is constant and conserved. In other words, there has always been, and always will be, exactly the same amount of energy in the universe. Energy exists in many different forms. According to the first law of thermodynamics, energy may be transferred from place to place or transformed into different forms, but it cannot be created or destroyed. The transfers and transformations of energy take place around us all the time. Light bulbs transform electrical energy into light and heat energy. Gas stoves transform chemical energy from natural gas into heat

energy. Plants perform one of the most biologically useful energy transformations on earth: that of converting the energy of sunlight to chemical energy stored within organic molecules (Figure 4.3.1). Some examples of energy transformations are shown in Figure 4.3.3.

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

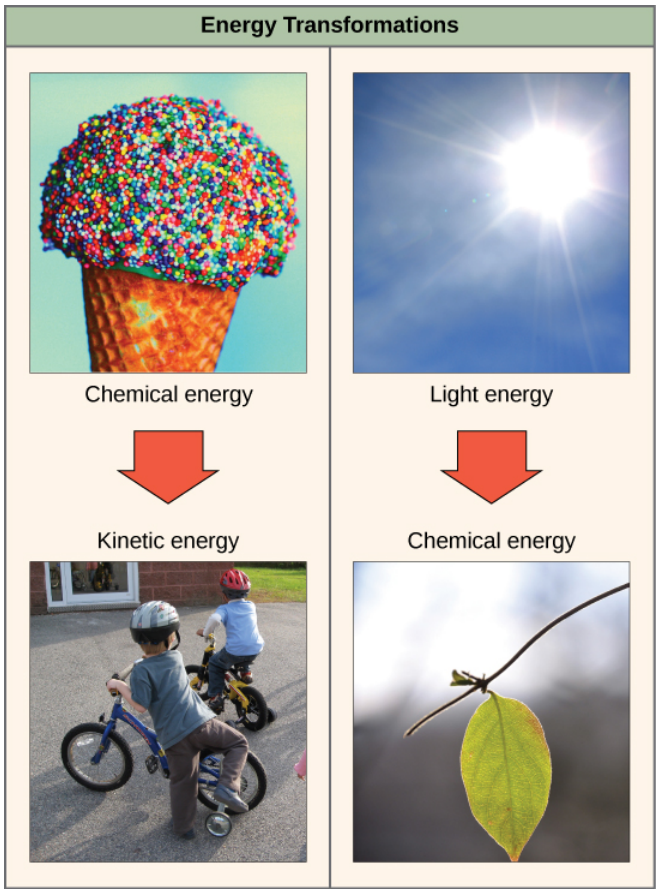


Figure 4.3.3: Shown are some examples of energy transferred and transformed from one system to another and from one form to another. The food we consume provides our cells with the energy required to carry out bodily functions, just as light energy provides plants with the means to create the chemical energy they need. (credit "ice cream": modification of work by D. Sharon Pruitt; credit "kids": modification of work by Max from Providence; credit "leaf": modification of work by Cory Zanker)

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

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

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

Potential and Kinetic Energy

When an object is in motion, there is energy associated with that object. Think of a wrecking ball. Even a slow-moving wrecking ball can do a great deal of damage to other objects. Energy associated with objects in motion is called kinetic energy (Figure 4.3.4). A speeding bullet, a walking person, and the rapid movement of molecules in the air (which produces heat) all have kinetic energy.

Now what if that same motionless wrecking ball is lifted two stories above ground with a crane? If the suspended wrecking ball is unmoving, is there energy associated with it? The answer is yes. The energy that was required to lift the wrecking ball did not disappear, but is now stored in the wrecking ball by virtue of its position and the force of gravity acting on it. This type of energy is called potential energy (Figure 4.3.4). If the ball were to fall, the potential energy would be transformed into kinetic energy until all of the potential energy was exhausted when the ball rested on the ground. Wrecking balls also swing like a pendulum; through the swing, there is a constant change of potential energy (highest at the top of the swing) to kinetic energy (highest at the bottom of the swing). Other examples of potential energy include the energy of water held behind a dam or a person about to skydive out of an airplane.



Figure 4.3.4: Still water has potential energy; moving water, such as in a waterfall or a rapidly flowing river, has kinetic energy. (credit "dam": modification of work by "Pascal"/Flickr; credit "waterfall": modification of work by Frank Gualtieri)

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

CONCEPT IN ACTION

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

Free and Activation Energy

After learning that chemical reactions release energy when energy-storing bonds are broken, an important next question is the following: How is the energy associated with these chemical reactions quantified and expressed? How can the energy released from one reaction be compared to that of another reaction? A measurement of free energy is used to quantify these energy transfers. Recall that according to the second law of thermodynamics, all energy transfers involve the loss of some amount of energy in an

unusable form such as heat. Free energy specifically refers to the energy associated with a chemical reaction that is available after the losses are accounted for. In other words, free energy is usable energy, or energy that is available to do work.

If energy is released during a chemical reaction, then the change in free energy, signified as ΔG (delta G) will be a negative number. A negative change in free energy also means that the products of the reaction have less free energy than the reactants, because they release some free energy during the reaction. Reactions that have a negative change in free energy and consequently release free energy are called exergonic reactions. Think: *ex*ergonic means energy is *ex*iting the system. These reactions are also referred to as spontaneous reactions, and their products have less stored energy than the reactants. An important distinction must be drawn between the term spontaneous and the idea of a chemical reaction occurring immediately. Contrary to the everyday use of the term, a spontaneous reaction is not one that suddenly or quickly occurs. The rusting of iron is an example of a spontaneous reaction that occurs slowly, little by little, over time.

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

ART CONNECTION

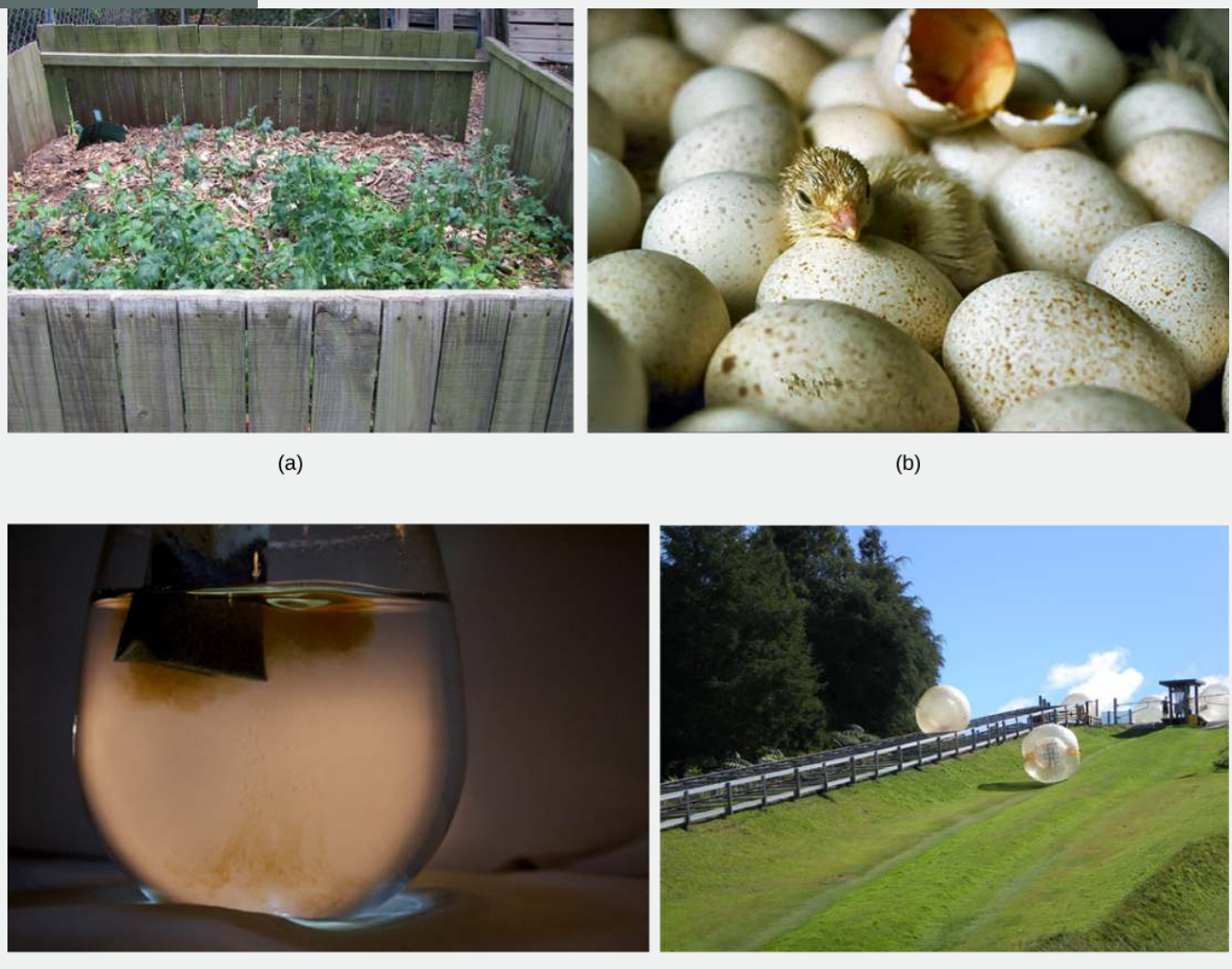
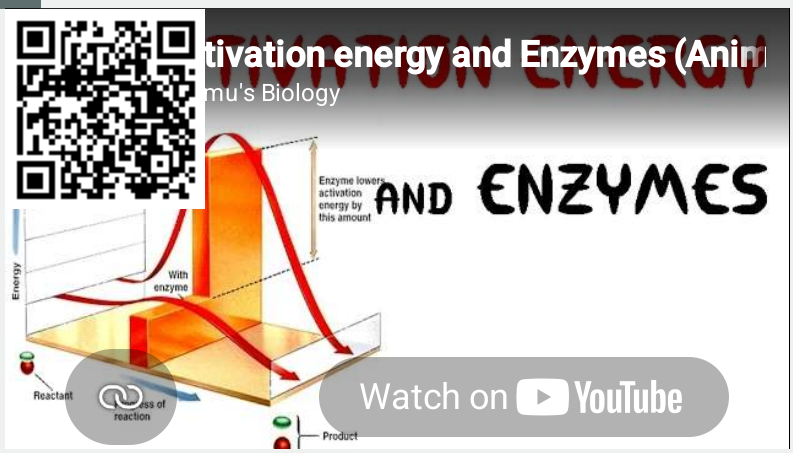


Figure 4.3.5: Shown are some examples of endergonic processes (ones that require energy) and exergonic processes (ones that release energy). (credit a: modification of work by Natalie Maynor; credit b: modification of work by USDA; credit c: modification of work by Cory Zanker; credit d: modification of work by Harry Malsch)

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

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

CONCEPT IN ACTION



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

Enzymes

A substance that helps a chemical reaction to occur is called a catalyst, and the molecules that catalyze biochemical reactions are called enzymes. Most enzymes are proteins and perform the critical task of lowering the activation energies of chemical reactions inside the cell. Most of the reactions critical to a living cell happen too slowly at normal temperatures to be of any use to the cell. Without enzymes to speed up these reactions, life could not persist. Enzymes do this by binding to the reactant molecules and holding them in such a way as to make the chemical bond-breaking and -forming processes take place more easily. It is important to remember that enzymes do not change whether a reaction is exergonic (spontaneous) or endergonic. This is because they do not change the free energy of the reactants or products. They only reduce the activation energy required for the reaction to go forward (Figure 4.3.6). In addition, an enzyme itself is unchanged by the reaction it catalyzes. Once one reaction has been catalyzed, the enzyme is able to participate in other reactions.

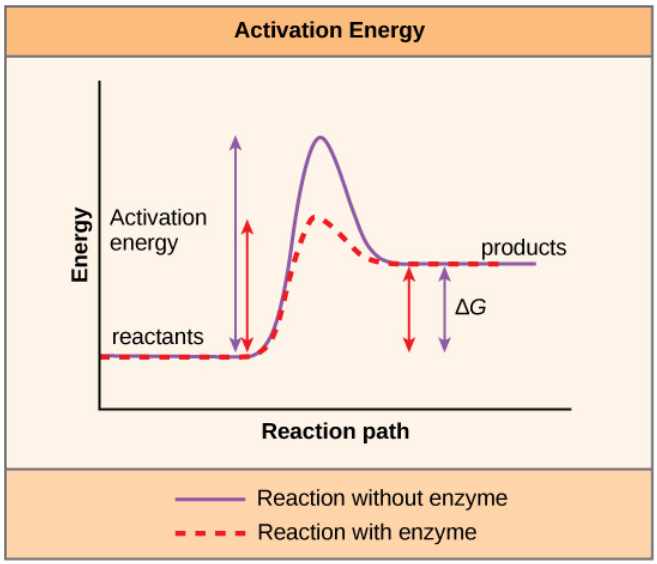


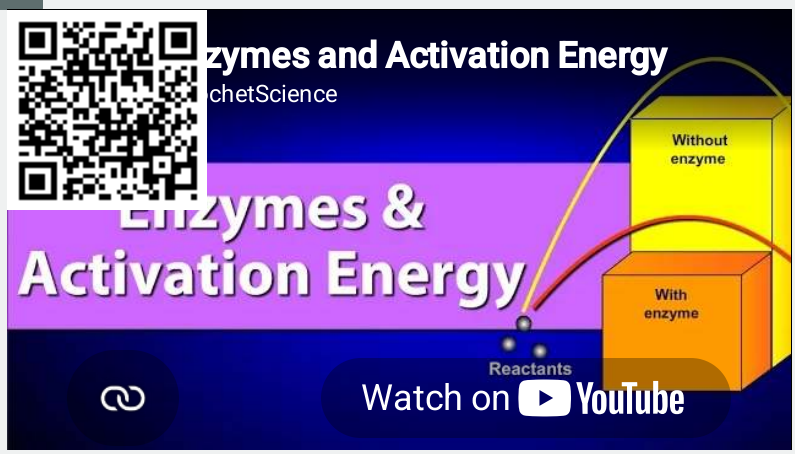
Figure 4.3.6: Enzymes lower the activation energy of the reaction but do not change the free energy of the reaction.

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

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

For many years, scientists thought that enzyme-substrate binding took place in a simple "lock and key" fashion. This model asserted that the enzyme and substrate fit together perfectly in one instantaneous step. However, current research supports a model called induced fit (Figure 4.3.7). The induced-fit model expands on the lock-and-key model by describing a more dynamic binding between enzyme and substrate. As the enzyme and substrate come together, their interaction causes a mild shift in the enzyme's structure that forms an ideal binding arrangement between enzyme and substrate.

CONCEPT IN ACTION



View an animation of induced fit.

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

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

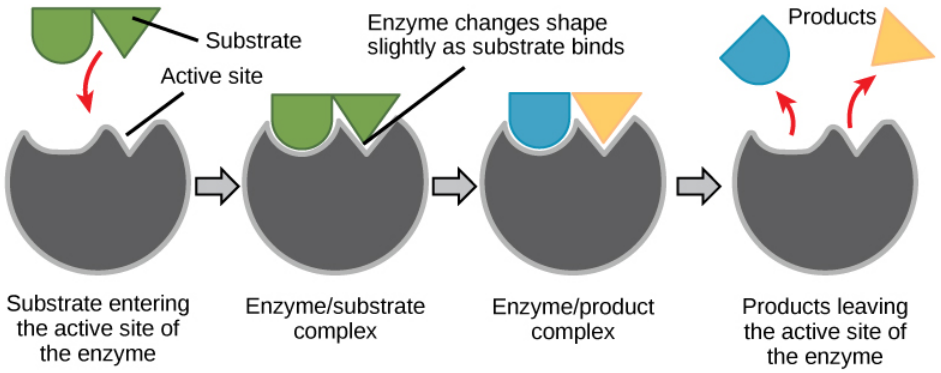


Figure 4.3.7: The induced-fit model is an adjustment to the lock-and-key model and explains how enzymes and substrates undergo dynamic modifications during the transition state to increase the affinity of the substrate for the active site.

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

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

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

On the other hand, in noncompetitive inhibition, an inhibitor molecule binds to the enzyme in a location other than the active site, called an allosteric site, but still manages to block substrate binding to the active site. Some inhibitor molecules bind to enzymes in a location where their binding induces a conformational change that reduces the affinity of the enzyme for its substrate. This type of inhibition is called allosteric inhibition(Figure 4.3.8). Most allosterically regulated enzymes are made up of more than one polypeptide, meaning that they have more than one protein subunit. When an allosteric inhibitor binds to a region on an enzyme, all active sites on the protein subunits are changed slightly such that they bind their substrates with less efficiency. There are allosteric activators as well as inhibitors. Allosteric activators bind to locations on an enzyme away from the active site, inducing a conformational change that increases the affinity of the enzyme's active site(s) for its substrate(s) (Figure 4.3.8).

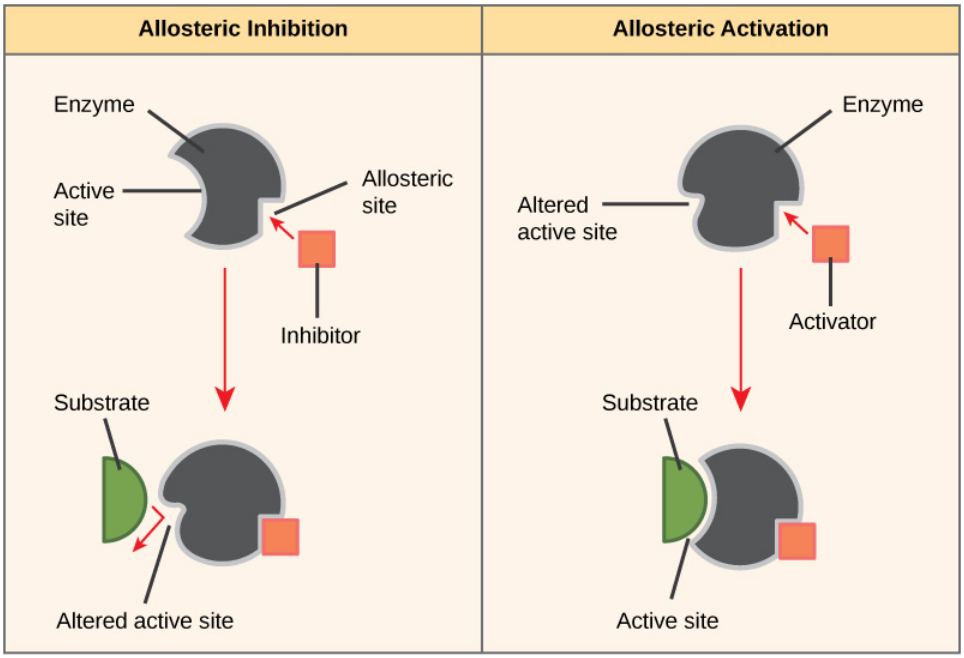


Figure 4.3.8: Allosteric inhibition works by indirectly inducing a conformational change to the active site such that the substrate no longer fits. In contrast, in allosteric activation, the activator molecule modifies the shape of the active site to allow a better fit of the substrate.

CAREERS IN ACTION: Pharmaceutical Drug Developer



Figure 4.3.9: Have you ever wondered how pharmaceutical drugs are developed? (credit: Deborah Austin)

Enzymes are key components of metabolic pathways. Understanding how enzymes work and how they can be regulated are key principles behind the development of many of the pharmaceutical drugs on the market today. Biologists working in this field collaborate with other scientists to design drugs (Figure 4.3.9).

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

How are drugs discovered? One of the biggest challenges in drug discovery is identifying a drug target. A drug target is a molecule that is literally the target of the drug. In the case of statins, HMG-CoA reductase is the drug target. Drug targets are identified through painstaking research in the laboratory. Identifying the target alone is not enough; scientists also need to know how the target acts inside the cell and which reactions go awry in the case of disease. Once the target and the pathway are identified, then the actual process of drug design begins. In this stage, chemists and biologists work together to design and synthesize molecules that can block or activate a particular reaction. However, this is only the beginning: If and when a drug

prototype is successful in performing its function, then it is subjected to many tests from in vitro experiments to clinical trials before it can get approval from the U.S. Food and Drug Administration to be on the market.

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

Feedback Inhibition in Metabolic Pathways

Molecules can regulate enzyme function in many ways. The major question remains, however: What are these molecules and where do they come from? Some are cofactors and coenzymes, as you have learned. What other molecules in the cell provide enzymatic regulation such as allosteric modulation, and competitive and non-competitive inhibition? Perhaps the most relevant sources of regulatory molecules, with respect to enzymatic cellular metabolism, are the products of the cellular metabolic reactions themselves. In a most efficient and elegant way, cells have evolved to use the products of their own reactions for feedback inhibition of enzyme activity. Feedback inhibition involves the use of a reaction product to regulate its own further production (Figure 4.3.10). The cell responds to an abundance of the products by slowing down production during anabolic or catabolic reactions. Such reaction products may inhibit the enzymes that catalyzed their production through the mechanisms described above.

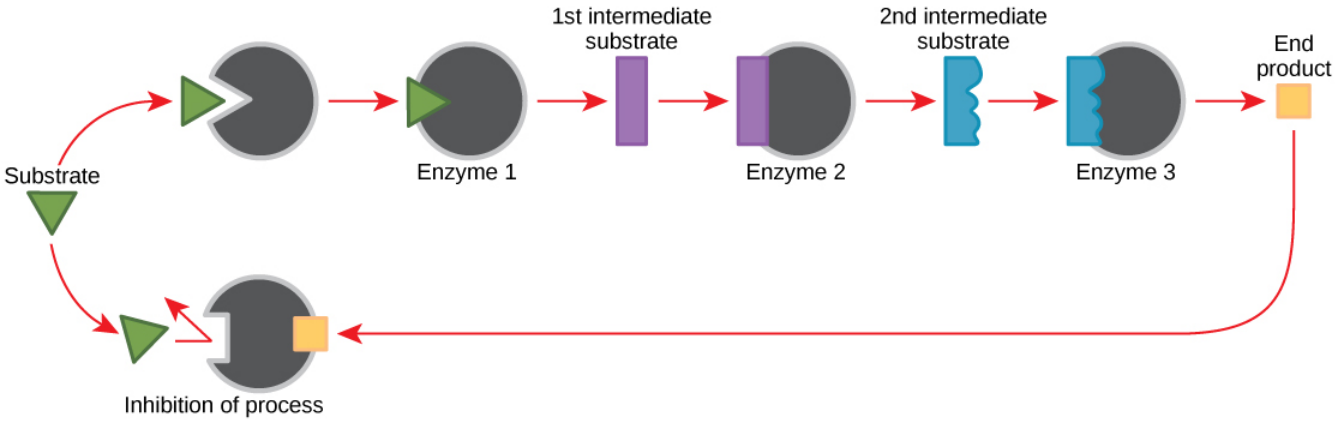


Figure 4.3.10: Metabolic pathways are a series of reactions catalyzed by multiple enzymes. Feedback inhibition, where the end product of the pathway inhibits an upstream process, is an important regulatory mechanism in cells.

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

Section Summary

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

In studying energy, the term system refers to the matter and environment involved in energy transfers. Entropy is a measure of the disorder of a system. The physical laws that describe the transfer of energy are the laws of thermodynamics. The first law states that the total amount of energy in the universe is constant. The second law of thermodynamics states that every energy transfer involves

some loss of energy in an unusable form, such as heat energy. Energy comes in different forms: kinetic, potential, and free. The change in free energy of a reaction can be negative (releases energy, exergonic) or positive (consumes energy, endergonic). All reactions require an initial input of energy to proceed, called the activation energy.

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

Art Connections

Figure 4.3.5: Look at each of the processes shown and decide if it is endergonic or exergonic.

Answer

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

Glossary

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

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

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

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

bioenergetics
the concept of energy flow through living systems

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

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

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

enzyme
a molecule that catalyzes a biochemical reaction

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

feedback inhibition

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

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

kinetic energy
the type of energy associated with objects in motion

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

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

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

substrate
a molecule on which the enzyme acts

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

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4.A: Cell Structure and Function (Exercises)

Passive Transport

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

Multiple Choice

Water moves via osmosis _____.

A. throughout the cytoplasm
B. from an area with a high concentration of other solutes to a lower one
C. from an area with a low concentration of solutes to an area with a higher one
D. from an area with a low concentration of water to one of higher concentration

Answer

C

The principal force driving movement in diffusion is _____.

A. temperature
B. particle size
C. concentration gradient
D. membrane surface area

Answer

C

Free Response

Why does osmosis occur?

Answer

Water moves through a semipermeable membrane in osmosis because there is a concentration gradient across the membrane of solute and solvent. The solute cannot effectively move to balance the concentration on both sides of the membrane, so water moves to achieve this balance.

Active Transport

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

Multiple Choice

Active transport must function continuously because _____.

A. plasma membranes wear out
B. cells must be in constant motion
C. facilitated transport opposes active transport
D. diffusion is constantly moving the solutes in the other direction

Answer

D

Free Response

Where does the cell get energy for active transport processes?

Answer

The cell harvests energy from ATP produced by its own metabolism to power active transport processes, such as pumps.

Energy and Metabolism

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

Review Questions

Which of the following is not an example of an energy transformation?

A. Heating up dinner in a microwave
B. Solar panels at work
C. Formation of static electricity
D. None of the above

Answer

D

Which of the following is not true about enzymes?

A. They are consumed by the reactions they catalyze.
B. They are usually made of amino acids.
C. They lower the activation energy of chemical reactions.
D. Each one is specific to the particular substrate(s) to which it binds.

Answer

A

Free Response

Does physical exercise to increase muscle mass involve anabolic and/or catabolic processes? Give evidence for your answer.

Answer

Physical exercise involves both anabolic and catabolic processes. Body cells break down sugars to provide ATP to do the work necessary for exercise, such as muscle contractions. This is catabolism. Muscle cells also must repair muscle tissue damaged by exercise by building new muscle. This is anabolism.

Explain in your own terms the difference between a spontaneous reaction and one that occurs instantaneously, and what causes this difference.

Answer

A spontaneous reaction is one that has a negative ΔG and thus releases energy. However, a spontaneous reaction need not occur quickly or suddenly like an instantaneous reaction. It may occur over long periods of time due to a large energy of activation, which prevents the reaction from occurring quickly.

With regard to enzymes, why are vitamins and minerals necessary for good health? Give examples.

Answer

Most vitamins and minerals act as cofactors and coenzymes for enzyme action. Many enzymes require the binding of certain cofactors or coenzymes to be able to catalyze their reactions. Since enzymes catalyze many important reactions, it is critical to

obtain sufficient vitamins and minerals from diet and supplements. Vitamin C (ascorbic acid) is a coenzyme necessary for the action of enzymes that build collagen.

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CHAPTER OVERVIEW

5: How Cells Obtain Energy

5.1: Glycolysis

5.2: Citric Acid Cycle and Oxidative Phosphorylation

5.3: Fermentation

5.4: Connections to Other Metabolic Pathways

5.A: How Cells Obtain Energy (Exercises)

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5.1: Glycolysis

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

ATP in Living Systems

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

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

ATP Structure and Function

At the heart of ATP is a molecule of adenosine monophosphate (AMP), which is composed of an adenine molecule bonded to both a ribose molecule and a single phosphate group (Figure 5.1.1). Ribose is a five-carbon sugar found in RNA and AMP is one of the nucleotides in RNA. The addition of a second phosphate group to this core molecule results in adenosine diphosphate (ADP); the addition of a third phosphate group forms adenosine triphosphate (ATP).

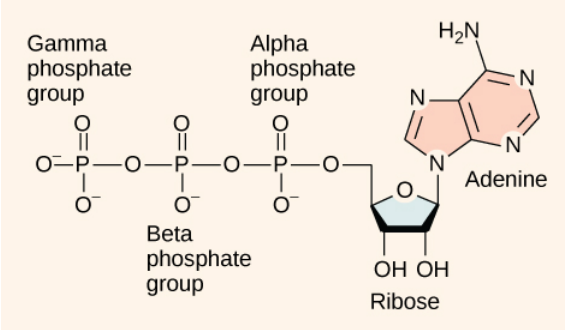


Figure 5.1.1: The structure of ATP shows the basic components of a two-ring adenine, five-carbon ribose, and three phosphate groups.

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

Glycolysis

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

Glycolysis begins with the six-carbon, ring-shaped structure of a single glucose molecule and ends with two molecules of a three-carbon sugar called pyruvate. Glycolysis consists of two distinct phases. In the first part of the glycolysis pathway, energy is used to make adjustments so that the six-carbon sugar molecule can be split evenly into two three-carbon pyruvate molecules. In the second part of glycolysis, ATP and nicotinamide-adenine dinucleotide (NADH) are produced (Figure 5.1.2).

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

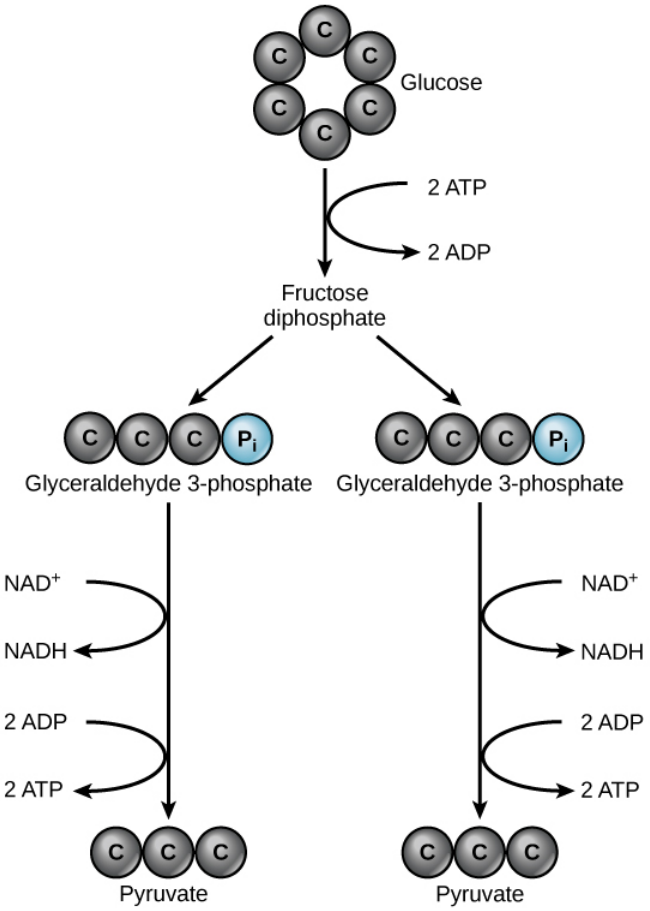


Figure 5.1.2**:** In glycolysis, a glucose molecule is converted into two pyruvate molecules.

Summary

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

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

Glossary

ATP

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

glycolysis

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

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5.2: Citric Acid Cycle and Oxidative Phosphorylation

The Citric Acid Cycle

In eukaryotic cells, the pyruvate molecules produced at the end of glycolysis are transported into mitochondria, which are sites of cellular respiration. If oxygen is available, aerobic respiration will go forward. In mitochondria, pyruvate will be transformed into a two-carbon acetyl group (by removing a molecule of carbon dioxide) that will be picked up by a carrier compound called coenzyme A (CoA), which is made from vitamin B_5. The resulting compound is called acetyl CoA. (Figure 5.2.1). Acetyl CoA can be used in a variety of ways by the cell, but its major function is to deliver the acetyl group derived from pyruvate to the next pathway in glucose catabolism.

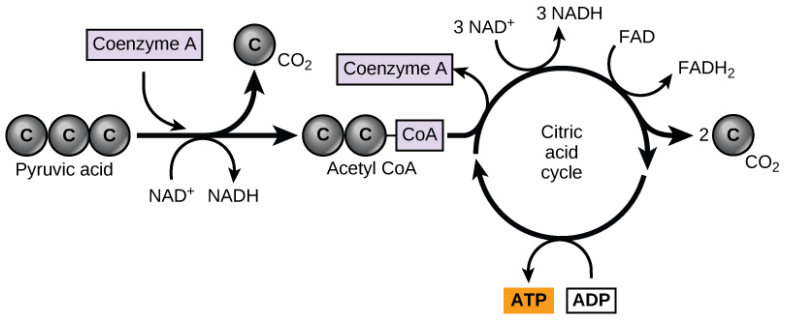


Figure 5.2.1**:** Pyruvate is converted into acetyl-CoA before entering the citric acid cycle.

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

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

Oxidative Phosphorylation

You have just read about two pathways in glucose catabolism—glycolysis and the citric acid cycle—that generate ATP. Most of the ATP generated during the aerobic catabolism of glucose, however, is not generated directly from these pathways. Rather, it derives from a process that begins with passing electrons through a series of chemical reactions to a final electron acceptor, oxygen. These reactions take place in specialized protein complexes located in the inner membrane of the mitochondria of eukaryotic organisms and on the inner part of the cell membrane of prokaryotic organisms. The energy of the electrons is harvested and used to generate a electrochemical gradient across the inner mitochondrial membrane. The potential energy of this gradient is used to generate ATP. The entirety of this process is called oxidative phosphorylation.

The electron transport chain (Figure 5.2.2**a**) is the last component of aerobic respiration and is the only part of metabolism that uses atmospheric oxygen. Oxygen continuously diffuses into plants for this purpose. In animals, oxygen enters the body through the respiratory system. Electron transport is a series of chemical reactions that resembles a bucket brigade in that electrons are passed rapidly from one component to the next, to the endpoint of the chain where oxygen is the final electron acceptor and water is produced. There are four complexes composed of proteins, labeled I through IV in Figure 5.2.2**c**, and the aggregation of these four

complexes, together with associated mobile, accessory electron carriers, is called the electron transport chain. The electron transport chain is present in multiple copies in the inner mitochondrial membrane of eukaryotes and in the plasma membrane of prokaryotes. In each transfer of an electron through the electron transport chain, the electron loses energy, but with some transfers, the energy is stored as potential energy by using it to pump hydrogen ions across the inner mitochondrial membrane into the intermembrane space, creating an electrochemical gradient.

ART CONNECTION

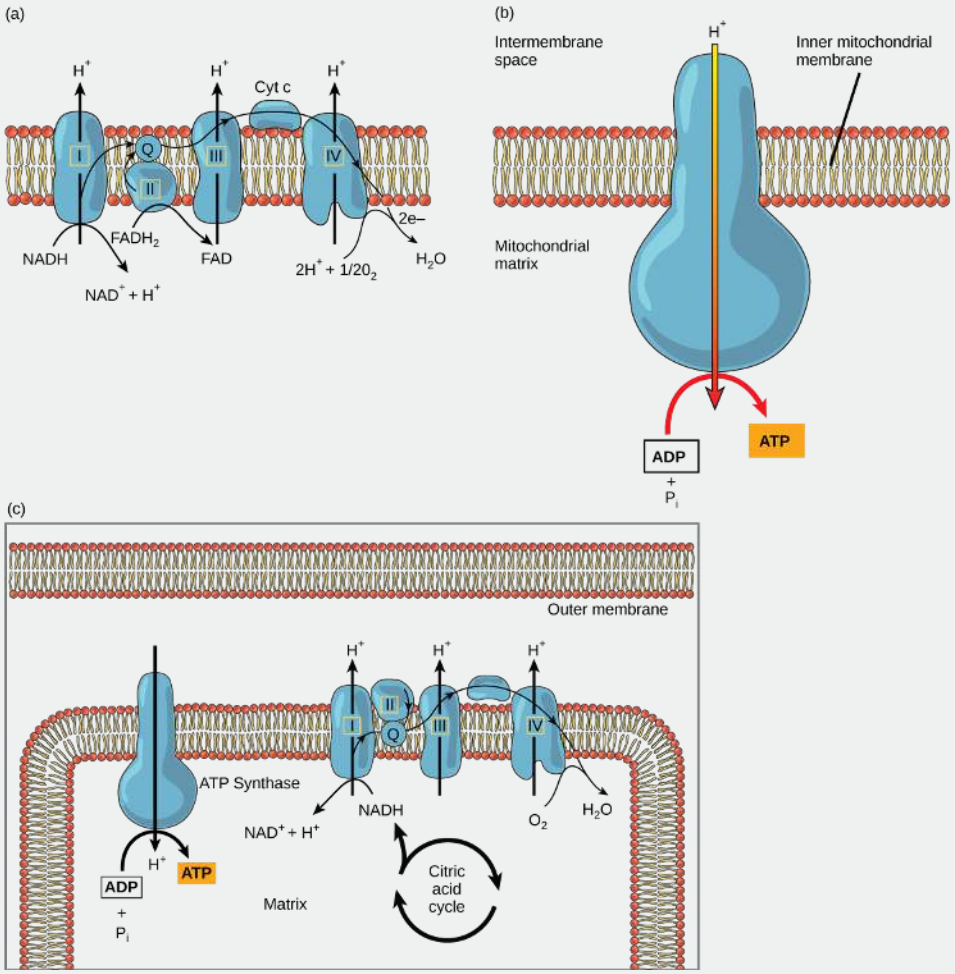


Figure 5.2.2**:** (a) The electron transport chain is a set of molecules that supports a series of oxidation-reduction reactions. (b) ATP synthase is a complex, molecular machine that uses an H^+ gradient to regenerate ATP from ADP. (c) Chemiosmosis relies on the potential energy provided by the H^+ gradient across the membrane.

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

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

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

Hydrogen ions diffuse through the inner membrane through an integral membrane protein called ATP synthase (Figure 5.2.2**b**). This complex protein acts as a tiny generator, turned by the force of the hydrogen ions diffusing through it, down their electrochemical gradient from the intermembrane space, where there are many mutually repelling hydrogen ions to the matrix, where there are few. The turning of the parts of this molecular machine regenerate ATP from ADP. This flow of hydrogen ions across the membrane through ATP synthase is called chemiosmosis.

Chemiosmosis (Figure 5.2.2**c**) is used to generate 90 percent of the ATP made during aerobic glucose catabolism. The result of the reactions is the production of ATP from the energy of the electrons removed from hydrogen atoms. These atoms were originally part of a glucose molecule. At the end of the electron transport system, the electrons are used to reduce an oxygen molecule to oxygen ions. The extra electrons on the oxygen ions attract hydrogen ions (protons) from the surrounding medium, and water is formed. The electron transport chain and the production of ATP through chemiosmosis are collectively called oxidative phosphorylation.

ATP Yield

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

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

CAREERS IN ACTION: Mitochondrial Disease Physician

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

Summary

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

The electron transport chain is the portion of aerobic respiration that uses free oxygen as the final electron acceptor for electrons removed from the intermediate compounds in glucose catabolism. The electrons are passed through a series of chemical reactions, with a small amount of free energy used at three points to transport hydrogen ions across the membrane. This contributes to the gradient used in chemiosmosis. As the electrons are passed from NADH or $FADH_2$ down the electron transport chain, they lose energy. The products of the electron transport chain are water and ATP. A number of intermediate compounds can be diverted into

the anabolism of other biochemical molecules, such as nucleic acids, non-essential amino acids, sugars, and lipids. These same molecules, except nucleic acids, can serve as energy sources for the glucose pathway.

Art Connections

Figure 5.2.2: Cyanide inhibits cytochrome c oxidase, a component of the electron transport chain. If cyanide poisoning occurs, would you expect the pH of the intermembrane space to increase or decrease? What affect would cyanide have on ATP synthesis?

Answer

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

Glossary

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

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

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

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

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

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

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5.3: Fermentation

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

Lactic Acid Fermentation

The fermentation method used by animals and some bacteria like those in yogurt is lactic acid fermentation (Figure 5.3.1). This occurs routinely in mammalian red blood cells and in skeletal muscle that has insufficient oxygen supply to allow aerobic respiration to continue (that is, in muscles used to the point of fatigue). In muscles, lactic acid produced by fermentation must be removed by the blood circulation and brought to the liver for further metabolism. The chemical reaction of lactic acid fermentation is the following:

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

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

ART CONNECTION

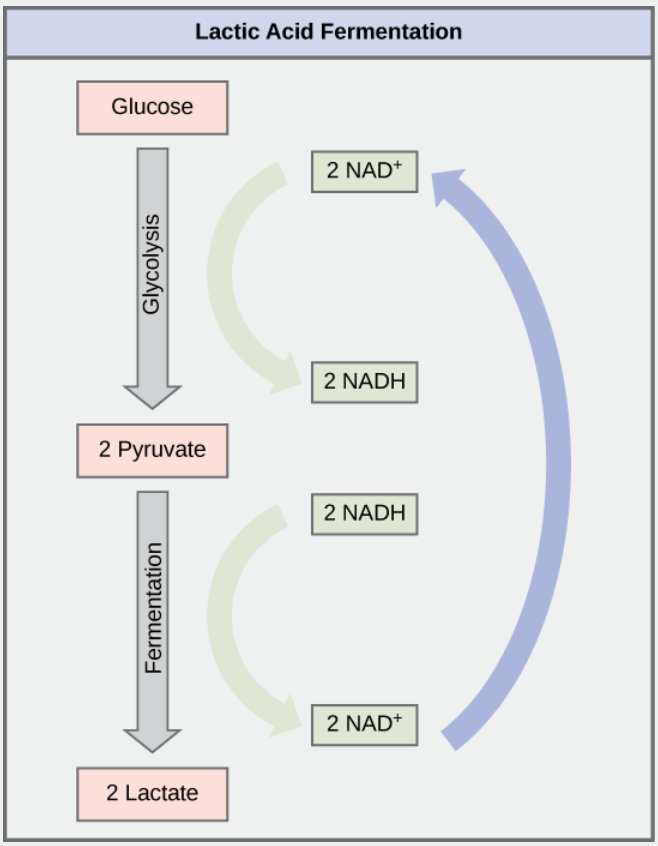


Figure 5.3.1: Lactic acid fermentation is common in muscles that have become exhausted by use.

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

Alcohol Fermentation

Another familiar fermentation process is alcohol fermentation (Figure 5.3.2), which produces ethanol, an alcohol. The alcohol fermentation reaction is the following:

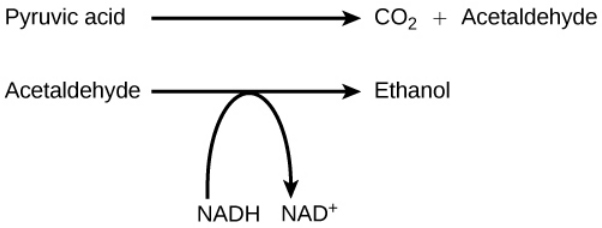


Figure 5.3.2: The reaction resulting in alcohol fermentation is shown.

In the first reaction, a carboxyl group is removed from pyruvic acid, releasing carbon dioxide as a gas. The loss of carbon dioxide reduces the molecule by one carbon atom, making acetaldehyde. The second reaction removes an electron from NADH, forming NAD^+ and producing ethanol from the acetaldehyde, which accepts the electron. The fermentation of pyruvic acid by yeast produces the ethanol found in alcoholic beverages (Figure 5.3.3). If the carbon dioxide produced by the reaction is not vented from the fermentation chamber, for example in beer and sparkling wines, it remains dissolved in the medium until the pressure is released. Ethanol above 12 percent is toxic to yeast, so natural levels of alcohol in wine occur at a maximum of 12 percent.



Figure 5.3.3: Fermentation of grape juice to make wine produces CO_2 as a byproduct. Fermentation tanks have valves so that pressure inside the tanks can be released.

Anaerobic Cellular Respiration

Certain prokaryotes, including some species of bacteria and Archaea, use anaerobic respiration. For example, the group of Archaea called methanogens reduces carbon dioxide to methane to oxidize NADH. These microorganisms are found in soil and in the digestive tracts of ruminants, such as cows and sheep. Similarly, sulfate-reducing bacteria and Archaea, most of which are anaerobic (Figure 5.3.4), reduce sulfate to hydrogen sulfide to regenerate NAD^+ from NADH.

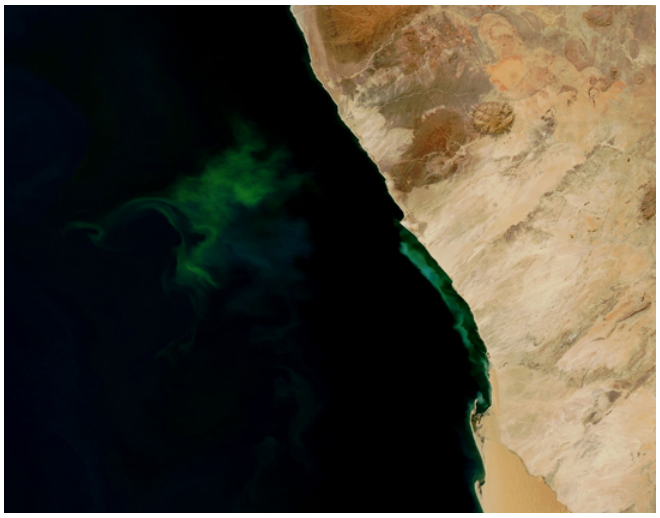
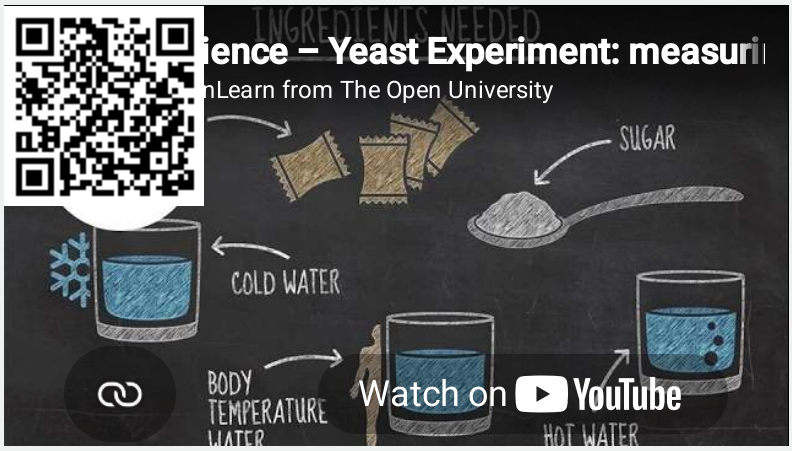


Figure 5.3.4**:** The green color seen in these coastal waters is from an eruption of hydrogen sulfide. Anaerobic, sulfate-reducing bacteria release hydrogen sulfide gas as they decompose algae in the water. (credit: NASA image courtesy Jeff Schmaltz, MODIS Land Rapid Response Team at NASA GSFC)

CONCEPT IN ACTION



Visit this site to see anaerobic cellular respiration in action.

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

Section Summary

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

Art Connections

Figure 5.3.1: Tremetol, a metabolic poison found in white snake root plant, prevents the metabolism of lactate. When cows eat this plant, Tremetol is concentrated in the milk. Humans who consume the milk become ill. Symptoms of this disease, which include vomiting, abdominal pain, and tremors, become worse after exercise. Why do you think this is the case?

Answer

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

Glossary

anaerobic cellular respiration

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

fermentation

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

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5.4: Connections to Other Metabolic Pathways

You have learned about the catabolism of glucose, which provides energy to living cells. But living things consume more than just glucose for food. How does a turkey sandwich, which contains protein, provide energy to 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 (Figure 5.4.1). Metabolic pathways should be thought of as porous—that is, substances enter from other pathways, and other substances leave for other pathways. These pathways are not closed systems. Many of the products in a particular pathway are reactants in other pathways.

Connections of Other Sugars to Glucose Metabolism

Glycogen, a polymer of glucose, is a short-term energy storage molecule in animals. When there is adequate ATP present, excess glucose is converted into glycogen for storage. Glycogen is made and stored in the liver and muscle. Glycogen will be taken out of storage if blood sugar levels drop. The presence of glycogen in muscle cells as a source of glucose allows ATP to be produced for a longer time during exercise.

Sucrose is a disaccharide made from glucose and fructose bonded together. Sucrose is broken down in the small intestine, and the glucose and fructose are absorbed separately. Fructose is one of the three dietary monosaccharides, along with glucose and galactose (which is part of milk sugar, the disaccharide lactose), that are absorbed directly into the bloodstream during digestion. The catabolism of both fructose and galactose produces the same number of ATP molecules as glucose.

Connections of Proteins to Glucose Metabolism

Proteins are broken down by a variety of enzymes in cells. Most of the time, amino acids are recycled into new proteins. If there are excess amino acids, however, or if the body is in a state of famine, some amino acids will be shunted into pathways of glucose catabolism. Each amino acid must have its amino group removed prior to entry into these pathways. The amino group is converted into ammonia. In mammals, the liver synthesizes urea from two ammonia molecules and a carbon dioxide molecule. Thus, urea is the principal waste product in mammals from the nitrogen originating in amino acids, and it leaves the body in urine.

Connections of Lipids to Glucose Metabolism

The lipids that are connected to the glucose pathways are cholesterol and triglycerides. Cholesterol is a lipid that contributes to cell membrane flexibility and is a precursor of steroid hormones. The synthesis of cholesterol starts with acetyl CoA and proceeds in only one direction. The process cannot be reversed, and ATP is not produced.

Triglycerides are a form of long-term energy storage in animals. Triglycerides store about twice as much energy as carbohydrates. Triglycerides 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 and proceeds through glycolysis. Fatty acids are broken into two-carbon units that enter the citric acid cycle.

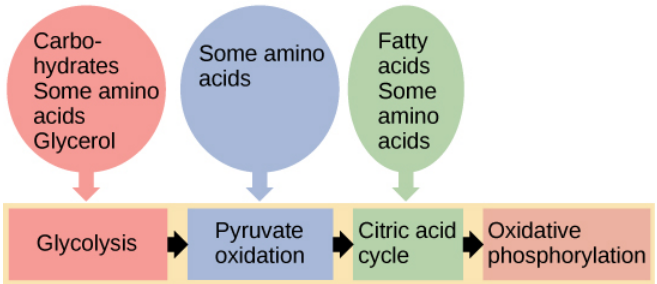


Figure 5.4.1: Glycogen from the liver and muscles, together with fats, can feed into the catabolic pathways for carbohydrates.

EVOLUTION IN ACTION: Pathways of Photosynthesis and Cellular Metabolism

Photosynthesis and cellular metabolism consist of several very complex pathways. It is generally thought that the first cells arose in an aqueous environment—a “soup” of nutrients. If these cells reproduced successfully and their numbers climbed steadily, it follows that the cells would begin to deplete the nutrients from the medium in which they lived, as they shifted the

nutrients into their own cells. This hypothetical situation would have resulted in natural selection favoring those organisms that could exist by using the nutrients that remained in their environment and by manipulating these nutrients into materials that they could use to survive. Additionally, selection would favor those organisms that could extract maximal value from the available nutrients.

An early form of photosynthesis developed that harnessed the sun's energy using compounds other than water as a source of hydrogen atoms, but this pathway did not produce free oxygen. It is thought that glycolysis developed prior to this time and could take advantage of simple sugars being produced, but these reactions were not able to fully extract the energy stored in the carbohydrates. A later form of photosynthesis used water as a source of hydrogen ions and generated free oxygen. Over time, the atmosphere became oxygenated. Living things adapted to exploit this new atmosphere and allowed respiration as we know it to evolve. When the full process of photosynthesis as we know it developed and the atmosphere became oxygenated, cells were finally able to use the oxygen expelled by photosynthesis to extract more energy from the sugar molecules using the citric acid cycle.

Summary

The breakdown and synthesis of carbohydrates, proteins, and lipids connect with the pathways of glucose catabolism. The carbohydrates that can also feed into glucose catabolism include galactose, fructose, and glycogen. These connect with glycolysis. The amino acids from proteins connect with glucose catabolism through pyruvate, acetyl CoA, and components of the citric acid cycle. Cholesterol synthesis starts with acetyl CoA, and the components of triglycerides are picked up by acetyl CoA and enter the citric acid cycle.

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5.A: How Cells Obtain Energy (Exercises)

Glycolysis

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

Multiple Choice

Energy is stored long-term in the bonds of _____ and used short-term to perform work from a(n) _____ molecule.

A. ATP : glucose
B. an anabolic molecule : catabolic molecule
C. glucose : ATP
D. a catabolic molecule : anabolic molecule

Answer

C

The energy currency used by cells is _____.

A. ATP
B. ADP
C. AMP
D. adenosine

Answer

A

The glucose that enters the glycolysis pathway is split into two molecules of _____.

A. ATP
B. phosphate
C. NADH
D. pyruvate

Answer

D

Free Response

Both prokaryotic and eukaryotic organisms carry out some form of glycolysis. How does that fact support or not support the assertion that glycolysis is one of the oldest metabolic pathways?

Answer

If glycolysis evolved relatively late, it likely would not be as universal in organisms as it is. It probably evolved in very primitive organisms and persisted, with the addition of other pathways of carbohydrate metabolism that evolved later.

Citric Acid Cycle and Oxidative Phosphorylation

The citric acid cycle is a series of chemical reactions that removes high-energy electrons and uses them in the electron transport chain to generate ATP. One molecule of ATP (or an equivalent) is produced per each turn of the cycle. The electron transport chain is the portion of aerobic respiration that uses free oxygen as the final electron acceptor for electrons removed from the intermediate compounds in glucose catabolism.

Multiple Choice

What do the electrons added to NAD^+ do?

A. They become part of a fermentation pathway.
B. They go to another pathway for ATP production.
C. They energize the entry of the acetyl group into the citric acid cycle.
D. They are converted into NADP.

Answer

B

Chemiosmosis involves

A. the movement of electrons across the cell membrane
B. the movement of hydrogen atoms across a mitochondrial membrane
C. the movement of hydrogen ions across a mitochondrial membran
D. the movement of glucose through the cell membrane

Answer

C

Free Response

We inhale oxygen when we breathe and exhale carbon dioxide. What is the oxygen used for and where does the carbon dioxide come from?

Answer

The oxygen we inhale is the final electron acceptor in the electron transport chain and allows aerobic respiration to proceed, which is the most efficient pathway for harvesting energy in the form of ATP from food molecules. The carbon dioxide we breathe out is formed during the citric acid cycle when the bonds in carbon compounds are broken.

Fermentation

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

Review Questions

Which of the following fermentation methods can occur in animal skeletal muscles?

A. lactic acid fermentation
B. alcohol fermentation
C. mixed acid fermentation
D. propionic fermentation

Answer

A

Free Response

When muscle cells run out of oxygen, what happens to the potential for energy extraction from sugars and what pathways do the cell use?

Answer

Without oxygen, oxidative phosphorylation and the citric acid cycle stop, so ATP is no longer generated through this mechanism, which extracts the greatest amount of energy from a sugar molecule. In addition, NADH accumulates, preventing glycolysis from going forward because of an absence of NAD^+. Lactic acid fermentation uses the electrons in NADH to generate lactic acid from pyruvate, which allows glycolysis to continue and thus a smaller amount of ATP can be generated by the cell.

Connections to Other Metabolic Pathways

Metabolic pathways should be thought of as porous—that is, substances enter from other pathways, and other substances leave for other pathways. These pathways are not closed systems. Many of the products in a particular pathway are reactants in other pathways.

Multiple Choice

The cholesterol synthesized by cells uses which component of the glycolytic pathway as a starting point?

A. glucose
B. acetyl CoA
C. pyruvate
D. carbon dioxide

Answer

B

Beta oxidation is _____.

A. the breakdown of sugars
B. the assembly of sugars
C. the breakdown of fatty acids
D. the removal of amino groups from amino acids

Answer

C

Free Response

Would you describe metabolic pathways as inherently wasteful or inherently economical, and why?

Answer

They are very economical. The substrates, intermediates, and products move between pathways and do so in response to finely tuned feedback inhibition loops that keep metabolism overall on an even keel. Intermediates in one pathway may occur in another, and they can move from one pathway to another fluidly in response to the needs of the cell.

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CHAPTER OVERVIEW

6: Reproduction at the Cellular Level

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

6.1: The Genome
6.2: The Cell Cycle
6.3: Cancer and the Cell Cycle
6.4: Prokaryotic Cell Division
6.5: Sexual Reproduction
6.6: Meiosis
6.7: Errors in Meiosis
6.A: Reproduction at the Cellular Level (Exercises)

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6.1: The Genome

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

Genomic DNA

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

In eukaryotes, the genome comprises several double-stranded, linear DNA molecules (Figure 6.1.1) bound with proteins to form complexes called chromosomes. Each species of eukaryote has a characteristic number of chromosomes in the nuclei of its cells. Human body cells (somatic cells) have 46 chromosomes. A somatic cell contains two matched sets of chromosomes, a configuration known as diploid. The letter *n* is used to represent a single set of chromosomes; therefore a diploid organism is designated 2*n*. Human cells that contain one set of 23 chromosomes are called gametes, or sex cells; these eggs and sperm are designated *n*, or haploid.

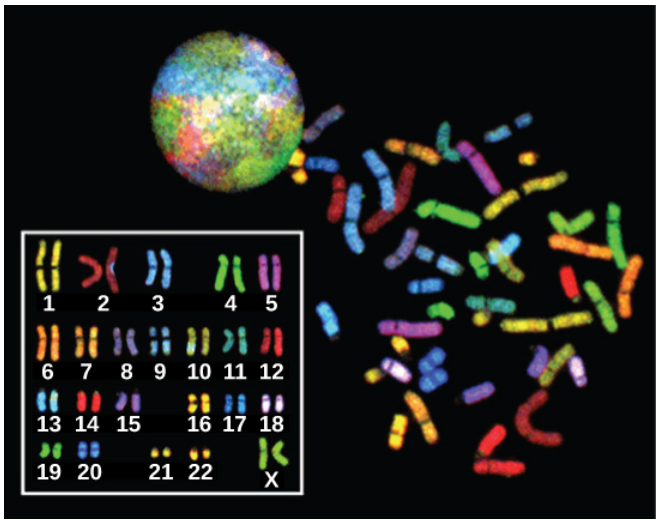


Figure 6.1.1**:** There are 23 pairs of homologous chromosomes in a female human somatic cell. These chromosomes are viewed within the nucleus (top), removed from a cell in mitosis (right), and arranged according to length (left) in an arrangement called a karyotype. In this image, the chromosomes were exposed to fluorescent stains to distinguish them. (credit: "718 Bot"/Wikimedia Commons, National Human Genome Research)

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

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

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

Summary

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

Glossary

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

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

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

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

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

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

locus
: the position of a gene on a chromosome

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6.2: The Cell Cycle

The cell cycle is an ordered series of events involving cell growth and cell division that produces two new daughter cells. Cells on the path to cell division proceed through a series of precisely timed and carefully regulated stages of growth, DNA replication, and division that produce two genetically identical cells. The cell cycle has two major phases: interphase and the mitotic phase (Figure 6.2.1). During interphase, the cell grows and DNA is replicated. During the mitotic phase, the replicated DNA and cytoplasmic contents are separated and the cell divides.

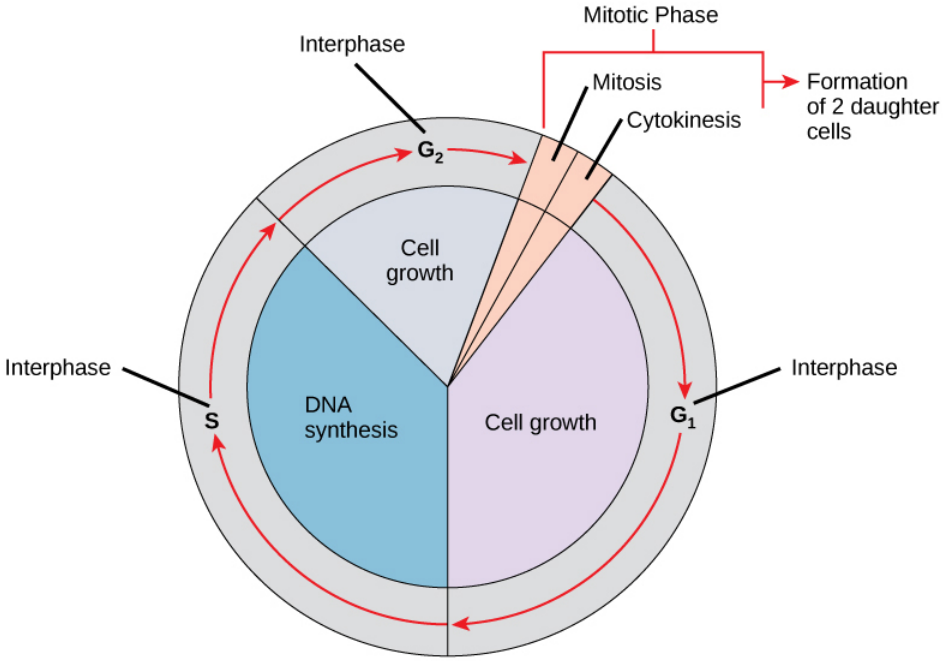


Figure 6.2.1**:** A cell moves through a series of phases in an orderly manner. During interphase, G_1 involves cell growth and protein synthesis, the S phase involves DNA replication and the replication of the centrosome, and G_2 involves further growth and protein synthesis. The mitotic phase follows interphase. Mitosis is nuclear division during which duplicated chromosomes are segregated and distributed into daughter nuclei. Usually the cell will divide after mitosis in a process called cytokinesis in which the cytoplasm is divided and two daughter cells are formed.

Interphase

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

G_1 Phase

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

S Phase

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

G_2 Phase

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

The Mitotic Phase

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

Mitosis

Mitosis is divided into a series of phases—prophase, prometaphase, metaphase, anaphase, and telophase—that result in the division of the cell nucleus (Figure 6.2.2).

ART CONNECTION

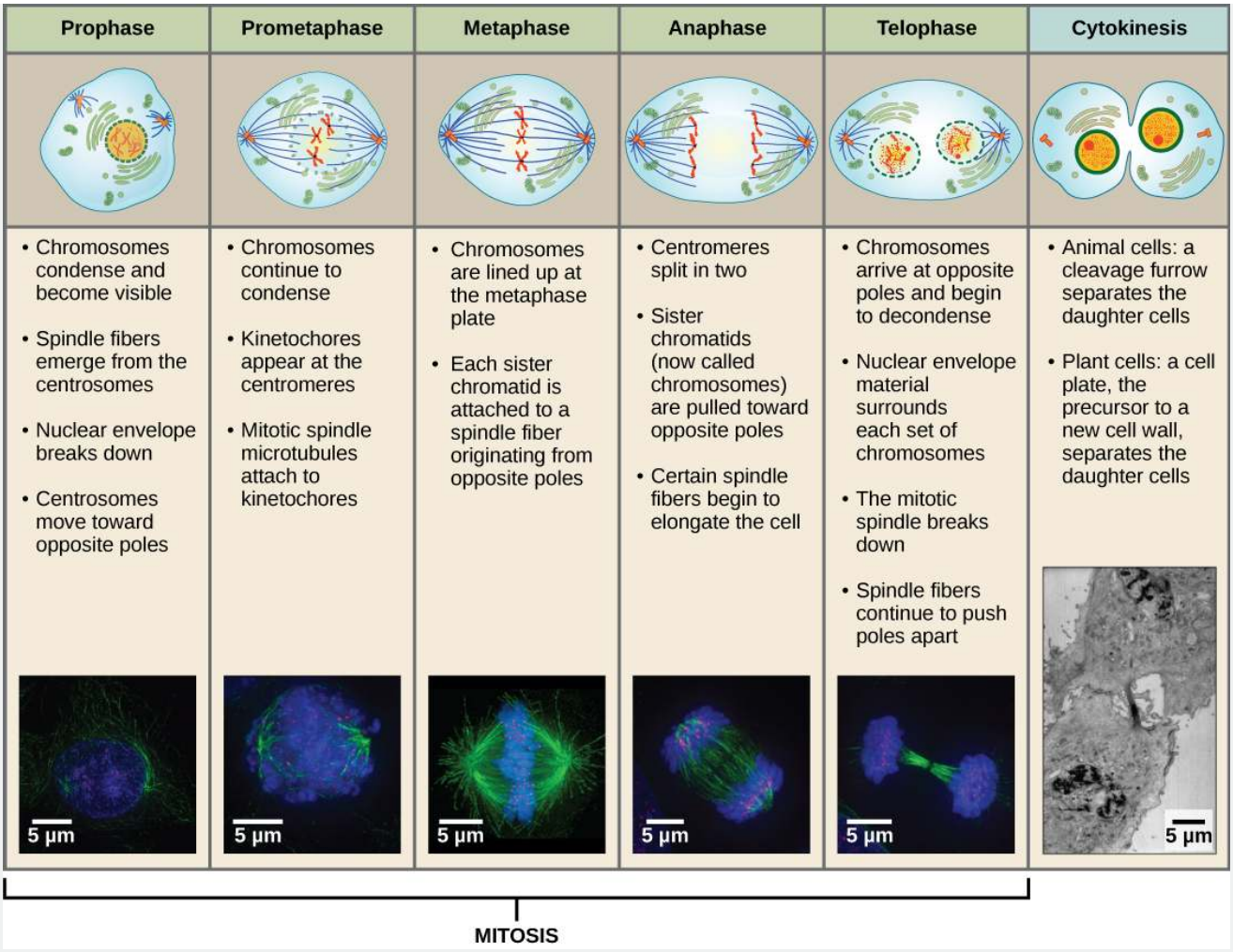


Figure 6.2.2**:** Animal cell mitosis is divided into five stages—prophase, prometaphase, metaphase, anaphase, and telophase—visualized here by light microscopy with fluorescence. Mitosis is usually accompanied by cytokinesis, shown here by a transmission electron microscope. (credit "diagrams": modification of work by Mariana Ruiz Villareal; credit "mitosis micrographs": modification of work by Roy van Heesbeen; credit "cytokinesis micrograph": modification of work by the Wadsworth Center, NY State Department of Health; donated to the Wikimedia foundation; scale-bar data from Matt Russell)

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

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

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

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

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

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

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

CONCEPT IN ACTION

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

Cytokinesis

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

In cells such as animal cells that lack cell walls, cytokinesis begins following the onset of anaphase. A contractile ring composed of actin filaments forms just inside the plasma membrane at the former metaphase plate. The actin filaments pull the equator of the cell inward, forming a fissure. This fissure, or “crack,” is called the cleavage furrow. The furrow deepens as the actin ring contracts, and eventually the membrane and cell are cleaved in two (Figure 6.2.3).

In plant cells, a cleavage furrow is not possible because of the rigid cell walls surrounding the plasma membrane. A new cell wall must form between the daughter cells. During interphase, the Golgi apparatus accumulates enzymes, structural proteins, and glucose molecules prior to breaking up into vesicles and dispersing throughout the dividing cell. During telophase, these Golgi vesicles move on microtubules to collect at the metaphase plate. There, the vesicles fuse from the center toward the cell walls; this structure is called a cell plate. As more vesicles fuse, the cell plate enlarges until it merges with the cell wall at the periphery of the cell. Enzymes use the glucose that has accumulated between the membrane layers to build a new cell wall of cellulose. The Golgi membranes become the plasma membrane on either side of the new cell wall (Figure 6.2.3).

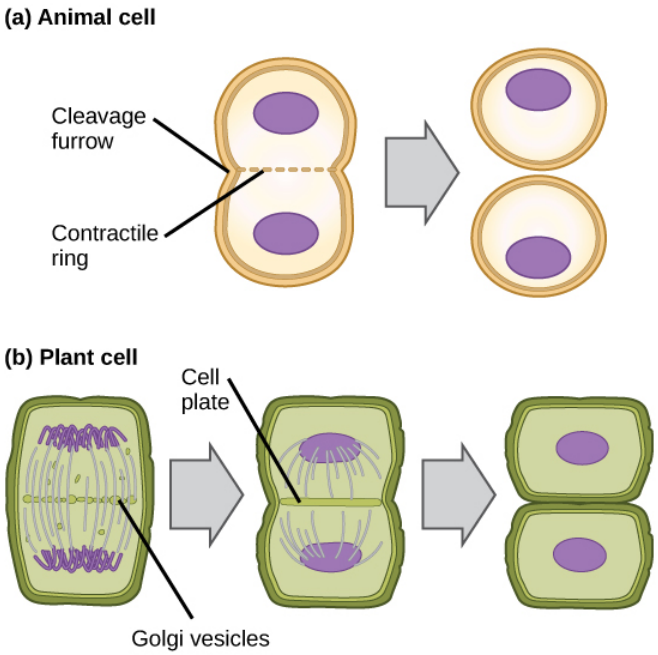


Figure 6.2.3**:** In part (a), a cleavage furrow forms at the former metaphase plate in the animal cell. The plasma membrane is drawn in by a ring of actin fibers contracting just inside the membrane. The cleavage furrow deepens until the cells are pinched in two. In part (b), Golgi vesicles coalesce at the former metaphase plate in a plant cell. The vesicles fuse and form the cell plate. The cell plate grows from the center toward the cell walls. New cell walls are made from the vesicle contents.

G_0 Phase

Not all cells adhere to the classic cell-cycle pattern in which a newly formed daughter cell immediately enters interphase, closely followed by the mitotic phase. Cells in the G_0 phase are not actively preparing to divide. The cell is in a quiescent (inactive) stage, having exited the cell cycle. Some cells enter G_0 temporarily until an external signal triggers the onset of G_1. Other cells that never or rarely divide, such as mature cardiac muscle and nerve cells, remain in G_0 permanently (Figure 6.2.4).

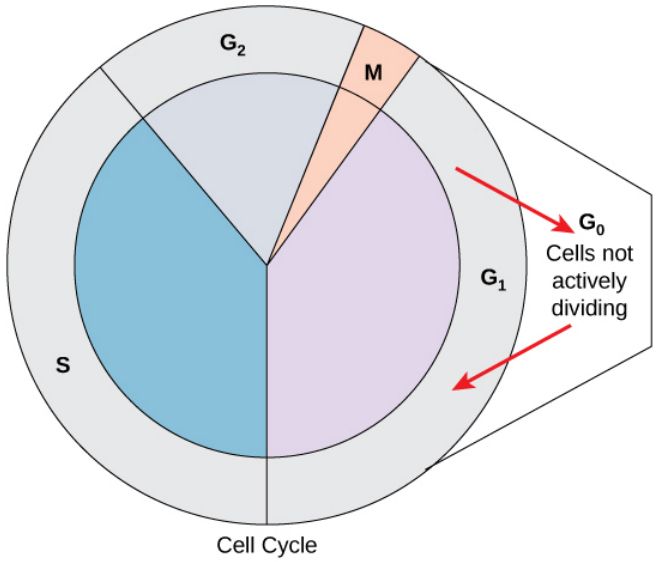


Figure 6.2.4: Cells that are not actively preparing to divide enter an alternate phase called G_0. In some cases, this is a temporary condition until triggered to enter G_1. In other cases, the cell will remain in G_0 permanently.

Control of the Cell Cycle

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

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

Regulation at Internal Checkpoints

It is essential that daughter cells be exact duplicates of the parent cell. Mistakes in the duplication or distribution of the chromosomes lead to mutations that may be passed forward to every new cell produced from the abnormal cell. To prevent a compromised cell from continuing to divide, there are internal control mechanisms that operate at three main cell cycle checkpoints at which the cell cycle can be stopped until conditions are favorable. These checkpoints occur near the end of G_1, at the G_2–M transition, and during metaphase (Figure 6.2.5).

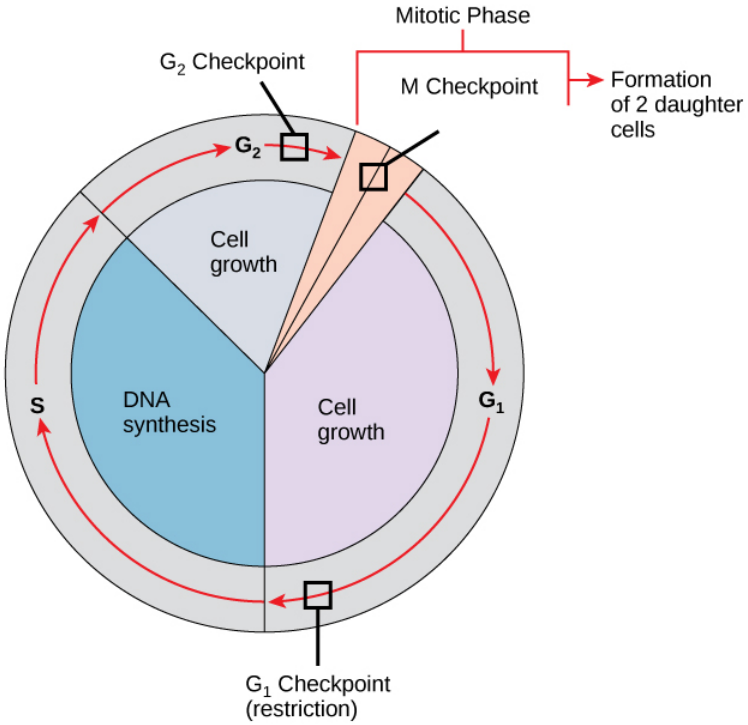


Figure 6.2.5: The cell cycle is controlled at three checkpoints. Integrity of the DNA is assessed at the G_1 checkpoint. Proper chromosome duplication is assessed at the G_2 checkpoint. Attachment of each kinetochore to a spindle fiber is assessed at the M checkpoint.

The G_1 Checkpoint

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

The G_2 Checkpoint

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

The M Checkpoint

The M checkpoint occurs near the end of the metaphase stage of mitosis. The M checkpoint is also known as the spindle checkpoint because it determines if all the sister chromatids are correctly attached to the spindle microtubules. Because the

separation of the sister chromatids during anaphase is an irreversible step, the cycle will not proceed until the kinetochores of each pair of sister chromatids are firmly anchored to spindle fibers arising from opposite poles of the cell.

CONCEPT IN ACTION

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

Summary

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

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

Art Connections

Figure 6.2.2: Which of the following is the correct order of events in mitosis?

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

Answer

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

Glossary

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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6.3: Cancer and the Cell Cycle

Cancer is a collective name for many different diseases caused by a common mechanism: uncontrolled cell division. Despite the redundancy and overlapping levels of cell-cycle control, errors occur. One of the critical processes monitored by the cell-cycle checkpoint surveillance mechanism is the proper replication of DNA during the S phase. Even when all of the cell-cycle controls are fully functional, a small percentage of replication errors (mutations) will be passed on to the daughter cells. If one of these changes to the DNA nucleotide sequence occurs within a gene, a gene mutation results. All cancers begin when a gene mutation gives rise to a faulty protein that participates in the process of cell reproduction. The change in the cell that results from the malformed protein may be minor. Even minor mistakes, however, may allow subsequent mistakes to occur more readily. Over and over, small, uncorrected errors are passed from parent cell to daughter cells and accumulate as each generation of cells produces more non-functional proteins from uncorrected DNA damage. Eventually, the pace of the cell cycle speeds up as the effectiveness of the control and repair mechanisms decreases. Uncontrolled growth of the mutated cells outpaces the growth of normal cells in the area, and a tumor can result.

Proto-oncogenes

The genes that code for the positive cell-cycle regulators are called proto-oncogenes. Proto-oncogenes are normal genes that, when mutated, become oncogenes—genes that cause a cell to become cancerous. 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 Cdk, a protein involved in cell-cycle regulation, to be activated before it should be 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 undertake further cell divisions, the mutation would not be propagated and no harm comes to the organism. However, if the atypical daughter cells are able to divide further, the subsequent generation of cells will likely accumulate even more mutations, some possibly in additional genes that regulate the cell cycle.

The Cdk 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. Once a proto-oncogene has been altered such that there is an increase in the rate of the cell cycle, it is then called an oncogene.

Tumor Suppressor Genes

Like proto-oncogenes, many of the negative cell-cycle regulatory proteins were discovered in cells that had become cancerous. Tumor suppressor genes are genes that code for the negative regulator proteins, the type of regulator that—when activated—can prevent the cell from undergoing uncontrolled division. The collective function of the best-understood tumor suppressor gene proteins, retinoblastoma protein (RB1), p53, and p21, is to put up a roadblock to cell-cycle progress 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.

Mutated p53 genes have been identified in more than 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. The p53 protein activates other genes whose products halt the cell cycle (allowing time for DNA repair), activates genes whose products participate in DNA repair, or activates genes that initiate cell death when DNA damage cannot be repaired. A damaged p53 gene can result in the cell behaving as if there are no mutations (Figure 6.3.1). This allows cells to divide, propagating the mutation in daughter cells and allowing the accumulation of new mutations. In addition, the damaged version of p53 found in cancer cells cannot trigger cell death.

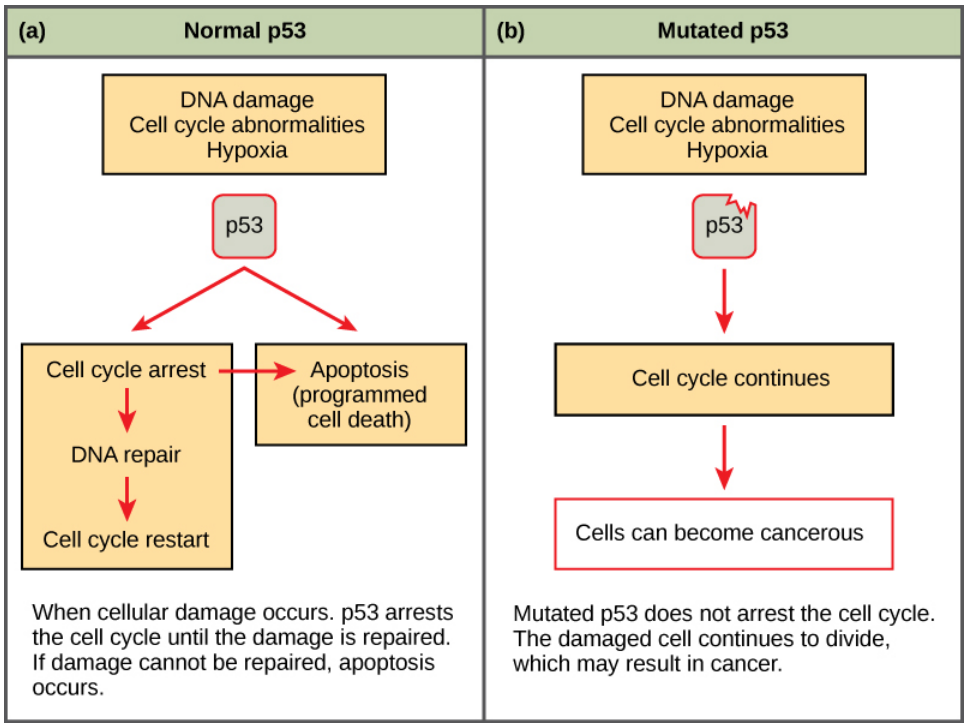
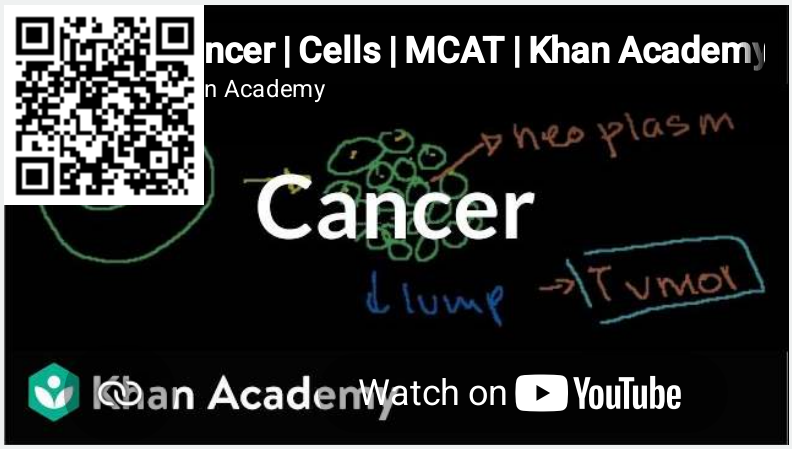


Figure 6.3.1**:** (a) The role of p53 is to monitor DNA. If damage is detected, p53 triggers repair mechanisms. If repairs are unsuccessful, p53 signals apoptosis. (b) A cell with an abnormal p53 protein cannot repair damaged DNA and cannot signal apoptosis. Cells with abnormal p53 can become cancerous. (credit: modification of work by Thierry Soussi)

CONCEPT IN ACTION



Go to this website to watch an animation of how cancer results from errors in the cell cycle.

Summary

Cancer is the result of unchecked cell division caused by a breakdown of the mechanisms regulating the cell cycle. The loss of control begins with a change in the DNA sequence of a gene that codes for one of the regulatory molecules. Faulty instructions lead to a protein that does not function as it should. Any disruption of the monitoring system can allow other mistakes to be passed on to the daughter cells. Each successive cell division will give rise to daughter cells with even more accumulated damage. Eventually, all checkpoints become nonfunctional, and rapidly reproducing cells crowd out normal cells, resulting in tumorous growth.

Glossary

oncogene

a mutated version of a proto-oncogene, which allows for uncontrolled progression of the cell cycle, or uncontrolled cell reproduction

proto-oncogene

a normal gene that controls cell division by regulating the cell cycle that becomes an oncogene if it is mutated

tumor suppressor gene

a gene that codes for regulator proteins that prevent the cell from undergoing uncontrolled division

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6.4: Prokaryotic Cell Division

Prokaryotes such as bacteria propagate by binary fission. For unicellular organisms, cell division is the only method 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.

To achieve the outcome of identical daughter cells, some steps are essential. The genomic DNA must be replicated and then allocated into the daughter cells; the cytoplasmic contents must also be divided to give both new cells the machinery to sustain life. In bacterial cells, the genome consists of a single, circular DNA chromosome; therefore, the process of cell division is simplified. Mitosis is unnecessary because there is no nucleus or multiple chromosomes. This type of cell division is called binary fission.

Binary Fission

The cell division process of prokaryotes, called binary fission, is a less complicated and much quicker process than cell division in eukaryotes. Because of the speed of bacterial cell division, populations of bacteria can grow very rapidly. The single, circular DNA chromosome of bacteria is not enclosed in a nucleus, but instead occupies a specific location, the nucleoid, within the cell. As in eukaryotes, the DNA of the nucleoid is associated with proteins that aid in packaging the molecule into a compact size. The packing proteins of bacteria are, however, related to some of the proteins involved in the chromosome compaction of eukaryotes.

The starting point of replication, the origin, is close to the binding site of the chromosome to the plasma membrane (Figure 6.4.1). Replication of the DNA is bidirectional—moving away from the origin on both strands of the DNA loop simultaneously. As the new double strands are formed, each origin point moves away from the cell-wall attachment toward 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. A septum is formed between the nucleoids from the periphery toward the center of the cell. When the new cell walls are in place, the daughter cells separate.

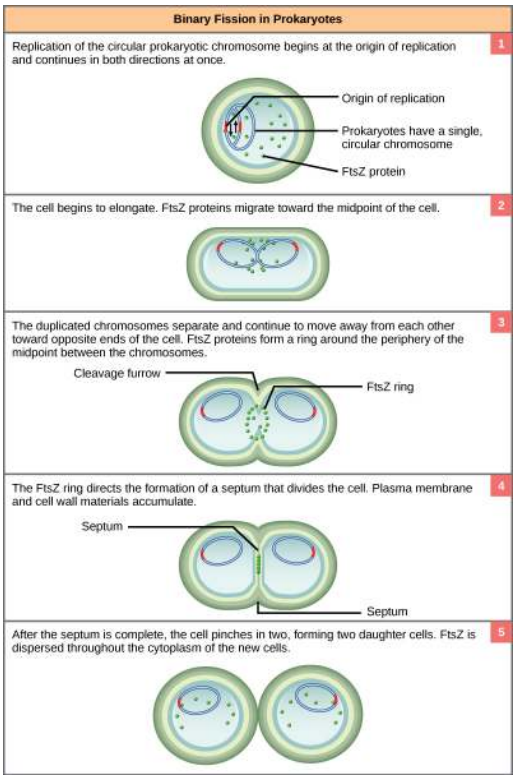


Figure 6.4.1**:** The binary fission of a bacterium is outlined in five steps. (credit: modification of work by “Mcstrother”/Wikimedia Commons)

EVOLUTION IN ACTION: 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 mitosis 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. The formation of a ring composed of repeating units of a protein called FtsZ directs the partition between the nucleoids in prokaryotes. 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. FtsZ proteins can form filaments, rings, and other three-dimensional structures resembling the way tubulin forms microtubules, centrioles, and various cytoskeleton 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 an example of homology, structures derived from the same evolutionary origins. In this example, FtsZ is presumed to be similar to the ancestor protein to both the modern FtsZ and tubulin. While both proteins are found in extant organisms, tubulin function has evolved and diversified tremendously since the evolution from its FtsZ-like prokaryotic origin. A survey of cell-division machinery in present-day unicellular eukaryotes reveals crucial intermediary steps to the complex mitotic machinery of multicellular eukaryotes (Table 6.4.1).

Table 6.4.1**:** Mitotic Spindle Evolution

	Structure of genetic material	Division of nuclear material	Separation of daughter cells
Prokaryotes	There is no nucleus. The single, circular chromosome exists in a region of cytoplasm called the nucleoid.	Occurs through binary fission. As the chromosome is replicated, the two copies move to opposite ends of the cell by an unknown mechanism.	FtsZ proteins assemble into a ring that pinches the cell in two.
Some protists	Linear chromosomes exist in the nucleus.	Chromosomes attach to the nuclear envelope, which remains intact. The mitotic spindle passes through the envelope and elongates the cell. No centrioles exist.	Microfilaments form a cleavage furrow that pinches the cell in two.
Other protists	Linear chromosomes exist in the nucleus.	A mitotic spindle forms from the centrioles and passes through the nuclear membrane, which remains intact. Chromosomes attach to the mitotic spindle. The mitotic spindle separates the chromosomes and elongates the cell.	Microfilaments form a cleavage furrow that pinches the cell in two.
Animal cells	Linear chromosomes exist in the nucleus.	A mitotic spindle forms from the centrioles. The nuclear envelope dissolves. Chromosomes attach to the mitotic spindle, which separates them and elongates the cell.	Microfilaments form a cleavage furrow that pinches the cell in two.

Summary

In both prokaryotic and eukaryotic cell division, the genomic DNA is replicated and each copy is allocated into a daughter cell. The cytoplasmic contents are also divided evenly to the new cells. However, there are many differences between prokaryotic and eukaryotic cell division. Bacteria have a single, circular DNA chromosome and no nucleus. Therefore, mitosis is not necessary in bacterial cell division. Bacterial cytokinesis is directed by a ring composed of a protein called FtsZ. Ingrowth of membrane and cell-wall material from the periphery of the cells results in a septum that eventually forms the separate cell walls of the daughter cells.

Glossary

binary fission
: the process of prokaryotic cell division

FtsZ
: a tubulin-like protein component of the prokaryotic cytoskeleton that is important in prokaryotic cytokinesis (name origin: **F**ilamenting **t**emperature-**s**ensitive mutant **Z**)

origin
: the region of the prokaryotic chromosome at which replication begins

septum
: a wall formed between bacterial daughter cells as a precursor to cell separation

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6.5: Sexual Reproduction

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

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

EVOLUTION IN ACTION: The Red Queen Hypothesis

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

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

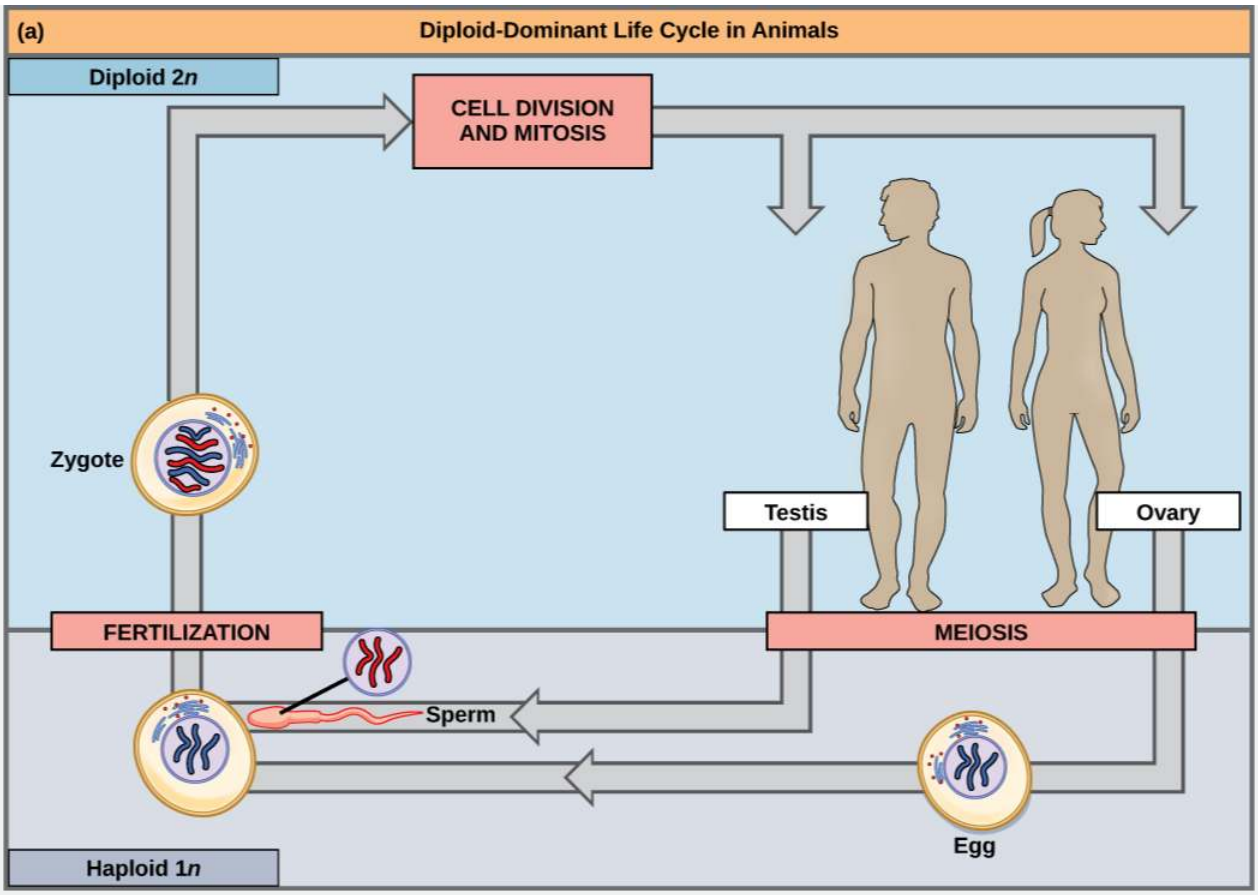
Each tiny advantage gained by favorable variation gives a species an edge over close competitors, predators, parasites, or even prey. The only method that will allow a coevolving species to keep its own share of the resources is also to continually improve its ability to survive and produce offspring.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

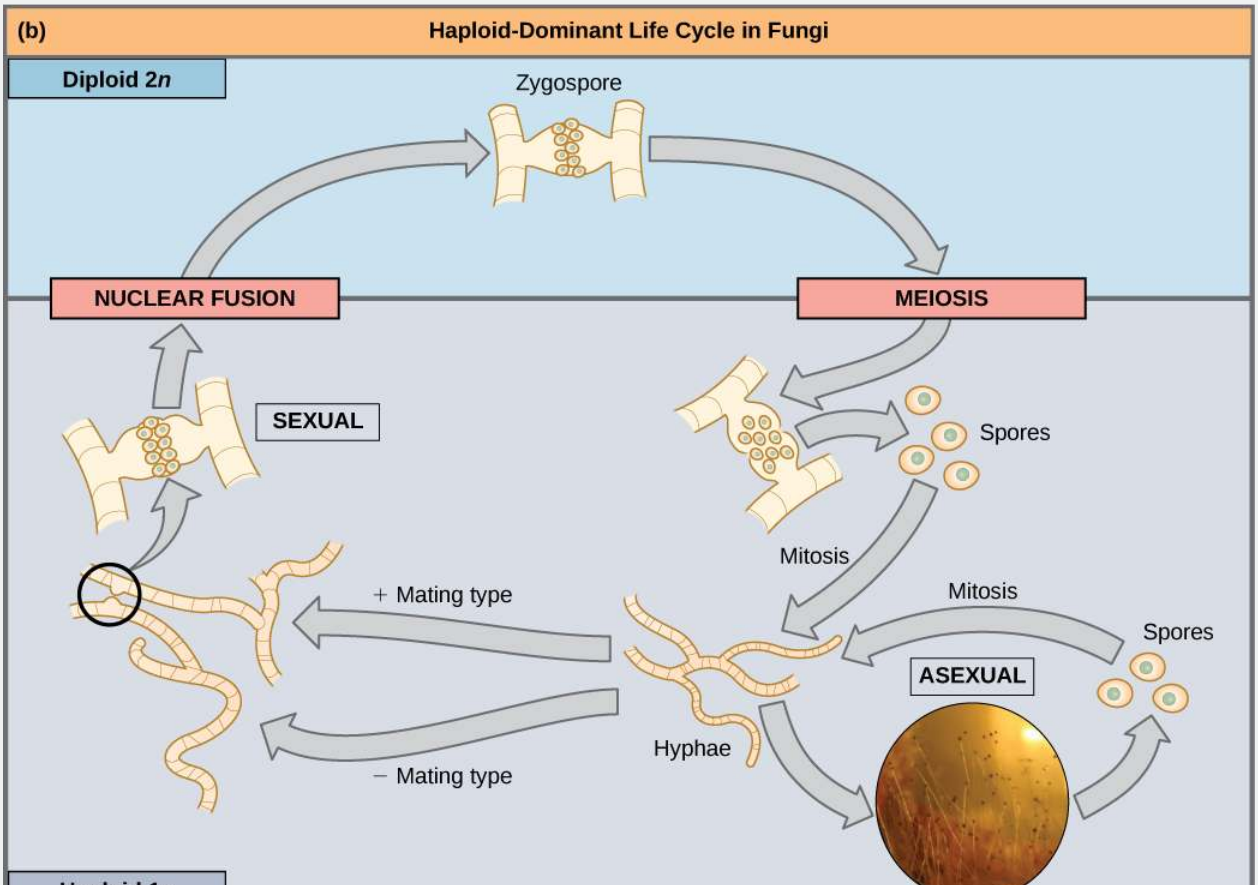
Life Cycles of Sexually Reproducing Organisms

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

Nearly all animals employ a diploid-dominant life-cycle strategy in which the only haploid cells produced by the organism are the gametes. The gametes are produced from diploid germ cells, a special cell line that only produces gametes. Once the haploid gametes are formed, they lose the ability to divide again. There is no multicellular haploid life stage. Fertilization occurs with the fusion of two gametes, usually from different individuals, restoring the diploid state (Figure 6.5.1**a**).

ART CONNECTION


(a)
Diploid-Dominant Life Cycle in Animals
Diploid 2n
CELL DIVISION AND MITOSIS
Zygote
Testis
Ovary
FERTILIZATION
MEIOSIS
Sperm
Egg
Haploid 1n


(b)
Haploid-Dominant Life Cycle in Fungi
Diploid 2n
Zygospore
NUCLEAR FUSION
MEIOSIS
SEXUAL
Spores
Mitosis
+ Mating type
Mitosis
Spores
ASEXUAL
Hyphae
− Mating type

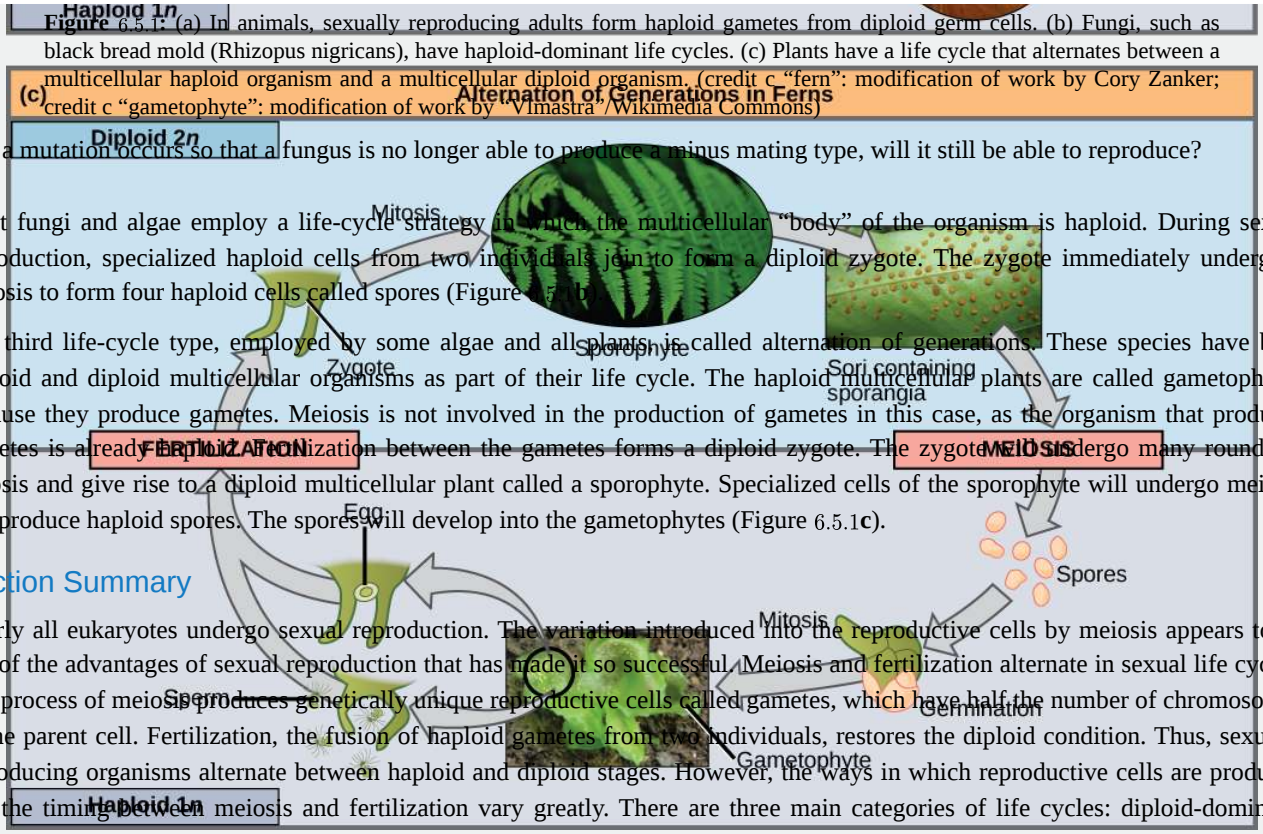


Figure 6.5.1: (a) In animals, sexually reproducing adults form haploid gametes from diploid germ cells. (b) Fungi, such as black bread mold (Rhizopus nigricans), have haploid-dominant life cycles. (c) Plants have a life cycle that alternates between a multicellular haploid organism and a multicellular diploid organism. (credit c "fern": modification of work by Cory Zanker; credit c "gametophyte": modification of work by "Vlmastra"/Wikimedia Commons)

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

Most fungi and algae employ a life-cycle strategy in which the multicellular "body" of the organism is haploid. During sexual reproduction, specialized haploid cells from two individuals join to form a diploid zygote. The zygote immediately undergoes meiosis to form four haploid cells called spores (Figure 6.5.1b).

The third life-cycle type, employed by some algae and all plants, is called alternation of generations. These species have both haploid and diploid multicellular organisms as part of their life cycle. The haploid multicellular plants are called gametophytes because they produce gametes. Meiosis is not involved in the production of gametes in this case, as the organism that produces gametes is already haploid. Fertilization between the gametes forms a diploid zygote. The zygote will undergo many rounds of mitosis and give rise to a diploid multicellular plant called a sporophyte. Specialized cells of the sporophyte will undergo meiosis and produce haploid spores. The spores will develop into the gametophytes (Figure 6.5.1c).

Section Summary

Nearly all eukaryotes undergo sexual reproduction. The variation introduced into the reproductive cells by meiosis appears to be one of the advantages of sexual reproduction that has made it so successful. Meiosis and fertilization alternate in sexual life cycles. The process of meiosis produces genetically unique reproductive cells called gametes, which have half the number of chromosomes as the parent cell. Fertilization, the fusion of haploid gametes from two individuals, restores the diploid condition. Thus, sexually reproducing organisms alternate between haploid and diploid stages. However, the ways in which reproductive cells are produced and the timing between meiosis and fertilization vary greatly. There are three main categories of life cycles: diploid-dominant, demonstrated by most animals; haploid-dominant, demonstrated by all fungi and some algae; and alternation of generations, demonstrated by plants and some algae.

Art Connections

Figure 6.5.1: If a mutation occurs so that a fungus is no longer able to produce a minus mating type, will it still be able to reproduce?

Answer

Yes, it will be able to reproduce asexually.

Footnotes

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

Glossary

alternation of generations

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

diploid-dominant

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

haploid-dominant

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

gametophyte

a multicellular haploid life-cycle stage that produces gametes

germ cell

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

life cycle

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

meiosis

a nuclear division process that results in four haploid cells

sporophyte

a multicellular diploid life-cycle stage that produces spores

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6.6: Meiosis

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

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

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

Interphase

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

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

Meiosis I

Early in prophase I, the chromosomes can be seen clearly microscopically. As the nuclear envelope begins to break down, the proteins associated with homologous chromosomes bring the pair close to each other. The tight pairing of the homologous chromosomes is called synapsis. In synapsis, the genes on the chromatids of the homologous chromosomes are precisely aligned with each other. An exchange of chromosome segments between non-sister homologous chromatids occurs and is called crossing over. This process is revealed visually after the exchange as chiasmata (singular = *chiasma*) (Figure 6.6.1).

As prophase I progresses, the close association between homologous chromosomes begins to break down, and the chromosomes continue to condense, although the homologous chromosomes remain attached to each other at chiasmata. The number of chiasmata varies with the species and the length of the chromosome. At the end of prophase I, the pairs are held together only at chiasmata (Figure 6.6.1) and are called tetrads because the four sister chromatids of each pair of homologous chromosomes are now visible.

The crossover events are the first source of genetic variation produced by meiosis. A single crossover event between homologous non-sister chromatids leads to a reciprocal exchange of equivalent DNA between a maternal chromosome and a paternal chromosome. Now, when that sister chromatid is moved into a gamete, it will carry some DNA from one parent of the individual

and some DNA from the other parent. The recombinant sister chromatid has a combination of maternal and paternal genes that did not exist before the crossover.

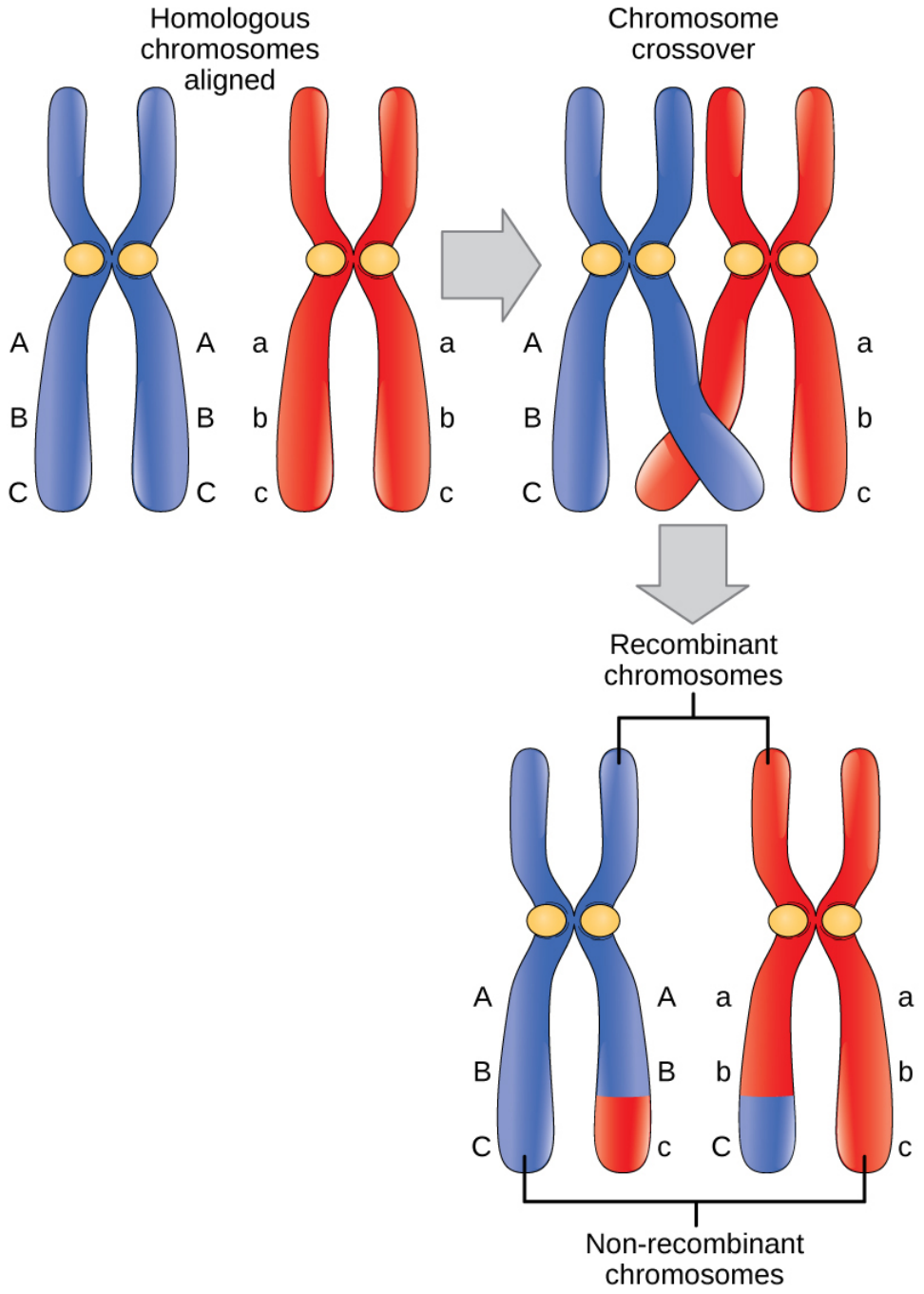


Figure 6.6.1**:** In this illustration of the effects of crossing over, the blue chromosome came from the individual's father and the red chromosome came from the individual's mother. Crossover occurs between non-sister chromatids of homologous chromosomes. The result is an exchange of genetic material between homologous chromosomes. The chromosomes that have a mixture of maternal and paternal sequence are called recombinant and the chromosomes that are completely paternal or maternal are called non-recombinant.

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

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

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

In each cell that undergoes meiosis, the arrangement of the tetrads is different. The number of variations depends on the number of chromosomes making up a set. There are two possibilities for orientation (for each tetrad); thus, the possible number of alignments equals 2^n where n is the number of chromosomes per set. Humans have 23 chromosome pairs, which results in over eight million (2^{23}) possibilities. This number does not include the variability previously created in the sister chromatids by crossover. Given these two mechanisms, it is highly unlikely that any two haploid cells resulting from meiosis will have the same genetic composition (Figure 6.6.2).

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

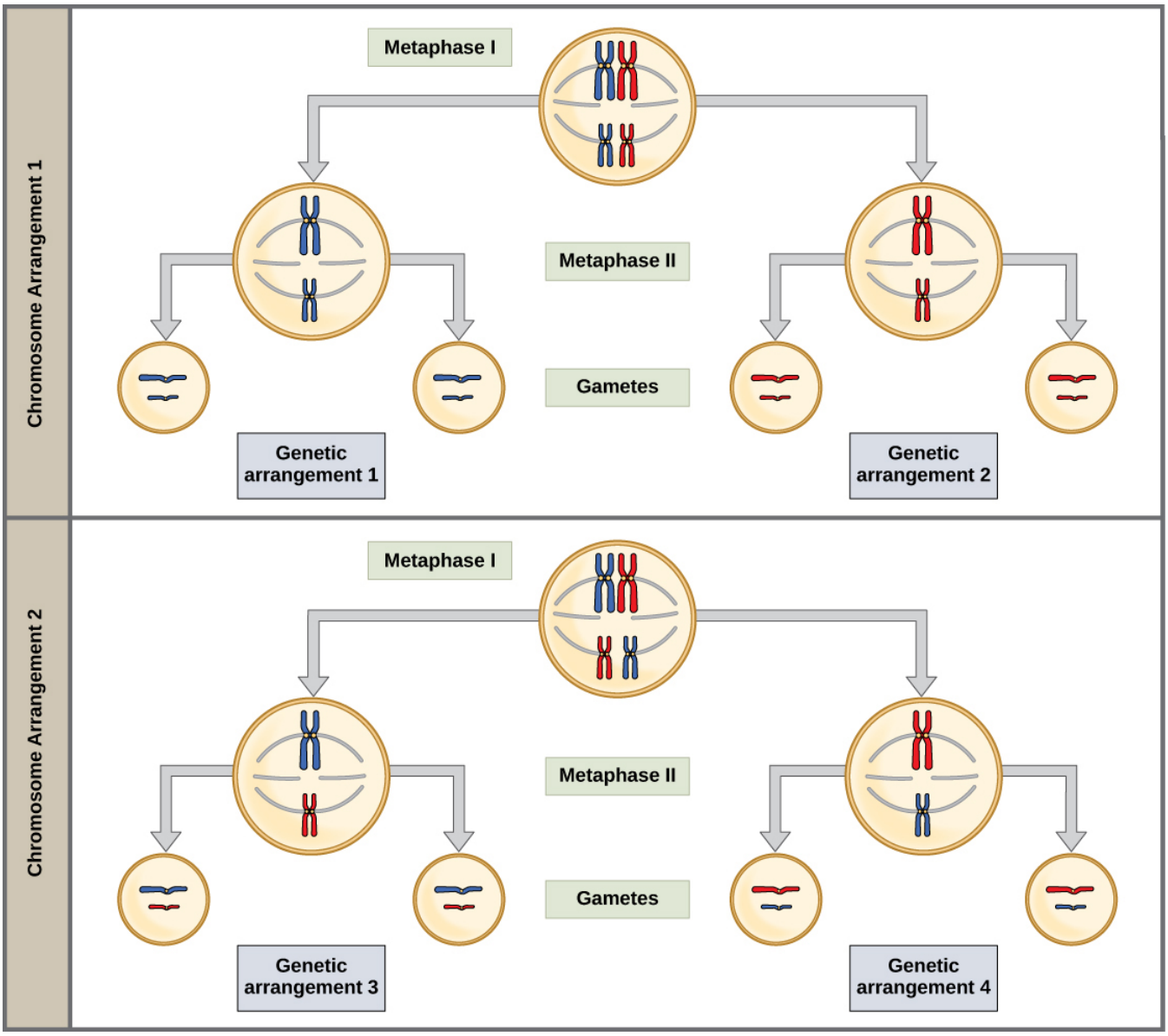


Figure 6.6.2**:** To demonstrate random, independent assortment at metaphase I, consider a cell with n = 2. In this case, there are two possible arrangements at the equatorial plane in metaphase I, as shown in the upper cell of each panel. These two possible orientations lead to the production of genetically different gametes. With more chromosomes, the number of possible arrangements increases dramatically.

In anaphase I, the spindle fibers pull the linked chromosomes apart. The sister chromatids remain tightly bound together at the centromere. It is the chiasma connections that are broken in anaphase I as the fibers attached to the fused kinetochores pull the homologous chromosomes apart (Figure 6.6.3).

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

Cytokinesis, the physical separation of the cytoplasmic components into two daughter cells, occurs without reformation of the nuclei in other organisms. In nearly all species, cytokinesis separates the cell contents by either a cleavage furrow (in animals and some fungi), or a cell plate that will ultimately lead to formation of cell walls that separate the two daughter cells (in plants). At each pole, there is just one member of each pair of the homologous chromosomes, so only one full set of the chromosomes is present. This is why the cells are considered haploid—there is only one chromosome set, even though there are duplicate copies of

the set because each homolog still consists of two sister chromatids that are still attached to each other. However, although the sister chromatids were once duplicates of the same chromosome, they are no longer identical at this stage because of crossovers.

CONCEPT IN ACTION



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

Meiosis II

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

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

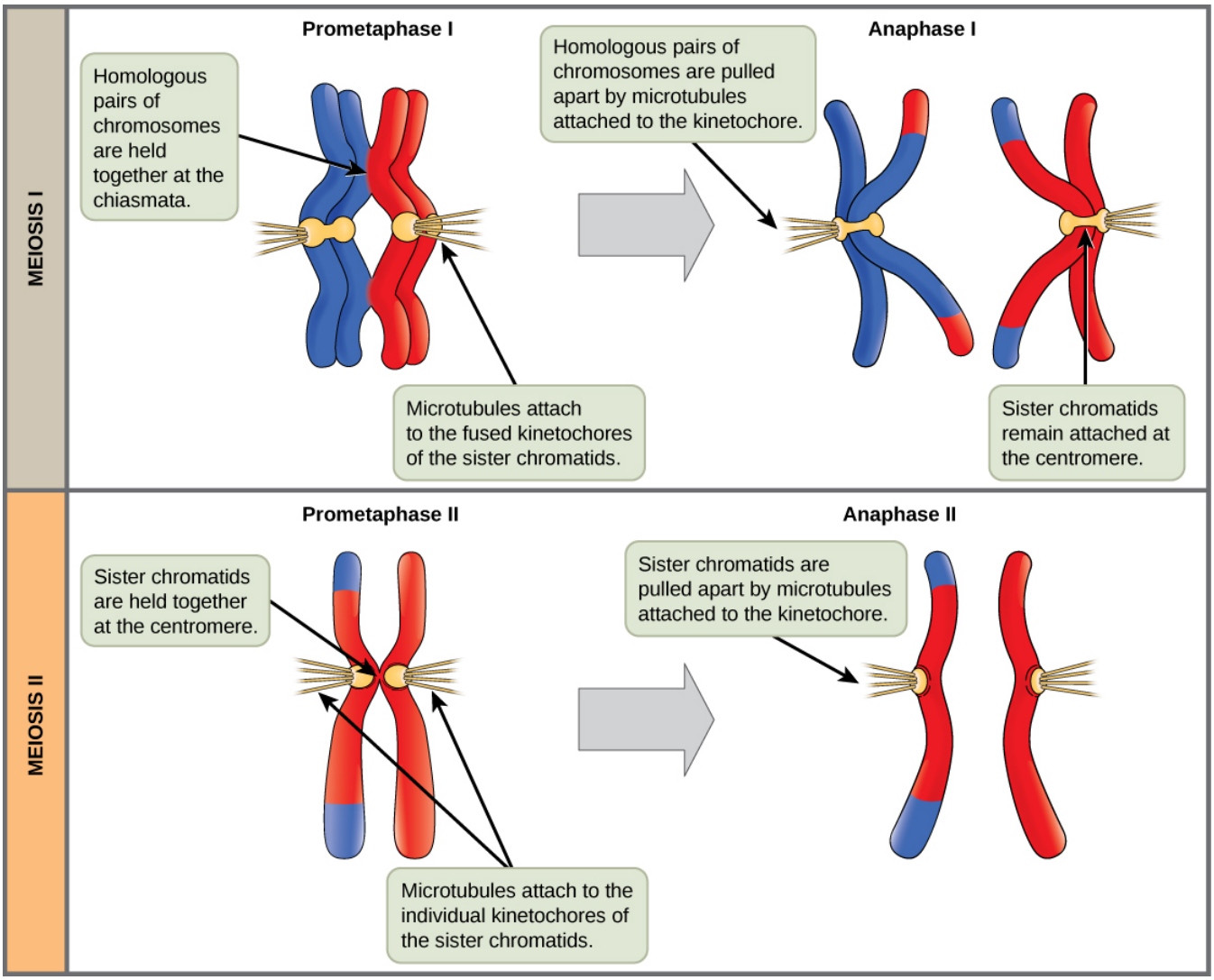


Figure 6.6.3**:** In prometaphase I, microtubules attach to the fused kinetochores of homologous chromosomes. In anaphase I, the homologous chromosomes are separated. In prometaphase II, microtubules attach to individual kinetochores of sister chromatids. In anaphase II, the sister chromatids are separated.

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

Comparing Meiosis and Mitosis

Mitosis and meiosis, which are both forms of division of the nucleus in eukaryotic cells, share some similarities, but also exhibit distinct differences that lead to their very different outcomes. Mitosis is a single nuclear division that results in two nuclei, usually partitioned into two new cells. The nuclei resulting from a mitotic division are genetically identical to the original. They have the same number of sets of chromosomes: one in the case of haploid cells, and two in the case of diploid cells. On the other hand, meiosis is two nuclear divisions that result in four nuclei, usually partitioned into four new cells. The nuclei resulting from meiosis are never genetically identical, and they contain one chromosome set only—this is half the number of the original cell, which was diploid (Figure 6.6.4).

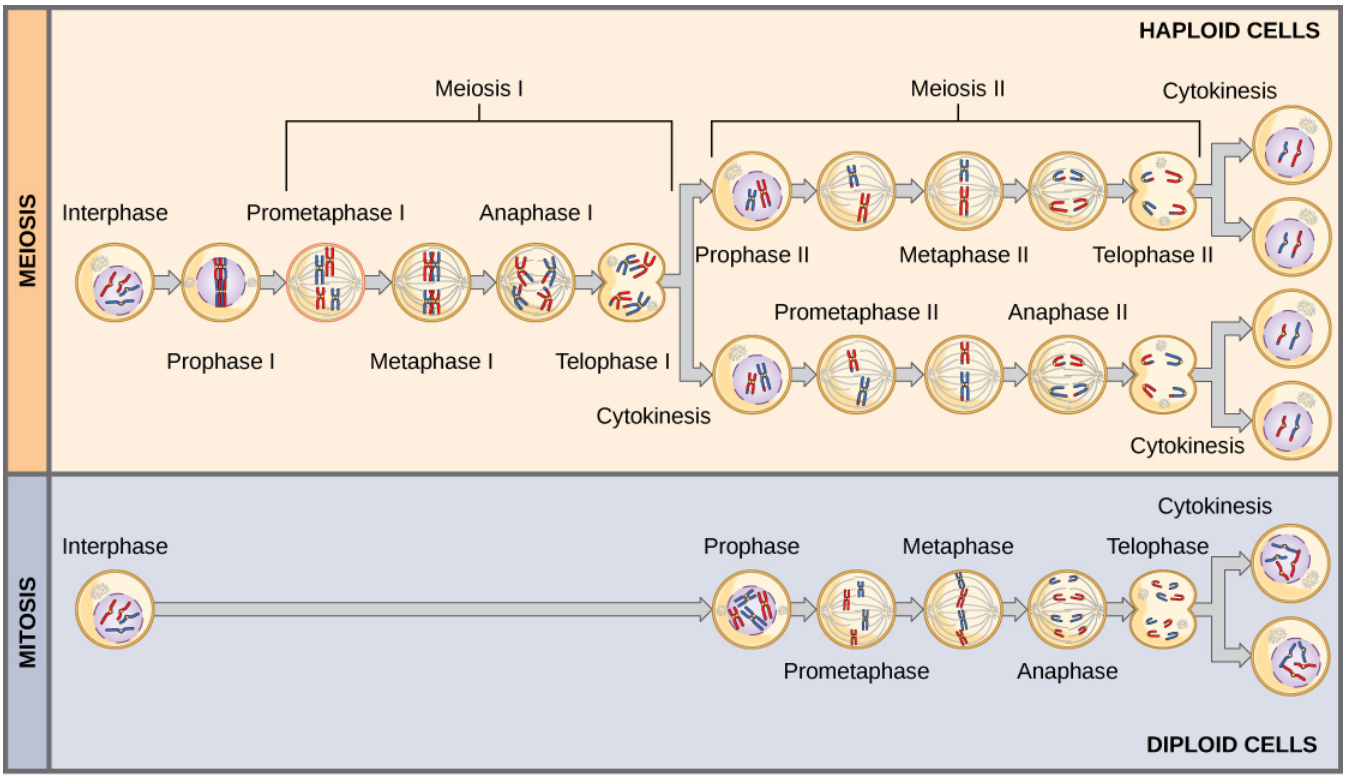
The differences in the outcomes of meiosis and mitosis occur because of differences in the behavior of the chromosomes during each process. Most of these differences in the processes occur in meiosis I, which is a very different nuclear division than mitosis.

In meiosis I, the homologous chromosome pairs become associated with each other, are bound together, experience chiasmata and crossover between sister chromatids, and line up along the metaphase plate in tetrads with spindle fibers from opposite spindle poles attached to each kinetochore of a homolog in a tetrad. All of these events occur only in meiosis I, never in mitosis.

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

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

Cells produced by mitosis will function in different parts of the body as a part of growth or replacing dead or damaged cells. They may even be involved in asexual reproduction in some organisms. Cells produced by meiosis in a diploid-dominant organism such as an animal will only participate in sexual reproduction.



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

Figure 6.6.4**:** Meiosis and mitosis are both preceded by one round of DNA replication; however, meiosis includes two nuclear divisions. The four daughter cells resulting from meiosis are haploid and genetically distinct. The daughter cells resulting from mitosis are diploid and identical to the parent cell.

CONCEPT IN ACTION

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

Section Summary

Sexual reproduction requires that diploid organisms produce haploid cells that can fuse during fertilization to form diploid offspring. The process that results in haploid cells is called meiosis. Meiosis is a series of events that arrange and separate

chromosomes into daughter cells. During the interphase of meiosis, each chromosome is duplicated. In meiosis, there are two rounds of nuclear division resulting in four nuclei and usually four haploid daughter cells, each with half the number of chromosomes as the parent cell. During meiosis, variation in the daughter nuclei is introduced because of crossover in prophase I and random alignment at metaphase I. The cells that are produced by meiosis are genetically unique.

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

Glossary

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

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

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

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

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

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

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

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

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

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

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

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6.7: Errors in Meiosis

Inherited disorders can arise when chromosomes behave abnormally during meiosis. Chromosome disorders can be divided into two categories: abnormalities in chromosome number and chromosome structural rearrangements. Because even small segments of chromosomes can span many genes, chromosomal disorders are characteristically dramatic and often fatal.

Disorders in Chromosome Number

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, including their length, banding pattern, and centromere position. 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 (Figure 6.7.1).

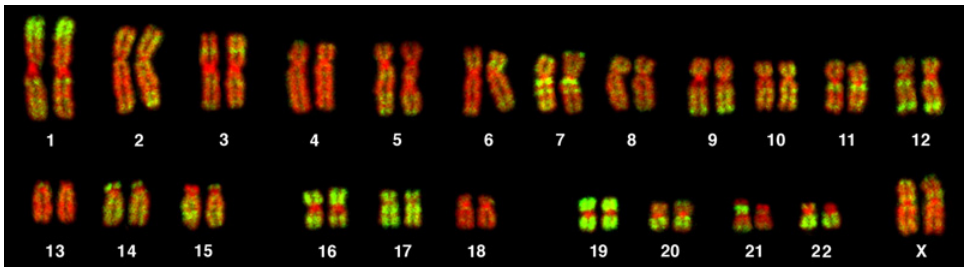


Figure 6.7.1**:** This karyogram shows the chromosomes of a female human immune cell during mitosis. (credit: Andreas Bolzer, et al)

CAREERS IN ACTION: Geneticists Use Karyograms to Identify Chromosomal Aberrations

The karyotype is a method by 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 is then applied to the cells to arrest mitosis during metaphase. The cells are then fixed 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, chromosomes are viewed using bright-field microscopy. An experienced cytogeneticist can identify each band. 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 6.7.1).

At its most basic, the karyogram 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 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.

By observing a karyogram, geneticists can actually visualize the chromosomal composition of an individual to confirm or predict genetic abnormalities in offspring even before birth.

Nondisjunctions, Duplications, and Deletions

Of all the chromosomal disorders, abnormalities in chromosome number are the most easily identifiable from a karyogram. Disorders of chromosome number include the duplication or loss of entire chromosomes, as well as changes in the number of complete sets of chromosomes. They are caused by nondisjunction, which occurs when pairs of homologous chromosomes or sister chromatids fail to separate during meiosis. The risk of nondisjunction increases with the age of the parents.

Nondisjunction can occur during either meiosis I or II, with different results (Figure 6.7.2). If homologous chromosomes fail to separate during meiosis I, the result is two gametes that lack that 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.

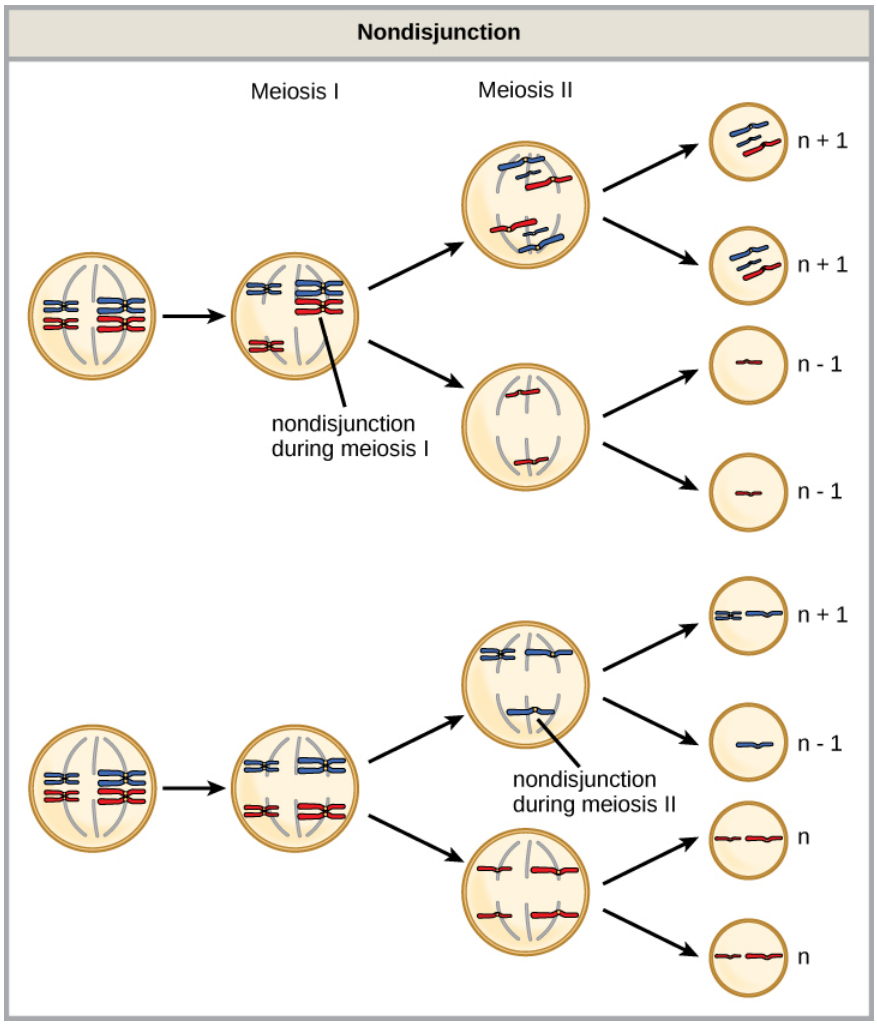


Figure 6.7.2**:** Following meiosis, each gamete has one copy of each chromosome. Nondisjunction occurs when homologous chromosomes (meiosis I) or sister chromatids (meiosis II) fail to separate during meiosis.

An individual with the appropriate number of chromosomes for their species is called euploid; in humans, euploidy corresponds to 22 pairs of autosomes and one pair of sex chromosomes. An individual with an error in chromosome number is described as aneuploid, a term that includes monosomy (loss of one chromosome) or trisomy (gain of an extraneous chromosome). Monosomic human zygotes missing any one copy of an autosome invariably fail to develop to birth because they have only one copy of essential genes. Most autosomal trisomies also fail to develop to birth; however, duplications of some of the smaller chromosomes (13, 15, 18, 21, or 22) can result in offspring that survive for several weeks to many years. Trisomic individuals suffer from a different type of genetic imbalance: an excess in gene dose. Cell functions are calibrated to the amount of gene product produced by two copies (doses) of each gene; adding a third copy (dose) disrupts this balance. The most common trisomy is that of chromosome 21, which leads to Down syndrome. Individuals with this inherited disorder have characteristic physical features and developmental delays in growth and cognition. The incidence of Down syndrome is correlated with maternal age, such that older women are more likely to give birth to children with Down syndrome (Figure 6.7.3).

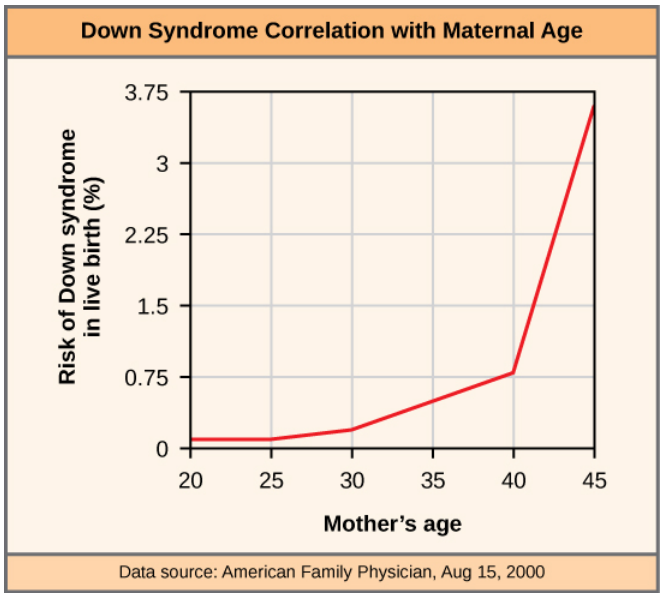


Figure 6.7.3**:** The incidence of having a fetus with trisomy 21 increases dramatically with maternal age.

CONCEPT IN ACTION



Visualize the addition of a chromosome that leads to Down syndrome in this video simulation.

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. In part, this occurs because of a process called X inactivation. Early in development, when female mammalian embryos consist of just a few thousand cells, one X chromosome in each cell inactivates by condensing into a structure called a Barr body. The genes on the inactive X chromosome are not expressed. The particular X chromosome (maternally or paternally derived) that is inactivated in each cell is random, but once the inactivation occurs, all cells descended from that cell will have the same inactive X chromosome. By this process, females compensate for their double genetic dose of X chromosome.

In so-called "tortoiseshell" cats, X inactivation is observed as coat-color variegation (Figure 6.7.4). Females heterozygous for an X-linked coat color gene will express one of two different coat colors over different regions of their body, corresponding to whichever X chromosome is inactivated in the embryonic cell progenitor of that region. When you see a tortoiseshell cat, you will know that it has to be a female.



Figure 6.7.4**:** Embryonic inactivation of one of two different X chromosomes encoding different coat colors gives rise to the tortoiseshell phenotype in cats. (credit: Michael Bodega)

In an individual carrying an abnormal number of X chromosomes, cellular mechanisms will inactivate all but one X in each of her cells. 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.

Several errors in sex chromosome number have been characterized. Individuals with three X chromosomes, called triplo-X, appear female but express developmental delays and reduced fertility. The XXY chromosome complement, corresponding to one type of Klinefelter syndrome, corresponds to male individuals with small testes, enlarged breasts, and reduced body hair. The extra X chromosome undergoes inactivation to compensate for the excess genetic dosage. Turner syndrome, characterized as an X0 chromosome complement (i.e., only a single sex chromosome), corresponds to a female individual with short stature, webbed skin in the neck region, hearing and cardiac impairments, and sterility.

An individual with more than the correct number of chromosome sets (two for diploid species) is called polyploid. For instance, fertilization of an abnormal diploid egg with a normal haploid sperm would yield a triploid zygote. Polyploid animals are extremely rare, with only a few examples among the flatworms, crustaceans, amphibians, fish, and lizards. Triploid animals are sterile because meiosis cannot proceed normally with an odd number of chromosome sets. In contrast, polyploidy is very common in the plant kingdom, and polyploid plants tend to be larger and more robust than euploids of their species.

Chromosome Structural Rearrangements

Cytologists have characterized numerous structural rearrangements in chromosomes, including partial duplications, deletions, inversions, and translocations. Duplications and deletions often produce offspring that survive but exhibit physical and mental abnormalities. Cri-du-chat (from the French for “cry of the cat”) is a syndrome associated with nervous system abnormalities and identifiable physical features that results from a deletion of most of the small arm of chromosome 5 (Figure 6.7.5). Infants with this genotype emit a characteristic high-pitched cry upon which the disorder’s name is based.

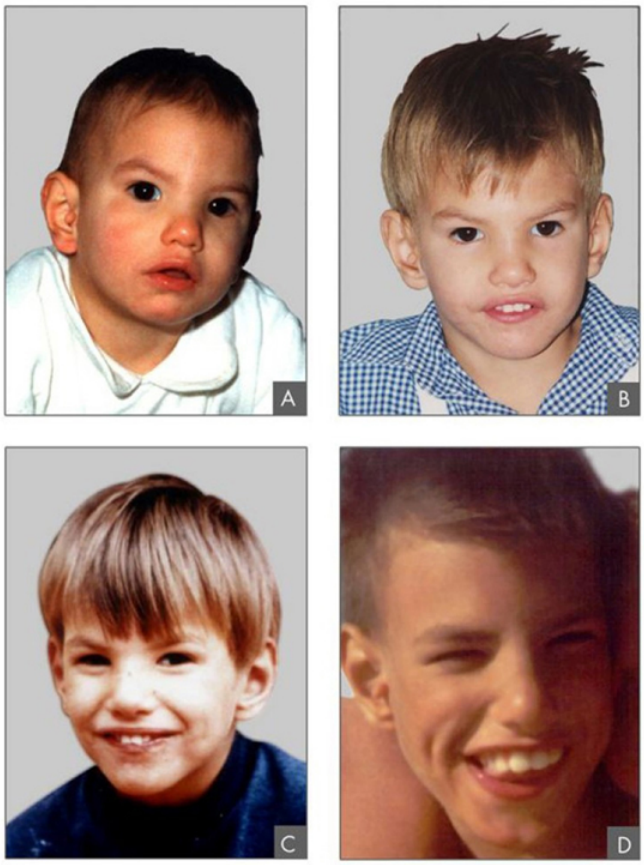


Figure 6.7.5**:** This individual with cri-du-chat syndrome is shown at various ages: (A) age two, (B) age four, (C) age nine, and (D) age 12. (credit: Paola Cerruti Mainardi)

Chromosome inversions and translocations can be identified by observing cells during meiosis because homologous chromosomes with a rearrangement in one of the pair must contort to maintain appropriate gene alignment and pair effectively during prophase I.

A chromosome inversion is the detachment, 180° rotation, and reinsertion of part of a chromosome (Figure 6.7.6). Unless they disrupt a gene sequence, inversions only change the orientation of genes and are likely to have more mild effects than aneuploid errors.

EVOLUTION IN ACTION: The Chromosome 18 Inversion

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, an 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.

The 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 have suggested that a long stretch of DNA was duplicated on chromosome 18 of an ancestor to humans, but that during the duplication it was inverted (inserted into the chromosome in reverse orientation.

A comparison of human and chimpanzee genes in the region of this inversion indicates that two genes—*ROCK1* and *USP14*—are farther apart on human chromosome 18 than they are on the corresponding chimpanzee chromosome. 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* code for 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.[1]

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 6.7.6).

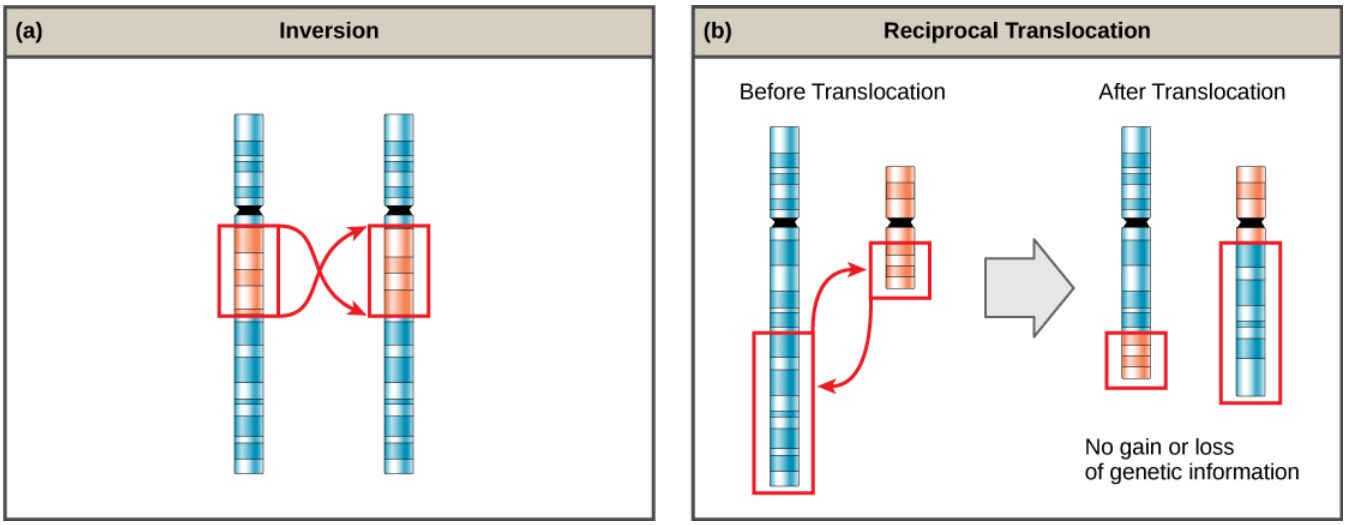


Figure 6.7.6: An (a) inversion occurs when a chromosome segment breaks from the chromosome, reverses its orientation, and then reattaches in the original position. A (b) reciprocal translocation occurs between two nonhomologous chromosomes and does not cause any genetic information to be lost or duplicated. (credit: modification of work by National Human Genome Research Institute (USA)

Section Summary

The number, size, shape, and banding pattern of chromosomes make them easily identifiable in a karyogram and allow for the assessment of many chromosomal abnormalities. Disorders in chromosome number, or aneuploidies, are typically lethal to the embryo, although a few trisomic genotypes are viable. Because of X inactivation, aberrations in sex chromosomes typically have milder effects on an individual. Aneuploidies also include instances in which segments of a chromosome are duplicated or deleted. Chromosome structures also may be rearranged, for example by inversion or translocation. Both of these aberrations can result in negative effects on development, or death. Because they force chromosomes to assume contorted pairings during meiosis I, inversions and translocations are often associated with reduced fertility because of the likelihood of nondisjunction.

Footnotes

1. 1 V Goidts, et al., “Segmental duplication associated with the human-specific inversion of chromosome 18: a further example of the impact of segmental duplications on karyotype and genome evolution in primates,” *Human Genetics*, 115 (2004):116–22.

Glossary

aneuploid
an individual with an error in chromosome number; includes deletions and duplications of chromosome segments

autosome
any of the non-sex chromosomes

chromosome inversion
the detachment, 180° rotation, and reinsertion of a chromosome arm

euploid
an individual with the appropriate number of chromosomes for their species

karyogram

the photographic image of a karyotype

karyotype
the number and appearance of an individuals chromosomes, including the size, banding patterns, and centromere position

monosomy
an otherwise diploid genotype in which one chromosome is missing

nondisjunction
the failure of synapsed homologs to completely separate and migrate to separate poles during the first cell division of meiosis

polyploid
an individual with an incorrect number of chromosome sets

translocation
the process by which one segment of a chromosome dissociates and reattaches to a different, nonhomologous chromosome

trisomy
an otherwise diploid genotype in which one entire chromosome is duplicated

X inactivation
the condensation of X chromosomes into Barr bodies during embryonic development in females to compensate for the double genetic dose

Contributors and Attributions

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6.A: Reproduction at the Cellular Level (Exercises)

The Genome

Prokaryotes have a single loop chromosome, whereas eukaryotes have multiple, linear chromosomes surrounded by a nuclear membrane. Human somatic cells have 46 chromosomes consisting of two sets of 22 homologous chromosomes and a pair of nonhomologous sex chromosomes. This is the 2*n*, or diploid, state. Human gametes have 23 chromosomes or one complete set of chromosomes. This is the *n*, or haploid, state. Genes are segments of DNA that code for a specific protein or RNA molecule.

Multiple Choice

A diploid cell has _____ the number of chromosomes as a haploid cell.

A. one-fourth
B. one-half
C. twice
D. four times

Answer

C

An organism's traits are determined by the specific combination of inherited _____.

A. cells
B. genes
C. proteins
D. chromatids

Answer

B

Free Response

Compare and contrast a human somatic cell to a human gamete.

Answer

Human somatic cells have 46 chromosomes, including 22 homologous pairs and one pair of nonhomologous sex chromosomes. This is the 2*n*, or diploid, condition. Human gametes have 23 chromosomes, one each of 23 unique chromosomes. This is the *n*, or haploid, condition.

The Cell Cycle

The cell cycle is an orderly sequence of events. Cells on the path to cell division proceed through a series of precisely timed and carefully regulated stages. In eukaryotes, the cell cycle consists of a long preparatory period, called interphase. Interphase is divided into G1, S, and G2 phases. Mitosis consists of five stages: prophase, prometaphase, metaphase, anaphase, and telophase. Mitosis is usually accompanied by cytokinesis.

Multiple Choice

Chromosomes are duplicated during what portion of the cell cycle?

A. G_1 phase
B. S phase
C. prophase
D. prometaphase

Answer

B

Separation of the sister chromatids is a characteristic of which stage of mitosis?

A. prometaphase
B. metaphase
C. anaphase
D. telophase

Answer

C

The individual chromosomes become visible with a light microscope during which stage of mitosis?

A. prophase
B. prometaphase
C. metaphase
D. anaphase

Answer

A

What is necessary for a cell to pass the G_2 checkpoint?

A. cell has reached a sufficient size
B. an adequate stockpile of nucleotides
C. accurate and complete DNA replication
D. proper attachment of mitotic spindle fibers to kinetochores

Answer

C

Free Response

Describe the similarities and differences between the cytokinesis mechanisms found in animal cells versus those in plant cells.

Answer

There are very few similarities between animal cell and plant cell cytokinesis. In animal cells, a ring of actin fibers is formed around the periphery of the cell at the former metaphase plate. The actin ring contracts inward, pulling the plasma membrane toward the center of the cell until the cell is pinched in two. In plant cells, a new cell wall must be formed between the daughter cells. Because of the rigid cell walls of the parent cell, contraction of the middle of the cell is not possible. Instead, a cell plate is formed in the center of the cell at the former metaphase plate. The cell plate is formed from Golgi vesicles that contain enzymes, proteins, and glucose. The vesicles fuse and the enzymes build a new cell wall from the proteins and glucose. The cell plate grows toward, and eventually fuses with, the cell wall of the parent cell.

Prokaryotic Cell Division

In both prokaryotic and eukaryotic cell division, the genomic DNA is replicated and each copy is allocated into a daughter cell. The cytoplasmic contents are also divided evenly to the new cells. However, there are many differences between prokaryotic and eukaryotic cell division. Bacteria have a single, circular DNA chromosome and no nucleus. Therefore, mitosis is not necessary in bacterial cell division. Bacterial cytokinesis is directed by a ring composed of a protein called FtsZ.

Multiple Choice

Which eukaryotic cell-cycle event is missing in binary fission?

A. cell growth
B. DNA duplication
C. mitosis
D. cytokinesis

Answer

C

FtsZ proteins direct the formation of a _____ that will eventually form the new cell walls of the daughter cells.

A. contractile ring
B. cell plate
C. cytoskeleton
D. septum

Answer

D

Free Response

Name the common components of eukaryotic cell division and binary fission.

Answer

The common components of eukaryotic cell division and binary fission are DNA duplication, segregation of duplicated chromosomes, and the division of the cytoplasmic contents.

Sexual Reproduction

Nearly all eukaryotes undergo sexual reproduction. The variation introduced into the reproductive cells by meiosis appears to be one of the advantages of sexual reproduction that has made it so successful. Meiosis and fertilization alternate in sexual life cycles. The process of meiosis produces genetically unique reproductive cells called gametes, which have half the number of chromosomes as the parent cell. Fertilization, the fusion of haploid gametes from two individuals, restores the diploid condition. Thus, sexually reproducing organisms alternate between haploid and diploid stages. However, the ways in which reproductive cells are produced and the timing between meiosis and fertilization vary greatly. There are three main categories of life cycles: diploid-dominant, demonstrated by most animals; haploid-dominant, demonstrated by all fungi and some algae; and alternation of generations, demonstrated by plants and some algae.

Multiple Choice

What is a likely evolutionary advantage of sexual reproduction over asexual reproduction?

A. sexual reproduction involves fewer steps
B. less chance of using up the resources in a given environment
C. sexual reproduction results in greater variation in the offspring
D. sexual reproduction is more cost-effective

Answer

C

Which type of life cycle has both a haploid and diploid multicellular stage?

A. an asexual life cycle
B. diploid-dominant
C. haploid-dominant
D. alternation of generations

Answer

D

Which event leads to a diploid cell in a life cycle?

A. meiosis
B. fertilization
C. alternation of generations
D. mutation

Answer

B

Free Response

Explain the advantage that populations of sexually reproducing organisms have over asexually reproducing organisms?

Answer

The offspring of sexually reproducing organisms are all genetically unique. Because of this, sexually reproducing organisms may have more successful survival of offspring in environments that change than asexually reproducing organisms, whose offspring are all genetically identical. In addition, the rate of adaptation of sexually reproducing organisms is higher, because of their increased variation. This may allow sexually reproducing organisms to adapt more quickly to competitors and parasites, who are evolving new ways to exploit or out-compete them.

Describe the two events that are common to all sexually reproducing organisms and how they fit into the different life cycles of those organisms.

Answer

The two events common to all sexually reproducing organisms are meiosis and fertilization. Meiosis reduces a diploid cell to a haploid state. The haploid cell may divide mitotically to produce an organism, some of whose cells will combine during fertilization, or the haploid cells produced by meiosis may immediately combine in fertilization to produce a diploid cell that divides to produce an organism.

Meiosis

Sexual reproduction requires that diploid organisms produce haploid cells that can fuse during fertilization to form diploid offspring. The process that results in haploid cells is called meiosis. Meiosis is a series of events that arrange and separate chromosomes into daughter cells. During the interphase of meiosis, each chromosome is duplicated. In meiosis, there are two rounds of nuclear division resulting in four nuclei and usually four haploid daughter cells, each with half the number of chromosomes as the parent cell. During meiosis, variation in the daughter nuclei is introduced because of crossover in prophase I and random alignment at metaphase I. The cells that are produced by meiosis are genetically unique.

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

Multiple Choice

Meiosis produces _____ daughter cells.

A. two haploid
B. two diploid
C. four haploid
D. four diploid

Answer

C

At which stage of meiosis are sister chromatids separated from each other?

A. prophase I
B. prophase II
C. anaphase I
D. anaphase II

Answer

D

The part of meiosis that is similar to mitosis is _____.

A. meiosis I
B. anaphase I
C. meiosis II
D. interkinesis

Answer

C

If a muscle cell of a typical organism has 32 chromosomes, how many chromosomes will be in a gamete of that same organism?

A. 8
B. 16
C. 32
D. 64

Answer

B

Free Response

Explain how the random alignment of homologous chromosomes during metaphase I contributes to variation in gametes produced by meiosis.

Answer

Random alignment leads to new combinations of traits. The chromosomes that were originally inherited by the gamete-producing individual came equally from the egg and the sperm. In metaphase I, the duplicated copies of these maternal and paternal homologous chromosomes line up across the center of the cell to form a tetrad. The orientation of each tetrad is random. There is an equal chance that the maternally derived chromosomes will be facing either pole. The same is true of the paternally derived chromosomes. The alignment should occur differently in almost every meiosis. As the homologous chromosomes are pulled apart in anaphase I, any combination of maternal and paternal chromosomes will move toward each pole. The gametes formed from these two groups of chromosomes will have a mixture of traits from the individual's parents. Each gamete is unique.

In what ways is meiosis II similar to and different from mitosis of a diploid cell?

Answer

The two divisions are similar in that the chromosomes line up along the metaphase plate individually, meaning unpaired with other chromosomes (as in meiosis I). In addition, each chromosome consists of two sister chromatids that will be pulled apart. The two divisions are different because in meiosis II there are half the number of chromosomes that are present in a diploid cell of the same species undergoing mitosis. This is because meiosis I reduced the number of chromosomes to a haploid state.

The genotype XXY corresponds to:

A. Klinefelter syndrome
B. Turner syndrome
C. Triplo-X
D. Jacob syndrome

Answer

A

Abnormalities in the number of X chromosomes tend to be milder than the same abnormalities in autosomes because of _____.

A. deletions
B. nonhomologous recombination
C. synapsis
D. X inactivation

Answer

D

Aneuploidies are deleterious for the individual because of what phenomenon?

A. nondisjunction
B. gene dosage
C. meiotic errors
D. X inactivation

Answer

B

Free Response

Individuals with trisomy 21 are more likely to survive to adulthood than individuals with trisomy 18. Based on what you know about aneuploidies from this module, what can you hypothesize about chromosomes 21 and 18?

Answer

The problems caused by trisomies arise because the genes on the chromosome that is present in three copies produce more product than genes on chromosomes with only two copies. The cell does not have a way to adjust the amount of product, and the lack of balance causes problems in development and the maintenance of the individual. Each chromosome is different, and the differences in survivability could have to do with the numbers of genes on the two chromosomes. Chromosome 21 may be a smaller chromosome, so there are fewer unbalanced gene products. It is also possible that chromosome 21 carries genes whose products are less sensitive to differences in dosage than chromosome 18. The genes may be less involved in critical pathways, or the differences in dosage may make less of a difference to those pathways.

Errors in Meiosis

The number, size, shape, and banding pattern of chromosomes make them easily identifiable in a karyogram and allow for the assessment of many chromosomal abnormalities. Disorders in chromosome number, or aneuploidies, are typically lethal to the embryo, although a few trisomic genotypes are viable. Because of X inactivation, aberrations in sex chromosomes typically have milder effects on an individual. Aneuploidies also include instances in which segments of a chromosome are duplicated or deleted. Chromosome structures also may be rearranged, for example by inversion or translocation. Both of these aberrations can result in negative effects on development, or death. Because they force chromosomes to assume contorted pairings during meiosis I, inversions and translocations are often associated with reduced fertility because of the likelihood of nondisjunction.

Multiple Choice

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D. Jacob syndrome

Answer

A

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Answer

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B. gene dosage
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Answer

Free Response

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B

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CHAPTER OVERVIEW

7: Patterns of Inheritance

7.1: Mendel’s Experiments

7.2: Laws of Inheritance

7.3: Extensions of the Laws of Inheritance

7.A: Patterns of Inheritance (Exercises)

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7.1: Mendel's Experiments

Johann Gregor Mendel (1822–1884) (Figure 7.1.1) was a lifelong learner, teacher, scientist, and man of faith. As a young adult, he joined the Augustinian Abbey of St. Thomas in Brno in what is now the Czech Republic. Supported by the monastery, he taught physics, botany, and natural science courses at the secondary and university levels. In 1856, he began a decade-long research pursuit involving inheritance patterns in honeybees and plants, ultimately settling on pea plants as his primary model system (a system with convenient characteristics that is used to study a specific biological phenomenon to gain understanding to be applied to other systems). In 1865, Mendel presented the results of his experiments with nearly 30,000 pea plants to the local natural history society. He demonstrated that traits are transmitted faithfully from parents to offspring in specific patterns. In 1866, he published his work, *Experiments in Plant Hybridization*,[1] in the proceedings of the Natural History Society of Brünn.



Figure 7.1.1**:** Johann Gregor Mendel set the framework for the study of genetics.

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

Mendel's Crosses

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

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

Plants used in first-generation crosses were called P, or parental generation, plants (Figure 7.1.2). Mendel collected the seeds produced by the P plants that resulted from each cross and grew them the following season. These offspring were called the F_1, or the first filial (filial = daughter or son), generation. Once Mendel examined the characteristics in the F_1 generation of plants, he allowed them to self-fertilize naturally. He then collected and grew the seeds from the F_1 plants to produce the F_2, or second filial, generation. Mendel's experiments extended beyond the F_2 generation to the F_3 generation, F_4 generation, and so on, but it was the ratio of characteristics in the P, F_1, and F_2 generations that were the most intriguing and became the basis of Mendel's postulates.

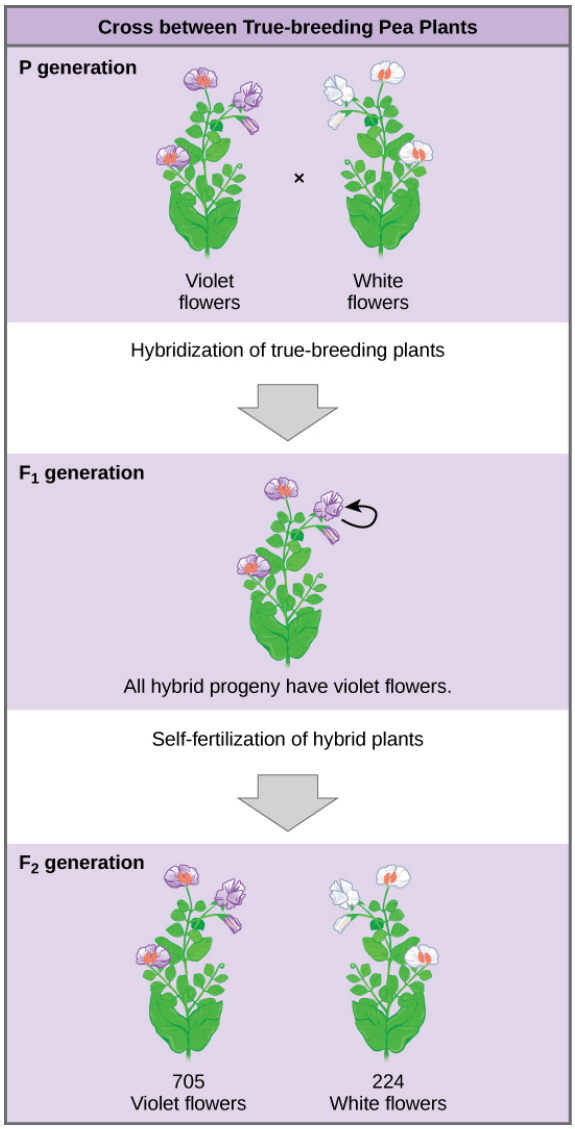


Figure 7.1.2**:** Mendel's process for performing crosses included examining flower color.

Garden Pea Characteristics Revealed the Basics of Heredity

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

What results did Mendel find in his crosses for flower color? First, Mendel confirmed that he was using plants that bred true for white or violet flower color. Irrespective of the number of generations that Mendel examined, all self-crossed offspring of parents with white flowers had white flowers, and all self-crossed offspring of parents with violet flowers had violet flowers. In addition,

Mendel confirmed that, other than flower color, the pea plants were physically identical. This was an important check to make sure that the two varieties of pea plants only differed with respect to one trait, flower color.

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

Importantly, Mendel did not stop his experimentation there. He allowed the F_1 plants to self-fertilize and found that 705 plants in the F_2 generation had violet flowers and 224 had white flowers. This was a ratio of 3.15 violet flowers to one white flower, or approximately 3:1. When Mendel transferred pollen from a plant with violet flowers to the stigma of a plant with white flowers and vice versa, he obtained approximately the same ratio irrespective of which parent—male or female—contributed which trait. This is called a reciprocal cross—a paired cross in which the respective traits of the male and female in one cross become the respective traits of the female and male in the other cross. For the other six characteristics that Mendel examined, the F_1 and F_2 generations behaved in the same way that they behaved for flower color. One of the two traits would disappear completely from the F_1 generation, only to reappear in the F_2 generation at a ratio of roughly 3:1 (Figure 7.1.3).

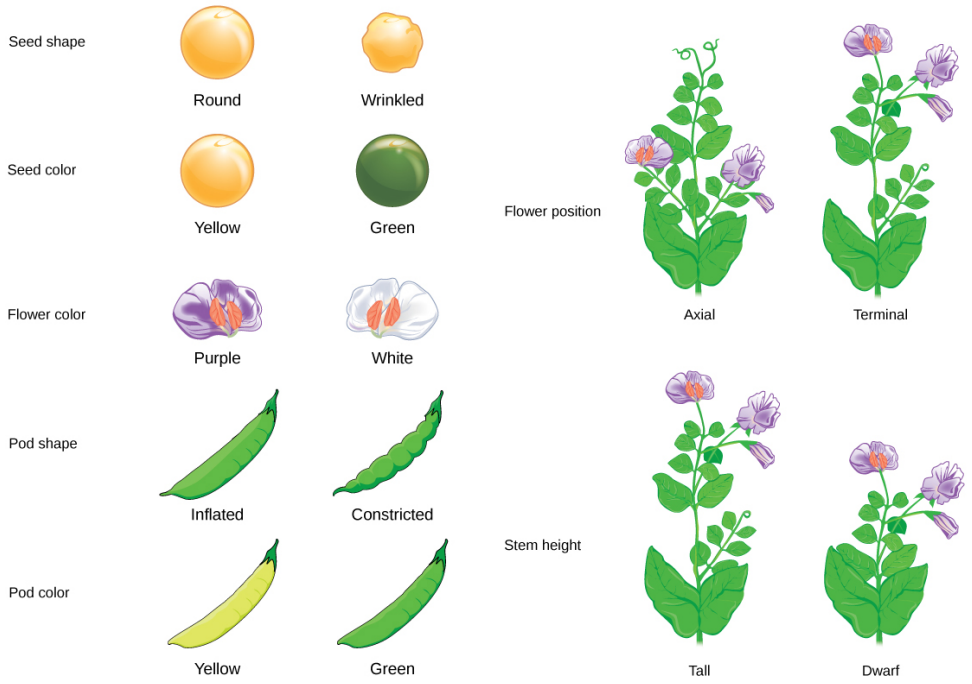


Figure 7.1.3**:** Mendel identified seven pea plant characteristics.

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

Section Summary

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

Footnotes

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

Glossary

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

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

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

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

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

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

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

P
: the parental generation in a cross

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

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

trait
: a variation in an inherited characteristic

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7.2: Laws of Inheritance

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

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

Phenotypes and Genotypes

Two alleles for a given gene in a diploid organism are expressed and interact to produce physical characteristics. The observable traits expressed by an organism are referred to as its phenotype. An organism's underlying genetic makeup, consisting of both the physically visible and the non-expressed alleles, is called its genotype. Mendel's hybridization experiments demonstrate the difference between phenotype and genotype. For example, the phenotypes that Mendel observed in his crosses between pea plants with differing traits are connected to the diploid genotypes of the plants in the P, F_1, and F_2 generations. We will use a second trait that Mendel investigated, seed color, as an example. Seed color is governed by a single gene with two alleles. The yellow-seed allele is dominant and the green-seed allele is recessive. When true-breeding plants were cross-fertilized, in which one parent had yellow seeds and one had green seeds, all of the F_1hybrid offspring had yellow seeds. That is, the hybrid offspring were phenotypically identical to the true-breeding parent with yellow seeds. However, we know that the allele donated by the parent with green seeds was not simply lost because it reappeared in some of the F_2 offspring (Figure 7.2.1). Therefore, the F_1 plants must have been genotypically different from the parent with yellow seeds.

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

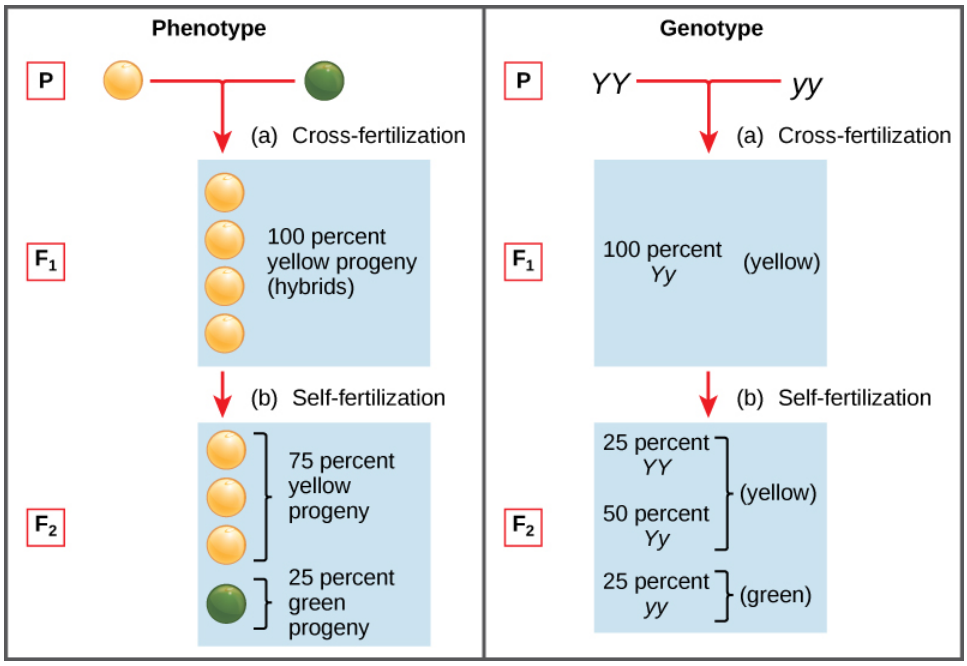


Figure 7.2.1**:** Phenotypes are physical expressions of traits that are transmitted by alleles. Capital letters represent dominant alleles and lowercase letters represent recessive alleles. The phenotypic ratios are the ratios of visible characteristics. The genotypic ratios are the ratios of gene combinations in the offspring, and these are not always distinguishable in the phenotypes.

Law of Dominance

Our discussion of homozygous and heterozygous organisms brings us to why the F_1 heterozygous offspring were identical to one of the parents, rather than expressing both alleles. In all seven pea-plant characteristics, one of the two contrasting alleles was dominant, and the other was recessive. Mendel called the dominant allele the expressed unit factor; the recessive allele was referred to as the latent unit factor. We now know that these so-called unit factors are actually genes on homologous chromosomes. For a gene that is expressed in a dominant and recessive pattern, homozygous dominant and heterozygous organisms will look identical (that is, they will have different genotypes but the same phenotype), and the recessive allele will only be observed in homozygous recessive individuals (Table 7.2.1).

Table 7.2.1***:*** Correspondence between Genotype and Phenotype for a Dominant-Recessive Characteristic.

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

Mendel's law of dominance states that in a heterozygote, one trait will conceal the presence of another trait for the same characteristic. For example, when crossing true-breeding violet-flowered plants with true-breeding white-flowered plants, all of the offspring were violet-flowered, even though they all had one allele for violet and one allele for white. Rather than both alleles contributing to a phenotype, the dominant allele will be expressed exclusively. The recessive allele will remain latent, but will be transmitted to offspring in the same manner as that by which the dominant allele is transmitted. The recessive trait will only be expressed by offspring that have two copies of this allele (Figure 7.2.2), and these offspring will breed true when self-crossed.



Figure 7.2.2**:** The allele for albinism, expressed here in humans, is recessive. Both of this child's parents carried the recessive allele.

Monohybrid Cross and the Punnett Square

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

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

To demonstrate this with a monohybrid cross, consider the case of true-breeding pea plants with yellow versus green seeds. The dominant seed color is yellow; therefore, the parental genotypes were *YY* for the plants with yellow seeds and *yy* for the plants with green seeds. A Punnett square, devised by the British geneticist Reginald Punnett, is useful for determining probabilities because it is drawn to predict all possible outcomes of all possible random fertilization events and their expected frequencies. Figure 7.2.5 shows a Punnett square for a cross between a plant with yellow peas and one with green peas. To prepare a Punnett square, all possible combinations of the parental alleles (the genotypes of the gametes) are listed along the top (for one parent) and side (for the other parent) of a grid. The combinations of egg and sperm gametes are then made in the boxes in the table on the basis of which alleles are combining. Each box then represents the diploid genotype of a zygote, or fertilized egg. Because each possibility is equally likely, genotypic ratios can be determined from a Punnett square. If the pattern of inheritance (dominant and recessive) is known, the phenotypic ratios can be inferred as well. For a monohybrid cross of two true-breeding parents, each parent contributes one type of allele. In this case, only one genotype is possible in the F_1 offspring. All offspring are *Yy* and have yellow seeds.

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

Law of Segregation

Observing that true-breeding pea plants with contrasting traits gave rise to F_1 generations that all expressed the dominant trait and F_2 generations that expressed the dominant and recessive traits in a 3:1 ratio, Mendel proposed the law of segregation. This law states that paired unit factors (genes) must segregate equally into gametes such that offspring have an equal likelihood of inheriting either factor. For the F_2 generation of a monohybrid cross, the following three possible combinations of genotypes result: homozygous dominant, heterozygous, or homozygous recessive. Because heterozygotes could arise from two different pathways (receiving one dominant and one recessive allele from either parent), and because heterozygotes and homozygous dominant individuals are phenotypically identical, the law supports Mendel's observed 3:1 phenotypic ratio. The equal segregation of alleles is the reason we can apply the Punnett square to accurately predict the offspring of parents with known genotypes. The physical basis of Mendel's law of segregation is the first division of meiosis in which the homologous chromosomes with their different versions of each gene are segregated into daughter nuclei. This process was not understood by the scientific community during Mendel's lifetime (Figure 7.2.3).

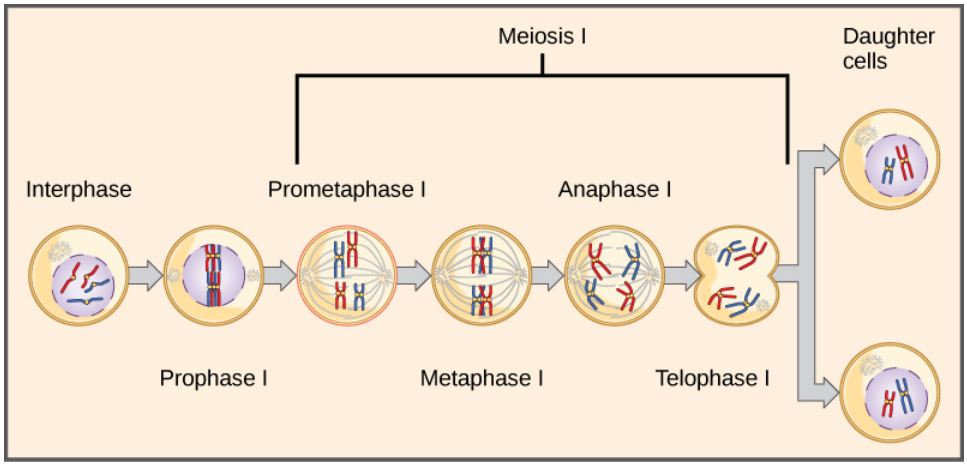


Figure 7.2.3**:** The first division in meiosis is shown.

Test Cross

Beyond predicting the offspring of a cross between known homozygous or heterozygous parents, Mendel also developed a way to determine whether an organism that expressed a dominant trait was a heterozygote or a homozygote. Called the test cross, this technique is still used by plant and animal breeders. In a test cross, the dominant-expressing organism is crossed with an organism that is homozygous recessive for the same characteristic. If the dominant-expressing organism is a homozygote, then all F_1 offspring will be heterozygotes expressing the dominant trait (Figure 7.2.4). Alternatively, if the dominant-expressing organism is a heterozygote, the F_1 offspring will exhibit a 1:1 ratio of heterozygotes and recessive homozygotes (Figure 7.2.4). The test cross further validates Mendel's postulate that pairs of unit factors segregate equally.

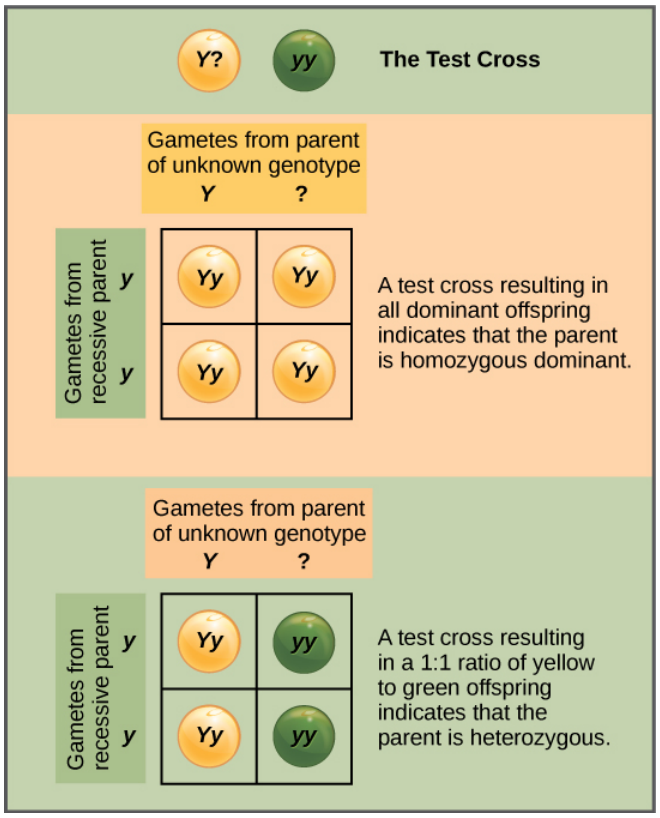


Figure 7.2.4**:** A test cross can be performed to determine whether an organism expressing a dominant trait is a homozygote or a heterozygote.

ART CONNECTION

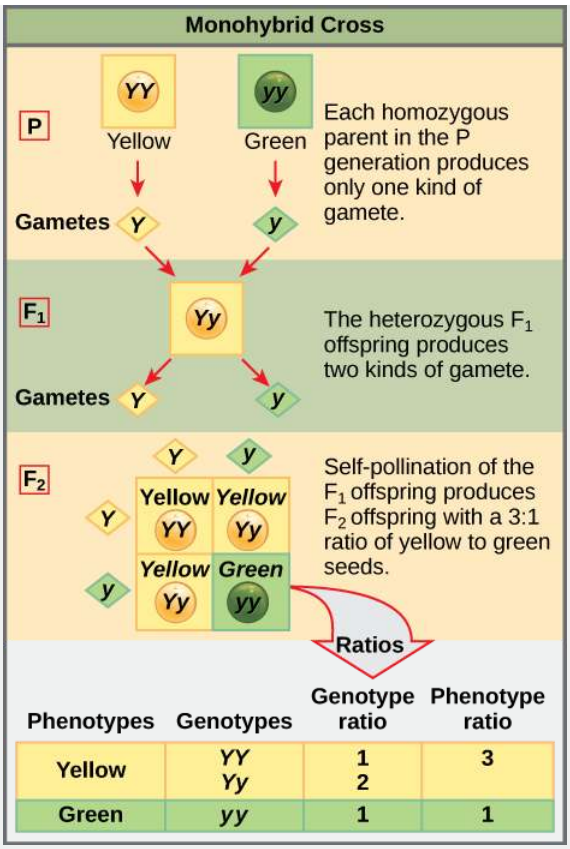


Figure 7.2.5**:** This Punnett square shows the cross between plants with yellow seeds and green seeds. The cross between the true-breeding P plants produces F_1 heterozygotes that can be self-fertilized. The self-cross of the F_1 generation can be analyzed with a Punnett square to predict the genotypes of the F_2 generation. Given an inheritance pattern of dominant–recessive, the genotypic and phenotypic ratios can then be determined.

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

Law of Independent Assortment

Mendel's law of independent assortment states that genes do not influence each other with regard to the sorting of alleles into gametes, and every possible combination of alleles for every gene is equally likely to occur. Independent assortment of genes can be illustrated by the dihybrid cross, a cross between two true-breeding parents that express different traits for two characteristics. Consider the characteristics of seed color and seed texture for two pea plants, one that has wrinkled, green seeds (*rryy*) and another that has round, yellow seeds (*RRYY*). Because each parent is homozygous, the law of segregation indicates that the gametes for the wrinkled–green plant all are *ry*, and the gametes for the round–yellow plant are all *RY*. Therefore, the F_1 generation of offspring all are *RrYy* (Figure 7.2.6).

ART CONNECTION

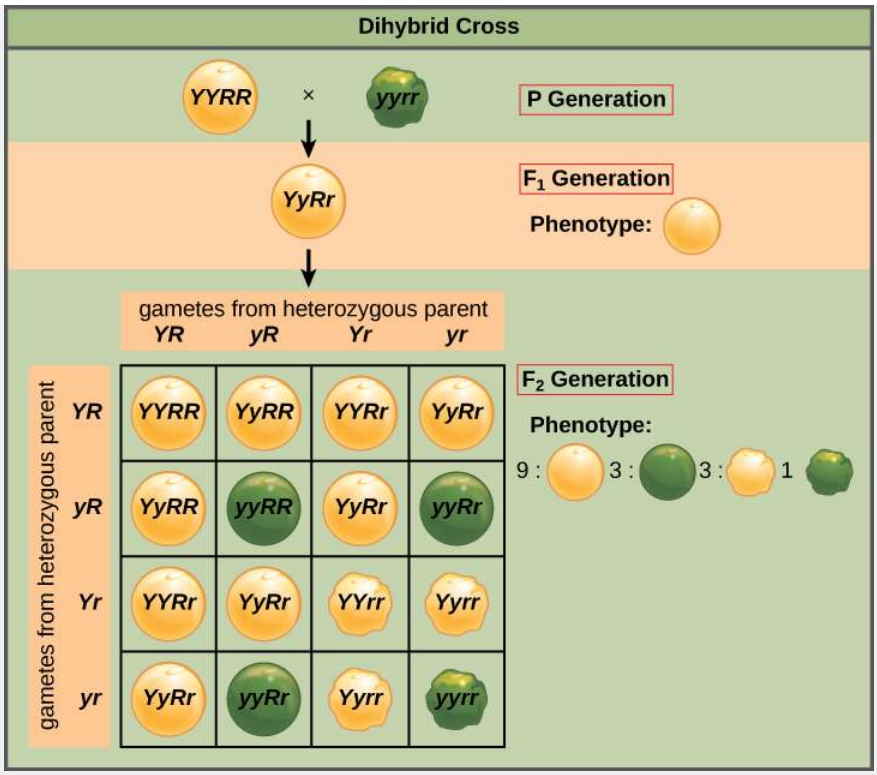


Figure 7.2.6**:** A dihybrid cross in pea plants involves the genes for seed color and texture. The P cross produces F_1 offspring that are all heterozygous for both characteristics. The resulting 9:3:3:1 F_2 phenotypic ratio is obtained using a Punnett square.

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

The gametes produced by the F_1 individuals must have one allele from each of the two genes. For example, a gamete could get an *R* allele for the seed shape gene and either a *Y* or a *y* allele for the seed color gene. It cannot get both an *R* and an *r* allele; each gamete can have only one allele per gene. The law of independent assortment states that a gamete into which an *r* allele is sorted would be equally likely to contain either a *Y* or a *y* allele. Thus, there are four equally likely gametes that can be formed when the *RrYy* heterozygote is self-crossed, as follows: *RY*, *rY*, *Ry*, and *ry*. Arranging these gametes along the top and left of a 4 × 4 Punnett square (Figure 7.2.6) gives us 16 equally likely genotypic combinations. From these genotypes, we find a phenotypic ratio of 9 round–yellow:3 round–green:3 wrinkled–yellow:1 wrinkled–green (Figure 7.2.6). These are the offspring ratios we would expect, assuming we performed the crosses with a large enough sample size.

The physical basis for the law of independent assortment also lies in meiosis I, in which the different homologous pairs line up in random orientations. Each gamete can contain any combination of paternal and maternal chromosomes (and therefore the genes on them) because the orientation of tetrads on the metaphase plane is random (Figure 7.2.7).

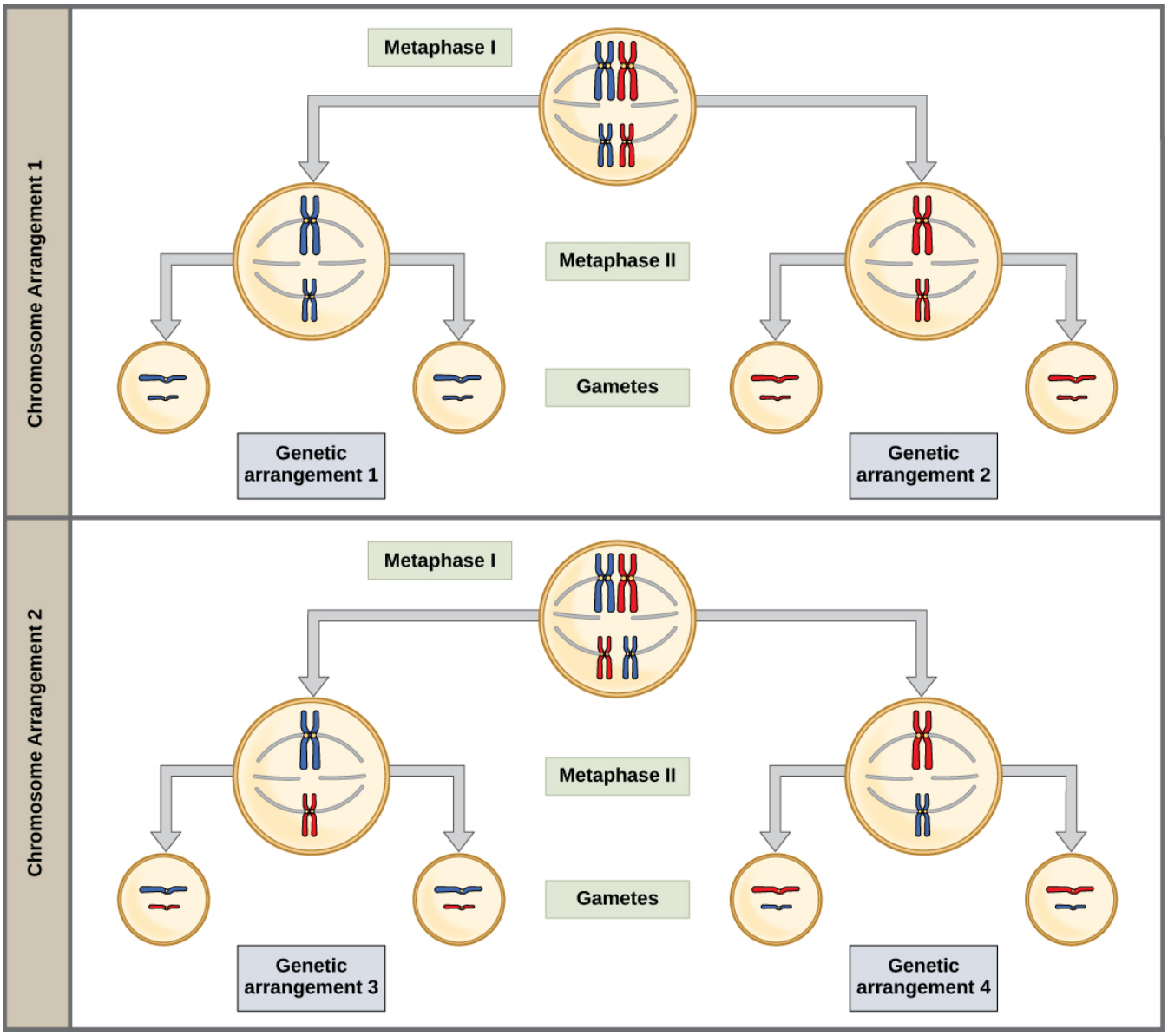


Figure 7.2.7**:** The random segregation into daughter nuclei that happens during the first division in meiosis can lead to a variety of possible genetic arrangements.

Section Summary

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

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

Art Connections

Figure 7.2.5: In pea plants, round peas (*R*) are dominant to wrinkled peas (*r*). You do a test cross between a pea plant with wrinkled peas (genotype *rr*) and a plant of unknown genotype that has round peas. You end up with three plants, all which have round peas. From this data, can you tell if the parent plant is homozygous dominant or heterozygous?

Answer

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

Figure 7.2.6: In pea plants, purple flowers (*P*) are dominant to white (*p*), and yellow peas (*Y*) are dominant to green (*y*). What are the possible genotypes and phenotypes for a cross between *PpYY* and *ppYy* pea plants? How many squares would you need to complete a Punnett square analysis of this cross?

Answer

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

Glossary

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

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

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

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

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

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

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

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

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

phenotype
the observable traits expressed by an organism

Punnett square

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

test cross

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

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7.3: Extensions of the Laws of Inheritance

Mendel studied traits with only one mode of inheritance in pea plants. The inheritance of the traits he studied all followed the relatively simple pattern of dominant and recessive alleles for a single characteristic. There are several important modes of inheritance, discovered after Mendel's work, that do not follow the dominant and recessive, single-gene model.

Alternatives to Dominance and Recessiveness

Mendel's experiments with pea plants suggested that: 1) two types of "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, with 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." Since then, genetic studies in other organisms have shown that much more complexity exists, but that the fundamental principles of Mendelian genetics still hold true. In the sections to follow, we consider some of the extensions of Mendelism.

Incomplete Dominance

Mendel's results, demonstrating 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* (Figure 7.3.1), 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). (Note that different genotypic abbreviations are used for Mendelian extensions to distinguish these patterns from simple dominance and recessiveness.) This pattern of inheritance is described as incomplete dominance, meaning that one of the alleles appears in the phenotype in the heterozygote, but not to the exclusion of the other, which can also be seen. 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. The basis for the intermediate color in the heterozygote is simply that the pigment produced by the red allele (anthocyanin) is diluted in the heterozygote and therefore appears pink because of the white background of the flower petals.



Figure 7.3.1**:** These pink flowers of a heterozygote snapdragon result from incomplete dominance. (credit: "storebukkebruse"/Flickr)

Codominance

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 occurs in the ABO blood groups of humans. The A and B alleles are expressed in the form of A or B molecules present on the surface of red blood cells. Homozygotes (I^AI^A and I^BI^B) express either the A or the B phenotype, and heterozygotes (I^AI^B) express both phenotypes equally. The I^AI^B individual has blood type AB. 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 (Figure 7.3.2).

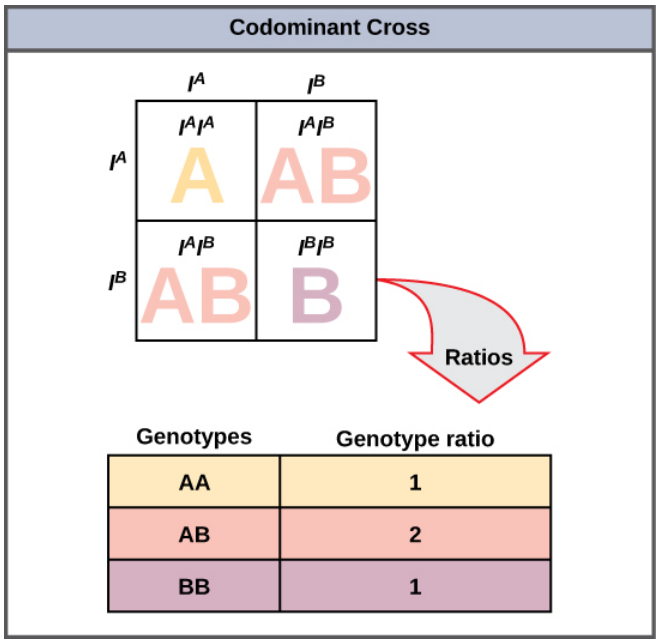


Figure 7.3.2**:** This Punnet square shows an AB/AB blood type cross.

Multiple Alleles

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 in the natural population as the wild type (often abbreviated "+"). All other phenotypes or genotypes are considered variants (mutants) of this typical form, meaning they deviate from the wild type. The variant may be recessive or dominant to the wild-type allele.

An example of multiple alleles is the ABO blood-type system in humans. In this case, there are three alleles circulating in the population. The I^A allele codes for A molecules on the red blood cells, the I^B allele codes for B molecules on the surface of red blood cells, and the i allele codes for no molecules on the red blood cells. In this case, the I^A and I^B alleles are codominant with each other and are both dominant over the i allele. Although there are three alleles present in a population, each individual only gets two of the alleles from their parents. This produces the genotypes and phenotypes shown in Figure 7.3.3. Notice that instead of three genotypes, there are six different genotypes when there are three alleles. The number of possible phenotypes depends on the dominance relationships between the three alleles.

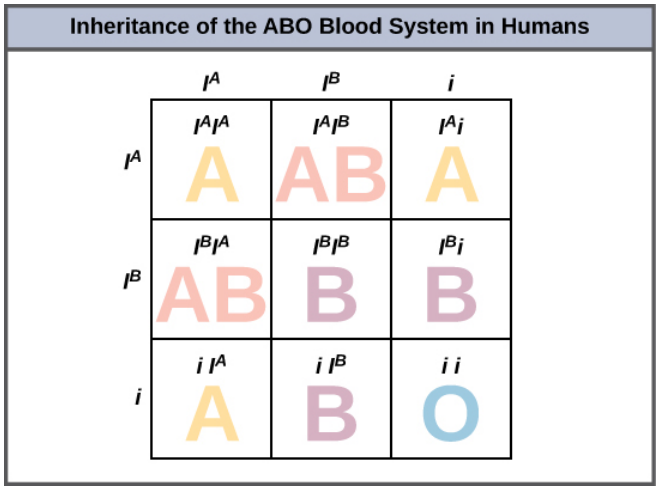


Figure 7.3.3**:** Inheritance of the ABO blood system in humans is shown.

EVOLUTION IN ACTION: Multiple Alleles Confer Drug Resistance in the Malaria Parasite

Malaria is a parasitic disease in humans that is transmitted by infected female mosquitoes, including *Anopheles gambiae*, and is characterized by cyclic high fevers, chills, flu-like symptoms, and severe anemia. *Plasmodium falciparum* and *P. vivax* are the most common causative agents of malaria, and *P. falciparum* is the most deadly. When promptly and correctly treated, *P. falciparum* malaria has a mortality rate of 0.1 percent. However, in some parts of the world, the parasite has evolved resistance to commonly used malaria treatments, so the most effective malarial treatments can vary by geographic region.

In Southeast Asia, Africa, and South America, *P. falciparum* has developed resistance to the anti-malarial drugs chloroquine, mefloquine, and sulfadoxine-pyrimethamine. *P. falciparum*, which is haploid during the life stage in which it is infective to humans, has evolved multiple drug-resistant mutant alleles of the *dhps* gene. Varying degrees of sulfadoxine resistance are associated with each of these alleles. Being haploid, *P. falciparum* needs only one drug-resistant allele to express this trait.

In Southeast Asia, different sulfadoxine-resistant alleles of the *dhps* gene are localized to different geographic regions. This is a common evolutionary phenomenon that comes about because drug-resistant mutants arise in a population and interbreed with other *P. falciparum* isolates in close proximity. Sulfadoxine-resistant parasites cause considerable human hardship in regions in which this drug is widely used as an over-the-counter malaria remedy. As is common with pathogens that multiply to large numbers within an infection cycle, *P. falciparum* evolves relatively rapidly (over a decade or so) in response to the selective pressure of commonly used anti-malarial drugs. For this reason, scientists must constantly work to develop new drugs or drug combinations to combat the worldwide malaria burden.[1]

Sex-Linked Traits

In humans, as well as in many other animals and some plants, the sex of the individual is determined by sex chromosomes—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 fewer genes. When a gene being examined is present on the X, but not the Y, chromosome, it is X-linked.

Eye color in *Drosophila*, the common fruit fly, was the first X-linked trait to be identified. Thomas Hunt Morgan mapped this trait to the X chromosome in 1910. Like humans, *Drosophila* males have an XY chromosome pair, and females are XX. In flies the wild-type eye color is red (X^W) and is dominant to white eye color (X^w) (Figure 7.3.4). Because of the location of the eye-color gene, reciprocal crosses do not produce the same offspring ratios. Males are said to be hemizygous, in that they have only one allele for any X-linked characteristic. Hemizygosity makes descriptions of dominance and recessiveness irrelevant for XY males. *Drosophila* males lack the white gene on the Y chromosome; that is, 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 7.3.4: 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.

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 generation. With respect to *Drosophila* eye color, when the P male expresses the white-eye phenotype and the female is homozygously red-eyed, all members of the F_1 generation exhibit red eyes (Figure 7.3.5). 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 female and their Y chromosome from the P 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^w genotypes) 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).

ART CONNECTION

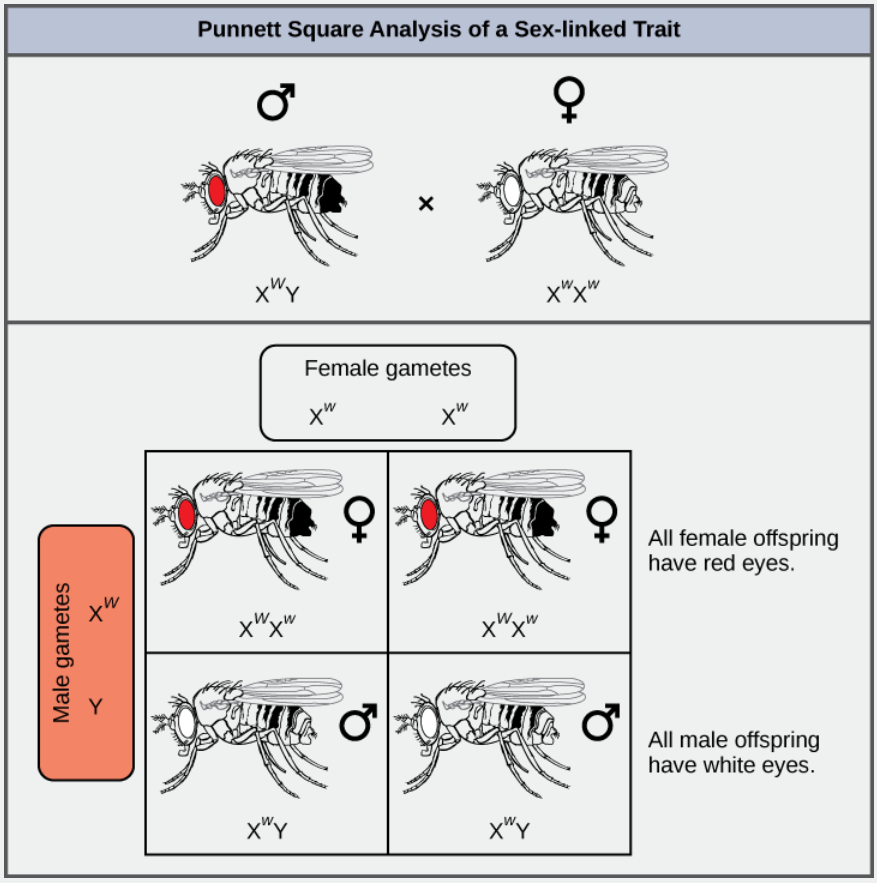


Figure 7.3.5: Crosses involving sex-linked traits often give rise to different phenotypes for the different sexes of offspring, as is the case for this cross involving red and white eye color in *Drosophila*. In the diagram, *w* is the white-eye mutant allele and *W* is the wild-type, red-eye allele.

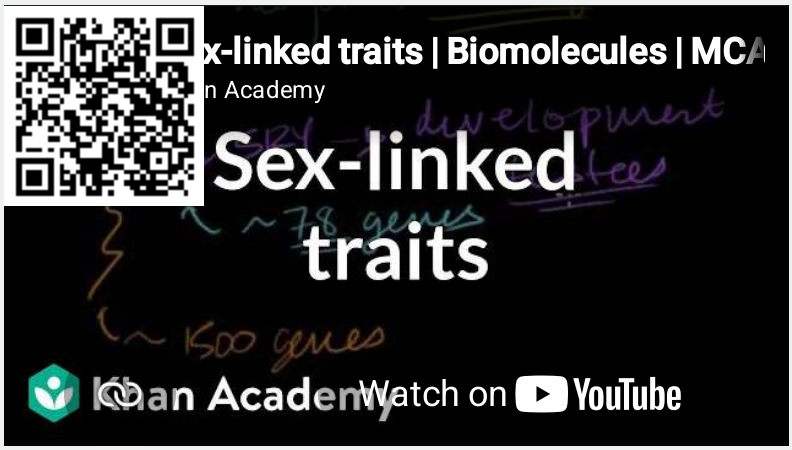
What ratio of offspring would result from a cross between a white-eyed male and a female that is heterozygous for red eye color?

Discoveries in fruit fly genetics can be applied to human genetics. When a female parent is homozygous for a recessive X-linked trait, she will pass the trait on to 100 percent of her male offspring, because the males will receive the Y chromosome from the male parent. In humans, the alleles for certain conditions (some color-blindness, hemophilia, and muscular dystrophy) are X-linked. Females who are heterozygous for these diseases are said to be carriers and may not exhibit any phenotypic effects. These females will pass the disease to half of their sons and will pass carrier status to half of their daughters; therefore, X-linked traits appear more frequently in males than females.

In some groups of organisms with sex chromosomes, the sex with the non-homologous sex chromosomes is the female rather than the male. This is the case for all birds. In this case, sex-linked traits will be more likely to appear in the female, in whom they are

hemizygous.

CONCEPT IN ACTION



Watch this video to learn more about sex-linked traits.

Linked Genes Violate the Law of Independent Assortment

Although all of Mendel's pea plant 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 us consider the biological basis of gene linkage and recombination.

Homologous chromosomes possess the same genes in the same order, though the specific alleles of the gene can be different on each of the two chromosomes. Recall that during interphase and prophase I of meiosis, homologous chromosomes first replicate and then synapse, with like genes on the homologs aligning with each other. At this stage, segments of homologous chromosomes exchange linear segments of genetic material (Figure 7.3.6). 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.

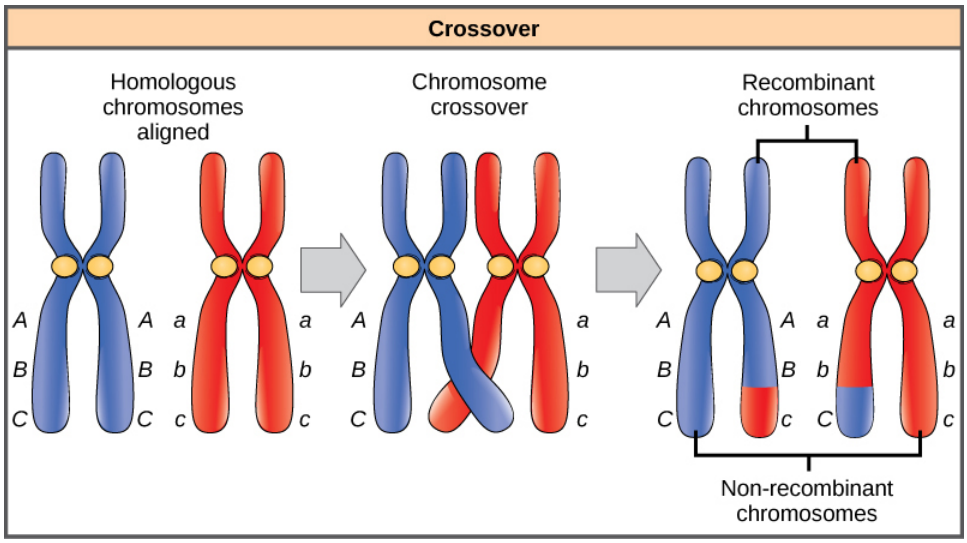


Figure 7.3.6**:** The process of crossover, or recombination, occurs when two homologous chromosomes align and exchange a segment of genetic material.

When two genes are located 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 tend to 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 a 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 linkage 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.

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), such that 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.

CONCEPT IN ACTION

Eye color in humans is determined by multiple alleles. Use the Eye Color Calculator to predict the eye color of children from parental eye color.

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, such that two or more genes expressed simultaneously affect a phenotype. An apparent example of this occurs with human skin color, which appears to involve the action of at least three (and probably more) genes. Cases in which inheritance for a characteristic like skin color or human height depend on the combined effects of numerous genes are called polygenic inheritance.

Genes may also oppose each other, with one gene suppressing the expression of another. In epistasis, the interaction between genes is antagonistic, such that one gene masks or interferes with the expression of another. “Epistasis” is a word composed of Greek roots meaning “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 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*, when present as the recessive homozygote (*cc*), negates any expression of pigment from the *A* gene and results in an albino mouse (Figure 7.3.7). 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 black:4 albino (Figure 7.3.7). In this case, the *C* gene is epistatic to the *A* gene.

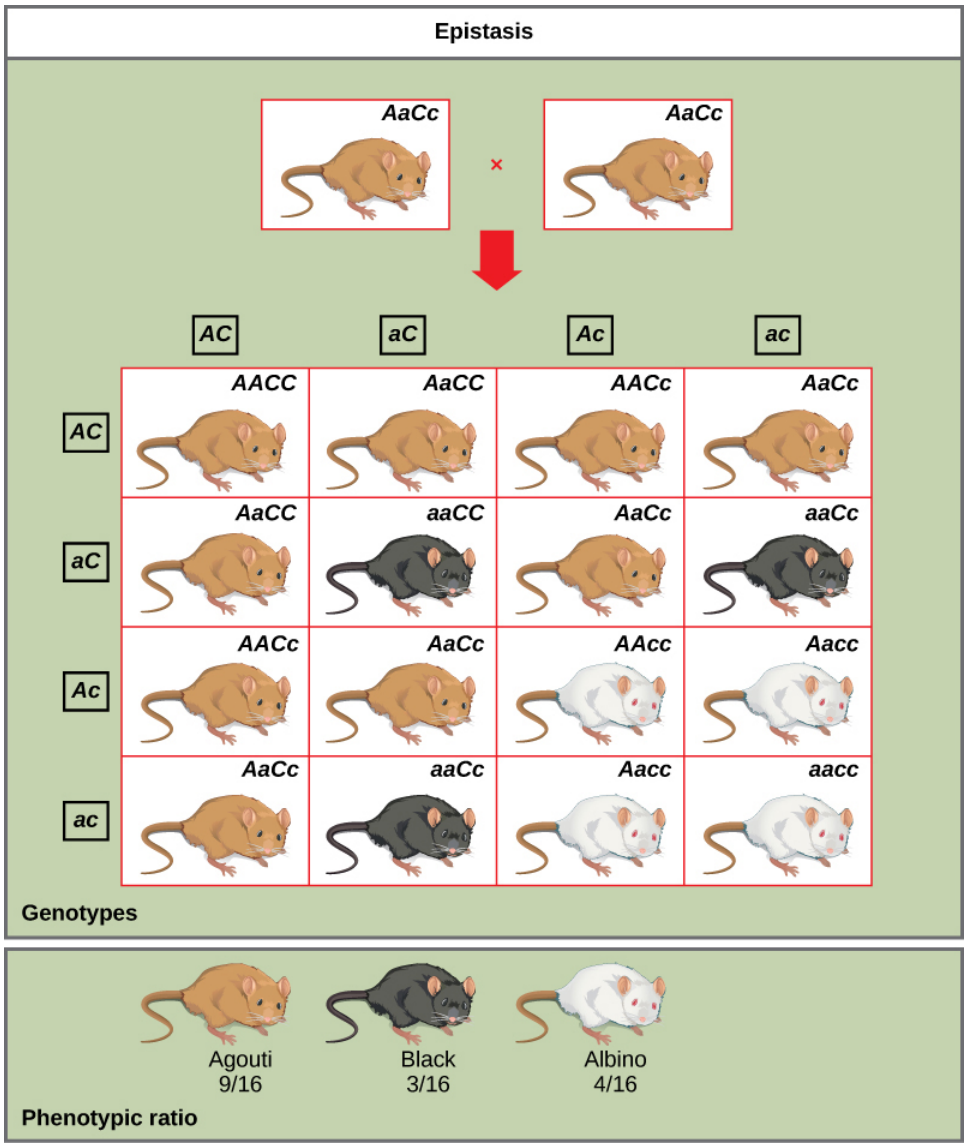


Figure 7.3.7**:** In this example of epistasis, one gene (*C*) masks the expression of another (*A*) for coat color. When the *C* allele is present, coat color is expressed; when it is absent (*cc*), no coat color is expressed. Coat color depends on the *A* gene, which shows dominance, with the recessive homozygote showing a different phenotype than the heterozygote or dominant homozygote.

Section Summary

Alleles do not always behave in dominant and recessive patterns. Incomplete dominance describes situations in which the heterozygote exhibits a phenotype that is intermediate between the homozygous phenotypes. Codominance describes the simultaneous expression of both of the alleles in the heterozygote. Although diploid organisms can only have two alleles for any given gene, it is common for more than two alleles for a gene to exist in a population. In humans, as in many animals and some plants, females have two X chromosomes and males have one X and one Y chromosome. Genes that are present on the X but not the Y chromosome are said to be X-linked, such that males only inherit one allele for the gene, and females inherit two.

According to Mendel's law of independent assortment, genes sort independently of each other into gametes during meiosis. This occurs because chromosomes, on which the genes reside, assort independently during meiosis and crossovers cause most genes on the same chromosomes to also behave independently. When genes are located in close proximity on the same chromosome, their alleles tend to be inherited together. This results in offspring ratios that violate Mendel's law of independent assortment. However, recombination serves to exchange genetic material on homologous chromosomes such that maternal and paternal alleles may be recombined on the same chromosome. This is why alleles on a given chromosome are not always inherited together. Recombination is a random event occurring anywhere on a chromosome. Therefore, genes that are far apart on the same

chromosome are likely to still assort independently because of recombination events that occurred in the intervening chromosomal space.

Whether or not they are sorting independently, genes may interact at the level of gene products, such that the expression of an allele for one gene masks or modifies the expression of an allele for a different gene. This is called epistasis.

Art Connections

Figure 7.3.5: What ratio of offspring would result from a cross between a white-eyed male and a female that is heterozygous for red eye color?

Answer

Half of the female offspring would be heterozygous (X^WX^w) with red eyes, and half would be homozygous recessive (X^wX^w) with white eyes. Half of the male offspring would be hemizygous dominant (X^WY) with red eyes, and half would be hemizygous recessive (X^wY) with white eyes.

Footnotes

1. 1 Sumiti Vinayak et al., "Origin and Evolution of Sulfadoxine Resistant *Plasmodium falciparum*," *PLoS Pathogens* 6 (2010): e1000830.

Glossary

codominance
in a heterozygote, complete and simultaneous expression of both alleles for the same characteristic

epistasis
an interaction between genes such that one gene masks or interferes with the expression of another

hemizygous
the presence of only one allele for a characteristic, as in X-linkage; hemizygosity makes descriptions of dominance and recessiveness irrelevant

incomplete dominance
in a heterozygote, expression of two contrasting alleles such that the individual displays an intermediate phenotype

linkage
a phenomenon in which alleles that are located in close proximity to each other on the same chromosome are more likely to be inherited together

recombination
the process during meiosis in which homologous chromosomes exchange linear segments of genetic material, thereby dramatically increasing genetic variation in the offspring and separating linked genes

wild type
the most commonly occurring genotype or phenotype for a given characteristic found in a population

X-linked
a gene present on the X chromosome, but not the Y chromosome

Contributors and Attributions

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

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7.A: Patterns of Inheritance (Exercises)

Mendel's Experiments

Multiple Choice

Imagine that you are performing a cross involving seed color in garden pea plants. What traits would you expect to observe in the F_1 offspring if you cross true-breeding parents with green seeds and yellow seeds? Yellow seed color is dominant over green.

A. only yellow-green seeds
B. only yellow seeds
C. 1:1 yellow seeds:green seeds
D. 1:3 green seeds:yellow seeds

Answer

B

Imagine that you are performing a cross involving seed texture in garden pea plants. You cross true-breeding round and wrinkled parents to obtain F_1 offspring. Which of the following experimental results in terms of numbers of plants are closest to what you expect in the F_2 progeny?

A. 810 round seeds
B. 810 wrinkled seeds
C. 405:395 round seeds:wrinkled seeds
D. 610:190 round seeds:wrinkled seeds

Answer

D

Free Response

Describe one of the reasons that made the garden pea an excellent choice of model system for studying inheritance.

Answer

The garden pea has flowers that close tightly during self-pollination. This helps to prevent accidental or unintentional fertilizations that could have diminished the accuracy of Mendel's data.

Laws of Inheritance

Multiple Choice

The observable traits expressed by an organism are described as its _____.

A. phenotype
B. genotype
C. alleles
D. zygote

Answer

A

A recessive trait will be observed in individuals that are _____ for that trait.

A. heterozygous
B. homozygous or heterozygous
C. homozygousdiploid

Answer

C

What are the types of gametes that can be produced by an individual with the genotype *AaBb*?

A. *Aa*, *Bb*
B. *AA*, *aa*, *BB*, *bb*
C. *AB*, *Ab*, *aB*, *ab*
D. *AB*, *ab*

Answer

C

What is the reason for doing a test cross?

A. to identify heterozygous individuals with the dominant phenotype
B. to determine which allele is dominant and which is recessive
C. to identify homozygous recessive individuals in the F_2
D. to determine if two genes assort independently

Answer

A

Free Response

Use a Punnett square to predict the offspring in a cross between a dwarf pea plant (homozygous recessive) and a tall pea plant (heterozygous). What is the phenotypic ratio of the offspring?

Answer

The Punnett square would be 2 × 2 and will have *T* and *T* along the top and *T* and *t* along the left side. Clockwise from the top left, the genotypes listed within the boxes will be *Tt*, *Tt*, *tt*, and *tt*. The phenotypic ratio will be 1 tall:1 dwarf.

Use a Punnett square to predict the offspring in a cross between a tall pea plant (heterozygous) and a tall pea plant (heterozygous). What is the genotypic ratio of the offspring?

Answer

The Punnett square will be 2 × 2 and will have *T* and *t* along the top and *T* and *t* along the left side. Clockwise from the top left, the genotypes listed within the boxes will be *TT*, *Tt*, *Tt*, and *tt*. The genotypic ratio will be 1*TT*:2*Tt*:1*tt*.

Extensions of the Laws of Inheritance

Multiple Choice

If black and white true-breeding mice are mated and the result is all gray offspring, what inheritance pattern would this be indicative of?

A. dominance
B. codominance
C. multiple alleles
D. incomplete dominance

Answer

D

The ABO blood groups in humans are expressed as the I^A, I^B, and *i* alleles. The I^A allele encodes the A blood group antigen, I^B encodes B, and *i* encodes O. Both A and B are dominant to O. If a heterozygous blood type A parent (I^Ai) and a heterozygous blood

type B parent (I^Bi) mate, one quarter of their offspring are expected to have the AB blood type (I^AI^B) in which both antigens are expressed equally. Therefore, ABO blood groups are an example of:

A. multiple alleles and incomplete dominance
B. codominance and incomplete dominance
C. incomplete dominance only
D. multiple alleles and codominance

Answer

D

In a cross between a homozygous red-eyed female fruit fly and a white-eyed male fruit fly, what is the expected outcome?

A. all white-eyed male offspring
B. all white-eyed female offspring
C. all red-eyed offspring
D. half white-eyed make offspring

Answer

C

When a population has a gene with four alleles circulating, how many possible genotypes are there?

A. 3
B. 6
C. 10
D. 16

Answer

C

Free Response

Can a male be a carrier of red-green color blindness?

Answer

No, males can only express color blindness and cannot carry it because an individual needs two X chromosomes to be a carrier.

Could an individual with blood type O (genotype *ii*) be a legitimate child of parents in which one parent had blood type A and the other parent had blood type B?

Answer

Yes this child could have come from these parents. The child would have inherited an *i* allele from each parent and for this to happen the type A parent had to have genotype I^Ai and the type b parent had to have genotype I^Bi.

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CHAPTER OVERVIEW

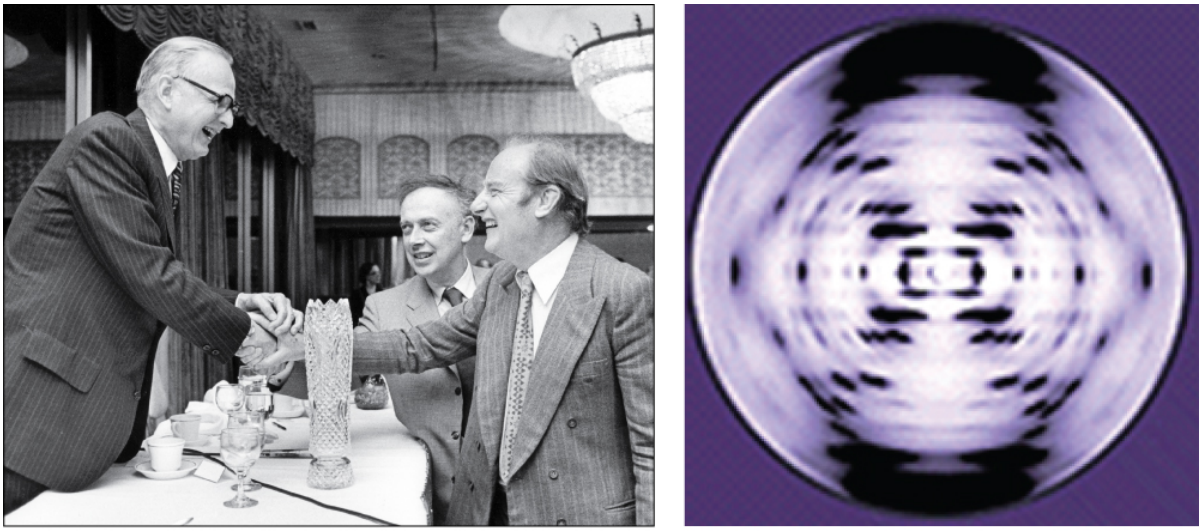
8: Molecular Biology

8.1: The Structure of DNA
8.2: DNA Replication
8.3: Transcription
8.4: Translation
8.5: How Genes Are Regulated
8.A: Molecular Biology (Exercises)

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8.1: The Structure of DNA

In the 1950s, Francis Crick and James Watson worked together at the University of Cambridge, England, to determine the structure of DNA. Other scientists, such as Linus Pauling and Maurice Wilkins, were also actively exploring this field. Pauling had discovered the secondary structure of proteins using X-ray crystallography. X-ray crystallography is a method for investigating molecular structure by observing the patterns formed by X-rays shot through a crystal of the substance. The patterns give important information about the structure of the molecule of interest. In Wilkins' lab, researcher Rosalind Franklin was using X-ray crystallography to understand the structure of DNA. Watson and Crick were able to piece together the puzzle of the DNA molecule using Franklin's data (Figure 8.1.1). Watson and Crick also had key pieces of information available from other researchers such as Chargaff's rules. Chargaff had shown that of the four kinds of monomers (nucleotides) present in a DNA molecule, two types were always present in equal amounts and the remaining two types were also always present in equal amounts. This meant they were always paired in some way. In 1962, James Watson, Francis Crick, and Maurice Wilkins were awarded the Nobel Prize in Medicine for their work in determining the structure of DNA.



(a) (b)

Figure 8.1.1**:** Pioneering scientists (a) James Watson and Francis Crick are pictured here with American geneticist Maclyn McCarty. Scientist Rosalind Franklin discovered (b) the X-ray diffraction pattern of DNA, which helped to elucidate its double helix structure. (credit a: modification of work by Marjorie McCarty; b: modification of work by NIH)

Now let's consider the structure of the two types of nucleic acids, deoxyribonucleic acid (DNA) and ribonucleic acid (RNA). The building blocks of DNA are nucleotides, which are made up of three parts: a deoxyribose (5-carbon sugar), a phosphate group, and a nitrogenous base (Figure 8.1.2). There are four types of nitrogenous bases in DNA. Adenine (A) and guanine (G) are double-ringed purines, and cytosine (C) and thymine (T) are smaller, single-ringed pyrimidines. The nucleotide is named according to the nitrogenous base it contains.

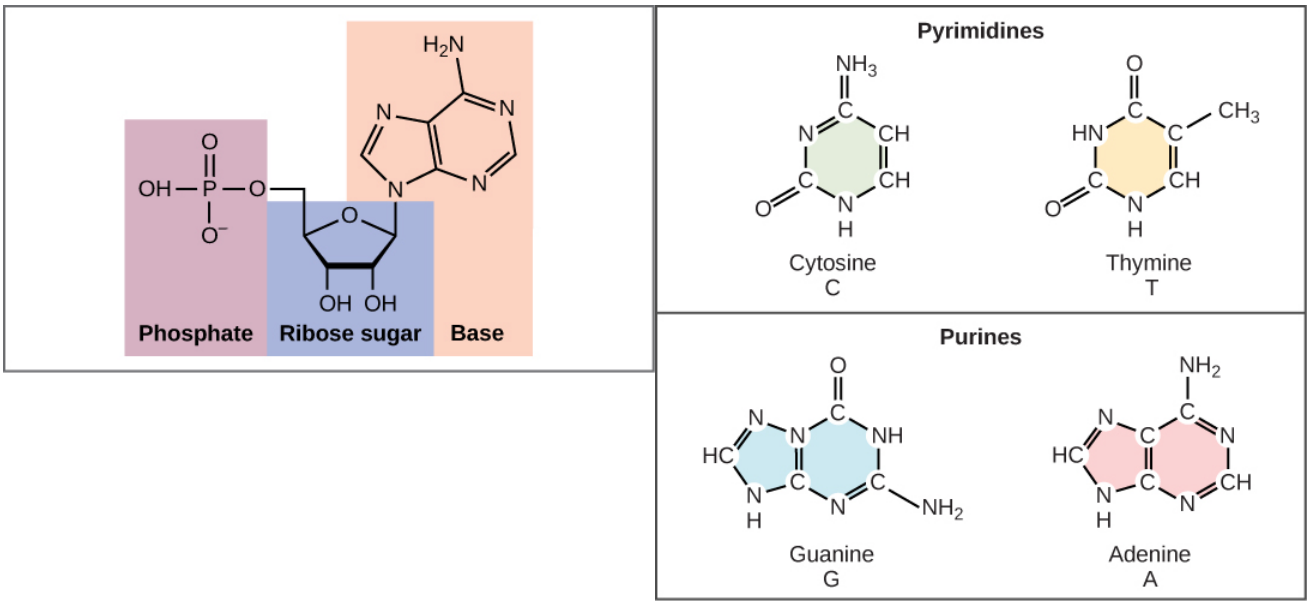


Figure 8.1.2**:** (a) Each DNA nucleotide is made up of a sugar, a phosphate group, and a base. (b) Cytosine and thymine are pyrimidines. Guanine and adenine are purines.

The phosphate group of one nucleotide bonds covalently with the sugar molecule of the next nucleotide, and so on, forming a long polymer of nucleotide monomers. The sugar–phosphate groups line up in a "backbone" for each single strand of DNA, and the nucleotide bases stick out from this backbone. The carbon atoms of the five-carbon sugar are numbered clockwise from the oxygen as 1', 2', 3', 4', and 5' (1' is read as "one prime"). The phosphate group is attached to the 5' carbon of one nucleotide and the 3' carbon of the next nucleotide. In its natural state, each DNA molecule is actually composed of two single strands held together along their length with hydrogen bonds between the bases.

Watson and Crick proposed that the DNA is made up of two strands that are twisted around each other to form a right-handed helix, called a double helix. Base-pairing takes place between a purine and pyrimidine: namely, A pairs with T, and G pairs with C. In other words, adenine and thymine are complementary base pairs, and cytosine and guanine are also complementary base pairs. This is the basis for Chargaff's rule; because of their complementarity, there is as much adenine as thymine in a DNA molecule and as much guanine as cytosine. Adenine and thymine are connected by two hydrogen bonds, and cytosine and guanine are connected by three hydrogen bonds. The two strands are anti-parallel in nature; that is, one strand will have the 3' carbon of the sugar in the "upward" position, whereas the other strand will have the 5' carbon in the upward position. The diameter of the DNA double helix is uniform throughout because a purine (two rings) always pairs with a pyrimidine (one ring) and their combined lengths are always equal (Figure 8.1.3).

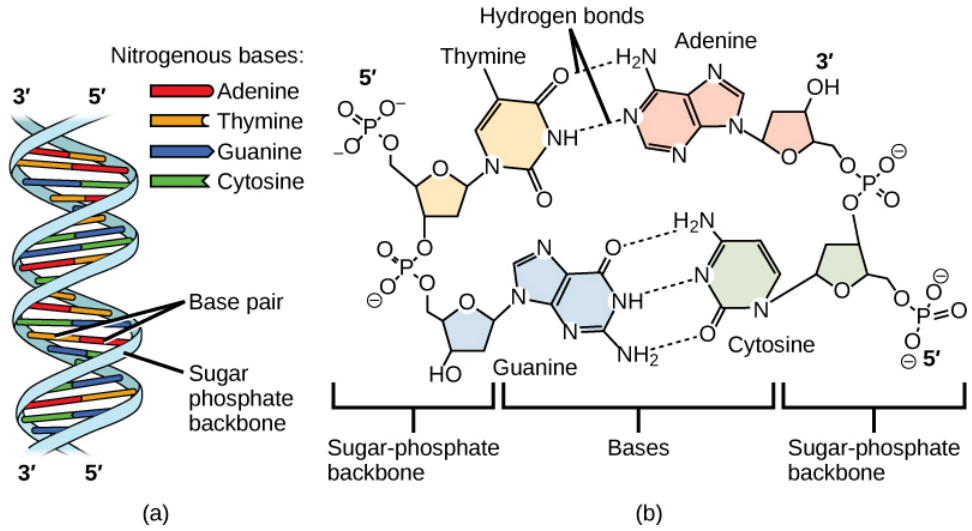


Figure 8.1.3**:** DNA (a) forms a double stranded helix, and (b) adenine pairs with thymine and cytosine pairs with guanine. (credit a: modification of work by Jerome Walker, Dennis Myts)

The Structure of RNA

There is a second nucleic acid in all cells called ribonucleic acid, or RNA. Like DNA, RNA is a polymer of nucleotides. Each of the nucleotides in RNA is made up of a nitrogenous base, a five-carbon sugar, and a phosphate group. In the case of RNA, the five-carbon sugar is ribose, not deoxyribose. Ribose has a hydroxyl group at the 2' carbon, unlike deoxyribose, which has only a hydrogen atom (Figure 8.1.4).

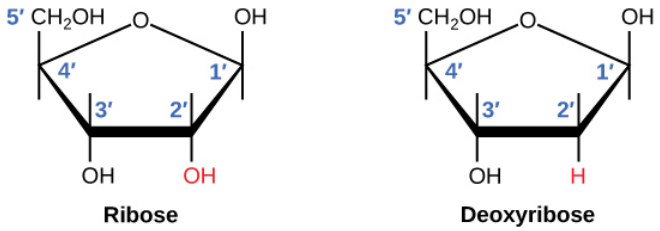


Figure 8.1.4**:** The difference between the ribose found in RNA and the deoxyribose found in DNA is that ribose has a hydroxyl group at the 2' carbon.

RNA nucleotides contain the nitrogenous bases adenine, cytosine, and guanine. However, they do not contain thymine, which is instead replaced by uracil, symbolized by a “U.” RNA exists as a single-stranded molecule rather than a double-stranded helix. Molecular biologists have named several kinds of RNA on the basis of their function. These include messenger RNA (mRNA), transfer RNA (tRNA), and ribosomal RNA (rRNA)—molecules that are involved in the production of proteins from the DNA code.

How DNA Is Arranged in the Cell

DNA is a working molecule; it must be replicated when a cell is ready to divide, and it must be “read” to produce the molecules, such as proteins, to carry out the functions of the cell. For this reason, the DNA is protected and packaged in very specific ways. In addition, DNA molecules can be very long. Stretched end-to-end, the DNA molecules in a single human cell would come to a length of about 2 meters. Thus, the DNA for a cell must be packaged in a very ordered way to fit and function within a structure (the cell) that is not visible to the naked eye. The chromosomes of prokaryotes are much simpler than those of eukaryotes in many of their features (Figure 8.1.5). Most prokaryotes contain a single, circular chromosome that is found in an area in the cytoplasm called the nucleoid.

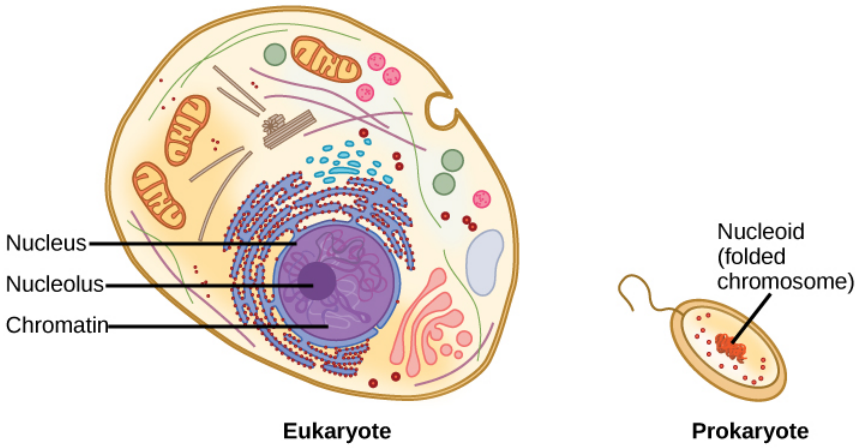


Figure 8.1.5**:** A eukaryote contains a well-defined nucleus, whereas in prokaryotes, the chromosome lies in the cytoplasm in an area called the nucleoid.

The size of the genome in one of the most well-studied prokaryotes, *Escherichia coli*, is 4.6 million base pairs, which would extend a distance of about 1.6 mm if stretched out. So how does this fit inside a small bacterial cell? The DNA is twisted beyond the double helix in what is known as supercoiling. Some proteins are known to be involved in the supercoiling; other proteins and enzymes 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 (Figure 8.1.6). At the most basic level, DNA is wrapped around proteins known as histones to form structures called nucleosomes. The DNA is wrapped tightly around the histone core. This nucleosome is linked to the next one by a short strand of DNA that is free of histones. This is also known as the “beads on a string” structure; the nucleosomes are the “beads” and the short lengths of DNA between them are the “string.” The nucleosomes, with their DNA coiled around them, stack compactly onto each other to form a 30-nm–wide fiber. This fiber is further coiled into a thicker and more compact structure. At the metaphase stage of mitosis, when the chromosomes are lined up in the center of the cell, the chromosomes are at their most compacted. They are approximately 700 nm in width, and are found in association with scaffold proteins.

In interphase, the phase of the cell cycle between mitoses at which the chromosomes are decondensed, eukaryotic chromosomes have two distinct regions that can be distinguished by staining. There is a tightly packaged region that stains darkly, and a less dense region. The darkly staining regions usually contain genes that are not active, and are found in the regions of the centromere and telomeres. The lightly staining regions usually contain genes that are active, with DNA packaged around nucleosomes but not further compacted.

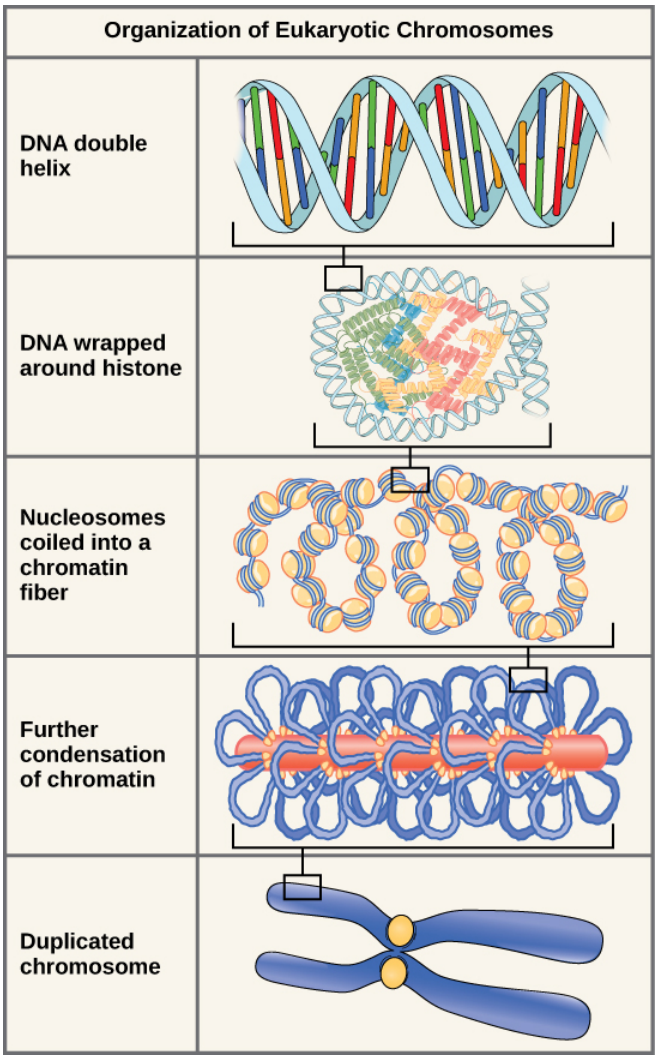


Figure 8.1.6**:** These figures illustrate the compaction of the eukaryotic chromosome.

CONCEPT IN ACTION



Watch this animation of DNA packaging.

Summary

The model of the double-helix structure of DNA was proposed by Watson and Crick. The DNA molecule is a polymer of nucleotides. Each nucleotide is composed of a nitrogenous base, a five-carbon sugar (deoxyribose), and a phosphate group. There

are four nitrogenous bases in DNA, two purines (adenine and guanine) and two pyrimidines (cytosine and thymine). A DNA molecule is composed of two strands. Each strand is composed of nucleotides bonded together covalently between the phosphate group of one and the deoxyribose sugar of the next. From this backbone extend the bases. The bases of one strand bond to the bases of the second strand with hydrogen bonds. Adenine always bonds with thymine, and cytosine always bonds with guanine. The bonding causes the two strands to spiral around each other in a shape called a double helix. Ribonucleic acid (RNA) is a second nucleic acid found in cells. RNA is a single-stranded polymer of nucleotides. It also differs from DNA in that it contains the sugar ribose, rather than deoxyribose, and the nucleotide uracil rather than thymine. Various RNA molecules function in the process of forming proteins from the genetic code in DNA.

Prokaryotes contain a single, double-stranded circular chromosome. Eukaryotes contain double-stranded linear DNA molecules packaged into chromosomes. The DNA helix is wrapped around proteins to form nucleosomes. The protein coils are further coiled, and during mitosis and meiosis, the chromosomes become even more greatly coiled to facilitate their movement. Chromosomes have two distinct regions which can be distinguished by staining, reflecting different degrees of packaging and determined by whether the DNA in a region is being expressed (euchromatin) or not (heterochromatin).

Glossary

deoxyribose
: a five-carbon sugar molecule with a hydrogen atom rather than a hydroxyl group in the 2' position; the sugar component of DNA nucleotides

double helix
: the molecular shape of DNA in which two strands of nucleotides wind around each other in a spiral shape

nitrogenous base
: a nitrogen-containing molecule that acts as a base; often referring to one of the purine or pyrimidine components of nucleic acids

phosphate group
: a molecular group consisting of a central phosphorus atom bound to four oxygen atoms

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8.2: DNA Replication

When a cell divides, it is important that each daughter cell receives an identical copy of the DNA. This is accomplished by the process of DNA replication. The replication of DNA occurs during the synthesis phase, or S phase, of the cell cycle, before the cell enters mitosis or meiosis.

The elucidation of the structure of the double helix provided a hint as to how DNA is copied. Recall that adenine nucleotides pair with thymine nucleotides, and cytosine with guanine. This means that the two strands are complementary to each other. For example, a strand of DNA with a nucleotide sequence of AGTCATGA will have a complementary strand with the sequence TCAGTACT (Figure 8.2.1).

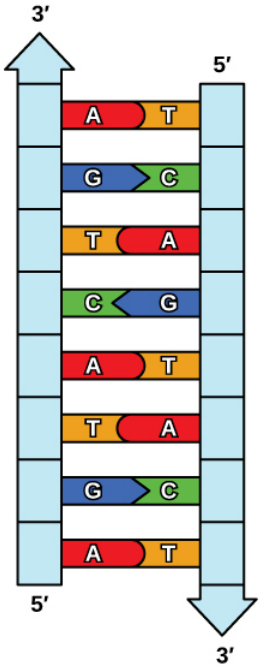


Figure 8.2.1**:** The two strands of DNA are complementary, meaning the sequence of bases in one strand can be used to create the correct sequence of bases in the other strand.

Because of the complementarity of the two strands, having one strand means that it is possible to recreate the other strand. This model for replication suggests that the two strands of the double helix separate during replication, and each strand serves as a template from which the new complementary strand is copied (Figure 8.2.2).

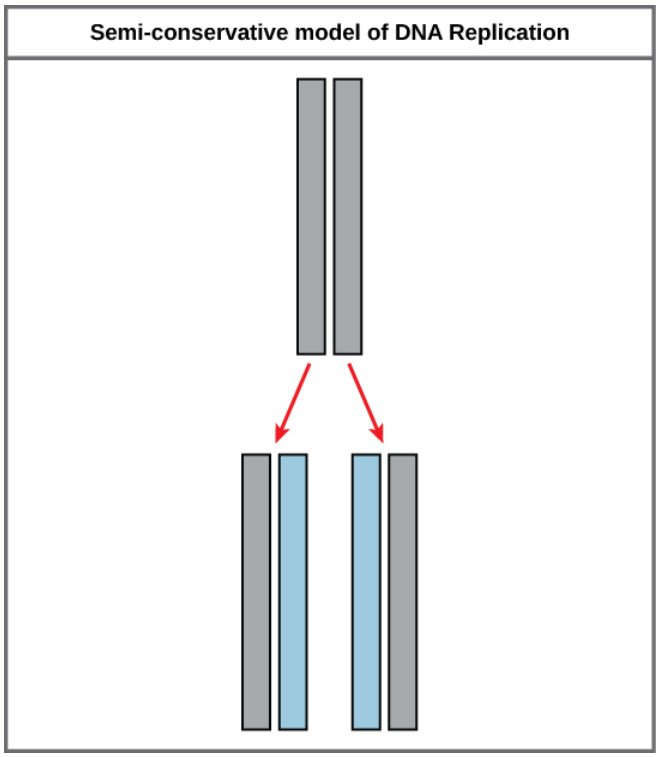


Figure 8.2.2**:** The semiconservative model of DNA replication is shown. Gray indicates the original DNA strands, and blue indicates newly synthesized DNA.

During DNA replication, each of the two strands that make up the double helix serves as a template from which new strands are copied. The new strand will be complementary to the parental or “old” strand. Each new double strand consists of one parental strand and one new daughter strand. This is known as semiconservative replication. When two DNA copies are formed, they have an identical sequence of nucleotide bases and are divided equally into two daughter cells.

DNA Replication in Eukaryotes

Because eukaryotic genomes are very 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.

Recall that 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. How does the replication machinery know where on the DNA double helix to begin? It turns out that there are specific nucleotide sequences called origins of replication at which replication begins. Certain proteins bind to the origin of replication while an enzyme called helicase unwinds and opens up the DNA helix. As the DNA opens up, Y-shaped structures called replication forks are formed (Figure 8.2.3). Two replication forks are formed at the origin of replication, and these get extended in both directions as replication proceeds. There are multiple origins of replication on the eukaryotic chromosome, such that replication can occur simultaneously from several places in the genome.

During elongation, an enzyme called DNA polymerase adds DNA nucleotides to the 3' end of the template. Because DNA polymerase can only add new nucleotides at the end of a backbone, a primer sequence, which provides this starting point, is added with complementary RNA nucleotides. This primer is removed later, and the nucleotides are replaced with DNA nucleotides. One strand, which is complementary to the parental DNA strand, is synthesized continuously toward the replication fork so the polymerase can add nucleotides in this direction. This continuously synthesized strand is known as the leading strand. Because DNA polymerase can only synthesize DNA in a 5' to 3' direction, the other new strand is put together in short pieces called Okazaki fragments. The Okazaki fragments each require a primer made of RNA to start the synthesis. The strand with the Okazaki fragments is known as the lagging strand. As synthesis proceeds, an enzyme removes the RNA primer, which is then replaced with DNA nucleotides, and the gaps between fragments are sealed by an enzyme called DNA ligase.

The process of DNA replication can be summarized as follows:

1. DNA unwinds at the origin of replication.
2. New bases are added to the complementary parental strands. One new strand is made continuously, while the other strand is made in pieces.
3. Primers are removed, new DNA nucleotides are put in place of the primers and the backbone is sealed by DNA ligase.

ART CONNECTION

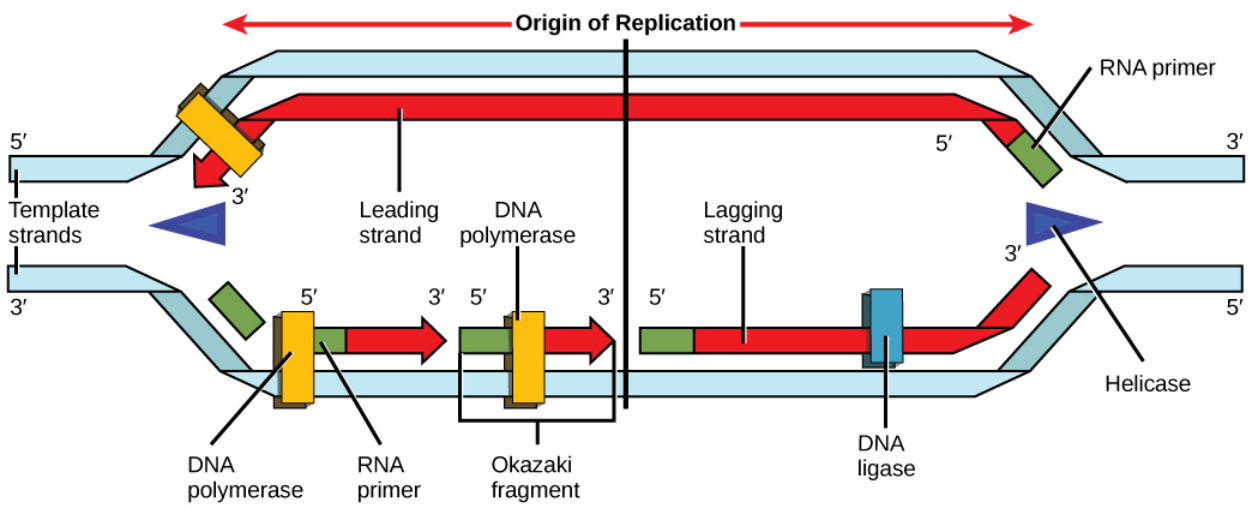


Figure 8.2.3**:** A replication fork is formed by the opening of the origin of replication, and helicase separates the DNA strands. An RNA primer is synthesized, and is elongated by the DNA polymerase. On the leading strand, DNA is synthesized continuously, whereas on the lagging strand, DNA is synthesized in short stretches. The DNA fragments are joined by DNA ligase (not shown).

You isolate a cell strain in which the joining together of Okazaki fragments is impaired and suspect that a mutation has occurred in an enzyme found at the replication fork. Which enzyme is most likely to be mutated?

Telomere Replication

Because eukaryotic chromosomes are linear, DNA replication comes to the end of a line in eukaryotic chromosomes. As you have learned, the DNA polymerase enzyme can add nucleotides in only one direction. In the leading strand, synthesis continues until the end of the chromosome is reached; however, on the lagging strand there is no place for a primer to be made for the DNA fragment to be copied at the end of the chromosome. This presents a problem for the cell because the ends remain unpaired, and over time these ends get progressively shorter as cells continue to divide. The ends of the linear chromosomes are known as telomeres, which have repetitive sequences that do not code for a particular gene. As a consequence, it is telomeres that are shortened with each round of DNA replication instead of genes. For example, in humans, a six base-pair sequence, TTAGGG, is repeated 100 to 1000 times. The discovery of the enzyme telomerase (Figure 8.2.4) helped in the understanding of how chromosome ends are maintained. The telomerase attaches to the end of the chromosome, and complementary bases to the RNA template are added on the end of the DNA strand. Once the lagging strand template is sufficiently elongated, DNA polymerase can now add nucleotides that are complementary to the ends of the chromosomes. Thus, the ends of the chromosomes are replicated.

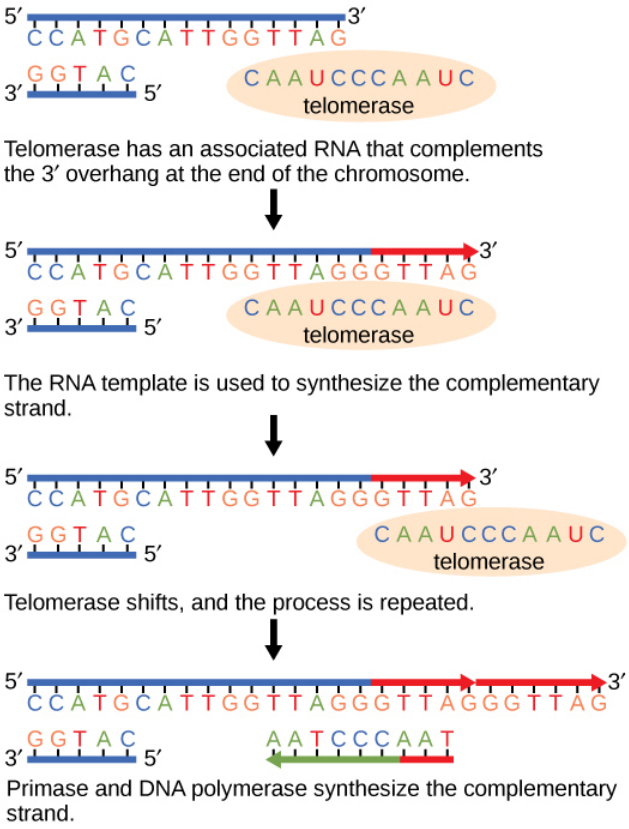


Figure 8.2.4**:** The ends of linear chromosomes are maintained by the action of the telomerase enzyme.

Telomerase is typically found to be active in germ cells, adult stem cells, and some cancer cells. For her discovery of telomerase and its action, Elizabeth Blackburn (Figure 8.2.5) received the Nobel Prize for Medicine and Physiology in 2009.



Figure 8.2.5**:** Elizabeth Blackburn, 2009 Nobel Laureate, was the scientist who discovered how telomerase works. (credit: U.S. Embassy, Stockholm, Sweden)

Telomerase is not active in adult somatic cells. Adult somatic cells that undergo cell division continue to have their telomeres shortened. This essentially means that telomere shortening is associated with aging. In 2010, scientists found that telomerase can reverse some age-related conditions in mice, and this may have potential in regenerative medicine.[1] Telomerase-deficient mice were used in these studies; these mice have tissue atrophy, stem-cell depletion, organ system failure, and impaired tissue injury responses. Telomerase reactivation in these mice caused extension of telomeres, reduced DNA damage, reversed neurodegeneration, and improved functioning of the testes, spleen, and intestines. Thus, telomere reactivation may have potential for treating age-related diseases in humans.

DNA Replication in Prokaryotes

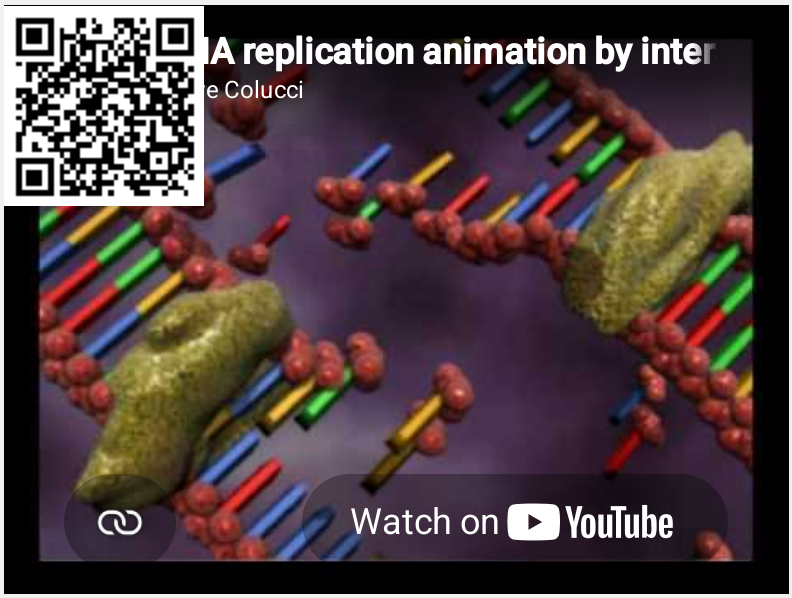
Recall that the prokaryotic chromosome is a circular molecule with a less extensive coiling structure than eukaryotic chromosomes. The eukaryotic chromosome is linear and highly coiled around proteins. While there are many similarities in the DNA replication process, these structural differences necessitate some differences in the DNA replication process in these two life forms.

DNA replication has been extremely well-studied in prokaryotes, primarily because of the small size of the genome and large number of variants available. *Escherichia coli* has 4.6 million base pairs in a single circular chromosome, and all of it gets replicated in approximately 42 minutes, starting from a single origin of replication and proceeding around the chromosome in both directions. This means that approximately 1000 nucleotides are added per second. The process is much more rapid than in eukaryotes. Table 8.2.1 summarizes the differences between prokaryotic and eukaryotic replications.

Table 8.2.1**:** Differences between Prokaryotic and Eukaryotic Replications

Property	Prokaryotes	Eukaryotes
Origin of replication	Single	Multiple
Rate of replication	1000 nucleotides/s	50 to 100 nucleotides/s
Chromosome structure	circular	linear
Telomerase	Not present	Present

CONCEPT IN ACTION



Click through a tutorial on DNA replication.

DNA Repair

DNA polymerase can make mistakes while adding nucleotides. It edits the DNA by proofreading every newly added base. Incorrect bases are removed and replaced by the correct base, and then polymerization continues (Figure 8.2.6**a**). Most mistakes are corrected during replication, although when this does not happen, the mismatch repair mechanism is employed. Mismatch repair enzymes recognize the wrongly incorporated base and excise it from the DNA, replacing it with the correct base (Figure 8.2.6**b**). In yet another type of repair, nucleotide excision repair, the DNA double strand is unwound and separated, the incorrect bases are removed along with a few bases on the 5' and 3' end, and these are replaced by copying the template with the help of DNA polymerase (Figure 8.2.6**c**). Nucleotide excision repair is particularly important in correcting thymine dimers, which are primarily caused by ultraviolet light. In a thymine dimer, two thymine nucleotides adjacent to each other on one strand are covalently bonded

to each other rather than their complementary bases. If the dimer is not removed and repaired it will lead to a mutation. Individuals with flaws in their nucleotide excision repair genes show extreme sensitivity to sunlight and develop skin cancers early in life.

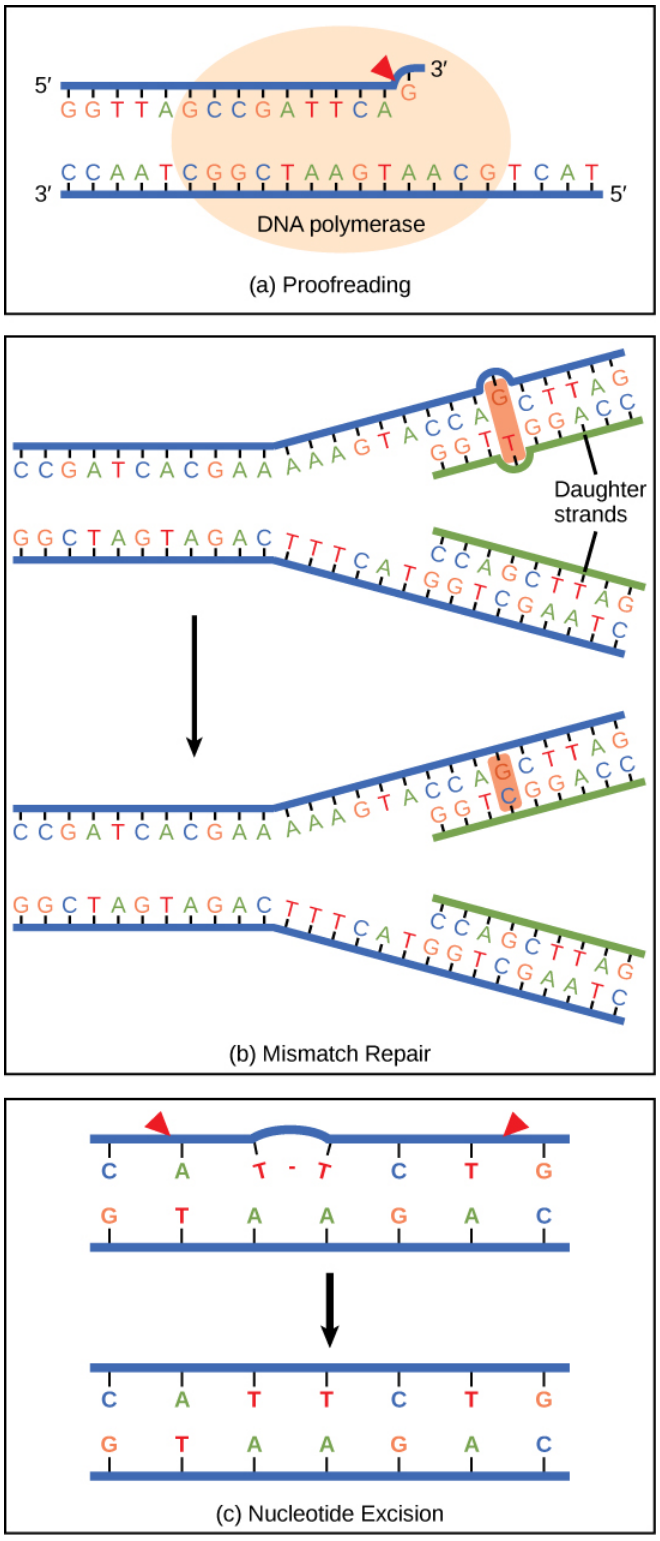


Figure 8.2.6**:** Proofreading by DNA polymerase (a) corrects errors during replication. In mismatch repair (b), the incorrectly added base is detected after replication. The mismatch repair proteins detect this base and remove it from the newly synthesized strand by nuclease action. The gap is now filled with the correctly paired base. Nucleotide excision (c) 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.

Most mistakes are corrected; if they are not, they may result in a mutation—defined as a permanent change in the DNA sequence. Mutations in repair genes may lead to serious consequences like cancer.

Summary

DNA replicates by a semi-conservative method in which each of the two parental DNA strands act as a template for new DNA to be synthesized. After replication, each DNA has one parental or “old” strand, and one daughter or “new” strand.

Replication in eukaryotes starts at multiple origins of replication, while replication in prokaryotes starts from a single origin of replication. The DNA is opened with enzymes, resulting in the formation of the replication fork. Primase synthesizes an RNA primer to initiate synthesis by DNA polymerase, which can add nucleotides in only one direction. One strand is synthesized continuously in the direction of the replication fork; this is called the leading strand. The other strand is synthesized in a direction away from the replication fork, in short stretches of DNA known as Okazaki fragments. This strand is known as the lagging strand. Once replication is completed, the RNA primers are replaced by DNA nucleotides and the DNA is sealed with DNA ligase.

The ends of eukaryotic chromosomes pose a problem, as polymerase is unable to extend them without a primer. Telomerase, an enzyme with an inbuilt RNA template, extends the ends by copying the RNA template and extending one end of the chromosome. DNA polymerase can then extend the DNA using the primer. In this way, the ends of the chromosomes are protected. Cells have mechanisms for repairing DNA when it becomes damaged or errors are made in replication. These mechanisms include mismatch repair to replace nucleotides that are paired with a non-complementary base and nucleotide excision repair, which removes bases that are damaged such as thymine dimers.

Art Connections

Figure 8.2.3: You isolate a cell strain in which the joining together of Okazaki fragments is impaired and suspect that a mutation has occurred in an enzyme found at the replication fork. Which enzyme is most likely to be mutated?

Answer

Ligase, as this enzyme joins together Okazaki fragments.

Footnotes

1. 1 Mariella Jaskelioff, et al., “Telomerase reactivation reverses tissue degeneration in aged telomerase-deficient mice,” *Nature*, 469 (2011):102–7.

Glossary

DNA ligase

the enzyme that catalyzes the joining of DNA fragments together

DNA polymerase

an enzyme that synthesizes a new strand of DNA complementary to a template strand

helicase

an enzyme that helps to open up the DNA helix during DNA replication by breaking the hydrogen bonds

lagging strand

during replication of the 3' to 5' strand, the strand that is replicated in short fragments and away from the replication fork

leading strand

the strand that is synthesized continuously in the 5' to 3' direction that is synthesized in the direction of the replication fork

mismatch repair

a form of DNA repair in which non-complementary nucleotides are recognized, excised, and replaced with correct nucleotides

mutation

a permanent variation in the nucleotide sequence of a genome

nucleotide excision repair
a form of DNA repair in which the DNA molecule is unwound and separated in the region of the nucleotide damage, the damaged nucleotides are removed and replaced with new nucleotides using the complementary strand, and the DNA strand is resealed and allowed to rejoin its complement

Okazaki fragments
the DNA fragments that are synthesized in short stretches on the lagging strand

primer
a short stretch of RNA nucleotides that is required to initiate replication and allow DNA polymerase to bind and begin replication

replication fork
the Y-shaped structure formed during the initiation of replication

semiconservative replication
the method used to replicate DNA in which the double-stranded molecule is separated and each strand acts as a template for a new strand to be synthesized, so the resulting DNA molecules are composed of one new strand of nucleotides and one old strand of nucleotides

telomerase
an enzyme that contains a catalytic part and an inbuilt RNA template; it functions to maintain telomeres at chromosome ends

telomere
the DNA at the end of linear chromosomes

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8.3: Transcription

In both prokaryotes and eukaryotes, the second function of DNA (the first was replication) is to provide the information needed to construct the proteins necessary so that the cell can perform all of its functions. To do this, the DNA is "read" or transcribed into an mRNA molecule. The mRNA then provides the code to form a protein by a process called translation. Through the processes of transcription and translation, a protein is built with a specific sequence of amino acids that was originally encoded in the DNA. This module discusses the details of transcription.

The Central Dogma: DNA Encodes RNA; RNA Encodes Protein

The flow of genetic information in cells from DNA to mRNA to protein is described by the central dogma (Figure 8.3.1), which states that genes specify the sequences of mRNAs, which in turn specify the sequences of proteins.

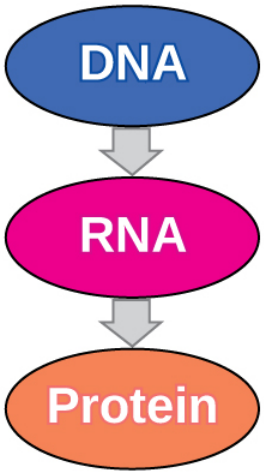


Figure 8.3.1: The central dogma states that DNA encodes RNA, which in turn encodes protein.

The copying of DNA to mRNA is relatively straightforward, with one nucleotide being added to the mRNA strand for every complementary nucleotide read in the DNA strand. The translation to protein is more complex because groups of three mRNA nucleotides correspond to one amino acid of the protein sequence. However, as we shall see in the next module, the translation to protein is still systematic, such that nucleotides 1 to 3 correspond to amino acid 1, nucleotides 4 to 6 correspond to amino acid 2, and so on.

Transcription: from DNA to mRNA

Both prokaryotes and eukaryotes perform fundamentally the same process of transcription, with the important difference of the membrane-bound nucleus in eukaryotes. With the genes bound in the nucleus, transcription occurs in the nucleus of the cell and the mRNA transcript must be transported to the cytoplasm. The prokaryotes, which include bacteria and archaea, lack membrane-bound nuclei and other organelles, and transcription occurs in the cytoplasm of the cell. In both prokaryotes and eukaryotes, transcription occurs in three main stages: initiation, elongation, and termination.

Initiation

Transcription requires the DNA double helix to partially unwind in the region of mRNA synthesis. The region of unwinding is called a transcription bubble. The DNA sequence onto which the proteins and enzymes involved in transcription bind to initiate the process is called a promoter. 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 of the time, some of the time, or hardly at all (Figure 8.3.2).

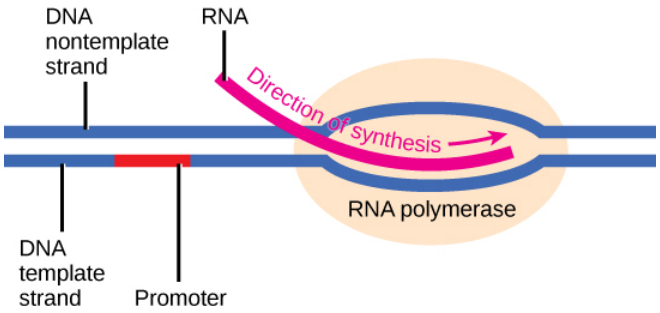


Figure 8.3.2**:** The initiation of transcription begins when DNA is unwound, forming a transcription bubble. Enzymes and other proteins involved in transcription bind at the promoter.

Elongation

Transcription always proceeds from one of the two DNA strands, which is called the template strand. The mRNA product is complementary to the template strand and is almost identical to the other DNA strand, called the nontemplate strand, with the exception that RNA contains a uracil (U) in place of the thymine (T) found in DNA. During elongation, an enzyme called RNA polymerase proceeds along the DNA template adding nucleotides by base pairing with the DNA template in a manner similar to DNA replication, with the difference that an RNA strand is being synthesized that does not remain bound to the DNA template. As elongation proceeds, the DNA is continuously unwound ahead of the core enzyme and rewound behind it (Figure 8.3.3).

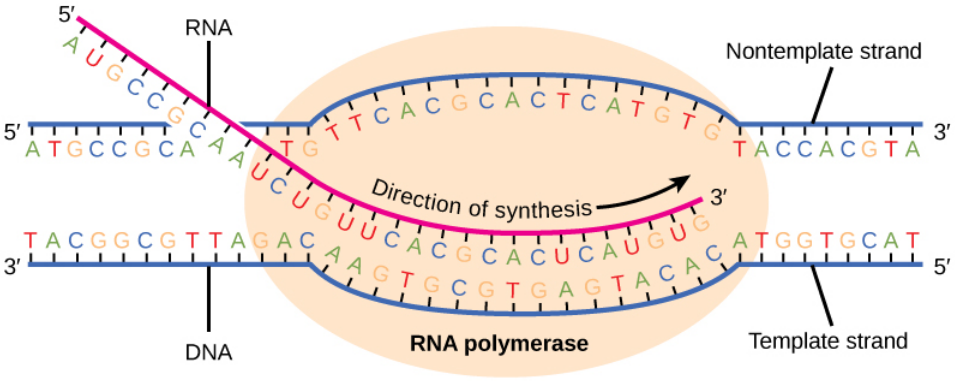


Figure 8.3.3**:** During elongation, RNA polymerase tracks along the DNA template, synthesizes mRNA in the 5' to 3' direction, and unwinds then rewinds the DNA as it is read.

Termination

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, but both involve repeated nucleotide sequences in the DNA template that result in RNA polymerase stalling, leaving the DNA template, and freeing the mRNA transcript.

On termination, the process of transcription is complete. In a prokaryotic cell, by the time termination occurs, the transcript would already have been used to partially synthesize numerous copies of the encoded protein because these processes can occur concurrently using multiple ribosomes (polyribosomes) (Figure 8.3.4). In contrast, the presence of a nucleus in eukaryotic cells precludes simultaneous transcription and translation.

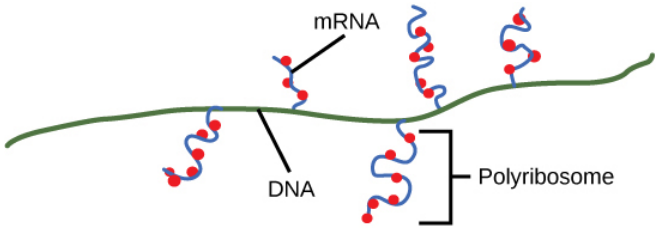


Figure 8.3.4**:** Multiple polymerases can transcribe a single bacterial gene while numerous ribosomes concurrently translate the mRNA transcripts into polypeptides. In this way, a specific protein can rapidly reach a high concentration in the bacterial cell.

Eukaryotic RNA Processing

The newly transcribed eukaryotic mRNAs must undergo several processing steps before they can be transferred from the nucleus to the cytoplasm and translated into a protein. The additional steps involved in eukaryotic mRNA maturation create a molecule that is much more stable than a prokaryotic mRNA. For example, eukaryotic mRNAs last for several hours, whereas the typical prokaryotic mRNA lasts no more than five seconds.

The mRNA transcript is first coated in RNA-stabilizing proteins to prevent it from degrading while it is processed and exported out of the nucleus. This occurs while the pre-mRNA still is being synthesized by adding a special nucleotide “cap” to the 5' end of the growing transcript. In addition to preventing degradation, factors involved in protein synthesis recognize the cap to help initiate translation by ribosomes.

Once elongation is complete, an enzyme then adds a string of approximately 200 adenine residues to the 3' end, called the poly-A tail. This modification further protects the pre-mRNA from degradation and signals to cellular factors that the transcript needs to be exported to the cytoplasm.

Eukaryotic genes are composed of protein-coding sequences called exons (*ex*-on signifies that they are *ex*pressed) and *int*ervening sequences called introns (*int*-ron denotes their *int*ervening role). Introns are removed from the pre-mRNA during processing. Intron sequences in mRNA do not encode functional proteins. It is essential that all of a pre-mRNA’s introns be completely and precisely removed before protein synthesis so that the exons join together to code for the correct amino acids. If the process errs by even a single nucleotide, the sequence of the rejoined exons would be shifted, and the resulting protein would be nonfunctional. The process of removing introns and reconnecting exons is called splicing (Figure 8.3.5). Introns are removed and degraded while the pre-mRNA is still in the nucleus.

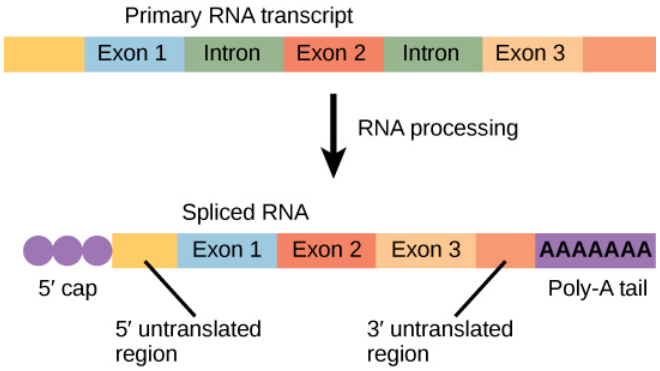


Figure 8.3.5**:** Eukaryotic mRNA contains introns that must be spliced out. A 5' cap and 3' tail are also added.

Summary

In prokaryotes, mRNA synthesis is initiated at a promoter sequence on the DNA template. Elongation synthesizes new mRNA. Termination liberates the mRNA and occurs by mechanisms that stall the RNA polymerase and cause it to fall off the DNA template. Newly transcribed eukaryotic mRNAs are modified with a cap and a poly-A tail. These structures protect the mature mRNA from degradation and help export it from the nucleus. Eukaryotic mRNAs also undergo splicing, in which introns are removed and exons are reconnected with single-nucleotide accuracy. Only finished mRNAs are exported from the nucleus to the cytoplasm.

Glossary

exon

a sequence present in protein-coding mRNA after completion of pre-mRNA splicing

intron

non–protein-coding intervening sequences that are spliced from mRNA during processing

mRNA

messenger RNA; a form of RNA that carries the nucleotide sequence code for a protein sequence that is translated into a polypeptide sequence

nontemplate strand
the strand of DNA that is not used to transcribe mRNA; this strand is identical to the mRNA except that T nucleotides in the DNA are replaced by U nucleotides in the mRNA

promoter
a sequence on DNA to which RNA polymerase and associated factors bind and initiate transcription

RNA polymerase
an enzyme that synthesizes an RNA strand from a DNA template strand

splicing
the process of removing introns and reconnecting exons in a pre-mRNA

template strand
the strand of DNA that specifies the complementary mRNA molecule

transcription bubble
the region of locally unwound DNA that allows for transcription of mRNA

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8.4: Translation

The synthesis of proteins is one of a cell's most energy-consuming metabolic processes. In turn, proteins account for more mass than any other component of living organisms (with the exception of water), and proteins perform a wide variety of the functions of a cell. The process of translation, or protein synthesis, involves decoding an mRNA message into a polypeptide product. Amino acids are covalently strung together in lengths ranging from approximately 50 amino acids to more than 1,000.

The Protein Synthesis Machinery

In addition to the mRNA template, many other molecules contribute to the process of translation. The composition of each component may vary across species; for instance, ribosomes may consist of different numbers of ribosomal RNAs (rRNA) and polypeptides depending on the organism. However, the general structures and functions of the protein synthesis machinery are comparable from bacteria to human cells. Translation requires the input of an mRNA template, ribosomes, tRNAs, and various enzymatic factors (Figure 8.4.1).

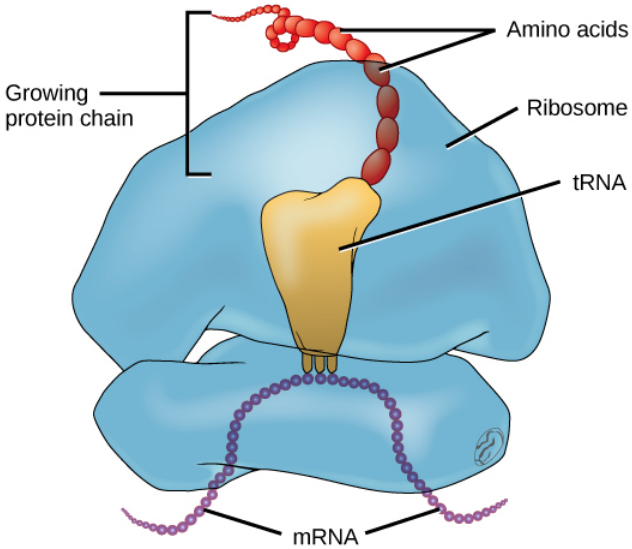


Figure 8.4.1: The protein synthesis machinery includes the large and small subunits of the ribosome, mRNA, and tRNA. (credit: modification of work by NIGMS, NIH)

In *E. coli*, there are 200,000 ribosomes present in every cell at any given time. A ribosome is a complex macromolecule composed of structural and catalytic rRNAs, and many distinct polypeptides. In eukaryotes, the nucleolus is completely specialized for the synthesis and assembly of rRNAs.

Ribosomes are located in the cytoplasm in prokaryotes and in the cytoplasm and endoplasmic reticulum of eukaryotes. Ribosomes are made up of a large and a small subunit that come together for translation. The small subunit is responsible for binding the mRNA template, whereas the large subunit sequentially binds tRNAs, a type of RNA molecule that brings amino acids to the growing chain of the polypeptide. Each mRNA molecule is simultaneously translated by many ribosomes, all synthesizing protein in the same direction.

Depending on the species, 40 to 60 types of tRNA 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. Therefore, tRNAs are the molecules that actually "translate" the language of RNA into the language of proteins. For each tRNA to function, it must have its specific amino acid bonded to it. In the process of tRNA "charging," each tRNA molecule is bonded to its correct amino acid.

The Genetic Code

To summarize what we know to this point, the cellular process of transcription generates messenger RNA (mRNA), a mobile molecular copy of one or more genes with an alphabet of A, C, G, and uracil (U). Translation of the mRNA template converts nucleotide-based genetic information into a protein product. Protein sequences consist of 20 commonly occurring amino acids;

therefore, it can be said that the protein alphabet consists of 20 letters. Each amino acid is defined by a three-nucleotide sequence called the triplet codon. The relationship between a nucleotide codon and its corresponding amino acid is called the genetic code.

Given the different numbers of “letters” in the mRNA and protein “alphabets,” combinations of nucleotides corresponded to single amino acids. Using a three-nucleotide code means that there are a total of 64 (4 × 4 × 4) possible combinations; therefore, a given amino acid is encoded by more than one nucleotide triplet (Figure 8.4.2).

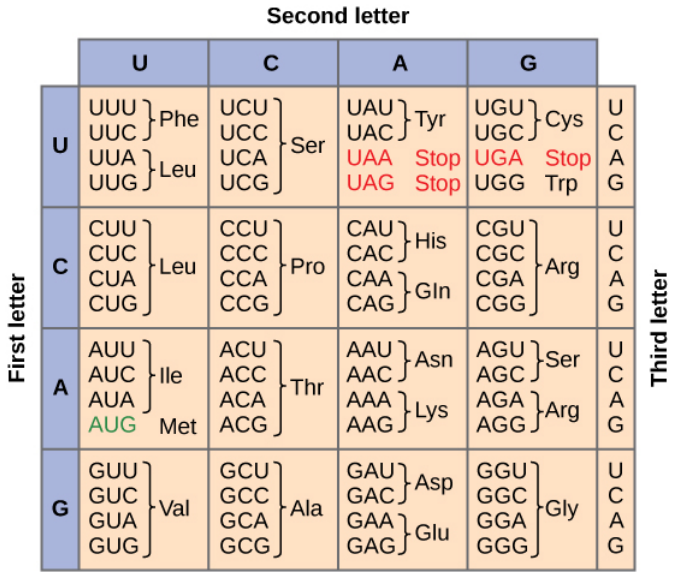


Figure 8.4.2**:** This figure shows the genetic code for translating each nucleotide triplet, or codon, in mRNA into an amino acid or a termination signal in a nascent protein. (credit: modification of work by NIH)

Three of the 64 codons terminate protein synthesis and release the polypeptide from the translation machinery. These triplets are called stop codons. Another 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 near the 5' end of the mRNA. The genetic code is universal. With a few exceptions, virtually all species use the same genetic code for protein synthesis, which is powerful evidence that all life on Earth shares a common origin.

The Mechanism of Protein Synthesis

Just as with mRNA synthesis, protein synthesis can be divided into three phases: initiation, elongation, and termination. The process of translation is similar in prokaryotes and eukaryotes. Here we will explore how translation occurs in *E. coli*, a representative prokaryote, and specify any differences between prokaryotic and eukaryotic translation.

Protein synthesis begins with the formation of an initiation complex. In *E. coli*, this complex involves the small ribosome subunit, the mRNA template, three initiation factors, and a special initiator tRNA. The initiator tRNA interacts with the AUG start codon, and links to a special form of the amino acid methionine that is typically removed from the polypeptide after translation is complete.

In prokaryotes and eukaryotes, the basics of polypeptide elongation are the same, so we will review elongation from the perspective of *E. coli*. The large ribosomal subunit of *E. coli* consists of three compartments: the A site binds incoming charged tRNAs (tRNAs with their attached specific amino acids). The P site binds charged tRNAs carrying amino acids that have formed bonds with the growing polypeptide chain but have not yet dissociated from their corresponding tRNA. The E site releases dissociated tRNAs so they can be recharged with free amino acids. The ribosome shifts one codon at a time, catalyzing each process that occurs in the three sites. With each step, a charged tRNA enters the complex, the polypeptide becomes one amino acid longer, and an uncharged tRNA departs. The energy for each bond between amino acids is derived from GTP, a molecule similar to ATP (Figure 8.4.3). Amazingly, the *E. coli* translation apparatus takes only 0.05 seconds to add each amino acid, meaning that a 200-amino acid polypeptide could be translated in just 10 seconds.

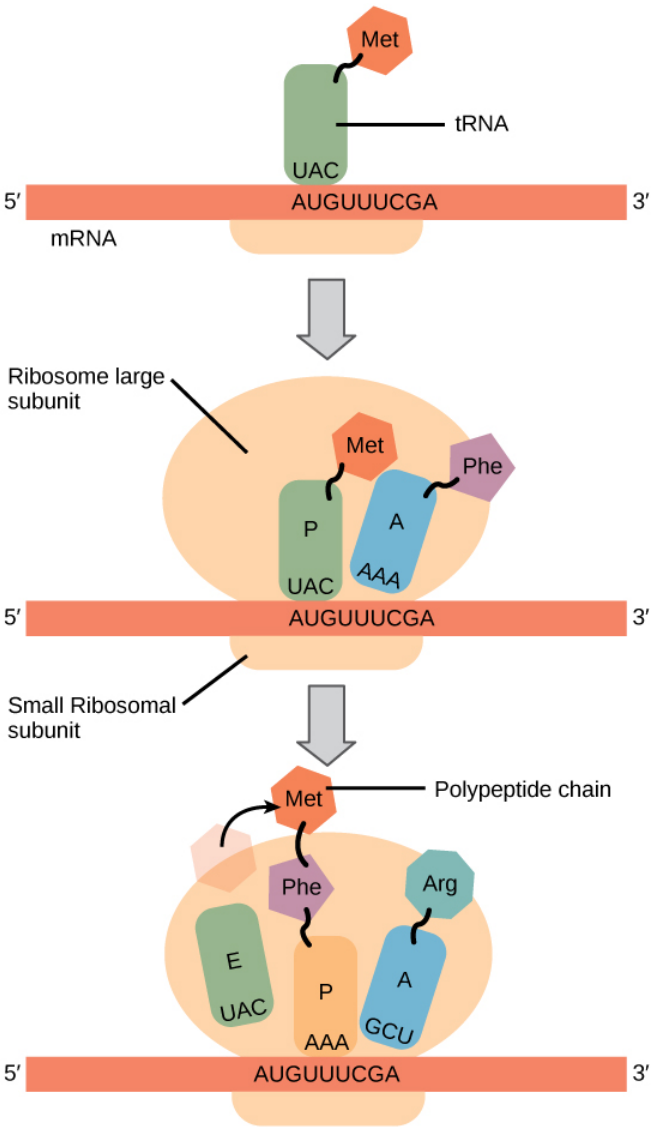


Figure 8.4.3**:** Translation begins when a tRNA anticodon recognizes a codon on the mRNA. The large ribosomal subunit joins the small subunit, and a second tRNA is recruited. As the mRNA moves relative to the ribosome, the polypeptide chain is formed. Entry of a release factor into the A site terminates translation and the components dissociate.

Termination of translation occurs when a stop codon (UAA, UAG, or UGA) is encountered. When the ribosome encounters the stop codon, the growing polypeptide is released and the ribosome subunits dissociate and leave the mRNA. After many ribosomes have completed translation, the mRNA is degraded so the nucleotides can be reused in another transcription reaction.

CONCEPT IN ACTION

Transcribe a gene and translate it to protein using complementary pairing and the genetic code at this site.

Summary

The central dogma describes the flow of genetic information in the cell from genes to mRNA to proteins. Genes are used to make mRNA by the process of transcription; mRNA is used to synthesize proteins by the process of translation. The genetic code is the correspondence between the three-nucleotide mRNA codon and an amino acid. The genetic code is "translated" by the tRNA molecules, which associate a specific codon with a specific amino acid. The genetic code is degenerate because 64 triplet codons in mRNA specify only 20 amino acids and three stop codons. This means that more than one codon corresponds to an amino acid. Almost every species on the planet uses the same genetic code.

The players in translation include the mRNA template, ribosomes, tRNAs, and various enzymatic factors. The small ribosomal subunit binds to the mRNA template. Translation begins at the initiating AUG on the mRNA. The formation of bonds occurs between sequential amino acids specified by the mRNA template according to the genetic code. The ribosome accepts charged tRNAs, and as it steps along the mRNA, it catalyzes bonding between the new amino acid and the end of the growing polypeptide. The entire mRNA is translated in three-nucleotide "steps" of the ribosome. When a stop codon is encountered, a release factor binds and dissociates the components and frees the new protein.

Glossary

codon
: three consecutive nucleotides in mRNA that specify the addition of a specific amino acid or the release of a polypeptide chain during translation

genetic code
: the amino acids that correspond to three-nucleotide codons of mRNA

rRNA
: ribosomal RNA; molecules of RNA that combine to form part of the ribosome

stop codon
: one of the three mRNA codons that specifies termination of translation

start codon
: the AUG (or, rarely GUG) on an mRNA from which translation begins; always specifies methionine

tRNA
: transfer RNA; an RNA molecule that contains a specific three-nucleotide anticodon sequence to pair with the mRNA codon and also binds to a specific amino acid

Contributors and Attributions

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8.5: How Genes Are Regulated

For a cell to function properly, necessary proteins must be synthesized at the proper time. All organisms and cells control or regulate the transcription and translation of their DNA into protein. The process of turning on a gene to produce RNA and protein is called gene expression. Whether in a simple unicellular organism or in a complex multicellular 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.

Cells in multicellular organisms are specialized; cells in different tissues look very different and perform different functions. For example, a muscle cell is very different from a liver cell, which is very different from a skin cell. These differences are a consequence of the expression of different sets of genes in each of these cells. All cells have certain basic functions they must perform for themselves, such as converting the energy in sugar molecules into energy in ATP. Each cell also has many genes that are not expressed, and expresses many that are not expressed by other cells, such that it can carry out its specialized functions. In addition, cells will turn on or off certain genes at different times in response to changes in the environment or at different times during the development of the organism. Unicellular organisms, both eukaryotic and prokaryotic, also turn on and off genes in response to the demands of their environment so that they can respond to special conditions.

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 becomes a functional protein in a cell. The process occurs in both prokaryotic and eukaryotic cells, just in slightly different fashions.

Because prokaryotic organisms lack a cell nucleus, the processes of transcription and translation occur almost simultaneously. When the protein is no longer needed, transcription stops. As a result, the primary method to control what type and how much protein is expressed in a prokaryotic cell is through the regulation of DNA transcription into RNA. All the subsequent steps happen automatically. When more protein is required, more transcription occurs. Therefore, in prokaryotic cells, the control of gene expression is almost entirely at the transcriptional level.

The first example of such control was discovered using *E. coli* in the 1950s and 1960s by French researchers and is called the *lac* operon. The *lac* operon is a stretch of DNA with three adjacent genes that code for proteins that participate in the absorption and metabolism of lactose, a food source for *E. coli*. When lactose is not present in the bacterium's environment, the *lac* genes are transcribed in small amounts. When lactose is present, the genes are transcribed and the bacterium is able to use the lactose as a food source. The operon also contains a promoter sequence to which the RNA polymerase binds to begin transcription; between the promoter and the three genes is a region called the operator. When there is no lactose present, a protein known as a repressor binds to the operator and prevents RNA polymerase from binding to the promoter, except in rare cases. Thus very little of the protein products of the three genes is made. When lactose is present, an end product of lactose metabolism binds to the repressor protein and prevents it from binding to the operator. This allows RNA polymerase to bind to the promoter and freely transcribe the three genes, allowing the organism to metabolize the lactose.

Eukaryotic cells, in contrast, have intracellular organelles and are much more complex. Recall that in eukaryotic cells, the DNA is contained inside the cell's nucleus and it is transcribed into mRNA there. The newly synthesized mRNA is then transported out of the nucleus into the cytoplasm, where ribosomes translate the mRNA into protein. The processes of transcription and translation are physically separated by the nuclear membrane; transcription occurs only within the nucleus, and translation only occurs outside the nucleus in the cytoplasm. The regulation of gene expression can occur at all stages of the process (Figure 8.5.1). 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 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).

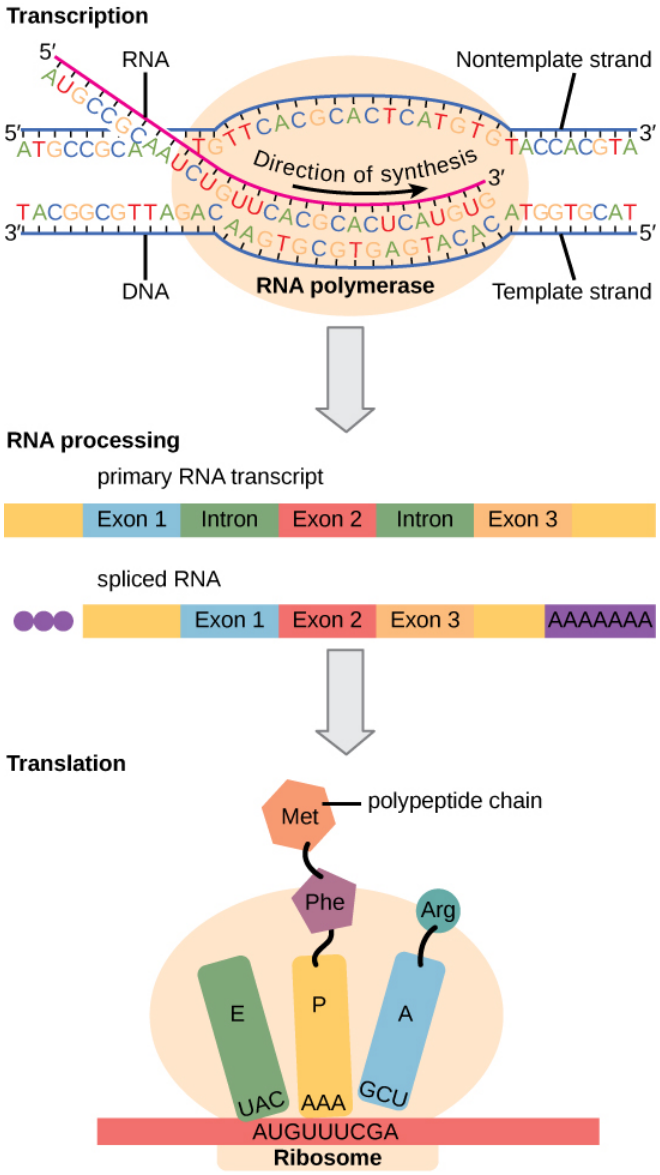


Figure 8.5.1**:** Eukaryotic gene expression is regulated during transcription and RNA processing, which take place in the nucleus, as well as during protein translation, which takes place in the cytoplasm. Further regulation may occur through post-translational modifications of proteins.

The differences in the regulation of gene expression between prokaryotes and eukaryotes are summarized in Table 8.5.1.

Table 8.5.1**:** Differences in the Regulation of Gene Expression of Prokaryotic and Eukaryotic Organisms

Prokaryotic organisms	Eukaryotic organisms
Lack nucleus	Contain nucleus
RNA transcription and protein translation occur almost simultaneously	• RNA transcription occurs prior to protein translation, and it takes place in the nucleus. RNA translation to protein occurs in the cytoplasm. • RNA post-processing includes addition of a 5' cap, poly-A tail, and excision of introns and splicing of exons.
Gene expression is regulated primarily at the transcriptional level	Gene expression is regulated at many levels (epigenetic, transcriptional, post-transcriptional, translational, and post-translational)

EVOLUTION IN ACTION: Alternative RNA Splicing

In the 1970s, genes were first observed that exhibited alternative RNA splicing. Alternative RNA splicing is a mechanism that allows different protein products to be produced from one gene when different combinations of introns (and sometimes exons) are removed from the transcript (Figure 8.5.2). This alternative splicing can be haphazard, but more often it is controlled and acts as a mechanism of gene regulation, with the frequency of different splicing alternatives controlled by the cell as a way to control the production of different protein products in different cells, or at different stages of development. Alternative splicing is now understood to be a common mechanism of gene regulation in eukaryotes; according to one estimate, 70% of genes in humans are expressed as multiple proteins through alternative splicing.

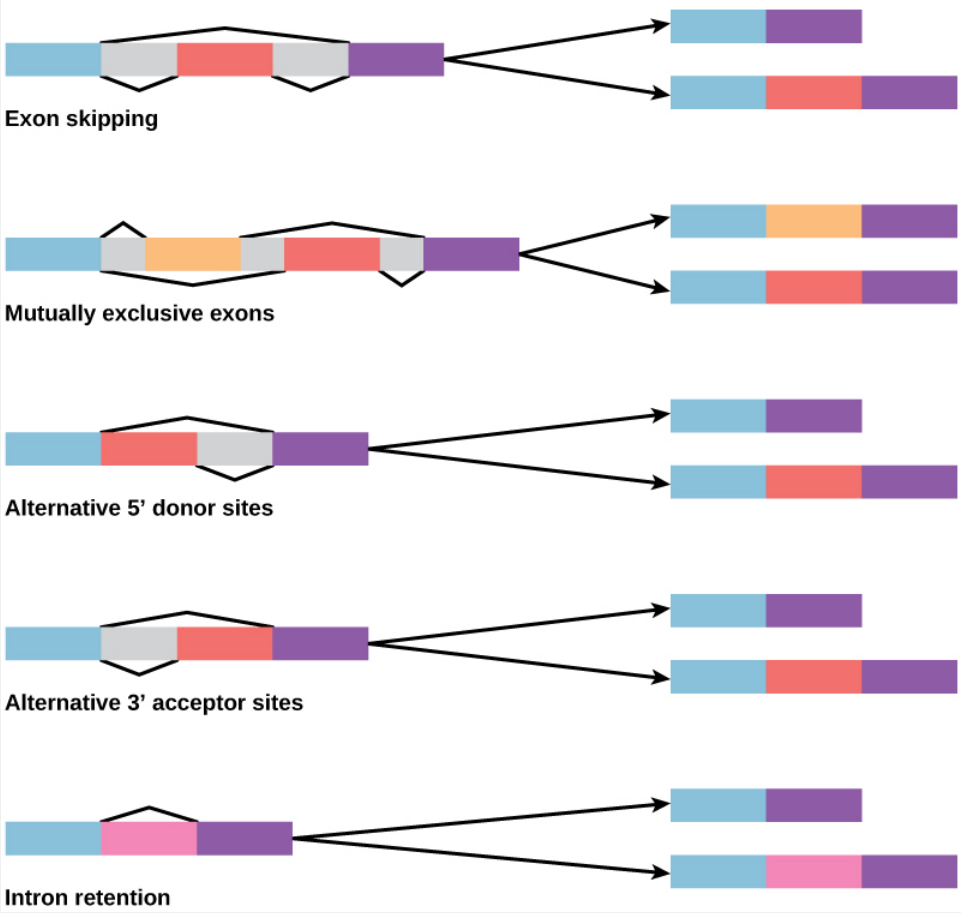


Figure 8.5.2**:** There are five basic modes of alternative splicing. Segments of pre-mRNA with exons shown in blue, red, orange, and pink can be spliced to produce a variety of new mature mRNA segments.

How could alternative splicing evolve? Introns have a beginning and ending recognition sequence, and it is easy to imagine the failure of the splicing mechanism to identify the end of an intron and find the end of the next intron, thus removing two introns and the intervening exon. In fact, there are mechanisms in place to prevent such exon skipping, but mutations are likely to lead to their failure. Such "mistakes" would more than likely produce a nonfunctional protein. Indeed, the cause of many genetic diseases is alternative splicing rather than mutations in a sequence. However, alternative splicing would create a protein variant without the loss of the original protein, opening up possibilities for adaptation of the new variant to new functions. Gene duplication has played an important role in the evolution of new functions in a similar way—by providing genes that may evolve without eliminating the original functional protein.

Summary

While all somatic cells within an organism contain the same DNA, not all cells within that organism express the same proteins. Prokaryotic organisms express the entire DNA they encode in every cell, but not necessarily all at the same time. Proteins are expressed only when they are needed. Eukaryotic organisms express a subset of the DNA that is encoded in any given cell. In each

cell type, the type and amount of protein is regulated by controlling gene expression. To express a protein, the DNA is first transcribed into RNA, which is then translated into proteins. In prokaryotic cells, these processes occur almost simultaneously. In eukaryotic cells, transcription occurs in the nucleus and is separate from the translation that occurs in the cytoplasm. Gene expression in prokaryotes is regulated only at the transcriptional level, whereas in eukaryotic cells, gene expression is regulated at the epigenetic, transcriptional, post-transcriptional, translational, and post-translational levels.

Glossary

alternative RNA splicing
: a post-transcriptional gene regulation mechanism in eukaryotes in which multiple protein products are produced by a single gene through alternative splicing combinations of the RNA transcript

epigenetic
: describing non-genetic regulatory factors, such as changes in modifications to histone proteins and DNA that control accessibility to genes in chromosomes

gene expression
: processes that control whether a gene is expressed

post-transcriptional
: control of gene expression after the RNA molecule has been created but before it is translated into protein

post-translational
: control of gene expression after a protein has been created

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8.A: Molecular Biology (Exercises)

The Structure of DNA

Multiple Choice

Which of the following does cytosine pair with?

A. guanine
B. thymine
C. adenine
D. a pyrimidine

Answer

A

Prokaryotes contain a _____chromosome, and eukaryotes contain _____ chromosomes.

A. single-stranded circular; single-stranded linear
B. single-stranded linear; single-stranded circular
C. double-stranded circular; double-stranded linear
D. double-stranded linear; double-stranded circular

Answer

C

Free Response

Describe the organization of the eukaryotic chromosome.

Answer

The DNA is wound around proteins called histones. The histones then stack together in a compact form that creates a fiber that is 30-nm thick. The fiber is further coiled for greater compactness. During metaphase of mitosis, the chromosome is at its most compact to facilitate chromosome movement. During interphase, there are denser areas of chromatin, called heterochromatin, that contain DNA that is not expressed, and less dense euchromatin that contains DNA that is expressed.

Describe the structure and complementary base pairing of DNA.

Answer

A single strand of DNA is a polymer of nucleic acids joined covalently between the phosphate group of one and the deoxyribose sugar of the next to form a “backbone” from which the nitrogenous bases stick out. In its natural state, DNA has two strands wound around each other in a double helix. The bases on each strand are bonded to each other with hydrogen bonds. Only specific bases bond with each other; adenine bonds with thymine, and cytosine bonds with guanine.

DNA Replication

Multiple Choice

DNA replicates by which of the following models?

A. conservative
B. semiconservative
C. dispersive
D. none of the above

Answer

B

The initial mechanism for repairing nucleotide errors in DNA is _____.

A. mismatch repair
B. DNA polymerase proofreading
C. nucleotide excision repair
D. thymine dimers

Answer

B

Free Response

How do the linear chromosomes in eukaryotes ensure that its ends are replicated completely?

Answer

Telomerase has an inbuilt RNA template that extends the 3' end, so a primer is synthesized and extended. Thus, the ends are protected.

Transcription

Multiple Choice

A promoter is _____.

A. a specific sequence of DNA nucleotides
B. a specific sequence of RNA nucleotides
C. a protein that binds to DNA
D. an enzyme that synthesizes RNA

Answer

A

Portions of eukaryotic mRNA sequence that are removed during RNA processing are _____.

A. exons
B. caps
C. poly-A tails
D. introns

Answer

D

Translation

Multiple Choice

The RNA components of ribosomes are synthesized in the _____.

A. cytoplasm
B. nucleus
C. nucleolus
D. endoplasmic reticulum

Answer

C

How long would the peptide be that is translated from this MRNA sequence: 5'-AUGGGCUACCGA-3'?

A. 0
B. 2
C. 3
D. 4

Answer

D

Free Response

Transcribe and translate the following DNA sequence (nontemplate strand): 5'-ATGGCCGGTTATTAAGCA-3'

Answer

The mRNA would be: 5'-AUGGCCGGUUAUUAAGCA-3'. The protein would be: MAGY. Even though there are six codons, the fifth codon corresponds to a stop, so the sixth codon would not be translated.

How Genes Are Regulated

Multiple Choice

Control of gene expression in eukaryotic cells occurs at which level(s)?

A. only the transcriptional level
B. epigenetic and transcriptional levels
C. epigenetic, transcriptional, and translational levels
D. epigenetic, transcriptional, post-transcriptional, translational, and post-translational levels

Answer

D

Post-translational control refers to:

A. regulation of gene expression after transcription
B. regulation of gene expression after translation
C. control of epigenetic activation
D. period between transcription and translation

Answer

B

Free Response

Describe how controlling gene expression will alter the overall protein levels in the cell.

Answer

The cell controls which protein is expressed, and to what level that protein is expressed, in the cell. Prokaryotic cells alter the transcription rate to turn genes on or off. This method will increase or decrease protein levels in response to what is needed by the cell. Eukaryotic cells change the accessibility (epigenetic), transcription, or translation of a gene. This will alter the amount of RNA, and the lifespan of the RNA, to alter the amount of protein that exists. Eukaryotic cells also change the protein's translation to increase or decrease its overall levels. Eukaryotic organisms are much more complex and can manipulate protein levels by changing many stages in the process.

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CHAPTER OVERVIEW

9: Biotechnology

9.1: Cloning and Genetic Engineering

9.2: Biotechnology in Medicine and Agriculture

9.3: Genomics and Proteomics

9.A: Biotechnology (Exercises)

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9.1: Cloning and Genetic Engineering

Biotechnology is the use of artificial methods to modify the genetic material of living organisms or cells to produce novel compounds or to perform new functions. Biotechnology has been used for improving livestock and crops since the beginning of agriculture through selective breeding. Since the discovery of the structure of DNA in 1953, and particularly since the development of tools and methods to manipulate DNA in the 1970s, biotechnology has become synonymous with the manipulation of organisms' DNA at the molecular level. The primary applications of this technology are in medicine (for the production of vaccines and antibiotics) and in agriculture (for the genetic modification of crops). Biotechnology also has many industrial applications, such as fermentation, the treatment of oil spills, and the production of biofuels, as well as many household applications such as the use of enzymes in laundry detergent.

Manipulating Genetic Material

To accomplish the applications described above, biotechnologists must be able to extract, manipulate, and analyze nucleic acids.

Review of Nucleic Acid Structure

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). The phosphate groups on these molecules each have a net negative charge. An entire set of DNA molecules in the nucleus of eukaryotic organisms is called the genome. DNA has two complementary strands linked by hydrogen bonds between the paired bases.

Unlike DNA in eukaryotic cells, RNA molecules leave the nucleus. Messenger RNA (mRNA) is analyzed most frequently because it represents the protein-coding genes that are being expressed in the cell.

Isolation of Nucleic Acids

To study or manipulate nucleic acids, the DNA must first be extracted from cells. Various techniques are used to extract different types of DNA (Figure 9.1.1). Most nucleic acid extraction techniques involve steps to break open the cell, and then the use of enzymatic reactions to destroy all undesired macromolecules. Cells are broken open using a detergent solution containing buffering compounds. To prevent degradation and contamination, macromolecules such as proteins and RNA are inactivated using enzymes. The DNA is then brought out of solution using alcohol. The resulting DNA, because it is made up of long polymers, forms a gelatinous mass.

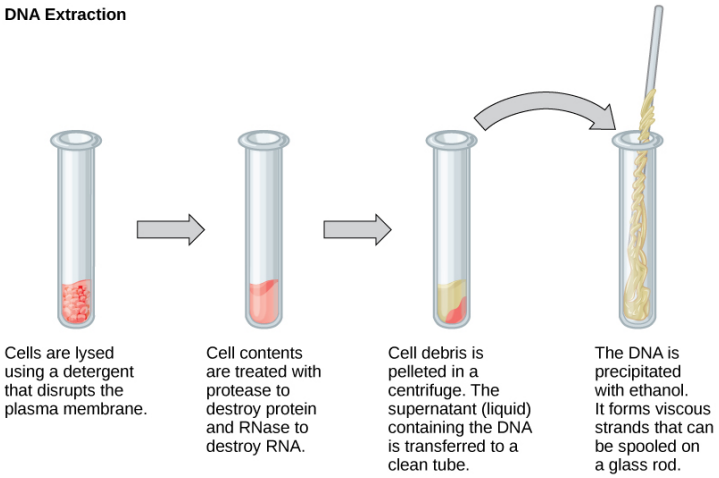


Figure 9.1.1**:** This diagram shows the basic method used for the extraction of DNA.

RNA is studied to understand gene expression patterns in cells. RNA is naturally very unstable because enzymes that break down RNA are commonly present in nature. Some are even secreted by our own skin and are very difficult to inactivate. Similar to DNA extraction, RNA extraction involves the use of various buffers and enzymes to inactivate other macromolecules and preserve only the RNA.

Gel Electrophoresis

Because nucleic acids are negatively charged ions at neutral or alkaline pH in an aqueous environment, they can be moved by an electric field. Gel electrophoresis is a technique used to separate charged molecules on the basis of size and charge. The nucleic acids can be separated as whole chromosomes or as fragments. The nucleic acids are loaded into a slot at one end of a gel matrix, an electric current is applied, and negatively charged molecules are pulled toward the opposite end of the gel (the end with the positive electrode). 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. The nucleic acids in a gel matrix are invisible until they are stained with a compound that allows them to be seen, such as a dye. Distinct fragments of nucleic acids appear as bands at specific distances from the top of the gel (the negative electrode end) that are based on their size (Figure 9.1.2). A mixture of many fragments of varying sizes appear as a long smear, whereas uncut genomic DNA is usually too large to run through the gel and forms a single large band at the top of the gel.

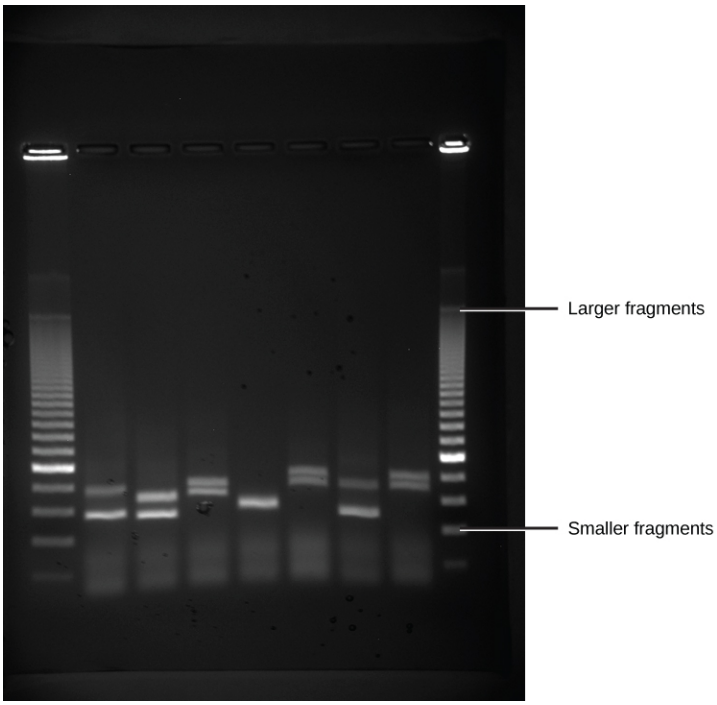


Figure 9.1.2: Shown are DNA fragments from six samples run on a gel, stained with a fluorescent dye and viewed under UV light. (credit: modification of work by James Jacob, Tompkins Cortland Community College)

Polymerase Chain Reaction

DNA analysis often requires focusing on one or more specific regions of the genome. It also frequently involves situations in which only one or a few copies of a DNA molecule are available for further analysis. These amounts are insufficient for most procedures, such as gel electrophoresis. Polymerase chain reaction (PCR)is a technique used to rapidly increase the number of copies of specific regions of DNA for further analyses (Figure 9.1.3). PCR uses a special form of DNA polymerase, the enzyme that replicates DNA, and other short nucleotide sequences called primers that base pair to a specific portion of the DNA being replicated. PCR is used for many purposes in laboratories. These include: 1) the identification of the owner of a DNA sample left at a crime scene; 2) paternity analysis; 3) the comparison of small amounts of ancient DNA with modern organisms; and 4) determining the sequence of nucleotides in a specific region.

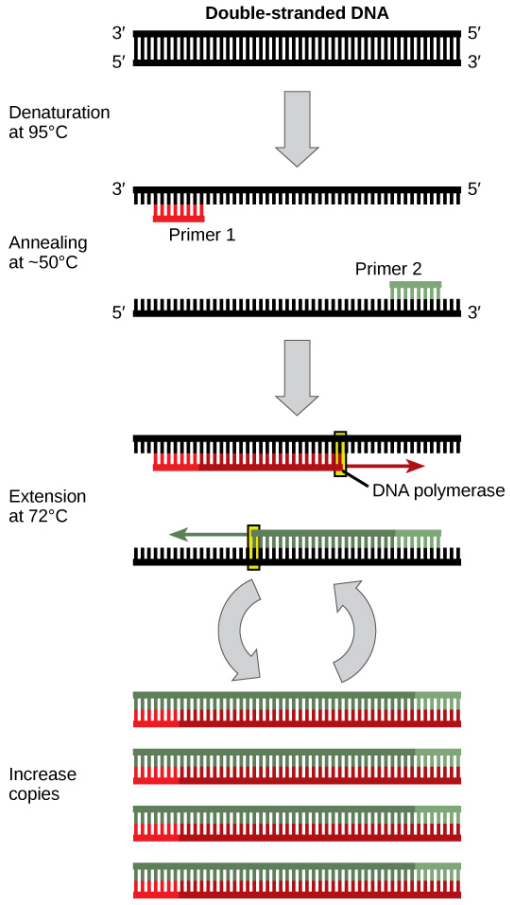


Figure 9.1.3**:** Polymerase chain reaction, or PCR, is used to produce many copies of a specific sequence of DNA using a special form of DNA polymerase.

Cloning

In general, cloning means the creation of a perfect replica. Typically, the word is used to describe the creation of a genetically identical copy. 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 copy short stretches of DNA—a process that is referred to as molecular cloning.

Molecular Cloning

Cloning allows for the creation of multiple copies of genes, expression of genes, and study of specific genes. To get the DNA fragment into a bacterial cell in a form that will be copied or expressed, the fragment is first inserted into a plasmid. A plasmid (also called a vector in this context) is a small circular DNA molecule that replicates independently of the chromosomal DNA in bacteria. In cloning, the plasmid molecules can be used to provide a "vehicle" in which to insert a desired DNA fragment. Modified plasmids are usually reintroduced into a bacterial host for replication. As the bacteria divide, they copy their own DNA (including the plasmids). The inserted DNA fragment is copied along with the rest of the bacterial DNA. In a bacterial cell, the fragment of DNA from the human genome (or another organism that is being studied) is referred to as foreign DNA to differentiate it from the DNA of the bacterium (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 highly engineered as vectors for molecular cloning and for the subsequent large-scale production of important molecules, such as insulin. A valuable characteristic of plasmid vectors is the ease with which a foreign DNA fragment can be introduced. These plasmid vectors contain many short DNA sequences that can be cut with different commonly available restriction enzymes. Restriction enzymes (also called 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 enzymes make staggered cuts in the two strands of DNA, such that the cut ends have a 2- to 4-nucleotide single-stranded overhang. The sequence that is recognized by the restriction enzyme is a four- to eight-nucleotide sequence that is a palindrome. Like with a word palindrome, this means the sequence reads the same forward and backward. In most cases, the sequence reads the same forward on one strand and backward on the complementary strand. When a staggered cut is made in a sequence like this, the overhangs are complementary (Figure 9.1.4).

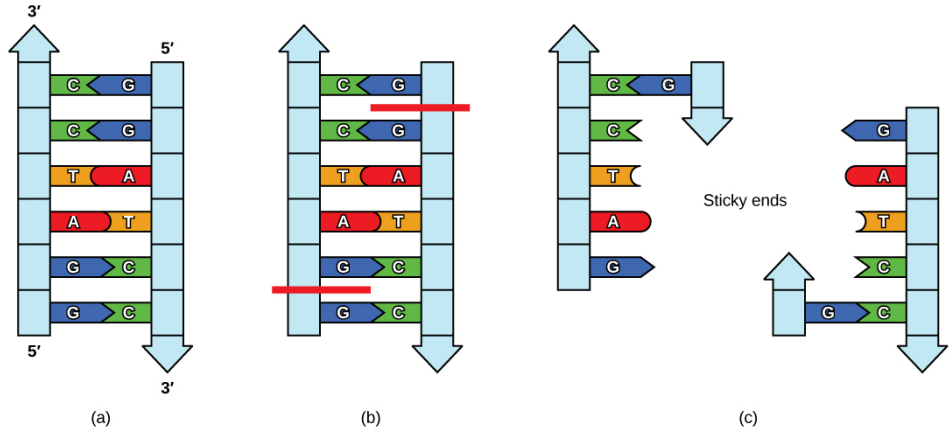


Figure 9.1.4**:** In this (a) six-nucleotide restriction enzyme recognition site, notice that the sequence of six nucleotides reads the same in the 5' to 3' direction on one strand as it does in the 5' to 3' direction on the complementary strand. This is known as a palindrome. (b) The restriction enzyme makes breaks in the DNA strands, and (c) the cut in the DNA results in “sticky ends”. Another piece of DNA cut on either end by the same restriction enzyme could attach to these sticky ends and be inserted into the gap made by this cut.

Because these overhangs are capable of coming back together by hydrogen bonding with complementary overhangs on a piece of DNA cut with the same restriction enzyme, these are called “sticky ends.” The process of forming hydrogen bonds between complementary sequences on single strands to form double-stranded DNA is called annealing. Addition of an enzyme called DNA ligase, which takes part in DNA replication in cells, permanently joins the DNA fragments when the sticky ends come together. In this way, any DNA fragment can be spliced between the two ends of a plasmid DNA that has been cut with the same restriction enzyme (Figure 9.1.5).

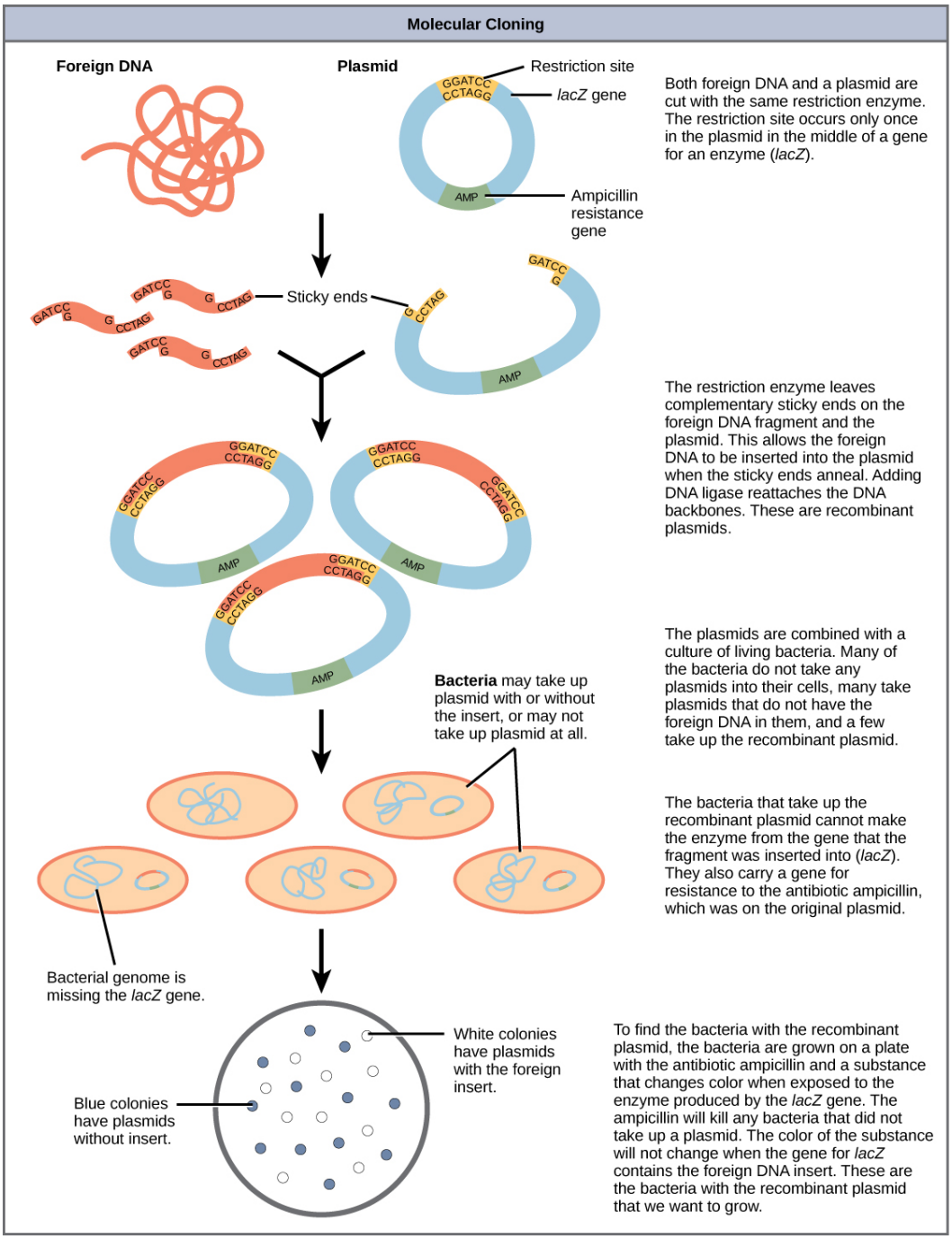


Figure 9.1.5**:** This diagram shows the steps involved in molecular cloning.

Plasmids with foreign DNA inserted into them are called recombinant DNA molecules because they contain new combinations of genetic material. Proteins that are produced from recombinant DNA molecules are called recombinant proteins. Not all recombinant plasmids are capable of expressing genes. 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.

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 the contribution of DNA from two individuals (parents), making it impossible to generate an identical copy or a clone of either parent. Recent advances in biotechnology have made it possible to reproductively clone mammals in the laboratory.

Natural sexual reproduction involves the union, during fertilization, of a sperm and an egg. Each of these gametes is haploid, meaning they contain one set of chromosomes in their nuclei. The resulting cell, or zygote, is then diploid and contains two sets of chromosomes. This cell divides mitotically to produce a multicellular organism. However, the union of just any two cells cannot produce a viable zygote; there are components in the cytoplasm of the egg cell that are essential for the early development of the embryo during its first few cell divisions. Without these provisions, there would be no subsequent development. Therefore, to produce a new individual, both a diploid genetic complement and an egg cytoplasm are required. The approach to producing an artificially cloned individual is to take the egg cell of one individual and to remove the haploid nucleus. Then a diploid nucleus from a body cell of a second individual, the donor, is put into the egg cell. The egg is then stimulated to divide so that development proceeds. This sounds simple, but in fact it takes many attempts before each of the steps is completed successfully.

The first cloned agricultural 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 six years and died of a lung tumor (Figure 9.1.6). There was speculation that because the cell DNA that gave rise to Dolly came from an older individual, the age of the DNA may have affected her life expectancy. Since Dolly, several species of animals (such as horses, bulls, and goats) have been successfully cloned.

There have been attempts at producing cloned human embryos as sources of embryonic stem cells. In the procedure, the DNA from an adult human is introduced into a human egg cell, which is then stimulated to divide. The technology is similar to the technology that was used to produce Dolly, but the embryo is never implanted into a surrogate mother. The cells produced are called embryonic stem cells because they have the capacity to develop into many different kinds of cells, such as muscle or nerve cells. The stem cells could be used to research and ultimately provide therapeutic applications, such as replacing damaged tissues. The benefit of cloning in this instance is that the cells used to regenerate new tissues would be a perfect match to the donor of the original DNA. For example, a leukemia patient would not require a sibling with a tissue match for a bone-marrow transplant.

ART CONNECTION

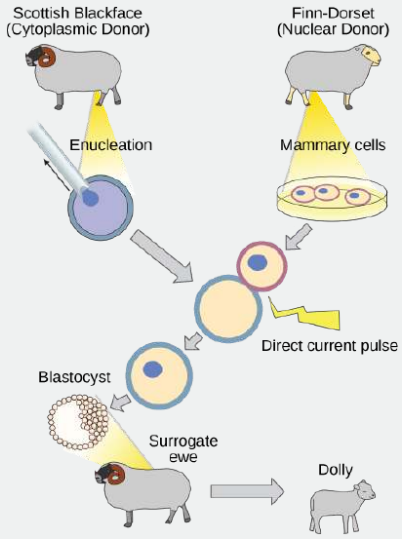


Figure 9.1.6**:** Dolly the sheep was the first agricultural animal to be cloned. To create Dolly, the nucleus was removed from a donor egg cell. The enucleated egg was placed next to the other cell, then they were shocked to fuse. They were shocked again to start division. The cells were allowed to divide for several days until an early embryonic stage was reached, before being implanted in a surrogate mother.

Why was Dolly a Finn-Dorset and not a Scottish Blackface sheep?

Genetic Engineering

Using recombinant DNA technology to modify an organism's DNA to achieve desirable traits is called genetic engineering. Addition of foreign DNA in the form of recombinant DNA vectors that are generated by molecular cloning is the most common method of genetic engineering. An 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. These applications will be examined in more detail in the next module.

CONCEPT IN ACTION



Watch this short video explaining how scientists create a transgenic animal.

Although the classic 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 classical genetic methodology. One example of this method is analogous to damaging a body part to determine its function. An insect that loses a wing cannot fly, which means that the wing's function is flight. The classic genetic method compares insects that cannot fly with insects that can fly, and observes that the non-flying insects have lost wings. Similarly in a reverse genetics approach, mutating or deleting genes provides researchers with clues about gene function. Alternately, reverse genetics can be used to cause a gene to overexpress itself to determine what phenotypic effects may occur.

Summary

Nucleic acids can be isolated from cells for the purposes of further analysis by breaking open the cells and enzymatically destroying all other major macromolecules. Fragmented or whole chromosomes can be separated on the basis of size by gel electrophoresis. Short stretches of DNA can be amplified by PCR. DNA can be cut (and subsequently re-spliced together) using restriction enzymes. The molecular and cellular techniques of biotechnology allow researchers to genetically engineer organisms, modifying them to achieve desirable traits.

Cloning may involve cloning small DNA fragments (molecular cloning), or cloning entire organisms (reproductive cloning). In molecular cloning with bacteria, a desired DNA fragment is inserted into a bacterial plasmid using restriction enzymes and the plasmid is taken up by a bacterium, which will then express the foreign DNA. Using other techniques, foreign genes can be inserted into eukaryotic organisms. In each case, the organisms are called transgenic organisms. In reproductive cloning, a donor nucleus is put into an enucleated egg cell, which is then stimulated to divide and develop into an organism.

In reverse genetics methods, a gene is mutated or removed in some way to identify its effect on the phenotype of the whole organism as a way to determine its function.

Art Connections

Figure 9.1.6: Why was Dolly a Finn-Dorset and not a Scottish Blackface sheep?

Answer

Because even though the original cell came from a Scottish Blackface sheep and the surrogate mother was a Scottish Blackface, the DNA came from a Finn-Dorset.

Glossary

anneal

in molecular biology, the process by which two single strands of DNA hydrogen bond at complementary nucleotides to form a double-stranded molecule

biotechnology

the use of artificial methods to modify the genetic material of living organisms or cells to produce novel compounds or to perform new functions

cloning
the production of an exact copy—specifically, an exact genetic copy—of a gene, cell, or organism

gel electrophoresis
a technique used to separate molecules on the basis of their ability to migrate through a semisolid gel in response to an electric current

genetic engineering
alteration of the genetic makeup of an organism using the molecular methods of biotechnology

genetically modified organism (GMO)
an organism whose genome has been artificially changed

plasmid
a small circular molecule of DNA found in bacteria that replicates independently of the main bacterial chromosome; plasmids code for some important traits for bacteria and can be used as vectors to transport DNA into bacteria in genetic engineering applications

polymerase chain reaction (PCR)
a technique used to make multiple copies of DNA

recombinant DNA
a combination of DNA fragments generated by molecular cloning that does not exist in nature

recombinant protein
a protein that is expressed from recombinant DNA molecules

restriction enzyme
an enzyme that recognizes a specific nucleotide sequence in DNA and cuts the DNA double strand at that recognition site, often with a staggered cut leaving short single strands or “sticky” ends

reverse genetics
a form of genetic analysis that manipulates DNA to disrupt or affect the product of a gene to analyze the gene’s function

reproductive cloning
cloning of entire organisms

transgenic
describing an organism that receives DNA from a different species

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9.2: Biotechnology in Medicine and Agriculture

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 diseases. Biotechnology in agriculture can enhance resistance to disease, pests, and environmental stress to improve both crop yield and quality.

Genetic Diagnosis and Gene Therapy

The process of testing for suspected genetic defects before administering treatment is called genetic diagnosis by genetic testing. In some cases in which a genetic disease is present in an individual's family, family members may be advised to undergo genetic testing. For example, mutations in the *BRCA* genes may increase the likelihood of developing breast and ovarian cancers in women and some other cancers in women and men. A woman with breast cancer can be screened for these mutations. If one of the high-risk mutations is found, her female relatives may also wish to be screened for that particular mutation, or simply be more vigilant for the occurrence of cancers. Genetic testing is also offered for fetuses (or embryos with in vitro fertilization) to determine the presence or absence of disease-causing genes in families with specific debilitating diseases.

CONCEPT IN ACTION



See how human DNA is extracted for uses such as genetic testing.

Gene therapy is a genetic engineering technique that may one day be used to cure certain genetic diseases. In its simplest form, it involves the introduction of a non-mutated gene at a random location in the genome to cure a disease by replacing a protein that may be absent in these individuals because of a genetic mutation. The non-mutated gene is usually introduced into diseased cells as part of a vector transmitted by a virus, such as an adenovirus, that can infect the host cell and deliver the foreign DNA into the genome of the targeted cell (Figure 9.2.1). To date, gene therapies have been primarily experimental procedures in humans. A few of these experimental treatments have been successful, but the methods may be important in the future as the factors limiting its success are resolved.

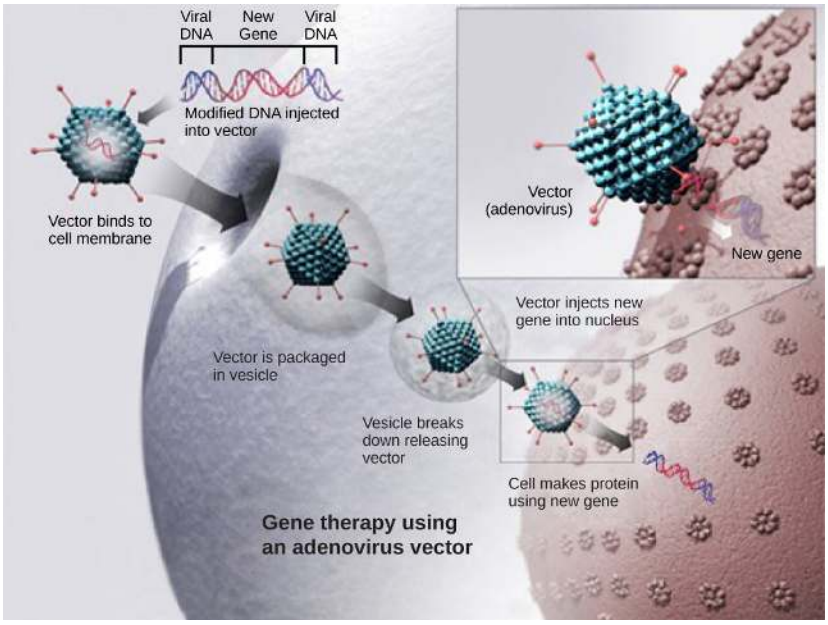


Figure 9.2.1**:** This diagram shows the steps involved in curing disease with gene therapy using an adenovirus vector. (credit: modification of work by NIH)

Production of Vaccines, Antibiotics, and Hormones

Traditional vaccination strategies use weakened or inactive forms of microorganisms or viruses to stimulate the immune system. Modern techniques use specific genes of microorganisms cloned into vectors and mass-produced in bacteria to make large quantities of specific substances to stimulate the immune system. The substance is then used as a vaccine. In some cases, such as the H1N1 flu vaccine, genes cloned from the virus have been used to combat the constantly changing strains of this virus.

Antibiotics kill bacteria and are naturally produced by microorganisms such as fungi; penicillin is perhaps the most well-known example. Antibiotics are produced on a large scale by cultivating and manipulating fungal cells. The fungal cells have typically been genetically modified to improve the yields of the antibiotic compound.

Recombinant DNA technology was used to produce large-scale quantities of the human hormone insulin in *E. coli* as early as 1978. Previously, it was only possible to treat diabetes with pig insulin, which caused allergic reactions in many humans because of differences in the insulin molecule. In addition, human growth hormone (HGH) is used to treat growth disorders in children. The HGH gene was cloned from a cDNA (complementary DNA) library and inserted into *E. coli* cells by cloning it into a bacterial vector.

Transgenic Animals

Although several recombinant proteins used in medicine are successfully produced in bacteria, some proteins need a eukaryotic animal host for proper processing. For this reason, genes have been 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 (Figure 9.2.2).



Figure 9.2.2**:** It can be seen that two of these mice are transgenic because they have a gene that causes them to fluoresce under a UV light. The non-transgenic mouse does not have the gene that causes fluorescence. (credit: Ingrid Moen et al.)

Several human proteins are expressed in the milk of transgenic sheep and goats. In one commercial example, the FDA has approved a blood anticoagulant protein that is produced in the milk of transgenic goats for use in humans. Mice have been used extensively for expressing and studying the effects of recombinant genes and mutations.

Transgenic Plants

Manipulating the DNA of plants (creating genetically modified organisms, or GMOs) has helped to create desirable traits such as disease resistance, herbicide, and pest resistance, better nutritional value, and better shelf life (Figure 9.2.3). 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.



Figure 9.2.3**:** Corn, a major agricultural crop used to create products for a variety of industries, is often modified through plant biotechnology. (credit: Keith Weller, USDA)

Transgenic plants have received DNA from other species. Because they contain unique combinations of genes and are not restricted to the laboratory, transgenic plants and other GMOs are closely monitored by government agencies to ensure that they are fit for human consumption and do not endanger other plant and animal life. Because foreign genes can spread to other species in the environment, particularly in the pollen and seeds of plants, extensive testing is required to ensure ecological stability. Staples like corn, potatoes, and tomatoes were the first crop plants to be genetically engineered.

Transformation of Plants Using *Agrobacterium tumefaciens*

In plants, tumors caused by the bacterium *Agrobacterium tumefaciens* occur by transfer of DNA from the bacterium to the plant. 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 that contain genes that integrate into the infected plant cell's genome. Researchers manipulate the plasmids to carry the desired DNA fragment and insert it into the plant genome.

The Organic Insecticide *Bacillus thuringiensis*

Bacillus thuringiensis (Bt) is a bacterium that produces protein crystals that are toxic to many insect species that feed on plants. 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. The crystal toxin genes have been cloned from the bacterium and introduced into plants, therefore allowing plants to produce their own crystal Bt toxin that acts against insects. Bt toxin is safe for the environment and non-toxic to mammals (including humans). As a result, it has been approved for use by organic farmers as a natural insecticide. There is some concern, however, that insects may evolve resistance to the Bt toxin in the same way that bacteria evolve resistance to antibiotics.

FlavrSavr Tomato

The first GM crop to be introduced into the market was the FlavrSavr Tomato produced in 1994. Molecular genetic 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 FlavrSavr tomato did not successfully stay in the market because of problems maintaining and shipping the crop.

Summary

Genetic testing is performed to identify disease-causing genes, and can be used to benefit affected individuals and their relatives who have not developed disease symptoms yet. Gene therapy—by which functioning genes are incorporated into the genomes of individuals with a non-functioning mutant gene—has the potential to cure heritable diseases. Transgenic organisms possess DNA from a different species, usually generated by molecular cloning techniques. Vaccines, antibiotics, and hormones are examples of products obtained by recombinant DNA technology. Transgenic animals have been created for experimental purposes and some are used to produce some human proteins.

Genes are inserted into plants, using plasmids in the bacterium *Agrobacterium tumefaciens*, which infects plants. Transgenic plants have been created to improve the characteristics of crop plants—for example, by giving them insect resistance by inserting a gene for a bacterial toxin.

Glossary

gene therapy
: the technique used to cure heritable diseases by replacing mutant genes with good genes

genetic testing
: identifying gene variants in an individual that may lead to a genetic disease in that individual

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9.3: Genomics and Proteomics

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 us to get detailed information about locations around the globe, genomic information is used to create similar maps of the DNA of different organisms.

Mapping Genomes

Genome mapping is the process of finding the location of genes on each chromosome. The maps that are created are comparable to the maps that we use to navigate streets. A genetic map is an illustration that lists genes and their location on a chromosome. Genetic maps provide the big picture (similar to a map of interstate highways) and use genetic markers (similar to landmarks). A genetic marker is a gene or sequence on a chromosome that shows genetic linkage with a trait of interest. The genetic marker tends to be inherited with the gene of interest, and one measure of distance between them is the recombination frequency during meiosis. Early geneticists called this linkage analysis.

Physical maps get into the intimate details of smaller regions of the chromosomes (similar to a detailed road map) (Figure 9.3.1). A physical map is a representation of the physical distance, in nucleotides, between genes or genetic markers. Both genetic linkage maps and physical maps are required to build a complete picture of the genome. Having a complete map of the genome makes it easier for researchers to study individual genes. Human genome maps help researchers in their efforts to identify human disease-causing genes related to illnesses such as cancer, heart disease, and cystic fibrosis, to name a few. In addition, genome mapping can be used to help identify organisms with beneficial traits, such as microbes with the ability to clean up pollutants or even prevent pollution. Research involving plant genome mapping may lead to methods that produce higher crop yields or to the development of plants that adapt better to climate change.

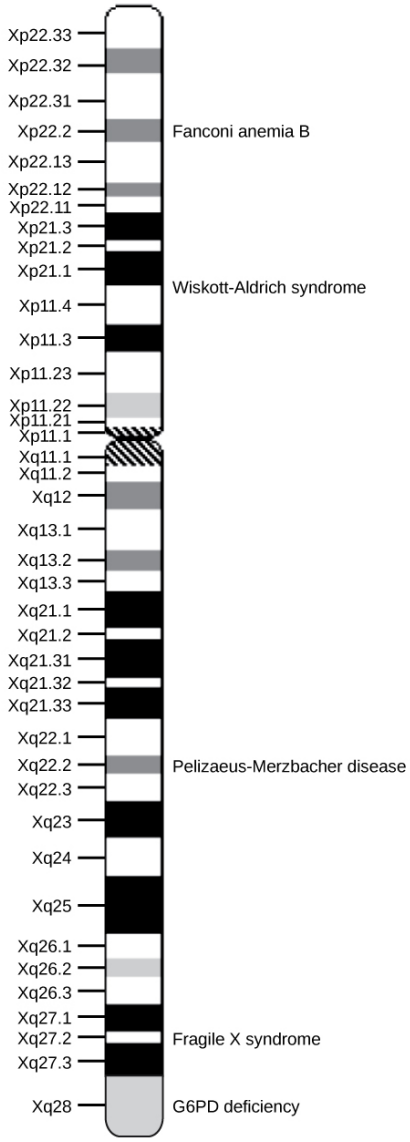


Figure 9.3.1**:** This is a physical map of the human X chromosome. (credit: modification of work by NCBI, NIH)

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 used with different model organisms that are used for research. Genome mapping is still an ongoing process, and as more advanced 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 all over the world is entered into central databases, such as the National Center for Biotechnology Information (NCBI). Efforts are 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 allows us to use a genome viewer tool to simplify the data mining process.

CONCEPT IN ACTION

Online Mendelian Inheritance in Man (OMIM) is a searchable online catalog of human genes and genetic disorders. This website shows genome mapping, and also details the history and research of each trait and disorder. Click the link to search for traits (such as handedness) and genetic disorders (such as diabetes).

Whole Genome Sequencing

Although there have been significant advances in the medical sciences in recent years, doctors are still confounded by many diseases and researchers are using whole genome sequencing to get to the bottom of the problem. Whole genome sequencing is a process that determines the DNA sequence of an entire genome. Whole genome sequencing is a brute-force approach to problem solving when there is a genetic basis at the core of a disease. Several laboratories now provide services to sequence, analyze, and interpret entire genomes.

In 2010, whole genome sequencing was used to save a young boy whose intestines had multiple mysterious abscesses. The child had several colon operations with no relief. Finally, a whole genome sequence revealed a defect in a pathway that controls apoptosis (programmed cell death). A bone marrow transplant was used to overcome this genetic disorder, leading to a cure for the boy. He was the first person to be successfully diagnosed using whole genome sequencing.

The first genomes to be sequenced, such as those belonging to viruses, bacteria, and yeast, were smaller in terms of the number of nucleotides than the genomes of multicellular organisms. The genomes of other model organisms, such as the mouse (*Mus musculus*), the fruit fly (*Drosophila melanogaster*), and the nematode (*Caenorhabditis elegans*) are now known. A great deal of basic research is performed in model organismsbecause the information can be applied to other organisms. A model organism is a species that is studied as a model to understand the biological processes in other species that can be represented by the model organism. For example, fruit flies are able to metabolize alcohol like humans, so the genes affecting sensitivity to alcohol have been studied in fruit flies in an effort to understand the variation in sensitivity to alcohol in humans. Having entire genomes sequenced helps with the research efforts in these model organisms (Figure 9.3.2).

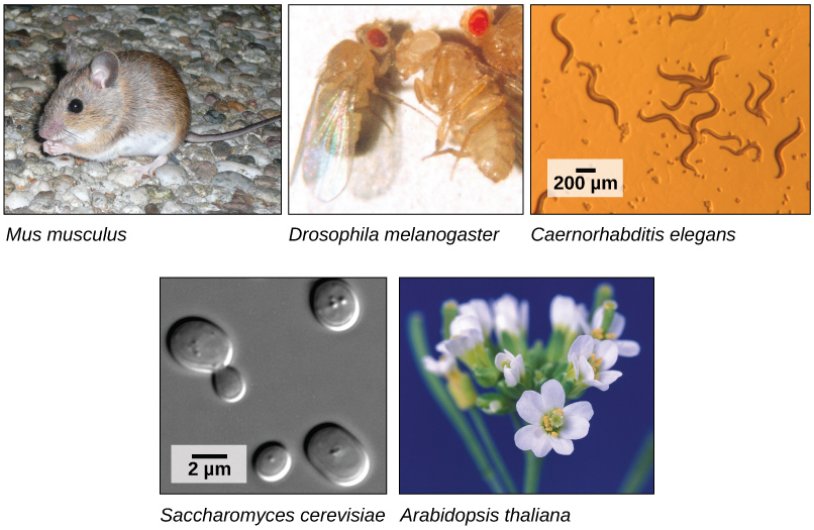


Figure 9.3.2**:** Much basic research is done with model organisms, such as the mouse, Mus musculus; the fruit fly, Drosophila melanogaster; the nematode Caenorhabditis elegans; the yeast Saccharomyces cerevisiae; and the common weed, Arabidopsis thaliana. (credit "mouse": modification of work by Florean Fortescue; credit "nematodes": modification of work by "snickclunk"/Flickr; credit "common weed": modification of work by Peggy Greb, USDA; scale-bar data from Matt Russell)

The first human genome sequence was published in 2003. The number of whole genomes that have been sequenced steadily increases and now includes hundreds of species and thousands of individual human genomes.

Applying Genomics

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 Disease Risk at the Individual Level

Predicting the risk of disease involves screening and identifying 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 arises from a single gene mutation. Such defects only account for about 5 percent of diseases found in developed countries. Most of the common diseases, such as heart disease, are multifactorial or polygenic, which refers to a phenotypic characteristic that is determined by two or more genes, and also 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 done to analyze Quake's percentage of risk for 55 different medical conditions. A rare genetic mutation was found that 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 disease. 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. For example, could such data be legitimately used to charge more or less for insurance or to affect credit ratings?

Genome-wide Association Studies

Since 2005, it has been possible to conduct a type of study called a genome-wide association study, or GWAS. A GWAS is a method that identifies differences between individuals in single nucleotide polymorphisms (SNPs) that may be involved in causing diseases. The method is particularly suited to diseases that may be affected by one or many genetic changes throughout the genome. It is very difficult to identify the genes involved in such a disease using family history information. The GWAS method relies on a genetic database that has been in development since 2002 called the International HapMap Project. The HapMap Project sequenced the genomes of several hundred individuals from around the world and identified groups of SNPs. The groups include SNPs that are located near to each other on chromosomes so they tend to stay together through recombination. The fact that the group stays together means that identifying one marker SNP is all that is needed to identify all the SNPs in the group. There are several million SNPs identified, but identifying them in other individuals who have not had their complete genome sequenced is much easier because only the marker SNPs need to be identified.

In a common design for a GWAS, two groups of individuals are chosen; one group has the disease, and the other group does not. The individuals in each group are matched in other characteristics to reduce the effect of confounding variables causing differences between the two groups. For example, the genotypes may differ because the two groups are mostly taken from different parts of the world. Once the individuals are chosen, and typically their numbers are a thousand or more for the study to work, samples of their DNA are obtained. The DNA is analyzed using automated systems to identify large differences in the percentage of particular SNPs between the two groups. Often the study examines a million or more SNPs in the DNA. The results of GWAS can be used in two ways: the genetic differences may be used as markers for susceptibility to the disease in undiagnosed individuals, and the particular genes identified can be targets for research into the molecular pathway of the disease and potential therapies. An offshoot of the discovery of gene associations with disease has been the formation of companies that provide so-called "personal genomics" that will identify risk levels for various diseases based on an individual's SNP complement. The science behind these services is controversial.

Because GWAS looks for associations between genes and disease, these studies provide data for other research into causes, rather than answering specific questions themselves. An association between a gene difference and a disease does not necessarily mean there is a cause-and-effect relationship. However, some studies have provided useful information about the genetic causes of diseases. For example, three different studies in 2005 identified a gene for a protein involved in regulating inflammation in the body that is associated with a disease-causing blindness called age-related macular degeneration. This opened up new possibilities for research into the cause of this disease. A large number of genes have been identified to be associated with Crohn's disease using GWAS, and some of these have suggested new hypothetical mechanisms for the cause of the disease.

Pharmacogenomics

Pharmacogenomics involves evaluating the effectiveness and safety of drugs on the basis of information from an individual's genomic sequence. 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. Studying changes in gene expression could provide information about

the gene 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. The gene signatures may not be completely accurate, but can be tested further before pathologic symptoms arise.

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. On the other hand, many 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 9.3.3). Metagenomics techniques can now also be applied to communities of higher eukaryotes, such as fish.

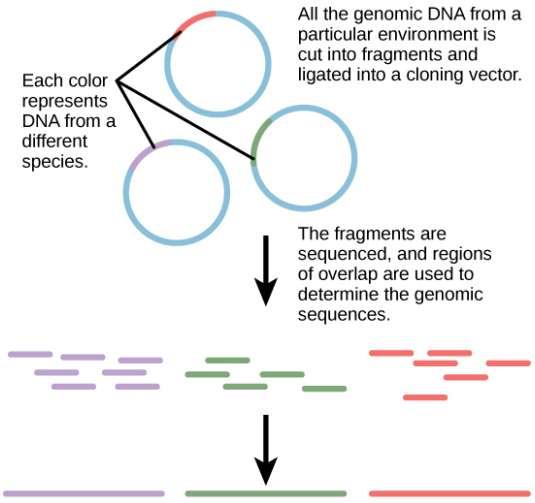


Figure 9.3.3: Metagenomics involves isolating DNA from multiple species within an environmental niche. The DNA is cut up and sequenced, allowing entire genome sequences of multiple species to be reconstructed from the sequences of overlapping pieces.

Creation of New Biofuels

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. This vast genetic resource holds the potential to provide new sources of biofuels (Figure 9.3.4).

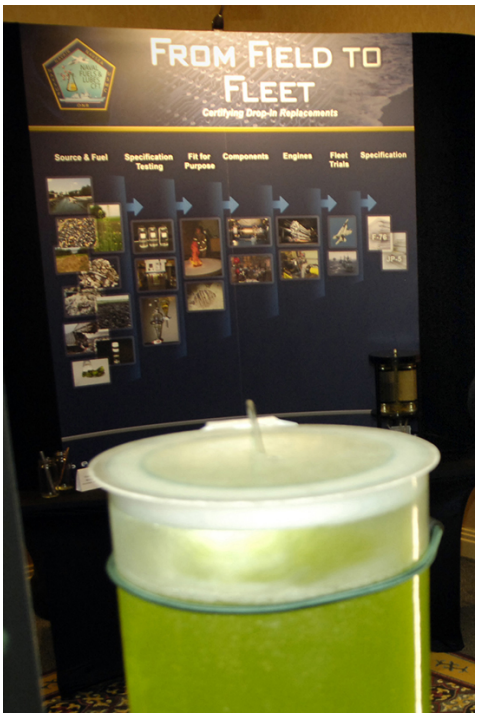


Figure 9.3.4**:** Renewable fuels were tested in Navy ships and aircraft at the first Naval Energy Forum. (credit: modification of work by John F. Williams, US Navy)

Mitochondrial Genomics

Mitochondria are intracellular organelles that contain their own DNA. Mitochondrial DNA mutates at a rapid rate and is often used to study evolutionary relationships. Another feature that makes studying the mitochondrial genome interesting is that in most multicellular organisms, the mitochondrial DNA is passed on from the mother during the process of fertilization. For this reason, mitochondrial genomics is often used to trace genealogy.

Genomics in Forensic Analysis

Information and clues obtained from DNA samples found at crime scenes have been used as evidence in court cases, and genetic markers have been used in forensic analysis. Genomic analysis has also become useful in this field. In 2001, the first use of genomics in forensics was published. It was a collaborative effort between academic research institutions and the FBI to solve the mysterious cases of anthrax (Figure 9.3.5) that was transported by the US Postal Service. Anthrax bacteria were made into an infectious powder and mailed to news media and two U.S. Senators. The powder infected the administrative staff and postal workers who opened or handled the letters. Five people died, and 17 were sickened from the bacteria. Using microbial genomics, researchers determined that a specific strain of anthrax was used in all the mailings; eventually, the source was traced to a scientist at a national biodefense laboratory in Maryland.

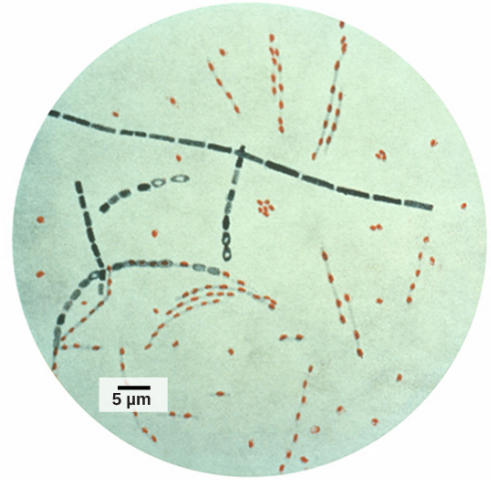


Figure 9.3.5**:** Bacillus anthracis is the organism that causes anthrax. (credit: modification of work by CDC; scale-bar data from Matt Russell)

Genomics in Agriculture

Genomics can reduce the trials and failures involved in scientific research to a certain extent, which could improve the quality and quantity of crop yields in agriculture (Figure 9.3.6). Linking traits to genes or gene signatures helps to improve crop breeding to generate hybrids with the most desirable qualities. Scientists use genomic data to identify desirable traits, and then transfer those traits to a different organism to create a new genetically modified organism, as described in the previous module. Scientists are discovering how genomics can improve the quality and quantity of agricultural production. For example, scientists could use desirable traits to create a useful product or enhance an existing product, such as making a drought-sensitive crop more tolerant of the dry season.



Figure 9.3.6**:** Transgenic agricultural plants can be made to resist disease. These transgenic plums are resistant to the plum pox virus. (credit: Scott Bauer, USDA ARS)

Proteomics

Proteins are the final products of genes that perform the function encoded by the gene. Proteins are composed of amino acids and play important roles in the cell. All enzymes (except ribozymes) are proteins and act as catalysts that affect the rate of reactions. Proteins are also regulatory molecules, and some are hormones. Transport proteins, such as hemoglobin, help transport oxygen to various organs. Antibodies that defend against foreign particles are also proteins. In the diseased state, protein function can be impaired because of changes at the genetic level or because of direct impact on a specific protein.

A proteome is the entire set of proteins produced by a cell type. Proteomes can be studied using the knowledge of genomes because genes code for mRNAs, and the mRNAs encode proteins. The study of the function of proteomes is called proteomics. Proteomics complements genomics and is useful when scientists want to test their hypotheses that were based on genes. Even though all cells in 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 alternatively spliced (cut and pasted to create novel combinations and novel proteins), and many proteins are modified after translation. Although the genome provides a blueprint, the final architecture depends on several factors that can change the progression of events that generate the proteome.

Genomes and proteomes of patients suffering from specific diseases are being studied to understand the genetic basis of the disease. The most prominent disease being studied with proteomic approaches is cancer (Figure 9.3.7). Proteomic approaches are being used to improve the screening and early detection of cancer; this is achieved by identifying proteins whose expression is affected by the disease process. An individual protein 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 such as sweat, blood, or urine, so that large-scale screenings can be performed in a noninvasive fashion. The current problem with using biomarkers for the early detection of cancer is the high rate of false-negative results. A false-negative result is a negative 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. 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 have. Proteomics is also being used to predict the possibility of disease recurrence.



Figure 9.3.7**:** This machine is preparing to do a proteomic pattern analysis to identify specific cancers so that an accurate cancer prognosis can be made. (credit: Dorie Hightower, NCI, NIH)

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.

Summary

Genome mapping is similar to solving a big, complicated puzzle with pieces of information coming from laboratories all over the world. Genetic maps provide an outline for the location of genes within a genome, and they estimate the distance between genes and genetic markers on the basis of the recombination frequency during meiosis. Physical maps provide detailed information about the physical distance between the genes. The most detailed information is available through sequence mapping. Information from all mapping and sequencing sources is combined to study an entire genome.

Whole genome sequencing is the latest available resource to treat genetic diseases. Some doctors are using whole genome sequencing to save lives. Genomics has many industrial applications, including biofuel development, agriculture, pharmaceuticals, and pollution control.

Imagination is the only barrier to the applicability of genomics. Genomics is being applied to most fields of biology; it can be used for personalized medicine, prediction of disease risks at an individual level, the study of drug interactions before the conduction of clinical trials, and the study of microorganisms in the environment as opposed to the laboratory. It is also being applied to the generation of new biofuels, genealogical assessment using mitochondria, advances in forensic science, and improvements in agriculture.

Proteomics is the study of the entire set of proteins expressed by a given type of cell under certain environmental conditions. In a multicellular organism, different cell types will have different proteomes, and these will vary with changes in the environment. Unlike a genome, a proteome is dynamic and under constant flux, which makes it more complicated and more useful than the knowledge of genomes alone.

Glossary

biomarker
: an individual protein that is uniquely produced in a diseased state

genetic map
: an outline of genes and their location on a chromosome that is based on recombination frequencies between markers

genomics
: 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

metagenomics
: the study of the collective genomes of multiple species that grow and interact in an environmental niche

model organism
: a species that is studied and used as a model to understand the biological processes in other species represented by the model organism

pharmacogenomics
: the study of drug interactions with the genome or proteome; also called toxicogenomics

physical map
: a representation of the physical distance between genes or genetic markers

protein signature
: a set of over- or under-expressed proteins characteristic of cells in a particular diseased tissue

proteomics
: study of the function of proteomes

whole genome sequencing
: a process that determines the nucleotide sequence of an entire genome

Contributors and Attributions

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

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9.A: Biotechnology (Exercises)

Cloning and Genetic Engineering

Multiple Choice

In gel electrophoresis of DNA, the different bands in the final gel form because the DNA molecules _____.

A. are from different organisms
B. have different lengths
C. have different nucleotide compositions
D. have different genes

Answer

B

In the reproductive cloning of an animal, the genome of the cloned individual comes from _____.

A. a sperm cell
B. an egg cell
C. any gamete cell
D. a body cell

Answer

D

What carries a gene from one organism into a bacteria cell?

A. a plasmid
B. an electrophoresis gel
C. a restriction enzyme
D. polymerase chain reaction

Answer

A

Free Response

What is the purpose and benefit of the polymerase chain reaction?

Answer

The polymerase chain reaction is used to quickly produce many copies of a specific segment of DNA when only one or a very few copies are originally present. The benefit of PCR is that there are many instances in which we would like to know something about a sample of DNA when only very small amounts are available. PCR allows us to increase the number of DNA molecules so that other tests, such as sequencing, can be performed with it.

Biotechnology in Medicine and Agriculture

Multiple Choice

What is a genetically modified organism (GMO)?

A. a plant with certain genes removed
B. an organism with an artificially altered genome
C. a hybrid organism
D. any agricultural organism produced by breeding or biotechnology

Answer

What is the role of *Agrobacterium tumefaciens* in the production of transgenic plants?

A. Genes from *A. tumefaciens* are inserted into plant DNA to give the plant different traits.
B. Transgenic plants have been given resistance to the pest *A. tumefaciens*.
C. *A. tumefaciens* is used as a vector to move genes into plant cells.
D. Plant genes are incorporated into the genome of *Agrobacterium tumefaciens*.

Answer

C

Free Response

Today, it is possible for a diabetic patient to purchase human insulin from a pharmacist. What technology makes this possible and why is it a benefit over how things used to be?

Answer

The human insulin comes from the gene that produces insulin in humans, which has been spliced into a bacterial genome using recombinant DNA technology. The bacterium produces the insulin, which is then purified for human use. Before there was genetically engineered human insulin, diabetics were given insulin extracted from pig pancreases, which was similar to, but not exactly like, human insulin. Because it was not exactly like human insulin, the pig insulin caused complications in some diabetic patients.

Genomics and Proteomics

Multiple Choice

What is the most challenging issue facing genome sequencing?

A. the inability to develop fast and accurate sequencing techniques
B. the ethics of using information from genomes at the individual level
C. the availability and stability of DNA
D. all of the above

Answer

B

Genomics can be used in agriculture to:

A. generate new hybrid strains
B. improve disease resistance
C. improve yield
D. all of the above

Answer

D

What kind of diseases are studied using genome-wide association studies?

A. viral diseases
B. single-gene inherited diseases
C. diseases caused by multiple genes
D. diseases caused by environmental factors

Answer

C

Free Response

Describe two of the applications for genome mapping.

Answer

Genome mapping helps researchers to study disease-causing genes in humans. It also helps to identify traits of organisms that can be used in applications such as cleaning up pollution.

Identify a possible advantage and a possible disadvantage of a genetic test that would identify genes in individuals that increase their probability of having Alzheimer's disease later in life.

Answer

The benefit of such a test is that the individual can make preparations for having the disease including taking treatments that slow the disease. The disadvantage of the test is that it might be used by insurance companies to deny coverage to the person.

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10: Evolution and Its Processes

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10.1: Discovering How Populations Change

The theory of evolution by natural selection describes a mechanism for species change over time. That species change had been suggested and debated well before Darwin. The view that species were static and unchanging was grounded in the writings of Plato, yet there were also ancient Greeks that expressed evolutionary ideas.

In the eighteenth century, ideas about the evolution of animals were reintroduced by the naturalist Georges-Louis Leclerc, Comte de Buffon and even by Charles Darwin's grandfather, Erasmus Darwin. During this time, it was also accepted that there were extinct species. At the same time, James Hutton, the Scottish naturalist, proposed that geological change occurred gradually by the accumulation of small changes from processes (over long periods of time) just like those happening today. This contrasted with the predominant view that the geology of the planet was a consequence of catastrophic events occurring during a relatively brief past. Hutton's view was later popularized by the geologist Charles Lyell in the nineteenth century. Lyell became a friend to Darwin and his ideas were very influential on Darwin's thinking. Lyell argued that the greater age of Earth gave more time for gradual change in species, and the process provided an analogy for gradual change in species.

In the early nineteenth century, Jean-Baptiste Lamarck published a book that detailed a mechanism for evolutionary change that is now referred to as inheritance of acquired characteristics. In Lamarck's theory, modifications in an individual caused by its environment, or the use or disuse of a structure during its lifetime, could be inherited by its offspring and, thus, bring about change in a species. While this mechanism for evolutionary change as described by Lamarck was discredited, Lamarck's ideas were an important influence on evolutionary thought. The inscription on the statue of Lamarck that stands at the gates of the Jardin des Plantes in Paris describes him as the "founder of the doctrine of evolution."

Charles Darwin and Natural Selection

The actual mechanism for evolution was independently conceived of and described by two naturalists, Charles Darwin and Alfred Russell Wallace, in the mid-nineteenth century. Importantly, each spent time exploring the natural world on expeditions to the tropics. From 1831 to 1836, Darwin traveled around the world on *H.M.S. Beagle*, visiting South America, Australia, and the southern tip of Africa. Wallace traveled to Brazil to collect insects in the Amazon rainforest from 1848 to 1852 and to the Malay Archipelago from 1854 to 1862. Darwin's journey, like Wallace's later journeys in the Malay Archipelago, included stops at several island chains, the last being the Galápagos Islands (west of Ecuador). On these islands, Darwin observed species of organisms on different islands that were clearly similar, yet had distinct differences. For example, the ground finches inhabiting the Galápagos Islands comprised several species that each had a unique beak shape (Figure 10.1.1). He observed both that these finches closely resembled another finch species on the mainland of South America and that the group of species in the Galápagos formed a graded series of beak sizes and shapes, with very small differences between the most similar. Darwin imagined that the island species might be all species modified from one original mainland species. In 1860, he wrote, "Seeing this gradation and diversity of structure in one small, intimately related group of birds, one might really fancy that from an original paucity of birds in this archipelago, one species had been taken and modified for different ends."[1]

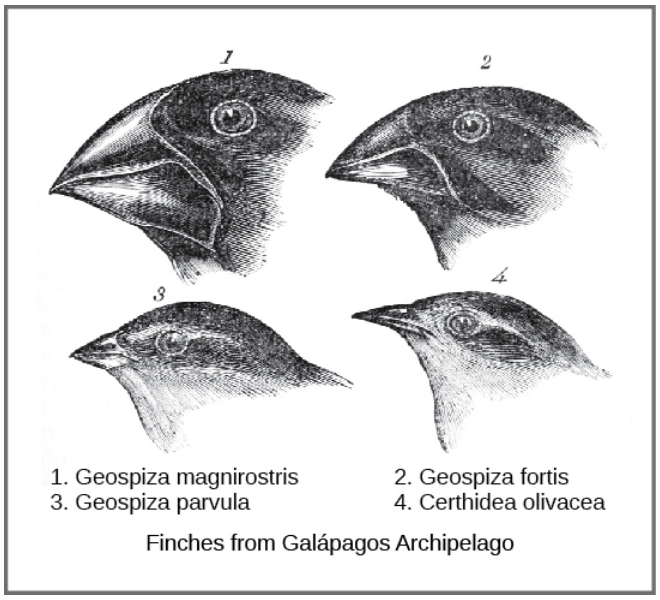


Figure 10.1.1**:** Darwin observed that beak shape varies among finch species. He postulated that the beak of an ancestral species had adapted over time to equip the finches to acquire different food sources. This illustration shows the beak shapes for four species of ground finch: 1. Geospiza magnirostris (the large ground finch), 2. G. fortis (the medium ground finch), 3. G. parvula (the small tree finch), and 4. Certhidea olivacea (the green-warbler finch).

Wallace and Darwin both observed similar patterns in other organisms and independently conceived a mechanism to explain how and why such changes could take place. Darwin called this mechanism natural selection. Natural selection, Darwin argued, was an inevitable outcome of three principles that operated in nature. First, the characteristics of organisms are inherited, or passed from parent to offspring. Second, more offspring are produced than are able to survive; in other words, resources for survival and reproduction are limited. The capacity for reproduction in all organisms outstrips the availability of resources to support their numbers. Thus, there is a competition for those resources in each generation. Both Darwin and Wallace's understanding of this principle came from reading an essay by the economist Thomas Malthus, who discussed this principle in relation to human populations. Third, offspring vary among each other in regard to their characteristics and those variations are inherited. Out of these three principles, Darwin and Wallace reasoned that offspring with inherited characteristics that allow them to best compete for limited resources will survive and have more offspring than those individuals with variations that are less able to compete. Because characteristics are inherited, these traits will be better represented in the next generation. This will lead to change in populations over generations in a process that Darwin called "descent with modification."

Papers by Darwin and Wallace (Figure 10.1.2) presenting the idea of natural selection were read together in 1858 before the Linnaean Society in London. The following year Darwin's book, *On the Origin of Species*, was published, which outlined in considerable detail his arguments for evolution by natural selection.



(a) (b)

Figure 10.1.2**:** (a) Charles Darwin and (b) Alfred Wallace wrote scientific papers on natural selection that were presented together before the Linnean Society in 1858.

Demonstrations of evolution by natural selection can be time consuming. One of the best demonstrations has been in the very birds that helped to inspire the theory, the Galápagos finches. Peter and Rosemary Grant and their colleagues have studied Galápagos finch populations every year since 1976 and have provided important demonstrations of the operation of natural selection. The Grants found changes from one generation to the next in the beak shapes of the medium ground finches on the Galápagos island of Daphne Major. The medium ground finch feeds on seeds. The birds have inherited variation in the bill shape with some individuals having wide, deep bills and others having thinner bills. Large-billed birds feed more efficiently on large, hard seeds, whereas smaller billed birds feed more efficiently on small, soft seeds. During 1977, a drought period altered vegetation on the island. After this period, the number of seeds declined dramatically: the decline in small, soft seeds was greater than the decline in large, hard seeds. The large-billed birds were able to survive better than the small-billed birds the following year. The year following the drought when the Grants measured beak sizes in the much-reduced population, they found that the average bill size was larger (Figure 10.1.3). This was clear evidence for natural selection (differences in survival) of bill size caused by the availability of seeds. The Grants had studied the inheritance of bill sizes and knew that the surviving large-billed birds would tend to produce offspring with larger bills, so the selection would lead to evolution of bill size. Subsequent studies by the Grants have demonstrated selection on and evolution of bill size in this species in response to changing conditions on the island. The evolution has occurred both to larger bills, as in this case, and to smaller bills when large seeds became rare.

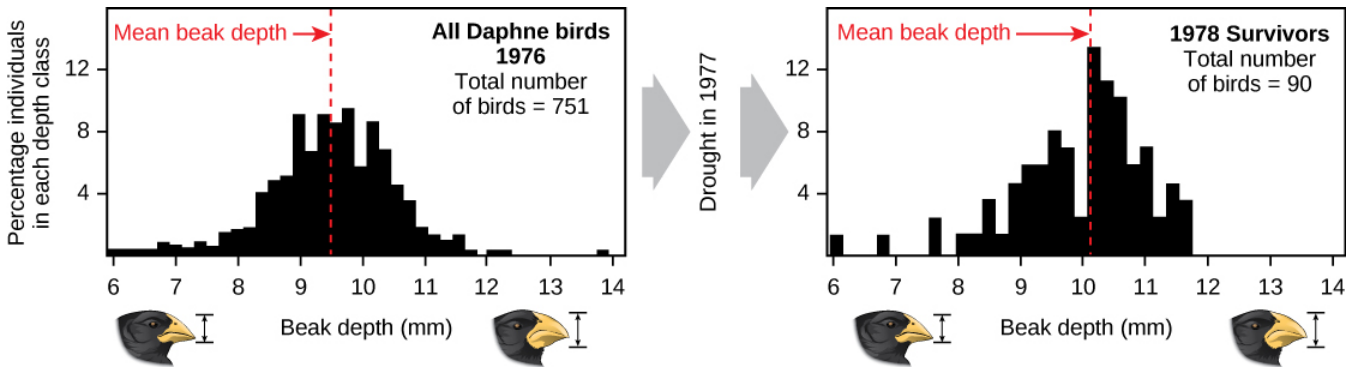


Figure 10.1.3**:** A drought on the Galápagos island of Daphne Major in 1977 reduced the number of small seeds available to finches, causing many of the small-beaked finches to die. This caused an increase in the finches' average beak size between 1976 and 1978.

Variation and Adaptation

Natural selection can only take place if there is variation, or differences, among individuals in a population. Importantly, these differences must have some genetic basis; otherwise, selection will not lead to change in the next generation. This is critical because variation among individuals can be caused by non-genetic reasons, such as an individual being taller because of better nutrition rather than different genes.

Genetic diversity in a population comes from two main sources: mutation and sexual reproduction. Mutation, a change in DNA, is the ultimate source of new alleles or new genetic variation in any population. An individual that has a mutated gene might have a different trait than other individuals in the population. However, this is not always the case. A mutation can have one of three outcomes on the organisms' appearance (or phenotype):

- A mutation may affect the phenotype of the organism in a way that gives it reduced fitness—lower likelihood of survival, resulting in fewer offspring.
- A mutation may produce a phenotype with a beneficial effect on fitness.
- Many mutations, called neutral mutations, will have no effect on fitness.

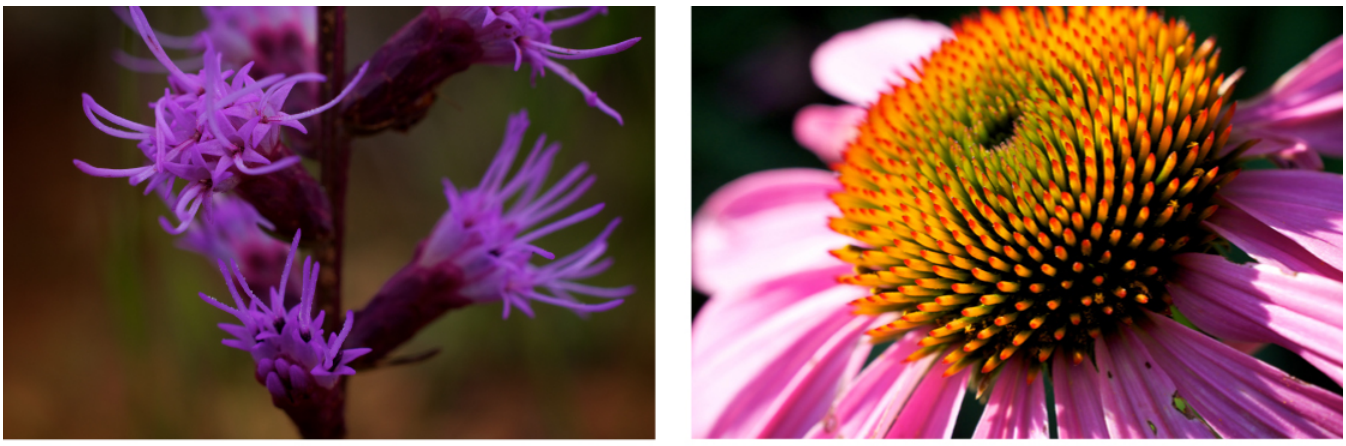
Mutations may also have a whole range of effect sizes on the fitness of the organism that expresses them in their phenotype, from a small effect to a great effect. Sexual reproduction and crossing over in meiosis also lead to genetic diversity: when two parents reproduce, unique combinations of alleles assemble to produce unique genotypes and, thus, phenotypes in each of the offspring.

A heritable trait that aids the survival and reproduction of an organism in its present environment is called an adaptation. An adaptation is a "match" of the organism to the environment. Adaptation to an environment comes about when a change in the range of genetic variation occurs over time that increases or maintains the match of the population with its environment. The variations in finch beaks shifted from generation to generation providing adaptation to food availability.

Whether or not a trait is favorable depends on the environment at the time. The same traits do not always have the same relative benefit or disadvantage because environmental conditions can change. For example, finches with large bills were benefited in one climate, while small bills were a disadvantage; in a different climate, the relationship reversed.

Patterns of Evolution

The evolution of species has resulted in enormous variation in form and function. When two species evolve in different directions from a common point, it is called divergent evolution. Such divergent evolution can be seen in the forms of the reproductive organs of flowering plants, which share the same basic anatomies; however, they can look very different as a result of selection in different physical environments, and adaptation to different kinds of pollinators (Figure 10.1.4).



(a) (b)

Figure 10.1.4**:** Flowering plants evolved from a common ancestor. Notice that the (a) dense blazing star and (b) purple coneflower vary in appearance, yet both share a similar basic morphology. (credit a, b: modification of work by Cory Zanker)

In other cases, similar phenotypes evolve independently in distantly related species. For example, flight has evolved in both bats and insects, and they both have structures we refer to as wings, which are adaptations to flight. The wings of bats and insects, however, evolved from very different original structures. When similar structures arise through evolution independently in different

species it is called convergent evolution. The wings of bats and insects are called analogous structures; they are similar in function and appearance, but do not share an origin in a common ancestor. Instead they evolved independently in the two lineages. The wings of a hummingbird and an ostrich are homologous structures, meaning they share similarities (despite their differences resulting from evolutionary divergence). The wings of hummingbirds and ostriches did not evolve independently in the hummingbird lineage and the ostrich lineage—they descended from a common ancestor with wings.

The Modern Synthesis

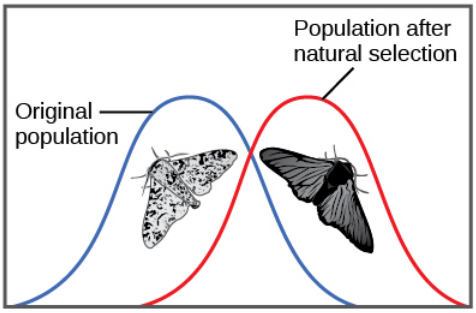
The mechanisms of inheritance, genetics, were not understood at the time Darwin and Wallace were developing their idea of natural selection. This lack of understanding was a stumbling block to comprehending many aspects of evolution. In fact, blending inheritance was the predominant (and incorrect) genetic theory of the time, which made it difficult to understand how natural selection might operate. Darwin and Wallace were unaware of the genetics work by Austrian monk Gregor Mendel, which was published in 1866, not long after publication of *On the Origin of Species*. Mendel's work was rediscovered in the early twentieth century at which time geneticists were rapidly coming to an understanding of the basics of inheritance. Initially, the newly discovered particulate nature of genes made it difficult for biologists to understand how gradual evolution could occur. But over the next few decades genetics and evolution were integrated in what became known as the modern synthesis—the coherent understanding of the relationship between natural selection and genetics that took shape by the 1940s and is generally accepted today. In sum, the modern synthesis describes how evolutionary pressures, such as natural selection, can affect a population's genetic makeup, and, in turn, how this can result in the gradual evolution of populations and species. The theory also connects this gradual change of a population over time, called microevolution, with the processes that gave rise to new species and higher taxonomic groups with widely divergent characters, called macroevolution.

Population Genetics

Recall that a gene for a particular character may have several variants, or alleles, that code for different traits associated with that character. For example, in the ABO blood type system in humans, three alleles determine the particular blood-type protein on the surface of red blood cells. Each individual in a population of diploid organisms can only carry two alleles for a particular gene, but more than two may be present in the individuals that make up the population. Mendel followed alleles as they were inherited from parent to offspring. In the early twentieth century, biologists began to study what happens to all the alleles in a population in a field of study known as population genetics.

Until now, we have defined evolution as a change in the characteristics of a population of organisms, but behind that phenotypic change is genetic change. In population genetic terms, evolution is defined as a change in the frequency of an allele in a population. Using the ABO system as an example, the frequency of one of the alleles, I^A, is the number of copies of that allele divided by all the copies of the ABO gene in the population. For example, a study in Jordan found a frequency of I^A to be 26.1 percent.[2] The I^B, I^0 alleles made up 13.4 percent and 60.5 percent of the alleles respectively, and all of the frequencies add up to 100 percent. A change in this frequency over time would constitute evolution in the population.

There are several ways the allele frequencies of a population can change. One of those ways is natural selection. If a given allele confers a phenotype that allows an individual to have more offspring that survive and reproduce, that allele, by virtue of being inherited by those offspring, will be in greater frequency in the next generation. Since allele frequencies always add up to 100 percent, an increase in the frequency of one allele always means a corresponding decrease in one or more of the other alleles. Highly beneficial alleles may, over a very few generations, become "fixed" in this way, meaning that every individual of the population will carry the allele. Similarly, detrimental alleles may be swiftly eliminated from the gene pool, the sum of all the alleles in a population. Part of the study of population genetics is tracking how selective forces change the allele frequencies in a population over time, which can give scientists clues regarding the selective forces that may be operating on a given population. The studies of changes in wing coloration in the peppered moth from mottled white to dark in response to soot-covered tree trunks and then back to mottled white when factories stopped producing so much soot is a classic example of studying evolution in natural populations (Figure 10.1.5).



Light-colored peppered moths are better camouflaged against a pristine environment; likewise, dark-colored peppered moths are better camouflaged against a sooty environment. Thus, as the Industrial Revolution progressed in nineteenth-century England, the color of the moth population shifted from light to dark.

Figure 10.1.5**:** As the Industrial Revolution caused trees to darken from soot, darker colored peppered moths were better camouflaged than the lighter colored ones, which caused there to be more of the darker colored moths in the population.

In the early twentieth century, English mathematician Godfrey Hardy and German physician Wilhelm Weinberg independently provided an explanation for a somewhat counterintuitive concept. Hardy's original explanation was in response to a misunderstanding as to why a "dominant" allele, one that masks a recessive allele, should not increase in frequency in a population until it eliminated all the other alleles. The question resulted from a common confusion about what "dominant" means, but it forced Hardy, who was not even a biologist, to point out that if there are no factors that affect an allele frequency those frequencies will remain constant from one generation to the next. This principle is now known as the Hardy-Weinberg equilibrium. The theory states that a population's allele and genotype frequencies are inherently stable—unless some kind of evolutionary force is acting on the population, the population would carry the same alleles in the same proportions generation after generation. Individuals would, as a whole, look essentially the same and this would be unrelated to whether the alleles were dominant or recessive. The four most important evolutionary forces, which will disrupt the equilibrium, are natural selection, mutation, genetic drift, and migration into or out of a population. A fifth factor, nonrandom mating, will also disrupt the Hardy-Weinberg equilibrium but only by shifting genotype frequencies, not allele frequencies. In nonrandom mating, individuals are more likely to mate with like individuals (or unlike individuals) rather than at random. Since nonrandom mating does not change allele frequencies, it does not cause evolution directly. Natural selection has been described. Mutation creates one allele out of another one and changes an allele's frequency by a small, but continuous amount each generation. Each allele is generated by a low, constant mutation rate that will slowly increase the allele's frequency in a population if no other forces act on the allele. If natural selection acts against the allele, it will be removed from the population at a low rate leading to a frequency that results from a balance between selection and mutation. This is one reason that genetic diseases remain in the human population at very low frequencies. If the allele is favored by selection, it will increase in frequency. Genetic drift causes random changes in allele frequencies when populations are small. Genetic drift can often be important in evolution, as discussed in the next section. Finally, if two populations of a species have different allele frequencies, migration of individuals between them will cause frequency changes in both populations. As it happens, there is no population in which one or more of these processes are not operating, so populations are always evolving, and the Hardy-Weinberg equilibrium will never be exactly observed. However, the Hardy-Weinberg principle gives scientists a baseline expectation for allele frequencies in a non-evolving population to which they can compare evolving populations and thereby infer what evolutionary forces might be at play. The population is evolving if the frequencies of alleles or genotypes deviate from the value expected from the Hardy-Weinberg principle.

Darwin identified a special case of natural selection that he called sexual selection. Sexual selection affects an individual's ability to mate and thus produce offspring, and it leads to the evolution of dramatic traits that often appear maladaptive in terms of survival but persist because they give their owners greater reproductive success. Sexual selection occurs in two ways: through male–male competition for mates and through female selection of mates. Male–male competition takes the form of conflicts between males, which are often ritualized, but may also pose significant threats to a male's survival. Sometimes the competition is for territory, with females more likely to mate with males with higher quality territories. Female choice occurs when females choose a male based on a particular trait, such as feather colors, the performance of a mating dance, or the building of an elaborate structure. In some cases male–male competition and female choice combine in the mating process. In each of these cases, the traits selected for, such as fighting ability or feather color and length, become enhanced in the males. In general, it is thought that sexual selection can proceed to a point at which natural selection against a character's further enhancement prevents its further evolution because it negatively impacts the male's ability to survive. For example, colorful feathers or an elaborate display make the male more obvious to predators.

Summary

Evolution by natural selection arises from three conditions: individuals within a species vary, some of those variations are heritable, and organisms have more offspring than resources can support. The consequence is that individuals with relatively advantageous variations will be more likely to survive and have higher reproductive rates than those individuals with different traits. The advantageous traits will be passed on to offspring in greater proportion. Thus, the trait will have higher representation in the next and subsequent generations leading to genetic change in the population.

The modern synthesis of evolutionary theory grew out of the reconciliation of Darwin's, Wallace's, and Mendel's thoughts on evolution and heredity. Population genetics is a theoretical framework for describing evolutionary change in populations through the change in allele frequencies. Population genetics defines evolution as a change in allele frequency over generations. In the absence of evolutionary forces allele frequencies will not change in a population; this is known as Hardy-Weinberg equilibrium principle. However, in all populations, mutation, natural selection, genetic drift, and migration act to change allele frequencies.

Footnotes

1. 1 Charles Darwin, *Journal of Researches into the Natural History and Geology of the Countries Visited during the Voyage of H.M.S. Beagle Round the World, under the Command of Capt. Fitz Roy, R.N*, 2nd. ed. (London: John Murray, 1860), http://www.archive.org/details/journalofresea00darw.
2. 2 Sahar S. Hanania, Dhia S. Hassawi, and Nidal M. Irshaid, "Allele Frequency and Molecular Genotypes of ABO Blood Group System in a Jordanian Population," *Journal of Medical Sciences* 7 (2007): 51-58, doi:10.3923/jms.2007.51.58

Glossary

adaptation
a heritable trait or behavior in an organism that aids in its survival in its present environment

analogous structure
a structure that is similar because of evolution in response to similar selection pressures resulting in convergent evolution, not similar because of descent from a common ancestor

convergent evolution
an evolution that results in similar forms on different species

divergent evolution
an evolution that results in different forms in two species with a common ancestor

gene pool
all of the alleles carried by all of the individuals in the population

genetic drift
the effect of chance on a population's gene pool

homologous structure
a structure that is similar because of descent from a common ancestor

inheritance of acquired characteristics
a phrase that describes the mechanism of evolution proposed by Lamarck in which traits acquired by individuals through use or disuse could be passed on to their offspring thus leading to evolutionary change in the population

macroevolution
a broader scale of evolutionary changes seen over paleontological time

microevolution
the changes in a population's genetic structure (i.e., allele frequency)

migration

the movement of individuals of a population to a new location; in population genetics it refers to the movement of individuals and their alleles from one population to another, potentially changing allele frequencies in both the old and the new population

modern synthesis

the overarching evolutionary paradigm that took shape by the 1940s and is generally accepted today

natural selection

the greater relative survival and reproduction of individuals in a population that have favorable heritable traits, leading to evolutionary change

population genetics

the study of how selective forces change the allele frequencies in a population over time

variation

the variety of alleles in a population

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10.2: Mechanisms of Evolution

The Hardy-Weinberg equilibrium principle says that allele frequencies in a population will remain constant in the absence of the four factors that could change them. Those factors are natural selection, mutation, genetic drift, and migration (gene flow). In fact, we know they are probably always affecting populations.

Natural Selection

Natural selection has already been discussed. Alleles are expressed in a phenotype. Depending on the environmental conditions, the phenotype confers an advantage or disadvantage to the individual with the phenotype relative to the other phenotypes in the population. If it is an advantage, then that individual will likely have more offspring than individuals with the other phenotypes, and this will mean that the allele behind the phenotype will have greater representation in the next generation. If conditions remain the same, those offspring, which are carrying the same allele, will also benefit. Over time, the allele will increase in frequency in the population.

Mutation

Mutation is a source of new alleles in a population. Mutation is a change in the DNA sequence of the gene. A mutation can change one allele into another, but the net effect is a change in frequency. The change in frequency resulting from mutation is small, so its effect on evolution is small unless it interacts with one of the other factors, such as selection. A mutation may produce an allele that is selected against, selected for, or selectively neutral. Harmful mutations are removed from the population by selection and will generally only be found in very low frequencies equal to the mutation rate. Beneficial mutations will spread through the population through selection, although that initial spread is slow. Whether or not a mutation is beneficial or harmful is determined by whether it helps an organism survive to sexual maturity and reproduce. It should be noted that mutation is the ultimate source of genetic variation in all populations—new alleles, and, therefore, new genetic variations arise through mutation.

Genetic Drift

Another way a population's allele frequencies can change is genetic drift (Figure 10.2.1), which is simply the effect of chance. Genetic drift is most important in small populations. Drift would be completely absent in a population with infinite individuals, but, of course, no population is this large. Genetic drift occurs because the alleles in an offspring generation are a random sample of the alleles in the parent generation. Alleles may or may not make it into the next generation due to chance events including mortality of an individual, events affecting finding a mate, and even the events affecting which gametes end up in fertilizations. If one individual in a population of ten individuals happens to die before it leaves any offspring to the next generation, all of its genes—a tenth of the population's gene pool—will be suddenly lost. In a population of 100, that 1 individual represents only 1 percent of the overall gene pool; therefore, it has much less impact on the population's genetic structure and is unlikely to remove all copies of even a relatively rare allele.

Imagine a population of ten individuals, half with allele *A* and half with allele *a* (the individuals are haploid). In a stable population, the next generation will also have ten individuals. Choose that generation randomly by flipping a coin ten times and let heads be *A* and tails be *a*. It is unlikely that the next generation will have exactly half of each allele. There might be six of one and four of the other, or some different set of frequencies. Thus, the allele frequencies have changed and evolution has occurred. A coin will no longer work to choose the next generation (because the odds are no longer one half for each allele). The frequency in each generation will drift up and down on what is known as a random walk until at one point either all *A* or all *a* are chosen and that allele is fixed from that point on. This could take a very long time for a large population. This simplification is not very biological, but it can be shown that real populations behave this way. The effect of drift on frequencies is greater the smaller a population is. Its effect is also greater on an allele with a frequency far from one half. Drift will influence every allele, even those that are being naturally selected.

ART CONNECTION

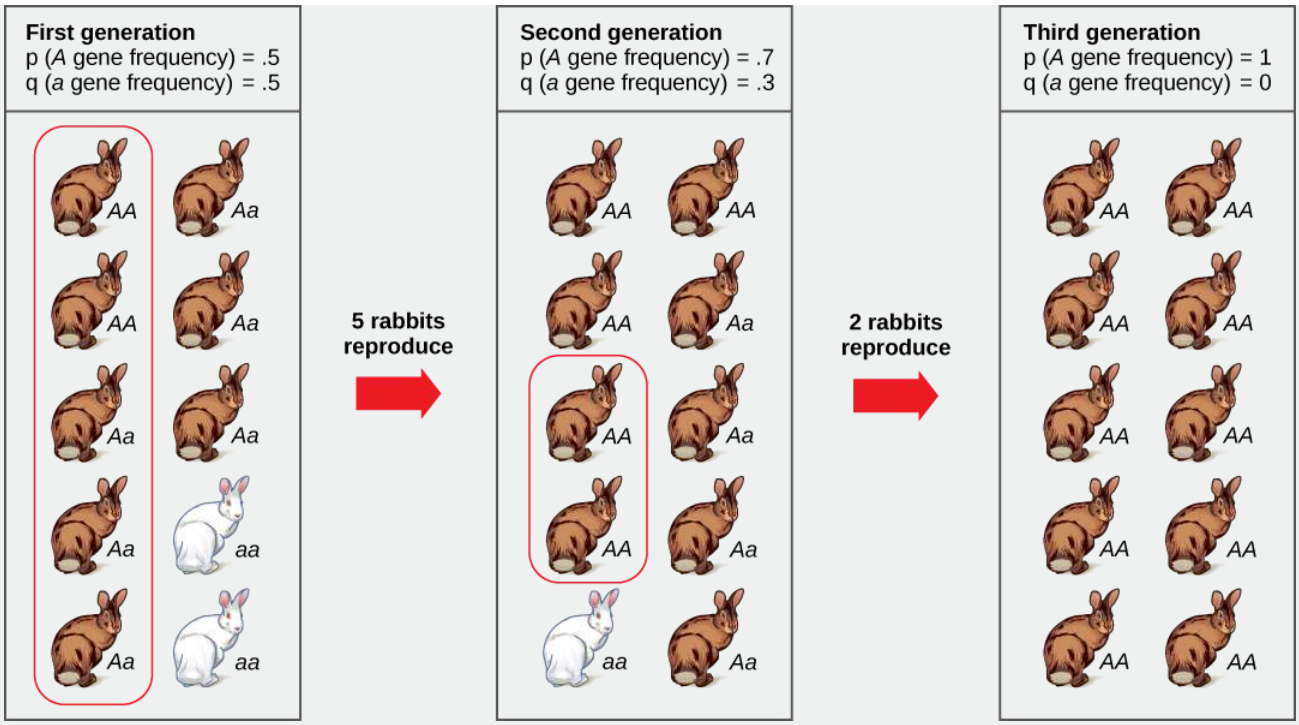


Figure 10.2.1**:** Genetic drift in a population can lead to the elimination of an allele from a population by chance. In each generation, a random set of individuals reproduces to produce the next generation. The frequency of alleles in the next generation is equal to the frequency of alleles among the individuals reproducing.

Do you think genetic drift would happen more quickly on an island or on the mainland?

Genetic drift can also be magnified by natural or human-caused events, such as a disaster that randomly kills a large portion of the population, which is known as the bottleneck effectthat results in a large portion of the genome suddenly being wiped out (Figure 10.2.2). In one fell swoop, the genetic structure of the survivors becomes the genetic structure of the entire population, which may be very different from the pre-disaster population. The disaster must be one that kills for reasons unrelated to the organism's traits, such as a hurricane or lava flow. A mass killing caused by unusually cold temperatures at night, is likely to affect individuals differently depending on the alleles they possess that confer cold hardiness.

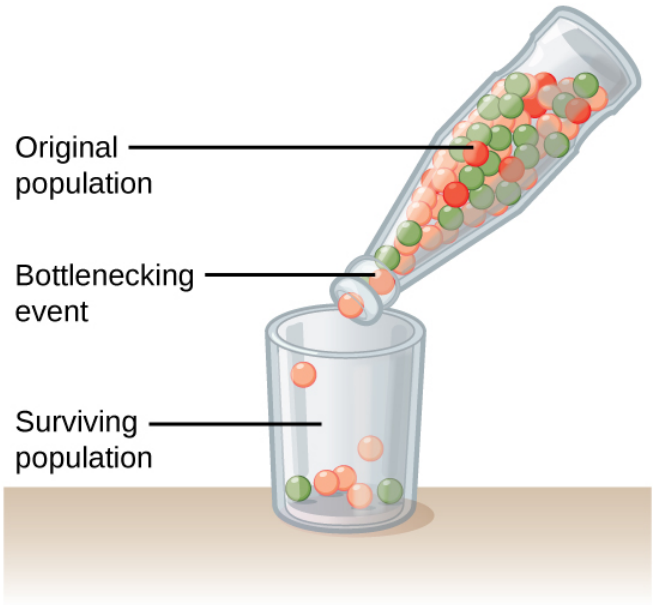


Figure 10.2.2**:** A chance event or catastrophe can reduce the genetic variability within a population.

Another scenario in which populations might experience a strong influence of genetic drift is if some portion of the population leaves to start a new population in a new location, or if a population gets divided by a physical barrier of some kind. In this situation, those individuals are unlikely to be representative of the entire population which results in the founder effect. The founder effect occurs when the genetic structure matches that of the new population's founding fathers and mothers. The founder effect is believed to have been a key factor in the genetic history of the Afrikaner population of Dutch settlers in South Africa, as evidenced by mutations that are common in Afrikaners but rare in most other populations. This is likely due to a higher-than-normal proportion of the founding colonists, which were a small sample of the original population, carried these mutations. As a result, the population expresses unusually high incidences of Huntington's disease (HD) and Fanconi anemia (FA), a genetic disorder known to cause bone marrow and congenital abnormalities, and even cancer.[1]

CONCEPT IN ACTION

Visit this site to learn more about genetic drift and to run simulations of allele changes caused by drift.

Gene Flow

Another important evolutionary force is gene flow, or the flow of alleles in and out of a population resulting from the migration of individuals or gametes (Figure 10.2.3). While some populations are fairly stable, others experience more flux. Many plants, for example, send their seeds far and wide, by wind or in the guts of animals; these seeds may introduce alleles common in the source population to a new population in which they are rare.

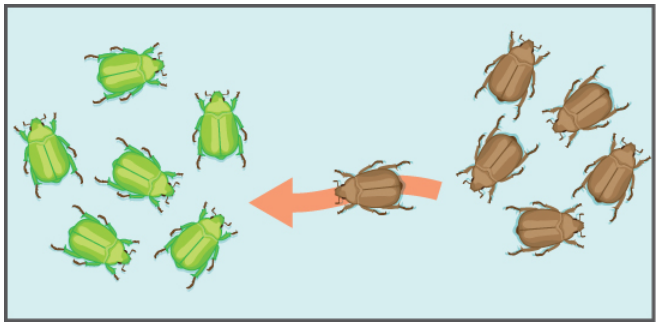


Figure 10.2.3: Gene flow can occur when an individual travels from one geographic location to another and joins a different population of the species. In the example shown here, the brown allele is introduced into the green population.

Summary

There are four factors that can change the allele frequencies of a population. Natural selection works by selecting for alleles that confer beneficial traits or behaviors, while selecting against those for deleterious qualities. Mutations introduce new alleles into a population. Genetic drift stems from the chance occurrence that some individuals have more offspring than others and results in changes in allele frequencies that are random in direction. When individuals leave or join the population, allele frequencies can change as a result of gene flow.

Art Connections

Figure 10.2.1: Do you think genetic drift would happen more quickly on an island or on the mainland?

Answer

Genetic drift is likely to occur more rapidly on an island, where smaller populations are expected to occur.

Footnotes

1. 1 A. J. Tipping et al., "Molecular and Genealogical Evidence for a Founder Effect in Fanconi Anemia Families of the Afrikaner Population of South Africa," *PNAS* 98, no. 10 (2001): 5734-5739, doi: 10.1073/pnas.091402398.

Glossary

bottleneck effect

the magnification of genetic drift as a result of natural events or catastrophes

founder effect

a magnification of genetic drift in a small population that migrates away from a large parent population carrying with it an unrepresentative set of alleles

gene flow

the flow of alleles in and out of a population due to the migration of individuals or gametes

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10.3: Evidence of Evolution

The evidence for evolution is compelling and extensive. Looking at every level of organization in living systems, biologists see the signature of past and present evolution. Darwin dedicated a large portion of his book, *On the Origin of Species*, identifying patterns in nature that were consistent with evolution and since Darwin our understanding has become clearer and broader.

Fossils

Fossils provide solid evidence that organisms from the past are not the same as those found today; fossils show a progression of evolution. Scientists determine the age of fossils and categorize them all over the world to determine when the organisms lived relative to each other. The resulting fossil record tells the story of the past, and shows the evolution of form over millions of years (Figure 10.3.1). For example, highly detailed fossil records have been recovered for sequences of species in the evolution of whales and modern horses. The fossil record of horses in North America is especially rich and many contain transition fossils: those showing intermediate anatomy between earlier and later forms. The fossil record extends back to a dog-like ancestor some 55 million years ago that gave rise to the first horse-like species 55 to 42 million years ago in the genus *Eohippus*. The series of fossils tracks the change in anatomy resulting from a gradual drying trend that changed the landscape from a forested one to a prairie. Successive fossils show the evolution of teeth shapes and foot and leg anatomy to a grazing habit, with adaptations for escaping predators, for example in species of *Mesohippus* found from 40 to 30 million years ago. Later species showed gains in size, such as those of *Hipparion*, which existed from about 23 to 2 million years ago. The fossil record shows several adaptive radiations in the horse lineage, which is now much reduced to only one genus, *Equus*, with several species.

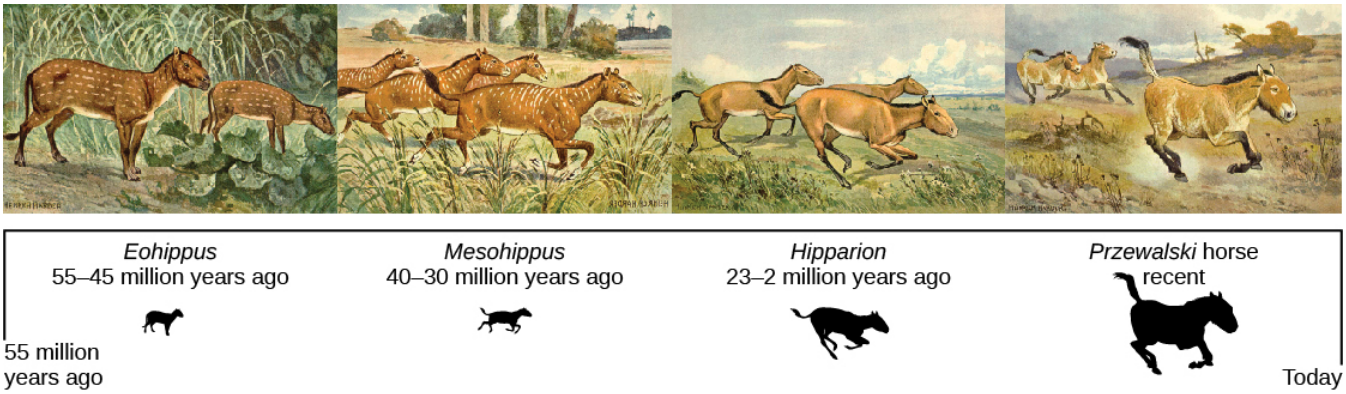


Figure 10.3.1**:** This illustration shows an artist's renderings of these species derived from fossils of the evolutionary history of the horse and its ancestors. The species depicted are only four from a very diverse lineage that contains many branches, dead ends, and adaptive radiations. One of the trends, depicted here is the evolutionary tracking of a drying climate and increase in prairie versus forest habitat reflected in forms that are more adapted to grazing and predator escape through running. Przewalski's horse is one of a few living species of horse.

Anatomy and Embryology

Another type of evidence for evolution is the presence of structures in organisms that share the same basic form. For example, the bones in the appendages of a human, dog, bird, and whale all share the same overall construction (Figure 10.3.2). That similarity results from their origin in the appendages of a common ancestor. Over time, evolution led to changes in the shapes and sizes of these bones in different species, but they have maintained the same overall layout, evidence of descent from a common ancestor. Scientists call these synonymous parts homologous structures. Some structures exist in organisms that have no apparent function at all, and appear to be residual parts from a past ancestor. For example, some snakes have pelvic bones despite having no legs because they descended from reptiles that did have legs. These unused structures without function are called vestigial structures. Other examples of vestigial structures are wings on flightless birds (which may have other functions), leaves on some cacti, traces of pelvic bones in whales, and the sightless eyes of cave animals.

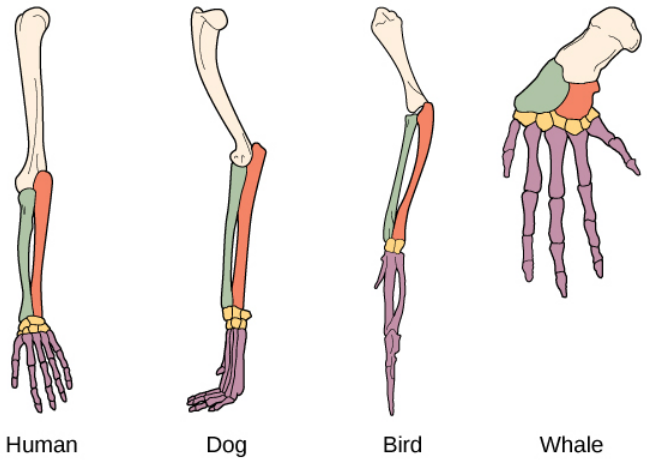


Figure 10.3.2**:** The similar construction of these appendages indicates that these organisms share a common ancestor.

Another evidence of evolution is the convergence of form in organisms that share similar environments. For example, species of unrelated animals, such as the arctic fox and ptarmigan (a bird), living in the arctic region have temporary white coverings during winter to blend with the snow and ice (Figure 10.3.3). The similarity occurs not because of common ancestry, indeed one covering is of fur and the other of feathers, but because of similar selection pressures—the benefits of not being seen by predators.



Figure 10.3.3**:** The white winter coat of (a) the arctic fox and (b) the ptarmigan's plumage are adaptations to their environments. (credit a: modification of work by Keith Morehouse)

Embryology, the study of the development of the anatomy of an organism to its adult form also provides evidence of relatedness between now widely divergent groups of organisms. Structures that are absent in some groups often appear in their embryonic forms and disappear by the time the adult or juvenile form is reached. For example, all vertebrate embryos, including humans, exhibit gill slits at some point in their early development. These disappear in the adults of terrestrial groups, but are maintained in adult forms of aquatic groups such as fish and some amphibians. Great ape embryos, including humans, have a tail structure during their development that is lost by the time of birth. The reason embryos of unrelated species are often similar is that mutational changes that affect the organism during embryonic development can cause amplified differences in the adult, even while the embryonic similarities are preserved.

Biogeography

The geographic distribution of organisms on the planet follows patterns that are best explained by evolution in conjunction with the movement of tectonic plates over geological time. Broad groups that evolved before the breakup of the supercontinent Pangaea

(about 200 million years ago) are distributed worldwide. Groups that evolved since the breakup appear uniquely in regions of the planet, for example the unique flora and fauna of northern continents that formed from the supercontinent Laurasia and of the southern continents that formed from the supercontinent Gondwana. The presence of Proteaceae in Australia, southern Africa, and South America is best explained by the plant family's presence there prior to the southern supercontinent Gondwana breaking up (Figure 10.3.4).

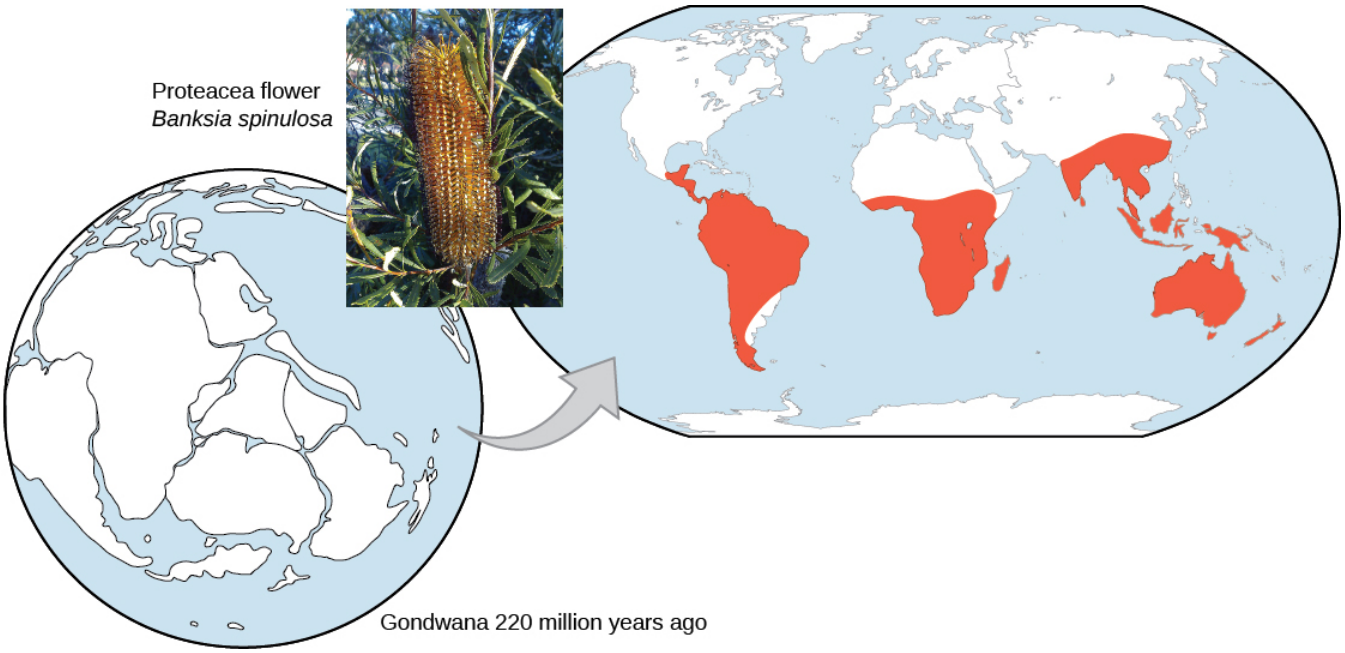


Figure 10.3.4**:** The Proteacea family of plants evolved before the supercontinent Gondwana broke up. Today, members of this plant family are found throughout the southern hemisphere (shown in red). (credit "Proteacea flower": modification of work by "dorofofoto"/Flickr)

The great diversification of the marsupials in Australia and the absence of other mammals reflects that island continent's long isolation. Australia has an abundance of endemic species—species found nowhere else—which is typical of islands whose isolation by expanses of water prevents migration of species to other regions. Over time, these species diverge evolutionarily into new species that look very different from their ancestors that may exist on the mainland. The marsupials of Australia, the finches on the Galápagos, and many species on the Hawaiian Islands are all found nowhere else but on their island, yet display distant relationships to ancestral species on mainlands.

Molecular Biology

Like anatomical structures, the structures of the molecules of life reflect descent with modification. Evidence of a common ancestor for all of life is reflected in the universality of DNA as the genetic material and of the near universality of the genetic code and the machinery of DNA replication and expression. Fundamental divisions in life between the three domains are reflected in major structural differences in otherwise conservative structures such as the components of ribosomes and the structures of membranes. In general, the relatedness of groups of organisms is reflected in the similarity of their DNA sequences—exactly the pattern that would be expected from descent and diversification from a common ancestor.

DNA sequences have also shed light on some of the mechanisms of evolution. For example, it is clear that the evolution of new functions for proteins commonly occurs after gene duplication events. These duplications are a kind of mutation in which an entire gene is added as an extra copy (or many copies) in the genome. These duplications allow the free modification of one copy by mutation, selection, and drift, while the second copy continues to produce a functional protein. This allows the original function for the protein to be kept, while evolutionary forces tweak the copy until it functions in a new way.

Section Summary

The evidence for evolution is found at all levels of organization in living things and in the extinct species we know about through fossils. Fossils provide evidence for the evolutionary change through now extinct forms that led to modern species. For example,

there is a rich fossil record that shows the evolutionary transitions from horse ancestors to modern horses that document intermediate forms and a gradual adaptation to changing ecosystems. The anatomy of species and the embryological development of that anatomy reveal common structures in divergent lineages that have been modified over time by evolution. The geographical distribution of living species reflects the origins of species in particular geographic locations and the history of continental movements. The structures of molecules, like anatomical structures, reflect the relationships of living species and match patterns of similarity expected from descent with modification.

Glossary

vestigial structure

a physical structure present in an organism but that has no apparent function and appears to be from a functional structure in a distant ancestor

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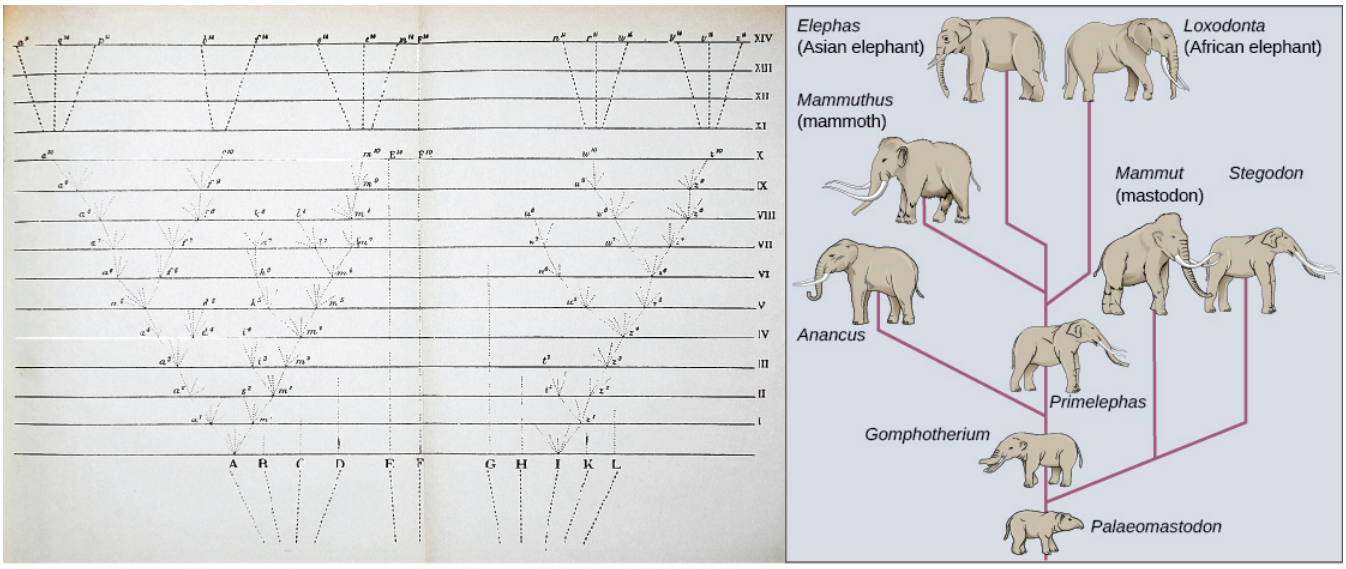
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10.4: Speciation

The biological definition of species, which works for sexually reproducing organisms, is a group of actually or potentially interbreeding individuals. According to this definition, one species is distinguished from another by the possibility of matings between individuals from each species to produce fertile offspring. There are exceptions to this rule. Many species are similar enough that hybrid offspring are possible and may often occur in nature, but for the majority of species this rule generally holds. In fact, the presence of hybrids between similar species suggests that they may have descended from a single interbreeding species and that the speciation process may not yet be completed.

Given the extraordinary diversity of life on the planet there must be mechanisms for speciation: the formation of two species from one original species. Darwin envisioned this process as a branching event and diagrammed the process in the only illustration found in *On the Origin of Species* (Figure 10.4.1**a**). For speciation to occur, two new populations must be formed from one original population, and they must evolve in such a way that it becomes impossible for individuals from the two new populations to interbreed. Biologists have proposed mechanisms by which this could occur that fall into two broad categories. Allopatric speciation, meaning speciation in "other homelands," involves a geographic separation of populations from a parent species and subsequent evolution. Sympatric speciation, meaning speciation in the "same homeland," involves speciation occurring within a parent species while remaining in one location.

Biologists think of speciation events as the splitting of one ancestral species into two descendant species. There is no reason why there might not be more than two species formed at one time except that it is less likely and such multiple events can also be conceptualized as single splits occurring close in time.



(a) (b)

Figure 10.4.1**:** The only illustration in Darwin's On the Origin of Species is (a) a diagram showing speciation events leading to biological diversity. The diagram shows similarities to phylogenetic charts that are drawn today to illustrate the relationships of species. (b) Modern elephants evolved from the Palaeomastodon, a species that lived in Egypt 35–50 million years ago.

Speciation through Geographic Separation

A geographically continuous population has a gene pool that is relatively homogeneous. Gene flow, the movement of alleles across the range of the species, is relatively free because individuals can move and then mate with individuals in their new location. Thus, the frequency of an allele at one end of a distribution will be similar to the frequency of the allele at the other end. When populations become geographically discontinuous that free-flow of alleles is prevented. When that separation lasts for a period of time, the two populations are able to evolve along different trajectories. Thus, their allele frequencies at numerous genetic loci gradually become more and more different as new alleles independently arise by mutation in each population. Typically, environmental conditions, such as climate, resources, predators, and competitors, for the two populations will differ causing natural

selection to favor divergent adaptations in each group. Different histories of genetic drift, enhanced because the populations are smaller than the parent population, will also lead to divergence.

Given enough time, the genetic and phenotypic divergence between populations will likely affect characters that influence reproduction enough that were individuals of the two populations brought together, mating would be less likely, or if a mating occurred, offspring would be non-viable or infertile. Many types of diverging characters may affect the reproductive isolation (inability to interbreed) of the two populations. These mechanisms of reproductive isolation can be divided into prezygotic mechanisms (those that operate before fertilization) and postzygotic mechanisms (those that operate after fertilization). Prezygotic mechanisms include traits that allow the individuals to find each other, such as the timing of mating, sensitivity to pheromones, or choice of mating sites. If individuals are able to encounter each other, character divergence may prevent courtship rituals from leading to a mating either because female preferences have changed or male behaviors have changed. Physiological changes may interfere with successful fertilization if mating is able to occur. Postzygotic mechanisms include genetic incompatibilities that prevent proper development of the offspring, or if the offspring live, they may be unable to produce viable gametes themselves as in the example of the mule, the infertile offspring of a female horse and a male donkey.

If the two isolated populations are brought back together and the hybrid offspring that formed from matings between individuals of the two populations have lower survivorship or reduced fertility, then selection will favor individuals that are able to discriminate between potential mates of their own population and the other population. This selection will enhance the reproductive isolation.

Isolation of populations leading to allopatric speciation can occur in a variety of ways: from a river forming a new branch, erosion forming a new valley, or a group of organisms traveling to a new location without the ability to return, such as seeds floating over the ocean to an island. The nature of the geographic separation necessary to isolate populations depends entirely on the biology of the organism and its potential for dispersal. If two flying insect populations took up residence in separate nearby valleys, chances are that individuals from each population would fly back and forth, continuing gene flow. However, if two rodent populations became divided by the formation of a new lake, continued gene flow would be unlikely; therefore, speciation would be more likely.

Biologists group allopatric processes into two categories. If a few members of a species move to a new geographical area, this is called dispersal. If a natural situation arises to physically divide organisms, this is called vicariance.

Scientists have documented numerous cases of allopatric speciation taking place. For example, along the west coast of the United States, two separate subspecies of spotted owls exist. The northern spotted owl has genetic and phenotypic differences from its close relative, the Mexican spotted owl, which lives in the south (Figure 10.4.2). The cause of their initial separation is not clear, but it may have been caused by the glaciers of the ice age dividing an initial population into two.[1]

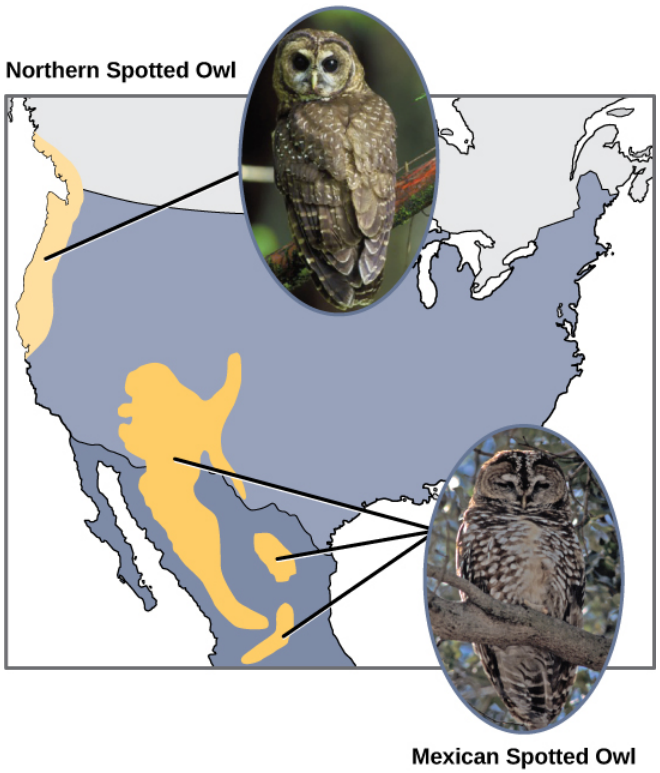


Figure 10.4.2**:** The northern spotted owl and the Mexican spotted owl inhabit geographically separate locations with different climates and ecosystems. The owl is an example of incipient speciation. (credit “northern spotted owl”: modification of work by John and Karen Hollingsworth, USFWS; credit “Mexican spotted owl”: modification of work by Bill Radke, USFWS)

Additionally, scientists have found that the further the distance between two groups that once were the same species, the more likely for speciation to take place. This seems logical because as the distance increases, the various environmental factors would likely have less in common than locations in close proximity. Consider the two owls; in the north, the climate is cooler than in the south; the other types of organisms in each ecosystem differ, as do their behaviors and habits; also, the hunting habits and prey choices of the owls in the south vary from the northern ones. These variances can lead to evolved differences in the owls, and over time speciation will likely occur unless gene flow between the populations is restored.

In some cases, a population of one species disperses throughout an area, and each finds a distinct niche or isolated habitat. Over time, the varied demands of their new lifestyles lead to multiple speciation events originating from a single species, which is called adaptive radiation. From one point of origin, many adaptations evolve causing the species to radiate into several new ones. Island archipelagos like the Hawaiian Islands provide an ideal context for adaptive radiation events because water surrounds each island, which leads to geographical isolation for many organisms (Figure 10.4.3). The Hawaiian honeycreeper illustrates one example of adaptive radiation. From a single species, called the founder species, numerous species have evolved, including the eight shown in Figure 10.4.3.

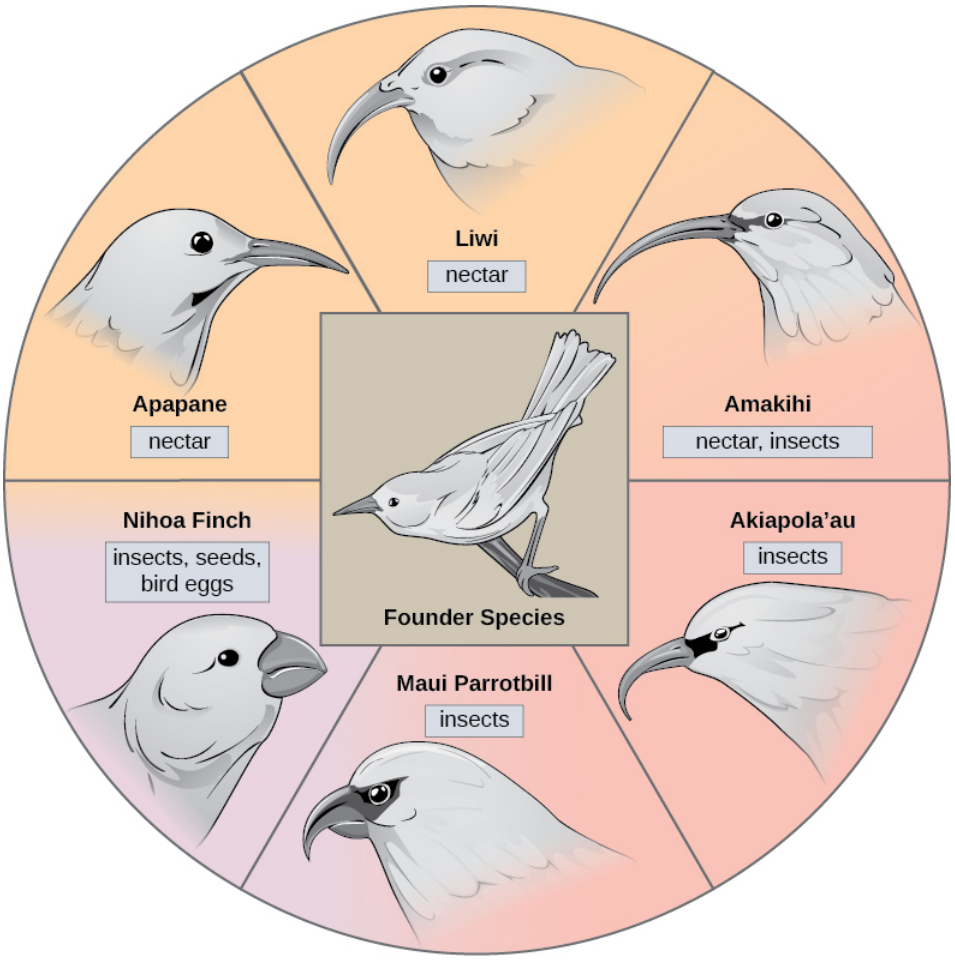


Figure 10.4.3**:** The honeycreeper birds illustrate adaptive radiation. From one original species of bird, multiple others evolved, each with its own distinctive characteristics.

Notice the differences in the species' beaks in Figure 10.4.3. Change in the genetic variation for beaks in response to natural selection based on specific food sources in each new habitat led to evolution of a different beak suited to the specific food source. The fruit and seed-eating birds have thicker, stronger beaks which are suited to break hard nuts. The nectar-eating birds have long beaks to dip into flowers to reach their nectar. The insect-eating birds have beaks like swords, appropriate for stabbing and impaling insects. Darwin's finches are another well-studied example of adaptive radiation in an archipelago.

Speciation without Geographic Separation

Can divergence occur if no physical barriers are in place to separate individuals who continue to live and reproduce in the same habitat? A number of mechanisms for sympatric speciation have been proposed and studied.

One form of sympatric speciation can begin with a chromosomal error during meiosis or the formation of a hybrid individual with too many chromosomes. Polyploidy is a condition in which a cell, or organism, has an extra set, or sets, of chromosomes. Scientists have identified two main types of polyploidy that can lead to reproductive isolation of an individual in the polyploid state. In some cases a polyploid individual will have two or more complete sets of chromosomes from its own species in a condition called autopolyploidy (Figure 10.4.4). The prefix "auto" means self, so the term means multiple chromosomes from one's own species. Polyploidy results from an error in meiosis in which all of the chromosomes move into one cell instead of separating.

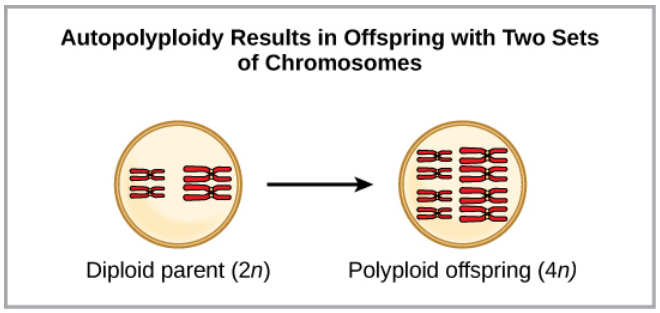


Figure 10.4.4**:** Autopolyploidy results when mitosis is not followed by cytokinesis.

For example, if a plant species with $2n = 6$ produces autopolyploid gametes that are also diploid ($2n = 6$, when they should be $n = 3$), the gametes now have twice as many chromosomes as they should have. These new gametes will be incompatible with the normal gametes produced by this plant species. But they could either self-pollinate or reproduce with other autopolyploid plants with gametes having the same diploid number. In this way, sympatric speciation can occur quickly by forming offspring with $4n$ called a tetraploid. These individuals would immediately be able to reproduce only with those of this new kind and not those of the ancestral species. The other form of polyploidy occurs when individuals of two different species reproduce to form a viable offspring called an allopolyploid. The prefix "allo" means "other" (recall from allopatric); therefore, an allopolyploid occurs when gametes from two different species combine. Figure 10.4.5 illustrates one possible way an allopolyploidy can form. Notice how it takes two generations, or two reproductive acts, before the viable fertile hybrid results.

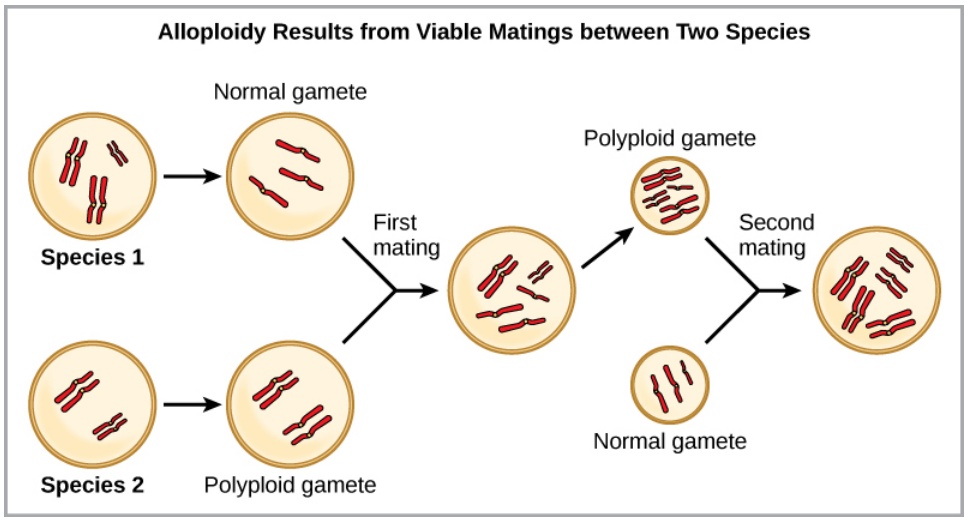


Figure 10.4.5**:** Alloploidy results when two species mate to produce viable offspring. In the example shown, a normal gamete from one species fuses with a polyploid gamete from another. Two matings are necessary to produce viable offspring.

The cultivated forms of wheat, cotton, and tobacco plants are all allopolyploids. Although polyploidy occurs occasionally in animals, most chromosomal abnormalities in animals are lethal; it takes place most commonly in plants. Scientists have discovered more than 1/2 of all plant species studied relate back to a species evolved through polyploidy.

Sympatric speciation may also take place in ways other than polyploidy. For example, imagine a species of fish that lived in a lake. As the population grew, competition for food also grew. Under pressure to find food, suppose that a group of these fish had the genetic flexibility to discover and feed off another resource that was unused by the other fish. What if this new food source was found at a different depth of the lake? Over time, those feeding on the second food source would interact more with each other than the other fish; therefore they would breed together as well. Offspring of these fish would likely behave as their parents and feed and live in the same area, keeping them separate from the original population. If this group of fish continued to remain separate from the first population, eventually sympatric speciation might occur as more genetic differences accumulated between them.

This scenario does play out in nature, as do others that lead to reproductive isolation. One such place is Lake Victoria in Africa, famous for its sympatric speciation of cichlid fish. Researchers have found hundreds of sympatric speciation events in these fish, which have not only happened in great number, but also over a short period of time. Figure 10.4.6 shows this type of speciation

among a cichlid fish population in Nicaragua. In this locale, two types of cichlids live in the same geographic location; however, they have come to have different morphologies that allow them to eat various food sources.

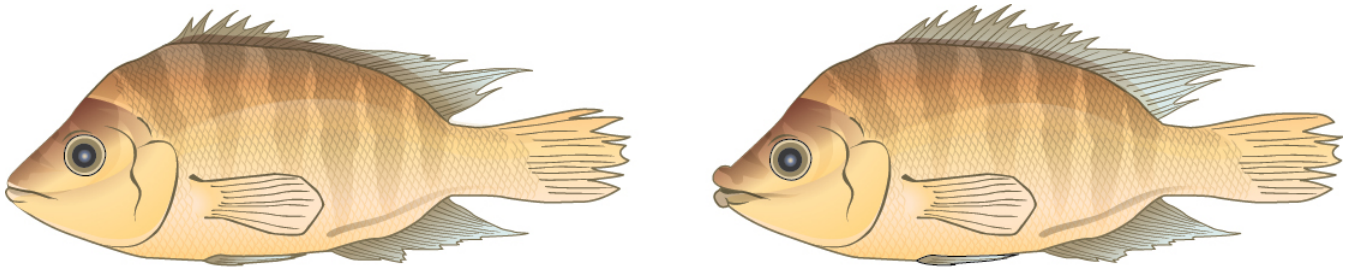


Figure 10.4.6**:** Cichlid fish from Lake Apoyeque, Nicaragua, show evidence of sympatric speciation. Lake Apoyeque, a crater lake, is 1800 years old, but genetic evidence indicates that the lake was populated only 100 years ago by a single population of cichlid fish. Nevertheless, two populations with distinct morphologies and diets now exist in the lake, and scientists believe these populations may be in an early stage of speciation.

Finally, a well-documented example of ongoing sympatric speciation occurred in the apple maggot fly, *Rhagoletis pomonella*, which arose as an isolated population sometime after the introduction of the apple into North America. The native population of flies fed on hawthorn species and is host-specific: it only infests hawthorn trees. Importantly, it also uses the trees as a location to meet for mating. It is hypothesized that either through mutation or a behavioral mistake, flies jumped hosts and met and mated in apple trees, subsequently laying their eggs in apple fruit. The offspring matured and kept their preference for the apple trees effectively dividing the original population into two new populations separated by host species, not by geography. The host jump took place in the nineteenth century, but there are now measureable differences between the two populations of fly. It seems likely that host specificity of parasites in general is a common cause of sympatric speciation.

Section Summary

Speciation occurs along two main pathways: geographic separation (allopatric speciation) and through mechanisms that occur within a shared habitat (sympatric speciation). Both pathways force reproductive isolation between populations. Sympatric speciation can occur through errors in meiosis that form gametes with extra chromosomes, called polyploidy. Autopolyploidy occurs within a single species, whereas allopolyploidy occurs because of a mating between closely related species. Once the populations are isolated, evolutionary divergence can take place leading to the evolution of reproductive isolating traits that prevent interbreeding should the two populations come together again. The reduced viability of hybrid offspring after a period of isolation is expected to select for stronger inherent isolating mechanisms.

Footnotes

1. 1 Courtney, S.P., et al, “Scientific Evaluation of the Status of the Northern Spotted Owl,” Sustainable Ecosystems Institute (2004), Portland, OR.

Glossary

adaptive radiation

a speciation when one species radiates out to form several other species

allopatric speciation

a speciation that occurs via a geographic separation

dispersal

an allopatric speciation that occurs when a few members of a species move to a new geographical area

speciation

a formation of a new species

sympatric speciation

a speciation that occurs in the same geographic space

vicariance

an allopatric speciation that occurs when something in the environment separates organisms of the same species into separate groups

Contributors and Attributions

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

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10.A: Evolution and Its Processes (Exercises)

Discovering How Populations Change

Multiple Choice

Which scientific concept did Charles Darwin and Alfred Wallace independently discover?

A. mutation
B. natural selection
C. over breeding
D. sexual reproduction

Answer

B

Which of the following situations will lead to natural selection?

A. The seeds of two plants land near each other and one grows larger than the other.
B. Two types of fish eat the same kind of food, and one is better able to gather food than the other.
C. Male lions compete for the right to mate with females, with only one possible winner.
D. all of the above

Answer

D

What is the difference between micro- and macroevolution?

A. Microevolution describes the evolution of small organisms, such as insects, while macroevolution describes the evolution of large organisms, like people and elephants.
B. Microevolution describes the evolution of microscopic entities, such as molecules and proteins, while macroevolution describes the evolution of whole organisms.
C. Microevolution describes the evolution of populations, while macroevolution describes the emergence of new species over long periods of time.
D. Microevolution describes the evolution of organisms over their lifetimes, while macroevolution describes the evolution of organisms over multiple generations.

Answer

C

Population genetics is the study of _____.

A. how allele frequencies in a population change over time
B. populations of cells in an individual
C. the rate of population growth
D. how genes affect embryological development

Answer

A

Free Response

If a person scatters a handful of plant seeds from one species in an area, how would natural selection work in this situation?

Answer

The plants that can best use the resources of the area, including competing with other individuals for those resources, will produce more seeds themselves and those traits that allowed them to better use the resources will increase in the population of the next generation.

Explain the Hardy-Weinberg principle of equilibrium.

Answer

The Hardy-Weinberg principle of equilibrium states that a population's allele frequencies are inherently stable. Unless an evolutionary force is acting upon the population, the population would carry the same genes at the same frequencies generation after generation, and individuals would, as a whole, look essentially the same.

Mechanisms of Evolution

Multiple Choice

Galápagos medium ground finches are found on Santa Cruz and San Cristóbal islands, which are separated by about 100 km of ocean. Occasionally, individuals from either island fly to the other island to stay. This can alter the allele frequencies of the population through which of the following mechanisms?

A. natural selection
B. genetic drift
C. gene flow
D. mutation

Answer

C

In which of the following pairs do both evolutionary processes introduce new genetic variation into a population?

A. natural selection and genetic drift
B. mutation and gene flow
C. natural selection and gene flow
D. gene flow and genetic drift

Answer

B

Free Response

Describe natural selection and give an example of natural selection at work in a population.

Answer

The theory of natural selection stems from the observation that some individuals in a population survive longer and have more offspring than others, thus passing on more of their genes to the next generation. For example, a big, powerful male gorilla is much more likely than a smaller, weaker gorilla to become the population's silverback, the pack's leader who mates far more than the other males of the group. The pack leader will, therefore, father more offspring, who share half of his genes, and are thus likely to also grow bigger and stronger like their father. Over time, the genes for bigger size will increase in frequency in the population, and the population will, as a result, grow larger on average.

Evidence of Evolution

Multiple Choice

The wing of a bird and the arm of a human are examples of _____.

A. vestigial structures
B. molecular structures
C. homologous structures
D. analogous structures

Answer

C

The fact that DNA sequences are more similar in more closely related organisms is evidence of what?

A. optimal design in organisms
B. adaptation
C. mutation
D. descent with modification

Answer

D

Free Response

Why do scientists consider vestigial structures evidence for evolution?

Answer

A vestigial structure is an example of a homologous structure that has apparently been reduced through evolution to a non-functional state because its function is no longer utilized by the species exhibiting it; therefore, any mutations which might reduce its structure are not selected against. The fact that the species has vestiges of the structure rather than no structure at all is evidence that it was present in an ancestor and evolved to non-functionality through accumulation of random mutations.

Speciation

Multiple Choice

Which situation would most likely lead to allopatric speciation?

A. A flood causes the formation of a new lake.
B. A storm causes several large trees to fall down.
C. A mutation causes a new trait to develop.
D. An injury causes an organism to seek out a new food source.

Answer

A

What are the three patterns that often appear once selective pressures have affected a population? Choose all that apply.

A. Bimodal.
B. Directional.
C. Diversifying.
D. Stabilizing.

Answers

B, C, D

What is the main difference between dispersal and vicariance?

A. One leads to allopatric speciation, whereas the other leads to sympatric speciation.
B. One involves the movement of the organism, whereas the other involves a change in the environment.

C. One depends on a genetic mutation occurring, whereas the other does not.
D. One involves closely related organisms, whereas the other involves only individuals of the same species.

Answer

B

Which variable increases the likelihood of allopatric speciation taking place more quickly?

A. lower rate of mutation
B. longer distance between divided groups
C. increased instances of hybrid formation
D. equivalent numbers of individuals in each population

Answer

B

Free Response

Why do island chains provide ideal conditions for adaptive radiation to occur?

Answer

Organisms of one species can arrive to an island together and then disperse throughout the chain, each settling into different niches, exploiting different food resources and, evolving independently with little gene flow between different islands.

Two species of fish had recently undergone sympatric speciation. The males of each species had a different coloring through which females could identify and choose a partner from her own species. After some time, pollution made the lake so cloudy it was hard for females to distinguish colors. What might take place in this situation?

Answer

It is likely the two species would start to reproduce with each other if hybridization is still possible. Depending on the viability of their offspring, they may fuse back into one species.

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CHAPTER OVERVIEW

11: ANIMAL STRUCTURE AND FUNCTION

In Unit 7, an introduction to the form and function of the animal body is followed by chapters on specific body systems and processes. This unit touches on the biology of all organisms while maintaining an engaging focus on human anatomy and physiology that helps students connect to the topics.

11.1: Introduction

11.2: Animal Form and Function

11.3: Animal Primary Tissues

11.4: Homeostasis

11.A: Key Terms

11.B: Animal Structure and Function (Exercises)

11.C: Critical Thinking Questions

Contributors

Connie Rye (East Mississippi Community College), Robert Wise (University of Wisconsin, Oshkosh), Vladimir Jurukovski (Suffolk County Community College), Jean DeSaix (University of North Carolina at Chapel Hill), Jung Choi (Georgia Institute of Technology), Yael Avissar (Rhode Island College) among other contributing authors. Original content by OpenStax (CC BY 4.0; Download for free at http://cnx.org/contents/185cbf87-c72...f21b5eabd@9.87).

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11.1: INTRODUCTION



Figure 11.1.1 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. (credit: modification of work by Keith Morehouse, USFWS)

CHAPTER OUTLINE

11.2 Animal Form and Function
11.3 Animal Primary Tissues
11.4 Homeostasis

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. The structures of animals consist of primary tissues that make up more complex organs and organ systems. Homeostasis allows an animal to maintain a balance between its internal and external environments.

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11.2: ANIMAL FORM AND FUNCTION

LEARNING OBJECTIVES

By the end of this section, you will be able to do the following:

- Describe the various types of body plans that occur in animals
- Describe limits on animal size and shape
- Relate bioenergetics to body size, levels of activity, and the environment

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. Animals' bodies are also designed to interact with their environments, whether in the deep sea, a rainforest canopy, or the desert. 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.

BODY PLANS

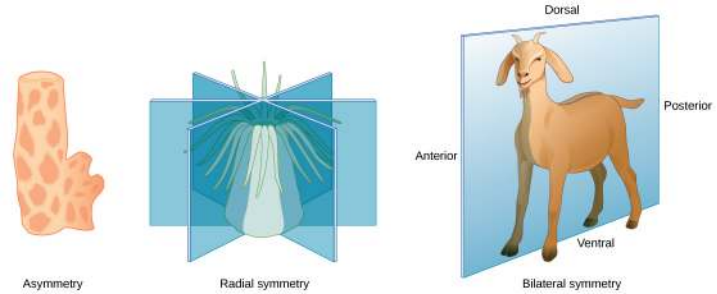


Figure 11.2.1 Animals exhibit different types of body symmetry. The sponge is asymmetrical, the sea anemone has radial symmetry, and the goat has bilateral symmetry.

Animal body plans follow set patterns related to symmetry. They are asymmetrical, radial, or bilateral in form as illustrated in Figure 33.2. Asymmetrical animals are animals with no pattern or symmetry; an example of an asymmetrical animal is a sponge. Radial symmetry, as illustrated in Figure 33.2, describes when an animal has 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, like a rock or a boat, and extract their food from the surrounding water as it flows around the organism. Bilateral symmetry is illustrated in the same figure by 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. Additional terms used when describing positions in the body are anterior (front), posterior (rear), dorsal (toward the back), and ventral (toward the stomach). Bilateral symmetry is found in both land-based and aquatic animals; it enables a high level of mobility.

LIMITS ON ANIMAL SIZE AND SHAPE

Animals with bilateral symmetry that live in water tend to have a fusiform shape: this is 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. Table 33.1 lists the maximum speed of various animals. Certain types of sharks can swim at fifty kilometers per hour and some dolphins at 32 to 40 kilometers per hour. Land animals frequently travel faster, although the tortoise and snail are significantly slower than cheetahs. 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. On the other hand, land-dwelling organisms are constrained mainly by gravity, and drag is relatively unimportant. For example, most adaptations in birds are for gravity not for drag.

Table 11.2.1 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

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 (Figure 33.3). 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, and 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. 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.

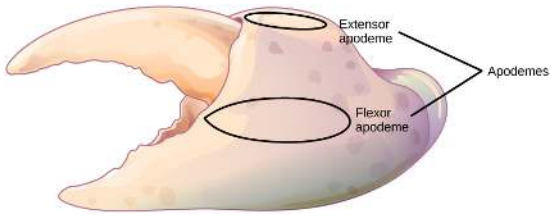


Figure 11.2.2 Apodemes are ingrowths on arthropod exoskeletons to which muscles attach. The apodemes on this crab leg are located above and below the fulcrum of the claw. Contraction of muscles attached to the apodemes pulls the claw closed.

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.

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 and the center of the cell does not receive adequate nutrients nor is it able to effectively dispel its waste.

An important concept in understanding how efficient diffusion is as a means of transport 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.

The solution to producing larger organisms is for them to become multicellular. Specialization occurs in complex organisms, allowing cells to become 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. Moreover, surface-to-volume ratio applies to other areas of animal development,

such as the relationship between muscle mass and cross-sectional surface area in supporting skeletons, and in the relationship between muscle mass and the generation and dissipation of heat.

LINK TO LEARNING

LINK TO LEARNING

Visit this interactive site to see an entire animal (a zebrafish embryo) at the cellular and sub-cellular level. Use the zoom and navigation functions for a virtual nanoscopy exploration.

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, and 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, and 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 and called 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 variously in joules, calories, or kilocalories (1000 calories). Carbohydrates and proteins contain about 4.5 to 5 kcal/g, and 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 to 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 (Figure 33.4). 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 O_2/g body mass/hr	75 mm^3 O_2/g body mass/hr

Figure 11.2.3 The mouse has a much higher metabolic rate than the elephant. (credit "mouse": modification of work by Magnus Kjaergaard; credit "elephant": modification of work by "TheLizardQueen"/Flickr)

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. For example: the type of grasses, leaves, or shrubs that an herbivore eats affects the number of calories that it takes in. The relative caloric content of herbivore foods, in descending order, is tall grasses > legumes > short grasses > forbs (any broad-leaved plant, not a grass) > subshrubs > annuals/biennials.

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 and allows animals to survive adverse conditions. Torpor can be used by animals for long periods, such as entering a state of hibernation during the winter months, in which case it 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 use this 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.

ANIMAL BODY PLANES AND CAVITIES

A standing vertebrate animal can be divided by several planes. 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 from the back. A transverse plane (or, horizontal plane) divides the animal into upper and lower portions. This is sometimes called a cross section, and, if the transverse cut is at an angle, it is called an oblique plane. Figure 33.5 illustrates these planes on a goat (a four-legged animal) and a human being.

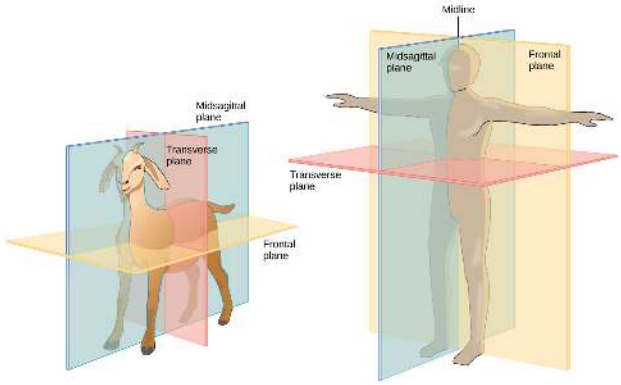


Figure 11.2.4 Shown are the planes of a quadrupedal goat and a bipedal human. The midsagittal plane divides the body exactly in half, into right and left portions. The frontal plane divides the front and back, and the transverse plane divides the body into upper and lower portions.

Vertebrate animals have a number of defined body cavities, as illustrated in Figure 33.6. Two of these are major cavities that contain smaller cavities within them. The dorsal cavity contains the cranial and the vertebral (or spinal) cavities. The ventral cavity contains the thoracic cavity, which in turn contains the pleural cavity around the lungs and the pericardial cavity, which surrounds the heart. The ventral cavity also contains the abdominopelvic cavity, which can be separated into the abdominal and the pelvic cavities.

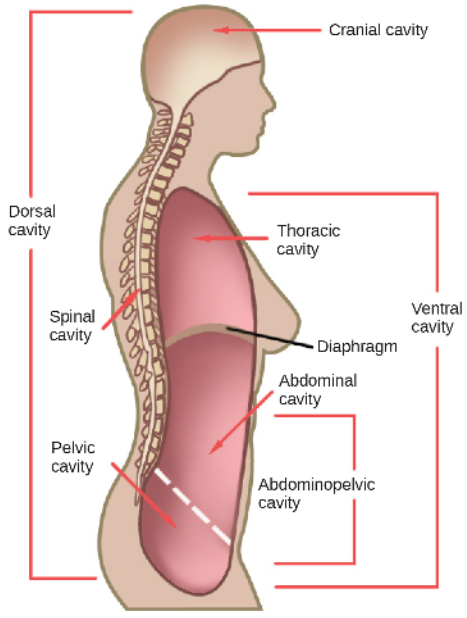


Figure 11.2.5 Vertebrate animals have two major body cavities. The dorsal cavity contains the cranial and the spinal cavity. The ventral cavity contains the thoracic cavity and the abdominopelvic cavity. The thoracic cavity is separated from the abdominopelvic cavity by the diaphragm. The abdominopelvic cavity is separated into the abdominal cavity and the pelvic cavity by an imaginary line parallel to the pelvis bones. (credit: modification of work by NCI)

CAREER CONNECTION

CAREER CONNECTIONS

Physical AnthropologistPhysical anthropologists study the adaptation, variability, and evolution of human beings, plus their living and fossil relatives. They can work in a variety of settings, although most will have an academic appointment at a university, usually in an anthropology department or a biology, genetics, or zoology department.

Nonacademic positions are available in the automotive and aerospace industries where the focus is on human size, shape, and anatomy. Research by these professionals might range from studies of how the human body reacts to car crashes to exploring how to make seats more comfortable. Other nonacademic positions can be obtained in museums of natural history, anthropology, archaeology, or science and technology. These positions involve educating students from grade school through graduate school. Physical anthropologists serve as education coordinators, collection managers, writers for museum publications, and as administrators. Zoos employ these professionals, especially if they have an expertise in primate biology; they work in collection management and captive breeding programs for endangered species. Forensic science utilizes physical anthropology expertise in identifying human and animal remains, assisting in determining the cause of death, and for expert testimony in trials.

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11.3: ANIMAL PRIMARY TISSUES

LEARNING OBJECTIVES

By the end of this section, you will be able to do the following:

- Describe epithelial tissues
- Discuss the different types of connective tissues in animals
- Describe three types of muscle tissues
- Describe nervous tissue

The tissues of multicellular, complex animals are four primary types: epithelial, connective, muscle, and nervous. Recall that tissues are groups of similar cells (cells carrying out related functions). These tissues combine to form organs—like the skin or kidney—that have specific, specialized functions within the body. Organs are organized into organ systems to perform functions; examples include the circulatory system, which consists of the heart and blood vessels, and the digestive system, consisting of several organs, including the stomach, intestines, liver, and pancreas. Organ systems come together to create an entire organism.

EPITHELIAL TISSUES

Epithelial tissues cover the outside of organs and structures in the body and 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. Table 33.2 summarizes the different types of epithelial tissues.

Table 11.3.1 Different Types of Epithelial Tissues

Cell shape	Description	Location
squamous	flat, irregular round shape	simple: lung alveoli, capillaries; stratified: skin, mouth, vagina
cuboidal	cube shaped, central nucleus	glands, renal tubules
columnar	tall, narrow, nucleus toward base; tall, narrow, nucleus along cell	simple: digestive tract; pseudostratified: respiratory tract
transitional	round, simple but appear stratified	urinary bladder

SQUAMOUS EPITHELIA

Squamous epithelial cells are generally round, flat, and have a small, centrally located nucleus. The cell outline is slightly irregular, and cells fit together to form a covering or lining. When the cells are arranged in a single layer (simple epithelia), they facilitate diffusion in tissues, such as the areas of gas exchange in the lungs and the exchange of nutrients and waste at blood capillaries.

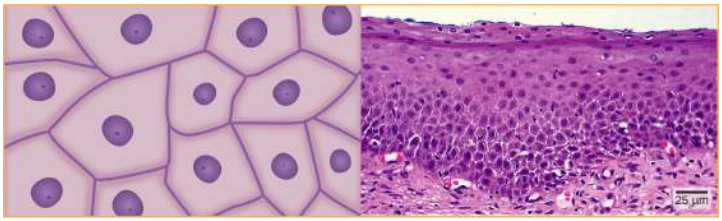


Figure 11.3.1 Squamous epithelia cells (a) have a slightly irregular shape, and a small, centrally located nucleus. These cells can be stratified into layers, as in (b) this human cervix specimen. (credit b: modification of work by Ed Uthman; scale-bar data from Matt Russell)

Figure 11.3.1a illustrates a layer of squamous cells with their membranes joined together to form an epithelium. Image Figure 11.3.1b illustrates squamous epithelial cells arranged in stratified layers, where protection is needed on the body from outside abrasion and damage. This is called a stratified squamous epithelium and occurs in the skin and in tissues lining the mouth and vagina.

CUBOIDAL EPITHELIA

Cuboidal epithelial cells, shown in Figure 11.3.2, are cube-shaped with a single, central nucleus. They are most commonly found in a single layer representing 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 11.3.2 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, and 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, as illustrated in Figure 11.3.3. 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.

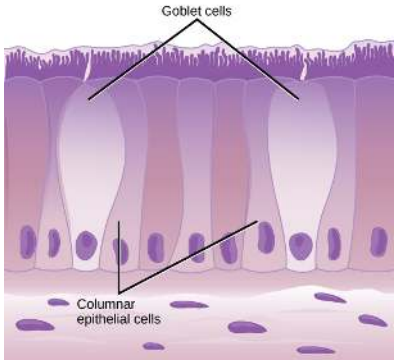


Figure 11.3.3 Simple columnar epithelial cells absorb material from the digestive tract. Goblet cells secrete mucus into the digestive tract lumen.

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, as seen in Figure 11.3.4. 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 mucus 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 mucus that traps irritants, which in the case of the trachea keep these irritants from getting into the lungs.

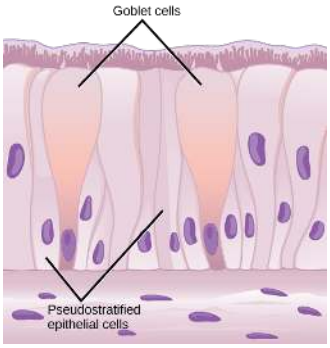


Figure 11.3.4 Pseudostratified columnar epithelia line the respiratory tract. They exist in one layer, but the arrangement of nuclei at different levels makes it appear that there is more than one layer. Goblet cells interspersed between the columnar epithelial cells secrete mucus into the respiratory tract.

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 illustrated in Figure 11.3.5. As the urinary bladder fills, the epithelial layer unfolds and expands to hold the volume of urine introduced into it. As the bladder fills, it expands and the lining becomes thinner. In other words, the tissue transitions from thick to thin.

VISUAL CONNECTION

VISUAL CONNECTION

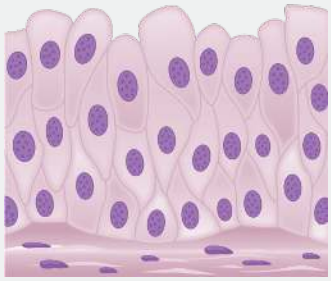


Figure 11.3.5 Transitional epithelia of the urinary bladder undergo changes in thickness depending on how full the bladder is.

Which of the following statements about types of epithelial cells is false?

a. Simple columnar epithelial cells line the tissue of the lung.
b. Simple cuboidal epithelial cells are involved in the filtering of blood in the kidney.
c. Pseudostratisfied columnar epithilia occur in a single layer, but the arrangement of nuclei makes it appear that more than one layer is present.
d. Transitional epithelia change in thickness depending on how full the bladder is.

CONNECTIVE TISSUES

Connective tissues are made up of a matrix consisting of living cells and a nonliving substance, called the ground substance. The ground substance is made 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. 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. Some tissues have specialized cells that are not found in the others. The matrix in connective tissues gives the tissue its density. When a connective tissue has a high concentration of cells or fibers, it has proportionally a 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 and return to its original size and shape. Elastic fibers provide flexibility to the tissues. Reticular fibers are the third type of protein fiber found in connective tissues. This fiber consists of thin strands of collagen that form a network of fibers to support the tissue and other organs to which it is connected. The various types of connective tissues, the types of cells and fibers they are made of, and sample locations of the tissues is summarized in Table 11.3.2.

Table 11.3.2 Connective Tissues

Tissue	Cells	Fibers	Location
loose/areolar	fibroblasts, macrophages, some lymphocytes, some neutrophils	few: collagen, elastic, reticular	around blood vessels; anchors epithelia
dense, fibrous connective tissue	fibroblasts, macrophages	mostly collagen	irregular: skin; regular: tendons, ligaments
cartilage	chondrocytes, chondroblasts	hyaline: few: collagen fibrocartilage: large amount of collagen	shark skeleton, fetal bones, human ears, intervertebral discs
bone	osteoblasts, osteocytes, osteoclasts	some: collagen, elastic	vertebrate skeletons
adipose	adipocytes	few	adipose (fat)
blood	red blood cells, white blood cells	none	blood

LOOSE/AREOLAR CONNECTIVE TISSUE

Loose connective tissue, also called areolar connective tissue, has a sampling of all of the components of a connective tissue. As illustrated in Figure 11.3.6, loose connective tissue has some fibroblasts; 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 and helps 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.

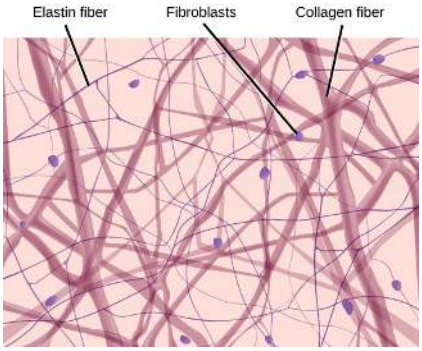


Figure 11.3.6 Loose connective tissue is composed of loosely woven collagen and elastic fibers. The fibers and other components of the connective tissue matrix are secreted by fibroblasts.

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, shown in Figure 11.3.7, is found in tendons (which connect muscles to bones) and ligaments (which connect bones to bones).

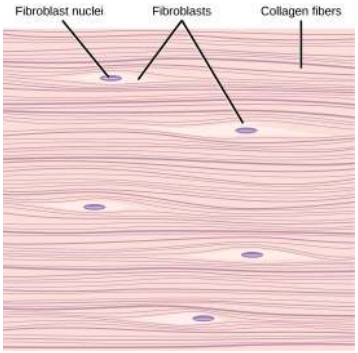


Figure 11.3.7 Fibrous connective tissue from the tendon has strands of collagen fibers lined up in parallel.

CARTILAGE

Cartilage is a connective tissue with a large amount of the matrix and variable amounts of fibers. The cells, called chondrocytes, 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, illustrated in Figure 11.3.8. The lacunae are randomly scattered throughout the tissue and the matrix takes on a milky or scrubbed appearance with routine histological stains. Sharks have cartilaginous skeletons, as does nearly the entire human skeleton during a specific pre-birth developmental stage. 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.

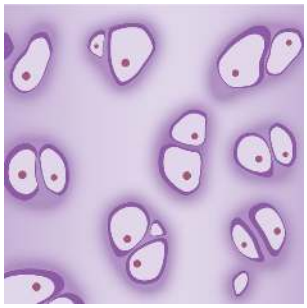


Figure 11.3.8 Hyaline cartilage consists of a matrix with cells called chondrocytes embedded in it. The chondrocytes exist in cavities in the matrix called lacunae.

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. Fibrocartilage contains a large amount of collagen fibers, giving the tissue tremendous strength. Fibrocartilage comprises the intervertebral discs in vertebrate animals. Hyaline cartilage found in movable joints such as the knee

and shoulder becomes damaged as a result of age or trauma. Damaged hyaline cartilage is replaced by fibrocartilage and results in the joints becoming “stiff.”

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 similar to the matrix material found in 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 salts—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. Osteoblasts 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. Osteoclasts are active in breaking down bone for bone remodeling, and they provide access to calcium stored in tissues. 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, as illustrated in Figure 11.3.9. A blood vessel and a nerve are found in the center of the structure within the Haversian canal, with radiating circles of lacunae around it known as lamellae. The wavy lines seen 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; these plates serve as struts to give the spongy bone strength. Over time, these plates can break causing the bone to become less resilient. Bone tissue forms the internal skeleton of vertebrate animals, providing structure to the animal and points of attachment for tendons.

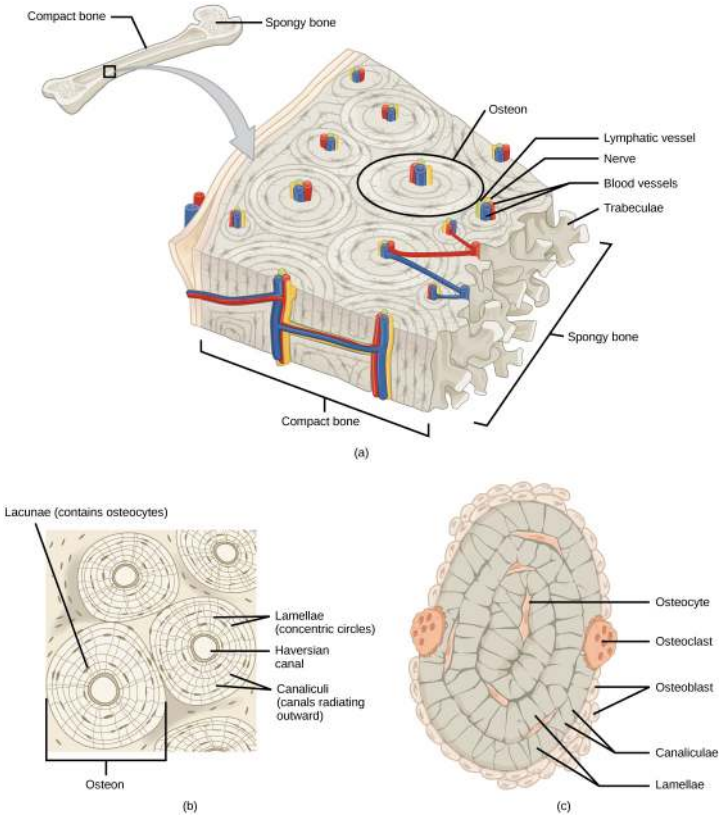


Figure 11.3.9 (a) Compact bone is a dense matrix on the outer surface of bone. Spongy bone, inside the compact bone, is porous with web-like trabeculae. (b) Compact bone is organized into rings called osteons. Blood vessels, nerves, and lymphatic vessels are found in the central Haversian canal. Rings of lamellae surround the Haversian canal. Between the lamellae are cavities called lacunae. Canaliculi are micro-channels 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 TISSUE

Adipose tissue, or fat tissue, is considered a connective tissue even though it does not have fibroblasts or a real matrix and only has a few fibers. Adipose tissue is made up 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, and they 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, as seen in Figure 11.3.10. The thin lines in the image are the cell membranes, and the nuclei are the small, black dots at the edges of the cells.

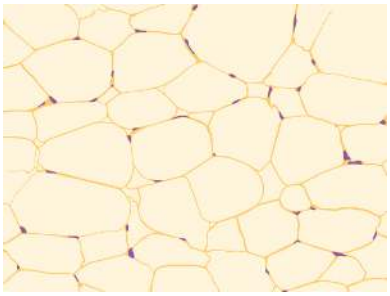


Figure 11.3.10 Adipose is a connective tissue is made up of cells called adipocytes. Adipocytes have small nuclei localized at the cell edge.

BLOOD

Blood is considered a connective tissue because it has a matrix, as shown in Figure 11.3.11. The living cell types are red blood cells (RBC), also called erythrocytes, and white blood cells (WBC), also called leukocytes. The fluid portion of whole blood, its matrix, is commonly called plasma.

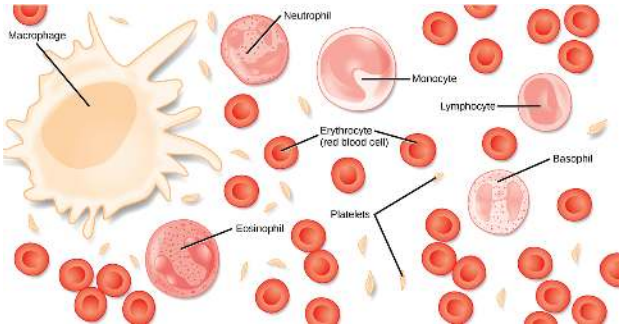


Figure 11.3.11 Blood is a connective tissue that has a fluid matrix, called plasma, and no fibers. Erythrocytes (red blood cells), the predominant cell type, are involved in the transport of oxygen and carbon dioxide. Also present are various leukocytes (white blood cells) involved in immune response.

The cell found in greatest abundance in blood is the erythrocyte. Erythrocytes are counted in millions in a blood sample: the average number of red blood cells in primates is 4.7 to 5.5 million cells per microliter. Erythrocytes are consistently the same size in a species, but vary in size between species. For example, the average diameter of a primate red blood cell is 7.5 µl, a dog is close at 7.0 µl, but a cat's RBC diameter is 5.9 µl. Sheep erythrocytes are even smaller at 4.6 µl. 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 the predominant white blood cells found in the peripheral blood. Leukocytes are counted in the thousands in the blood with measurements expressed as ranges: primate counts range from 4,800 to 10,800 cells per µl, dogs from 5,600 to 19,200 cells per µl, cats from 8,000 to 25,000 cells per µl, cattle from 4,000 to 12,000 cells per µl, and pigs from 11,000 to 22,000 cells per µl.

Lymphocytes function primarily in the immune response to foreign antigens or material. Different types of lymphocytes make antibodies tailored to the foreign antigens and control the production of those antibodies. Neutrophils are phagocytic cells and they 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. Monocytes 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 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.

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. Table

11.3 summarizes these differences.

Table 11.3.3 Types of Muscles

Type of Muscle	Striations	Nuclei	Control	Location
smooth	no	single, in center	involuntary	visceral organs
skeletal	yes	many, at periphery	voluntary	skeletal muscles
cardiac	yes	single, in center	involuntary	heart

SMOOTH MUSCLE

Smooth muscle does not have striations in its cells. It has a single, centrally located nucleus, as shown in Figure 11.3.12. Constriction of smooth muscle occurs under involuntary, autonomic nervous control and 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 of mostly smooth muscle.



Figure 11.3.12 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. 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. Figure 11.3.12 illustrates the histology of skeletal muscle.

CARDIAC MUSCLE

Cardiac muscle, shown in Figure 11.3.12, is found only in the heart. Like skeletal muscle, it has cross striations in its cells, but cardiac muscle has a single, centrally located nucleus. Cardiac muscle is not under voluntary control but can be influenced by the autonomic nervous system to speed up or slow down. An added feature to cardiac muscle cells is a line than extends along the end of the cell as it abuts the next cardiac cell in the row. This line is called an intercalated disc: it assists in passing electrical impulse efficiently from one cell to the next and maintains the strong connection between neighboring cardiac cells.

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. The main cell of the nervous system is the neuron, illustrated in Figure 11.3.13. The large structure with a central nucleus is the cell body of the neuron. Projections from the cell body are either dendrites specialized in receiving input or a single axon specialized in transmitting impulses. Some glial cells are also shown. Astrocytes regulate the chemical environment of the nerve cell, and oligodendrocytes insulate the axon so the electrical nerve impulse is transferred more efficiently. Other glial cells that are not shown support the nutritional and waste requirements of the neuron. Some of the glial cells are phagocytic and remove debris or damaged cells from the tissue. A nerve consists of neurons and glial cells.

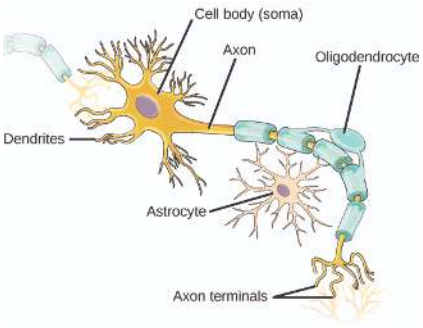


Figure 11.3.13 The neuron has projections called dendrites that receive signals and projections called axons that send signals. Also shown are two types of glial cells: astrocytes regulate the chemical environment of the nerve cell, and oligodendrocytes insulate the axon so the electrical nerve impulse is transferred more efficiently.

LINK TO LEARNING

LINK TO LEARNING

Click through the interactive review to learn more about epithelial tissues.

CAREER CONNECTION

CAREER CONNECTIONS

PathologistA pathologist is a medical doctor or veterinarian who has specialized in the laboratory detection of disease in animals, including humans. These professionals complete medical school education and follow it with an extensive post-graduate residency at a medical center. A pathologist may oversee clinical laboratories for the evaluation of body tissue and blood samples for the detection of disease or infection. They examine tissue specimens through a microscope to identify cancers and other diseases. Some pathologists perform autopsies to determine the cause of death and the progression of disease.

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11.4: HOMEOSTASIS

LEARNING OBJECTIVES

By the end of this section, you will be able to do the following:

- Define homeostasis
- Describe the factors affecting homeostasis
- Discuss positive and negative feedback mechanisms used in homeostasis
- Describe thermoregulation of endothermic and ectothermic animals

Animal organs and organ systems constantly adjust to internal and external changes through a process called homeostasis (“steady state”). These changes might be in the level of glucose or calcium in blood or in external temperatures. Homeostasis means to maintain dynamic equilibrium in the body. It is dynamic because it is constantly adjusting to the changes that the body’s systems encounter. It is equilibrium because body functions are kept within specific ranges. Even an animal that is apparently inactive is maintaining this homeostatic equilibrium.

HOMEOSTATIC PROCESS

The goal of homeostasis is the maintenance of equilibrium around a point or value called a set point. While there are normal fluctuations from the set point, the body’s systems will usually attempt to go back to this point. A change in the internal or external environment is called a stimulus and is detected by a receptor; the response of the system is to adjust the 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 getting the nutrient into tissues that need it or to store it for later use.

CONTROL OF HOMEOSTASIS

When a change occurs in an animal’s environment, an adjustment must be made. The receptor senses the change in the environment, then sends 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 (that contracts or relaxes) or a gland that secretes. Homeostatsis is maintained by negative feedback loops. Positive feedback loops actually push the organism further out of homeostasis, but may be necessary for life to occur. Homeostasis is controlled by the nervous and endocrine system of 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, and conversely, if a level is too low, the body does something to make it go up. Hence the term negative feedback. An example is animal maintenance of blood glucose levels. When an animal has eaten, blood glucose levels rise. This is sensed by the nervous system. Specialized cells in the pancreas sense this, and the hormone insulin is released by the endocrine system. Insulin causes blood glucose levels to decrease, as would be expected in a negative feedback system, as illustrated in Figure 11.4.1. However, if an animal has not eaten and blood glucose levels decrease, this is sensed in another group of cells in the pancreas, and 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 the 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 and, possibly, the breakdown of bone in order to liberate calcium. The effects of PTH are to raise blood levels of the element. Negative feedback loops are the predominant mechanism used in homeostasis.

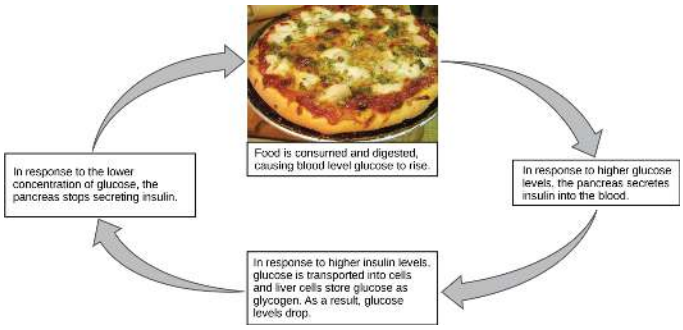


Figure 11.4.1 Blood sugar levels are controlled by a negative feedback loop. (credit: modification of work by Jon Sullivan)

POSITIVE FEEDBACK LOOP

A positive feedback loop maintains the direction of the stimulus, possibly accelerating it. Few examples of positive feedback loops 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, as illustrated in Figure 11.4.2. 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.

VISUAL CONNECTION

VISUAL CONNECTION

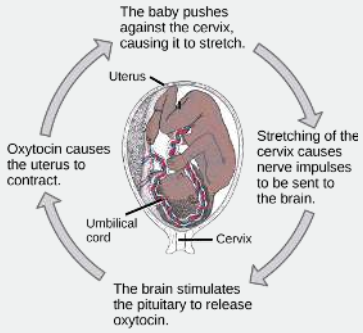


Figure 11.4.2 The birth of a human infant is the result of positive feedback.

State whether each of the following processes is regulated by a positive feedback loop or a negative feedback loop.

a. A person feels satiated after eating a large meal.
b. The blood has plenty of red blood cells. As a result, erythropoietin, a hormone that stimulates the production of new red blood cells, is no longer released from the kidney.

SET POINT

It is possible to adjust a system's set point. When this happens, the feedback loop works to maintain the new setting. An example of this is 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 and no attempt is made to return to the lower set point. The result is the maintenance of an elevated blood pressure that 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. This is called 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 that 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, and a light coat in summer assists in keeping body temperature from rising to harmful levels.

LINK TO LEARNING

LINK TO LEARNING

Feedback mechanisms can be understood in terms of driving a race car along a track: watch a short video lesson on positive and negative feedback loops.

Click to view content

HOMEOSTASIS: THERMOREGULATION

Body temperature affects body activities. Generally, as body temperature rises, enzyme activity rises as well. For every ten degree centigrade rise in temperature, enzyme activity doubles, up to a point. Body proteins, including enzymes, begin to denature and lose their function with high heat (around 50ºC for mammals). Enzyme activity will decrease by half for every ten degree centigrade drop in temperature, to the point of freezing, with a few exceptions. Some fish can withstand freezing solid and return to normal with thawing.

LINK TO LEARNING

LINK TO LEARNING

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

Click to view content

ENDOTHERMS AND ECTOTHERMS

Animals can be divided into two groups: some maintain a constant body temperature in the face of differing environmental temperatures, while others have a body temperature that is the same as their environment and thus varies with the environment. Animals that rely on external temperatures to set their body temperature are ectotherms. This group has been called cold-blooded, but the term may not apply to an animal in the desert with a very warm body temperature. In contrast to ectotherms, poikilotherms are animals with constantly varying internal temperatures. An animal that maintains a constant body temperature in the face of environmental changes is called a homeotherm. Endotherms are animals that rely on internal sources for maintenance of relatively constant body temperature in varying environmental temperatures. These animals are able to maintain a level of metabolic activity at cooler temperature, which an ectotherm cannot due to differing enzyme levels of activity. It is worth mentioning that some ectotherms and poikilotherms have relatively constant body temperatures due to the constant environmental temperatures in their habitats. These animals are so-called ectothermic homeotherms, like some deep sea fish species.

Heat can be exchanged between an animal and its environment through four mechanisms: radiation, evaporation, convection, and conduction (Figure 11.4.3). Radiation is the emission of electromagnetic “heat” waves. Heat comes from the sun in this manner and radiates from dry skin the same way. Heat can be removed with liquid from a surface during evaporation. This occurs when a mammal sweats. Convection currents of air remove heat from the surface of dry skin as the air passes over it. Heat will be conducted from one surface to another during direct contact with the surfaces, such as an animal resting on a warm rock.

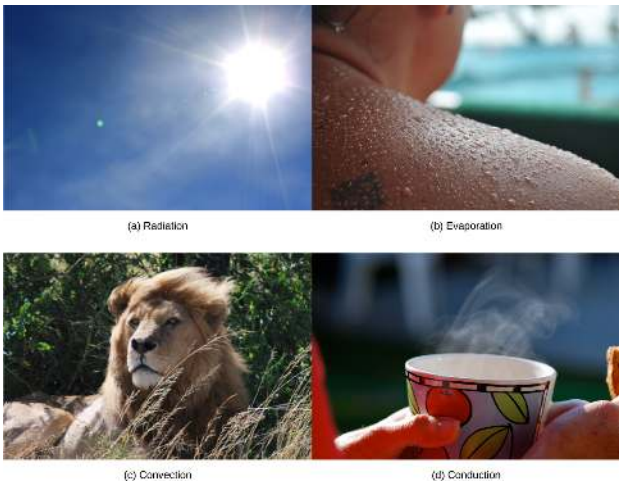


Figure 11.4.3 Heat can be exchanged by four mechanisms: (a) radiation, (b) evaporation, (c) convection, or (d) conduction. (credit b: modification of work by “Kullez”/Flickr; credit c: modification of work by Chad Rosenthal; credit d: modification of work by “stacey.d”/Flickr)

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 and yet maintain a constant, warm, body temperature. The arctic fox, for example, uses its fluffy tail as extra insulation when it curls up to sleep in cold weather. Mammals have a residual effect from shivering and increased muscle activity: arrector pili muscles cause “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. 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. Vasodilation brings more blood and heat to the body surface, facilitating radiation and evaporative heat loss, which helps to cool the body. Vasoconstriction reduces blood flow in peripheral blood vessels, forcing blood toward the core and the vital organs found there, and conserving heat. Some animals have adaptations to their circulatory system that enable them to transfer heat from arteries to veins, warming blood returning to the heart. This is called a countercurrent heat exchange; it prevents the cold venous blood from cooling the heart and other internal organs. This adaptation can be shut down in some animals to prevent overheating the internal organs. The countercurrent adaptation is found in many animals, including dolphins, sharks, bony fish, bees, and hummingbirds. In contrast, similar adaptations can help cool endotherms when needed, such as dolphin flukes and elephant ears.

Some ectothermic 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 getting 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.

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. Severe cold elicits a shivering reflex that generates heat for the body. Many species also have a type of adipose tissue called brown fat that specializes in generating heat.

NEURAL CONTROL OF THERMOREGULATION

The nervous system is important to thermoregulation, as illustrated in Figure 11.4.4. The processes of homeostasis and temperature control are centered in the hypothalamus of the advanced animal brain.

VISUAL CONNECTION

VISUAL CONNECTION

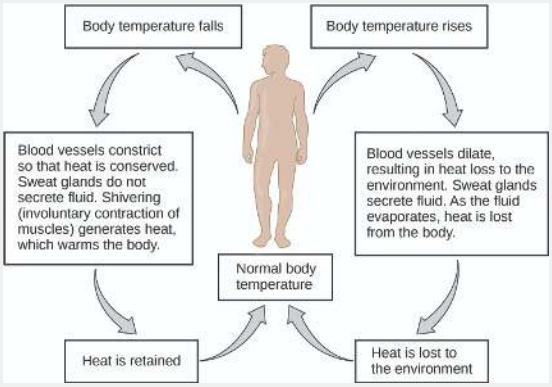


Figure 11.4.4 The body is able to regulate temperature in response to signals from the nervous system.

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

The hypothalamus maintains the set point for body temperature through reflexes that cause vasodilation and sweating when the body is too warm, or vasoconstriction and shivering when the body is too cold. It responds to chemicals from the body. When a bacterium is destroyed by phagocytic leukocytes, chemicals called endogenous pyrogens are released into the blood. These pyrogens circulate to the hypothalamus and reset the thermostat. This allows the body's temperature to increase in what is commonly called a fever. An increase in body temperature causes iron to be conserved, which reduces a nutrient needed by bacteria. An increase in body heat also increases the activity of the animal's enzymes and protective cells while inhibiting the enzymes and activity of the invading microorganisms. Finally, heat itself may also kill the pathogen. A fever that was once thought to be a complication of an infection is now understood to be a normal defense mechanism.

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11.A: KEY TERMS

acclimatization
alteration in a body system in response to environmental change

alteration
change of the set point in a homeostatic system

apodeme
ingrowth of an animal's exoskeleton that functions as an attachment site for muscles

asymmetrical
describes animals with no axis of symmetry in their body pattern

basal metabolic rate (BMR)
metabolic rate at rest in endothermic animals

canaliculus
microchannel that connects the lacunae and aids diffusion between cells

cartilage
type of connective tissue with a large amount of ground substance matrix, cells called chondrocytes, and some amount of fibers

chondrocyte
cell found in cartilage

columnar epithelia
epithelia made of cells taller than they are wide, specialized in absorption

connective tissue
type of tissue made of cells, ground substance matrix, and fibers

cuboidal epithelia
epithelia made of cube-shaped cells, specialized in glandular functions

dorsal cavity
body cavity on the posterior or back portion of an animal; includes the cranial and vertebral cavities

ectotherm
animal incapable of maintaining a relatively constant internal body temperature

endotherm
animal capable of maintaining a relatively constant internal body temperature

epithelial tissue
tissue that either lines or covers organs or other tissues

estivation
torpor in response to extremely high temperatures and low water availability

fibrous connective tissue
type of connective tissue with a high concentration of fibers

frontal (coronal) plane
plane cutting through an animal separating the individual into front and back portions

fusiform

animal body shape that is tubular and tapered at both ends

hibernation
torpor over a long period of time, such as a winter

homeostasis
dynamic equilibrium maintaining appropriate body functions

lacuna
space in cartilage and bone that contains living cells

loose (areolar) connective tissue
type of connective tissue with small amounts of cells, matrix, and fibers; found around blood vessels

matrix
component of connective tissue made of both living and nonliving (ground substances) cells

midsagittal plane
plane cutting through an animal separating the individual into even right and left sides

negative feedback loop
feedback to a control mechanism that increases or decreases a stimulus instead of maintaining it

osteon
subunit of compact bone

positive feedback loop
feedback to a control mechanism that continues the direction of a stimulus

pseudostratified
layer of epithelia that appears multilayered, but is a simple covering

sagittal plane
plane cutting through an animal separating the individual into right and left sides

set point
midpoint or target point in homeostasis

simple epithelia
single layer of epithelial cells

squamous epithelia
type of epithelia made of flat cells, specialized in aiding diffusion or preventing abrasion

standard metabolic rate (SMR)
metabolic rate at rest in ectothermic animals

stratified epithelia
multiple layers of epithelial cells

thermoregulation
regulation of body temperature

torpor
decrease in activity and metabolism that allows an animal to survive adverse conditions

trabecula
tiny plate that makes up spongy bone and gives it strength

transitional epithelia

epithelia that can transition for appearing multilayered to simple; also called uroepithelial

transverse (horizontal) plane

plane cutting through an animal separating the individual into upper and lower portions

ventral cavity

body cavity on the anterior or front portion of an animal that includes the thoracic cavities and the abdominopelvic cavities

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11.B: ANIMAL STRUCTURE AND FUNCTION (EXERCISES)

Which of the following statements about types of epithelial cells is false?

a. Simple columnar epithelial cells line the tissue of the lung.
b. Simple cuboidal epithelial cells are involved in the filtering of blood in the kidney.
c. Pseudostratisfied columnar epithilia occur in a single layer, but the arrangement of nuclei makes it appear that more than one layer is present.
d. Transitional epithelia change in thickness depending on how full the bladder is.

State whether each of the following processes are regulated by a positive feedback loop or a negative feedback loop.

a. A person feels satiated after eating a large meal.
b. The blood has plenty of red blood cells. As a result, erythropoietin, a hormone that stimulates the production of new red blood cells, is no longer released from the kidney.

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

Which type of animal maintains a constant internal body temperature?

a. endotherm
b. ectotherm
c. coelomate
d. mesoderm

The symmetry found in animals that move swiftly is _____.

a. radial
b. bilateral
c. sequential
d. interrupted

What term describes the condition of a desert mouse that lowers its metabolic rate and "sleeps" during the hot day?

a. turgid
b. hibernation
c. estivation
d. normal sleep pattern

A plane that divides an animal into equal right and left portions is _____.

a. diagonal
b. midsagittal
c. coronal
d. transverse

A plane that divides an animal into dorsal and ventral portions is _____.

a. sagittal
b. midsagittal
c. coronal
d. transverse

The pleural cavity is a part of which cavity?

a. dorsal cavity
b. thoracic cavity
c. abdominal cavity
d. pericardial cavity

How could the increasing global temperature associated with climate change impact ectotherms?

a. Ectotherm diversity will decrease in cool regions.
b. Ectotherms will be able to be active all day in the tropics.
c. Ectotherms will have to expend more energy to cool their body temperatures.

d. Ectotherms will be able to expand into new habitats.

Although most animals are bilaterally symmetrical, a few exhibit radial symmetry. What is an advantage of radial symmetry?

a. It confuses predators.
b. It allows the animal to gather food from all sides.
c. It allows the animal to undergo rapid, purposeful movement in any direction.
d. It lets an animal use its dorsal surface to sense its environment.

Which type of epithelial cell is best adapted to aid diffusion?

a. squamous
b. cuboidal
c. columnar
d. transitional

Which type of epithelial cell is found in glands?

a. squamous
b. cuboidal
c. columnar
d. transitional

Which type of epithelial cell is found in the urinary bladder?

a. squamous
b. cuboidal
c. columnar
d. transitional

Which type of connective tissue has the most fibers?

a. loose connective tissue
b. fibrous connective tissue
c. cartilage
d. bone

Which type of connective tissue has a mineralized different matrix?

a. loose connective tissue
b. fibrous connective tissue
c. cartilage
d. bone

The cell found in bone that breaks it down is called an _____.

a. osteoblast
b. osteocyte
c. osteoclast
d. osteon

The cell found in bone that makes the bone is called an _____.

a. osteoblast
b. osteocyte
c. osteoclast
d. osteon

Plasma is the _____.

a. fibers in blood
b. matrix of blood
c. cell that phagocytizes bacteria
d. cell fragment found in the tissue

The type of muscle cell under voluntary control is the _____.

a. smooth muscle
b. skeletal muscle
c. cardiac muscle
d. visceral muscle

The part of a neuron that contains the nucleus is the

a. cell body
b. dendrite
c. axon
d. glial

Why are intercalated discs essential to the function of cardiac muscle?

a. The discs maintain the barriers between the cells.
b. The discs pass nutrients between cells.
c. The discs ensure that all the cardiac muscle cells beat as a single unit.
d. The discs control the heart rate.

When faced with a sudden drop in environmental temperature, an endothermic animal will:

a. experience a drop in its body temperature
b. wait to see if it goes lower
c. increase muscle activity to generate heat
d. add fur or fat to increase insulation

Which is an example of negative feedback?

a. lowering of blood glucose after a meal
b. blood clotting after an injury
c. lactation during nursing
d. uterine contractions during labor

Which method of heat exchange occurs during direct contact between the source and animal?

a. radiation
b. evaporation
c. convection
d. conduction

The body's thermostat is located in the _____.

a. homeostatic receptor
b. hypothalamus
c. medulla
d. vasodilation center

Which of the following is **not** true about acclimatization?

a. Acclimatization allows animals to compensate for changes in their environment.
b. Acclimatization improves function in a new environment.
c. Acclimatization occurs when an animal tries to reestablish a homeostatic set point.
d. Acclimatization is passed on to offspring of acclimated individuals.

Which of the following is **not** a way that ectotherms can change their body temperatures?

a. Sweating for evaporative cooling.
b. Adjusting the timing of their daily activities.
c. Seek out or avoid direct sunlight.
d. Huddle in a group.

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11.C: CRITICAL THINKING QUESTIONS

How does diffusion limit the size of an organism? How is this counteracted?

What is the relationship between BMR and body size? Why?

Explain how using an open circulatory system constrains the size of animals.

Describe one key environmental constraint for ectotherms and one for endotherms. Why are they limited by different factors?

How can squamous epithelia both facilitate diffusion and prevent damage from abrasion?

What are the similarities between cartilage and bone?

Multiple sclerosis is a debilitating autoimmune disease that results in the loss of the insulation around neuron axons. What cell type is the immune system attacking, and how does this disrupt the transfer of messages by the nervous system?

When a person leads a sedentary life his skeletal muscles atrophy, but his smooth muscles do not. Why?

Why are negative feedback loops used to control body homeostasis?

Why is a fever a “good thing” during a bacterial infection?

How is a condition such as diabetes a good example of the failure of a set point in humans?

On a molecular level, how can endotherms produce their own heat by adjusting processes associated with cellular respiration?

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12: ANIMAL ORGAN SYSTEMS

This chapter showcases a few key animal organ systems. These will be useful when completing your Homeostasis Research Projects during the course of this class.

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SECTION OVERVIEW

12.1: RESPIRATORY SYSTEM

This chapter describes the structure and function of the respiratory system, including how breathing occurs and what controls it, as well as how the process of gas exchange takes place in the lungs. The chapter also describes several disorders of the respiratory system and details the adverse health effects of smoking.

12.1.1: STRUCTURE AND FUNCTION OF THE RESPIRATORY SYSTEM

12.1.2: BREATHING

12.1.3: DISORDERS OF THE RESPIRATORY SYSTEM

12.1.4: SMOKING AND HEALTH

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12.1.1: STRUCTURE AND FUNCTION OF THE RESPIRATORY SYSTEM

SEEING YOUR BREATH

Why can you "see your breath" on a cold day? The air you exhale through your nose and mouth is warm, like the inside of your body. Exhaled air also contains a lot of water vapor because it passes over moist surfaces from the lungs to the nose or mouth. The water vapor in your breath cools suddenly when it reaches the much colder outside air. This causes the water vapor to condense into a fog of tiny droplets of liquid water. You release water vapor and other gases from your body through the process of respiration.



Figure **12.1.1.1**: Breath on a cold day

WHAT IS RESPIRATION?

Respiration is the life-sustaining process in which gases are exchanged between the body and the outside atmosphere. Specifically, oxygen moves from the outside air into the body; and water vapor, carbon dioxide, and other waste gases move from inside the body into the outside air. Respiration is carried out mainly by the **respiratory system.** It is important to note that respiration by the respiratory system is not the same process as cellular respiration that occurs inside cells, although the two processes are closely connected. Cellular respiration is the metabolic process in which cells obtain energy, usually by "burning" glucose in the presence of oxygen. When cellular respiration is aerobic, it uses oxygen and releases carbon dioxide as a waste product. Respiration by the respiratory system supplies the oxygen needed by cells for aerobic cellular respiration and removes the carbon dioxide produced by cells during cellular respiration.

Respiration by the respiratory system actually involves two subsidiary processes. One process is ventilation or breathing. This is the physical process of conducting air to and from the lungs. The other process is gas exchange. This is the biochemical process in which oxygen diffuses out of the air and into the blood while carbon dioxide and other waste gases diffuse out of the blood and into the air. All of the organs of the respiratory system are involved in breathing, but only the lungs are involved in gas exchange.

RESPIRATORY ORGANS

The organs of the respiratory system form a continuous system of passages called the **respiratory tract,** through which air flows into and out of the body. The respiratory tract has two major divisions: the upper respiratory tract and the lower respiratory tract. The organs in each division are shown in Figure **12.1.1.2**. In addition to these organs, certain muscles of the thorax (the body cavity that fills the chest) are also involved in respiration by enabling breathing. Most important is a large muscle called the diaphragm, which lies below the lungs and separates the thorax from the abdomen. Smaller muscles between the ribs also play a role in breathing. You can learn more about breathing muscles in the concept of *Breathing*.

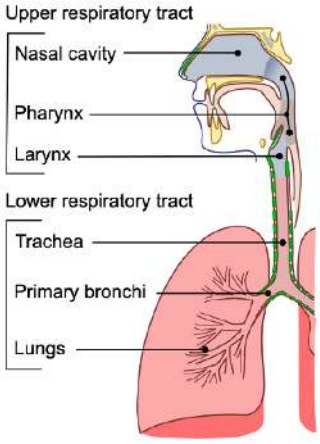


Figure **12.1.1.2**: During breathing, inhaled air enters the body through the nose and passes through the pharynx, larynx, trachea, bronchi, and then enters the lungs. Exhaled air travels from the lungs in the opposite direction.

UPPER RESPIRATORY TRACT

All of the organs and other structures of the upper respiratory tract are involved in the conduction or the movement of air into and out of the body. Upper respiratory tract organs provide a route for air to move between the outside atmosphere and the lungs. They also clean, humidity, and warm the incoming air. However, no gas exchange occurs in these organs.

NASAL CAVITY

The **nasal cavity** is a large, air-filled space in the skull above and behind the nose in the middle of the face. It is a continuation of the two nostrils. As inhaled air flows through the nasal cavity, it is warmed and humidified. Hairs in the nose help trap larger foreign particles in the air before they go deeper into the respiratory tract. In addition to its respiratory functions, the nasal cavity also contains chemoreceptors that are needed for the sense of smell and that contribute importantly to the sense of taste.

PHARYNX

The **pharynx** is a tube-like structure that connects the nasal cavity and the back of the mouth to other structures lower in the throat, including the larynx. The pharynx has dual functions: both air and

food (or other swallowed substances) pass through it, so it is part of both the respiratory and digestive systems. Air passes from the nasal cavity through the pharynx to the larynx (as well as in the opposite direction). Food passes from the mouth through the pharynx to the esophagus.

LARYNX

The **larynx** connects the pharynx and trachea and helps to conduct air through the respiratory tract. The larynx is also called the voice box because it contains the vocal cords, which vibrate when air flows over them, thereby producing sound. You can see the vocal cords in the larynx in Figure **12.1.1.3**. Certain muscles in the larynx move the vocal cords apart to allow breathing. Other muscles in the larynx move the vocal cords together to allow the production of vocal sounds. The latter muscles also control the pitch of sounds and help control their volume.

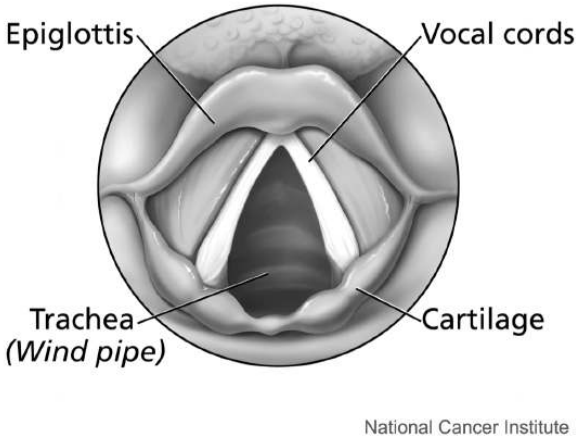


Figure **12.1.1.3**: The larynx is viewed from the top. opening to the trachea is closed by epiglottis during swallowing. Cartilage and vocal cords are also visible.

A very important function of the larynx is protecting the trachea from aspirated food. When swallowing occurs, the backward motion of the tongue forces a flap called the epiglottis to close over the entrance to the larynx. You can see the epiglottis in Figure **12.1.1.3**. This prevents swallowed material from entering the larynx and moving deeper into the respiratory tract. If swallowed material does start to enter the larynx, it irritates the larynx and stimulates a strong cough reflex. This generally expels the material out of the larynx and into the throat.

LOWER RESPIRATORY TRACT

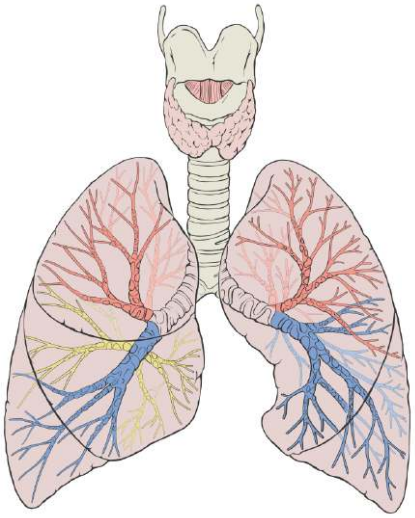


Figure **12.1.1.4**: This diagram illustrates the tree-like branching of the passages of the lower respiratory tract within the lungs.

The trachea and other passages of the lower respiratory tract conduct air between the upper respiratory tract and the lungs. These passages form an inverted tree-like shape (Figure **12.1.1.4**), with repeated branching as they move deeper into the lungs. All told, there are an astonishing 1,500 miles of airways conducting air through the human respiratory tract! It is only in the lungs, however, that gas exchange occurs between the air and the bloodstream.

TRACHEA

The **trachea,** or windpipe, is the widest passageway in the respiratory tract. It is about 2.5 cm (1 in.) wide and 10-15 cm (4-6 in.) long. It is formed by rings of cartilage, which make it relatively strong and resilient. The trachea connects the larynx to the lungs for the passage of air through the respiratory tract. The trachea branches at the bottom to form two bronchial tubes.

BRONCHI AND BRONCHIOLES

There are two main bronchial tubes, or **bronchi (singular, bronchus)**, called the right and left bronchi. The bronchi carry air between the trachea and lungs. Each bronchus branches into smaller, secondary bronchi; and secondary bronchi branch into still smaller tertiary bronchi. The smallest bronchi branch into very small tubules called bronchioles. The tiniest bronchioles end in alveolar ducts, which terminate in clusters of minuscule air sacs, called alveoli (singular, alveolus), in the lungs.

LUNGS

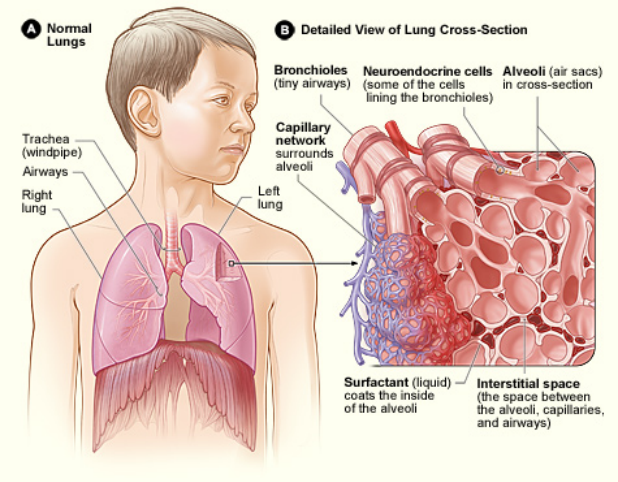


Figure **12.1.1.5**: The cross-section of lung tissue on the right shows the alveoli in which gas exchange takes place with the capillary network that surrounds them. Neuroendocrine cells lining the bronchioles control their diameter and the flow of air through them. A surfactant is a liquid that covers the inside of the alveoli and prevents them from collapsing and sticking together when air empties out of them during exhalation.

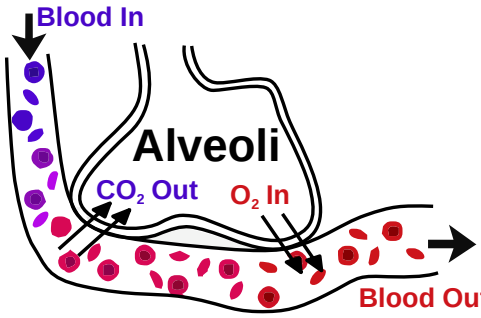


Figure **12.1.1.6**: The gaseous exchange between blood and outside air inside the lung alveoli.

The **lungs** are the largest organs of the respiratory tract. They are suspended within the pleural cavity of the thorax. In Figure **12.1.1.5**, you can see that each of the two lungs is divided into sections. These are called lobes, and they are separated from each other by connective tissues. The right lung is larger and contains three lobes. The left lung is smaller and contains only two lobes. The smaller left lung allows room for the heart, which is just left of the center of the chest.

Lung tissue consists mainly of alveoli (Figure **12.1.1.6**). These tiny air sacs are the functional units of the lungs where gas exchange takes place. The two lungs may contain as many as 700 million alveoli, providing a huge total surface area for gas exchange to take place. In fact, alveoli in the two lungs provide as much surface area as half a tennis court! Each time you breathe in, the alveoli fill with air, making the lungs expand. Oxygen in the air inside the alveoli is absorbed by the blood in the mesh-like network of tiny capillaries that surrounds each alveolus. The blood in these capillaries also releases carbon dioxide into the air inside the alveoli. Each time you breathe out, air leaves the alveoli and rushes into the outside atmosphere, carrying waste gases with it.

The lungs receive blood from two major sources. They receive deoxygenated blood from the heart. This blood absorbs oxygen in the lungs and carries it back to the heart to be pumped to cells throughout the body. The lungs also receive oxygenated blood from the heart that provides oxygen to the cells of the lungs for cellular respiration.

PROTECTING THE RESPIRATORY SYSTEM

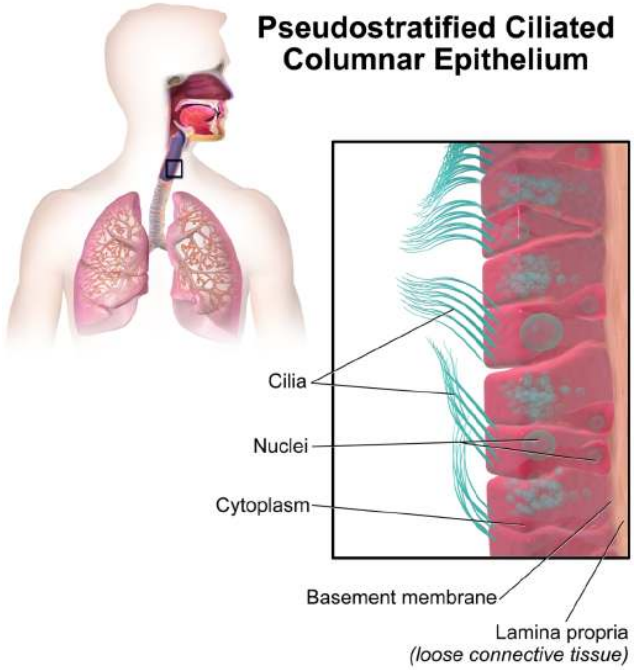


Figure **12.1.1.7**: The upward sweeping motion of cilia lining the respiratory tract helps keep it free from dust, pathogens, and other harmful substances.

You may be able to survive for weeks without food and for days without water, but you can survive without oxygen for only a matter of minutes except under exceptional circumstances. Therefore, protecting the respiratory system is vital. That's why making sure a patient has an open airway is the first step in treating many medical emergencies. Fortunately, the respiratory system is well protected by the ribcage of the skeletal system. However, the extensive surface area of the respiratory system is directly exposed to the outside world and all its potential dangers in inhaled air. Therefore, it should come as no surprise that the respiratory system has a variety of ways to protect itself from harmful substances such as dust and pathogens in the air.

The main way the respiratory system protects itself is called the mucociliary escalator. From the nose through the bronchi, the respiratory tract is covered in the epithelium that contains mucus-secreting goblet cells. The mucus traps particles and pathogens in the incoming air. The epithelium of the respiratory tract is also covered with tiny cell projections called cilia (singular, cilium), as shown in Figure **12.1.1.7**. The cilia constantly move in a sweeping motion upward toward the throat, moving the mucus and trapped particles and pathogens away from the lungs and toward the outside of the body.

What happens to the material that moves up the mucociliary escalator to the throat? It is generally removed from the respiratory tract by clearing the throat or coughing. Coughing is a largely involuntary response of the respiratory system that occurs when nerves lining the airways are irritated. The response causes air to be expelled forcefully from the trachea, helping to remove mucus and any debris it contains (called phlegm) from the upper respiratory tract to the mouth. The phlegm may spit out (expectorated), or it may be swallowed and destroyed by stomach acids.

Sneezing is a similar involuntary response that occurs when nerves lining the nasal passage are irritated. It results in forceful expulsion of air from the mouth, which sprays millions of tiny droplets of mucus and other debris out of the mouth and into the air, as shown in Figure **12.1.1.8**. This explains why it is so important to sneeze into a sleeve rather than the air to help prevent the transmission of respiratory pathogens.



Figure **12.1.1.8**: Sneezing results in tiny particles from the mouth being forcefully ejected into the air.

HOW THE RESPIRATORY SYSTEM WORKS WITH OTHER ORGAN SYSTEMS

The amount of oxygen and carbon dioxide in the blood must be maintained within a limited range for the survival of the organism. Cells cannot survive for long without oxygen, and if there is too much carbon dioxide in the blood, the blood becomes dangerously acidic (pH is too low). Conversely, if there is too little carbon dioxide in the blood, the blood becomes too basic (pH is too high). The respiratory system works hand-in-hand with the nervous and cardiovascular systems to maintain homeostasis in blood gases and pH.

It is the level of carbon dioxide rather than the level of oxygen that is most closely monitored to maintain blood gas and pH homeostasis. The level of carbon dioxide in the blood is detected by cells in the brain, which speed up or slow down the rate of breathing through the autonomic nervous system as needed to bring the carbon dioxide level within the normal range. Faster breathing lowers the carbon dioxide level (and raises the oxygen level and pH); slower breathing has the opposite effects. In this way, the levels of carbon dioxide and oxygen, as well as pH, are maintained within normal limits.

The respiratory system also works closely with the cardiovascular system to maintain homeostasis. The respiratory system exchanges gases between the blood and the outside air, but it needs the cardiovascular system to carry them to and from body cells. Oxygen is absorbed by the blood in the lungs and then transported through a vast network of blood vessels to cells throughout the body where it is needed for aerobic cellular respiration. The same system absorbs carbon dioxide from cells and carries it to the respiratory system for removal from the body.

FEATURE: MY HUMAN BODY

Choking is the mechanical obstruction of the flow of air from the atmosphere into the lungs. It prevents breathing and may be partial or complete. Partial choking allows some though inadequate airflow into the lung—prolonged or complete choking results in asphyxia, or suffocation, which is potentially fatal.

Obstruction of the airway typically occurs in the pharynx or trachea. Young children are more prone to choking than are older people, in part because they often put small objects in their mouths and do not appreciate the risk of choking that they pose. Young children may choke on small toys or parts of toys or on household objects in addition to food. Foods that can adapt their shape to that of the pharynx, such as bananas and marshmallows, are especially dangerous and may cause choking in adults as well as children.

How can you tell if a loved one is choking? The person cannot speak or cry out or has great difficulty doing so. Breathing, if possible, is labored, producing gasping or wheezing. The person may desperately clutch at his or her throat or mouth. If breathing is not soon restored, the person's face will start to turn blue from lack of oxygen. This will be followed by unconsciousness if oxygen deprivation continues beyond a few minutes.

If an infant is choking, turning the baby upside down and slapping on the back may dislodge the obstructing object. To help an older person who is choking, first, encourage the person to cough. Give them a few hardback slaps to help force the lodged object out of the airway. If these steps fail, perform the Heimlich maneuver on the person. You can easily find instructional videos online to learn how to do it. If the Heimlich maneuver also fails, call for emergency medical care immediately.



Figure **12.1.1.9**: The Heimlich maneuver may be needed to help force an aspirated object out of the respiratory tract.

REVIEW

1. What is respiration, as carried out by the respiratory system? Name the two subsidiary processes it involves.
2. Describe the respiratory tract.
3. Identify the organs of the upper respiratory tract, and state their functions.
4. List the organs of the lower respiratory tract. Which organs are involved only in conduction?
5. Where does gas exchange take place?
6. How does the respiratory system protect itself from potentially harmful substances in the air?
7. Explain how the rate of breathing is controlled.
8. Why does the respiratory system need the cardiovascular system to help it perform its main function of gas exchange?
9. Place the following organs or structures of the respiratory system in order of when they are encountered by air entering the body — from earliest to latest.

   trachea; nasal cavity; alveoli; bronchioles; larynx; bronchi; pharynx
10. Which organ is part of both the digestive and respiratory systems?

    A. Larynx

    B. Trachea

    C. Pharynx

    D. Bronchus
11. Describe two ways in which the body prevents food from entering the lungs.
12. *True or False.* The lungs receive some oxygenated blood.
13. *True or False.* Gas exchange occurs in both the upper and lower respiratory tracts.
14. Coughing can expel _____ from the body.

    A. mucus

    B. food particles

    C. phlegm

    D. All of the above
15. What is the relationship between respiration and cellular respiration?

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12.1.2: BREATHING

DOING THE 'FLY

The swimmer in this photo is doing the butterfly stroke. This swimming style requires the swimmer to carefully control his breathing so it is coordinated with his swimming movements. Breathing is the process of moving air into and out of the lungs, which are the organs in which gas exchange takes place between the atmosphere and the body. Breathing is also called **ventilation,** and it is one of two parts of the life-sustaining process of respiration, the other part being gas exchange. Before you can understand how breathing is controlled, you need to know how breathing occurs.



Figure **12.1.2.1**: Butterfly stroke

HOW BREATHING OCCURS

Breathing is a two-step process that includes drawing air into the lungs, or inhaling, and letting the air out of the lungs, or exhaling. Both processes are illustrated in Figure **12.1.2.2**.

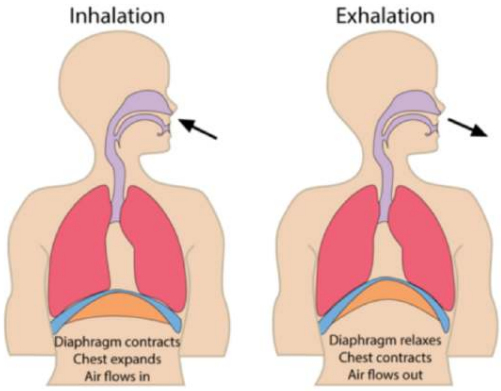


Figure **12.1.2.2**: Inhalation and exhalation during breathing depend mainly on repeated contractions of the diaphragm.

INHALING

Inhaling is an active process that results mainly from the contraction of a muscle called the diaphragm, shown in Figure **12.1.2.2**. The **diaphragm** is a large, dome-shaped muscle below the lungs that separates the thoracic (chest) and abdominal cavities. When the diaphragm contracts, the thoracic cavity expands and the contents of the abdomen are pushed downward. Other muscles, such as external intercostal muscles between the ribs, also contribute to the process of inhalation, especially when inhalation is forced, as when taking a deep breath. These muscles help increase thoracic volume by expanding the ribs outward. With the chest expanded, there is lower air pressure inside the lungs than outside the body, so outside air flows into the lungs via the respiratory tract.

EXHALING

Exhaling involves the opposite series of events. The diaphragm relaxes, so it moves upward and decreases the volume of the thorax (Figure **12.1.2.2**. Air pressure inside the lungs increases so it is higher than the air pressure outside the lungs. Exhaling, unlike inhaling, is typically a passive process that occurs mainly due to the elasticity of the lungs. With the change in air pressure, the lungs contract to their pre-inflated size, forcing out the air they contain in the process. Air flows out of the lungs, similar to the way air rushes out of a balloon when it is released. If exhalation is forced, internal intercostal and abdominal muscles may help move the air out of the lungs.

CONTROL OF BREATHING

Breathing is one of the few vital bodily functions that can be controlled consciously as well as unconsciously. Think about using your breath to blow up a balloon. You take a long, deep breath, and then you exhale the air as forcibly as you can into the balloon. Both the inhalation and exhalation are consciously controlled.

CONSCIOUS CONTROL OF BREATHING

You can control your breathing by holding your breath, slowing your breathing, or **hyperventilating,** which is breathing more quickly and shallowly than necessary. You can also exhale or inhale more forcefully or deeply than usual. Conscious control of breathing is common in many activities besides blowing up balloons, including swimming, speech training, singing, playing many different musical instruments (Figure **12.1.2.3**), and doing yoga, to name just a few.



Figure **12.1.2.3**: Playing the oboe is hard work. Exhaled air must be forced through a tiny opening between two very small wooden reeds.

There are limits on the conscious control of breathing. For example, it is not possible for a healthy person to voluntarily stop breathing indefinitely. Before long, there is an irrepressible urge to breathe. If you were able to stop breathing for a long enough time, you would lose consciousness. The same thing would happen if you were to

hyperventilate for too long. Once you lose consciousness so you can no longer exert conscious control over your breathing, involuntary control of breathing takes over.

UNCONSCIOUS CONTROL OF BREATHING

Unconscious breathing is controlled by **respiratory centers** in the medulla and pons of the brainstem (Figure **12.1.2.4**). The respiratory centers automatically and continuously regulate the rate of breathing depending on the body's needs. These are determined mainly by blood acidity or pH. When you exercise, for example, carbon dioxide levels increase in the blood because of increased cellular respiration by muscle cells. The carbon dioxide reacts with water in the blood to produce carbonic acid, making the blood more acidic, so pH falls. The drop in pH is detected by chemoreceptors in the medulla. Blood levels of oxygen and carbon dioxide, in addition to pH, are also detected by chemoreceptors in major arteries, which send the "data" to the respiratory centers. The respiratory center responds by sending nerve impulses to the diaphragm, "telling" it to contract more quickly so the rate of breathing speeds up. With faster breathing, more carbon dioxide is released into the air from the blood, and blood pH returns to the normal range.

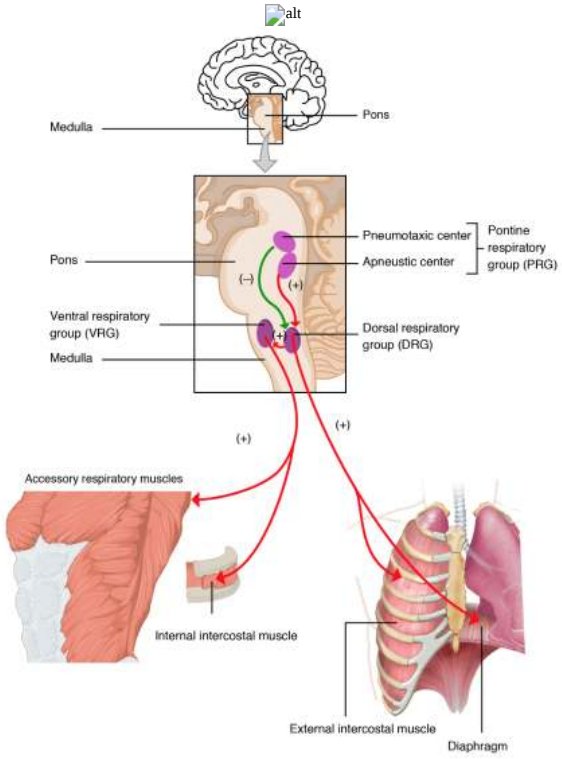


Figure **12.1.2.4**: Clusters of cells in the pons and medulla of the brain stem are the respiratory centers of the brain that have involuntary control over breathing muscles, such as the diaphragm and external and internal intercostal.

The opposite events occur when the level of carbon dioxide in the blood becomes too low and blood pH rises. This may occur with involuntary hyperventilation, which can happen in panic attacks, episodes of severe pain, asthma attacks, and many other situations. When you hyperventilate, you blow off a lot of carbon dioxide, leading to a drop in blood levels of carbon dioxide. The blood becomes more basic (alkaline), causing its pH to rise.

NASAL VS. MOUTH BREATHING

Nasal breathing is breathing through the nose rather than the mouth, and it is generally considered to be superior to mouth breathing. The hair-lined nasal passages do a better job of filtering particles out of the air before it moves deeper into the respiratory tract. The nasal passages are also better at warning and moistening the air, so nasal breathing is especially advantageous in the winter when the air is cold and dry. In addition, the smaller diameter of the nasal passages creates greater pressure in the lungs during exhalation. This slows the emptying of the lungs, giving them more time to extract oxygen from the air.

FEATURE: MYTH VS. REALITY

Drowning is defined as respiratory impairment from being in or under a liquid. It is further classified according to its outcome into death, ongoing health problems, or no ongoing health problems (full recovery). In the United States, accidental drowning is the second leading cause of death (after motor vehicle crashes) in children aged 12 years and younger. There are some potentially dangerous myths about drowning. Knowing what they are might save your life or the life of a loved one, especially a child.

Myth: People drown when they aspirate water into their lungs.

Reality: Generally, in the early stages of drowning, very little water enters the lungs. A small amount of water entering the trachea causes a muscular spasm in the larynx that seals the airway and prevents the passage of water into the lungs. This spasm is likely to last until unconsciousness occurs.

Myth: You can tell when someone is drowning because they will shout for help and wave their arms to attract attention.

Reality: The muscular spasm that seals the airway prevents the passage of air as well as water, so a person who is drowning is unable to shout or call for help. In addition, instinctive reactions that occur in the final minute or so before a drowning person sinks under the water may look similar to calm, safe behavior. The head is likely to be low in the water, tilted back with the mouth open. The person may have uncontrolled movements of the arms and legs, but they are unlikely to be visible above the water.

Myth: It is too late to save a person who is unconscious in the water.

Reality: An unconscious person rescued with an airway still sealed from the muscular spasm of the larynx stands a good chance of full recovery if they start receiving CPR within minutes. Without water in the lungs, CPR is much more effective. Even if the cardiac arrest has occurred so the heart is no longer beating, there is still a chance of recovery. However, the longer the brain goes without oxygen, the more likely brain

cells will die. Brain death is likely after about six minutes without oxygen, except in exceptional circumstances, such as young people drowning in very cold water. There are examples of children surviving, apparently without lasting ill effects, for as long as an hour in cold water (see Explore More below for an example). Therefore, rescuers retrieving a child from cold water should attempt resuscitation even after a protracted period of immersion.

Myth: If someone is drowning, you should start administering CPR immediately, even before you try to get the person out of the water.

Reality: Removing a drowning person from the water is the first priority because CPR is ineffective in the water. The goal should be to bring the person to stable ground as quickly as possible and then to start CPR.

Myth: You are unlikely to drown unless you are in water over your head.

Reality: Depending on circumstances, people have drowned in as little as 30 mm (about 1 ½ in.) of water. For example, inebriated people or those under the influence of drugs have been known to have drowned in puddles. Hundreds of children have drowned in the water in toilets, bathtubs, basins, showers, pails, and buckets (see figure below).



Figure **12.1.2.5**: Young children should never be left unattended around sources of water that pose a risk of drowning, including water in toilets, bathtubs, and buckets.

REVIEW

1. Define breathing.
2. What is another term for the process of breathing?
3. What is the main difference between the processes of inhaling and exhaling?
4. Give examples of activities in which breathing is consciously controlled.
5. Young children sometimes threaten to hold their breath until they get something they want. Why is this an idle threat?
6. Explain how unconscious breathing is controlled.
7. Why is nasal breathing generally considered to be superior to mouth breathing?
8. For each of the following, indicate whether it occurs during the process of inhalation (I) or exhalation (E).
   A. The diaphragm moves downward.
   B. The diaphragm relaxes.
   C. The thoracic cavity becomes smaller.
   D. The air pressure in the lungs is lower than outside the body.
9. Give one example of a situation that would cause blood pH to rise excessively and explain why this occurs.
10. Blood levels of oxygen and carbon dioxide and pH are detected by which of these:
    A. Mechanoreceptors
    B. Chemoreceptors
    C. Lung receptors
    D. Carbon receptors
11. True or False. The diaphragm can contract due to conscious control.
12. True or False. Hypoventilating is breathing that is fast and shallow.

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12.1.3: DISORDERS OF THE RESPIRATORY SYSTEM

A "MITEY" MONSTER

The scary beast in Figure **12.1.3.1** is likely to be lurking in your own home, where it feeds on organic debris, including human skin. What is it? It's the common dust mite, a close relative of spiders. The dust mite is so small that it is barely visible with the unaided eye, so it's obviously shown above greatly enlarged. If you think you can get rid of dust mites in your home by frequent and thorough cleaning, think again. There may be thousands of dust mites in just one gram of dust! Regardless of how clean you keep your house, you can't eliminate dust mites entirely. So why even bother trying? The feces of dust mites contain proteins that are a common trigger of asthma attacks.



Figure **12.1.3.1**: Dust mite

ASTHMA

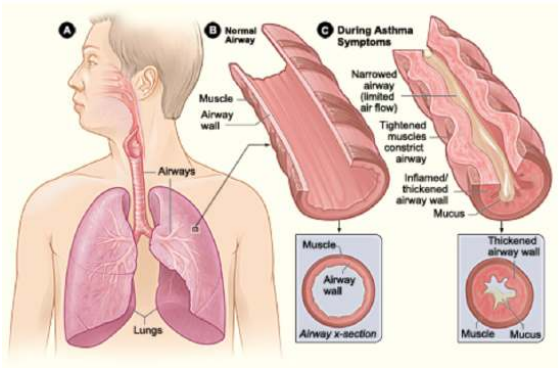


Figure **12.1.3.2**: During an asthma attack, airways narrow and may become clogged with mucus, making breathing difficult.

Asthma is a chronic inflammatory disease of the airways in the lungs, in which the airways periodically become inflamed. As you can see in Figure **12.1.3.2**, this causes swelling and narrowing of the airways, often accompanied by excessive mucus production. Symptoms of asthma include difficulty breathing, coughing, wheezing, shortness of breath, and chest tightness. Some people with asthma rarely experience symptoms, and then usually only in response to certain triggers in the environment. Other people may have symptoms almost all of the time.

Asthma is thought to be caused by a combination of genetic and environmental factors. A person with a family history of asthma is more likely to develop the disease. Dozens of genes have been found to be associated with asthma, many of which are related to the immune system. Additional risk factors include obesity and sleep apnea (see the feature My Human Body below). Environmental factors trigger asthma attacks in people who have a genetic predisposition to the disease. Besides dust mite feces, triggers may include other allergens (such as pet dander, cockroaches, and mold), certain medications including aspirin, air pollution, and stress, among other possible factors. Symptoms tend to be worse at night and early in the morning. They may also worsen during upper respiratory tract infections, strenuous exercise, or when the airways are exposed to cold air.

There is no cure for asthma at present, but the symptoms of asthma attacks usually can be reversed with the use of inhaled medications called bronchodilators. These medications soothe the constricted air passages and help to re-expand them, making breathing easier. The medications usually start to take effect almost immediately. Other medications can be taken for long-term control of the disease. These medications help prevent asthma attacks from occurring. Corticosteroids are generally considered the most effective treatment for long-term control. Another way to prevent asthma attacks is by avoiding triggers whenever possible.

PNEUMONIA

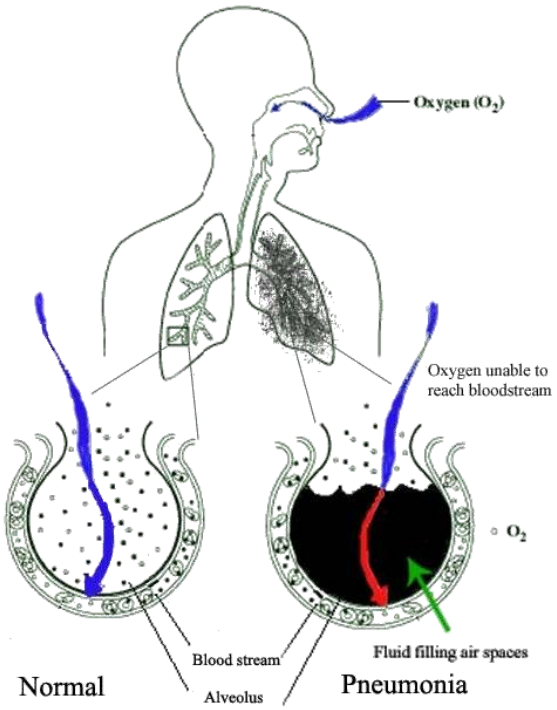


Figure **12.1.3.3**: Fluid-filled alveoli characteristic of pneumonia inhibit normal gas exchange with the blood.

Another common inflammatory disease of the respiratory tract is **pneumonia.** In pneumonia, the inflammation affects primarily the alveoli, which are the tiny air sacs of the lungs. Inflammation causes some of the alveoli to become filled with fluid so that gas exchange cannot occur. This is illustrated in Figure **12.1.3.3**. Symptoms of pneumonia typically include coughing, chest pain, difficulty breathing, and fever.

Pneumonia often develops as a consequence of an upper respiratory tract infection such as the common cold or flu, especially in the very young and the elderly. It is usually caused by bacteria or viruses, although some cases may be caused by other microorganisms such as fungi. The majority of cases are caused by just a few pathogens, the most common being the bacterium *Streptococcus pneumoniae.* Pneumonia is more likely to develop in people who have other lung diseases such as asthma, a history of smoking, heart failure, or a weakened immune system.

Vaccines are available to prevent certain types of bacterial and viral pneumonia, including pneumonia caused by *Streptococcus pneumoniae.* Treatment of pneumonia depends on the cause. For example, if it is caused by bacteria, antibiotics are generally prescribed. In cases of severe pneumonia, hospitalization and supplemental oxygen may be required.

CHRONIC OBSTRUCTIVE PULMONARY DISEASE

Chronic obstructive pulmonary disease (COPD) is a lung disease characterized by chronic poor airflow. The main symptoms include shortness of breath and a cough that produces phlegm. These symptoms are usually present for a long period of time and typically become worse over time. Eventually, walking upstairs and similar activities become difficult because of shortness of breath.

COPD formerly was referred to as chronic bronchitis or emphysema. Now, the term *chronic bronchitis* is used to refer to the symptoms of COPD, and the term *emphysema* is used to refer to the lung changes that occur with COPD. Some of these lung changes are shown in Figure **12.1.3.4**. They include a breakdown of connective tissues that reduces the number and elasticity of alveoli. As a result, the patient can no longer fully exhale air from the lungs, so the air becomes trapped in the lungs. Gas exchange is hampered and may lead to low oxygen levels and too much carbon dioxide in the blood.

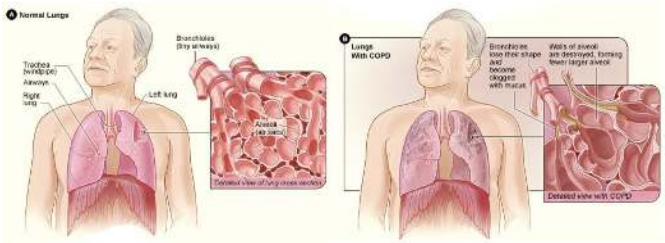


Figure **12.1.3.4**: The physiological changes that occur with COPD include a breakdown of alveolar walls, reducing the surface area for gas exchange.

Tobacco smoking is the major cause of COPD, with a number of other factors such as air pollution and genetics playing smaller roles. Of people who are life-long smokers, about half will eventually develop COPD. Exposure to secondhand smoke in nonsmokers also increases the risk of COPD and accounts for about 20 percent of cases. Most cases of COPD could have been prevented by never smoking. In people who have already been diagnosed with COPD, cessation of smoking can slow down the rate at which COPD worsens. People with COPD may be treated with supplemental oxygen and inhaled bronchodilators. These treatments may reduce the symptoms but there is no cure for COPD except, in very severe cases, lung transplantation (see the Explore More video below).

LUNG CANCER

Lung cancer is a malignant tumor characterized by uncontrolled cell growth in tissues of the lung. The tumor may arise directly from lung tissue (primary lung cancer) or as a result of metastasis from cancer in another part of the body (secondary lung cancer). Primary lung cancer may also metastasize and spread to other parts of the body. Lung cancer develops following genetic damage to DNA that affects the normal functions of the cell. As more damage accumulates, the risk of cancer increases. The most common symptoms of lung cancer include coughing (especially coughing up blood), wheezing, shortness of breath, chest pain, and weight loss.

The major cause of primary lung cancer is tobacco smoking, which accounts for about 85 percent of cases. Cigarette smoke contains numerous cancer-causing chemicals. Besides smoking, other potential causes of lung cancer include exposure to radon gas, asbestos, secondhand smoke, or other air pollutants. When tobacco smoking is combined with other risk factors such as exposure to radon or asbestos, the risk of lung cancer is heightened. People who have close biological relatives with lung cancer are also at increased risk of developing the disease.

Most cases of lung cancer cannot be cured. In many people, cancer has already spread beyond the original site by the time they have symptoms and seek medical attention. About 10 percent of people with lung cancer do not have symptoms when they are diagnosed, and the cancers are found when they have a chest X-ray for another problem. In part because of its typically late diagnosis, lung cancer is the most common cause of cancer-related death in men and the second most common cause in women (after breast cancer). Common treatments for lung cancer include surgical removal of the tumor, radiation therapy, chemotherapy, or some combination of these three types of treatment.

FEATURE: MY HUMAN BODY

Do you — or someone you love — snore? Snoring may be more than just an annoyance. It may also be a sign of a potentially dangerous and common disorder known as sleep apnea. **Sleep apnea** is characterized by pauses in breathing that occur most often because of physical blockage to airflow during sleep. When breathing is paused, carbon dioxide builds up in the bloodstream. The higher-than-normal level of carbon dioxide in the blood causes the respiratory centers in the brain to wake the person enough to start breathing normally. This reduces the carbon dioxide level, and the person falls back asleep. This occurs repeatedly throughout the night, causing serious disruption in sleep. Most people with sleep apnea are unaware that they have the disorder because they don't awake fully enough to remember the repeated awakenings throughout the night. Instead, sleep apnea is more commonly recognized by other people who witness the episodes.

Figure 12.1.3.5shows how sleep apnea typically occurs. The muscle tone of the body normally relaxes during sleep, allowing the soft tissues in the throat to collapse and block the airway. The relaxation of muscles may be exacerbated by the use of alcohol, tranquilizers, or muscle relaxants. The risk of sleep apnea is greater in people who are overweight, smoke tobacco, or have diabetes. The disorder is also more likely to occur in older people and males. Common symptoms of sleep apnea include loud snoring, restless sleep, and daytime sleepiness and fatigue. Daytime sleepiness, in turn, increases the risk of driving and work-related accidents. Continued sleep deprivation may cause moodiness and belligerence. Lack of adequate oxygen to the body because of sleep apnea may also lead to other health problems including fatty liver diseases and high blood pressure. Symptoms of sleep apnea may be present for years or even decades until (and if) a diagnosis is finally made.

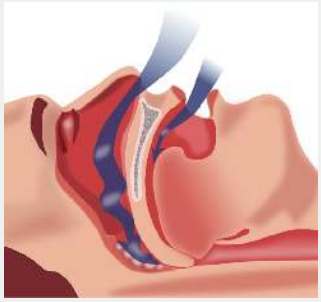


Figure 12.1.3.5: Sleeping on one's back may increase the risk of the airway becoming temporarily blocked during sleep, resulting in sleep apnea.

Treatment of sleep apnea may include avoiding alcohol, quitting smoking, or losing weight. Elevating the upper body during sleep or sleeping on one's side may help prevent airway collapse in many people with sleep apnea. Another type of treatment is the use of an oral device during sleep that shifts the lower jaw forward to help keep the airway open. The most common treatment for moderate to severe sleep apnea is the use during sleep of CPAP (continuous positive airway pressure), which keeps the airway open by means of pressurized air. In this treatment, the person typically wears a plastic facial mask that is connected by a flexible tube to a small bedside CPAP machine. Although CPAP is effective, long-term compliance is often poor because patients find the mask uncomfortable or they experience unpleasant side effects such as dry mouth and nose. A more extreme form of treatment is surgery to remove some of the tissues — such as the tonsils or part of the soft palate — that tend to collapse and block the airway in people with sleep apnea.

REVIEW

1. What is asthma, and what are its symptoms and causes?
2. Identify common risk factors and triggers of asthma attacks.
3. How can asthma attacks be prevented or controlled?
4. What are the causes and symptoms of pneumonia?
5. How can pneumonia be prevented? How is it treated?
6. Define COPD. How is it related to chronic bronchitis and emphysema?
7. Relate COPD to tobacco smoking.
8. What is the difference between primary and secondary lung cancer?
9. What is the major cause of primary lung cancer?
10. Discuss lung cancer as a cause of death.
11. How is lung cancer treated?
12. Define sleep apnea.
13. What is the difference between how COPD and pneumonia affect the alveoli?

EXPLORE MORE

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12.1.4: SMOKING AND HEALTH

SURE DEATH

The anti-smoking cartoon in Figure **12.1.4.1** clearly makes the point that smoking causes death. The cartoon is not using hyperbole, because smoking actually is deadly. It causes about six million deaths each year and is the single greatest cause of preventable death worldwide. As many as half of all people who smoke tobacco die from it. As a result of smoking's deadly effects, the life expectancy of long-term smokers is significantly less than that of non-smokers. In fact, long-term smokers can expect their lifespan to be reduced by as much as 18 years, and they are three times as likely to die before the age of 70 as non-smokers.



Figure **12.1.4.1**: Have another! Sure death

WHY IS SMOKING DEADLY?

As shown in Figure **12.1.4.2**, tobacco smoking has adverse effects on just about every bodily system and organ. The detrimental health effects of smoking depend on the number of years that a person smokes and how much the person smokes. Contrary to popular belief, all forms of tobacco smoke — including smoke from cigars and tobacco pipes — have similar health risks as those of cigarette smoke. Smokeless tobacco may be less of a danger to the lungs and heart, but it too has serious health effects. It significantly increases the risk of cancers of the mouth and throat, among other health problems.

Even non-smokers may not be spared the deadly risks of tobacco smoke. If you spend time around smokers either at home or on the job, then you are at risk of the dangers of secondhand smoke. **Secondhand smoke** enters the air directly from burning cigarettes (and cigars and pipes) and indirectly from the lungs of smokers. This smoke may linger in indoor air for hours and increase the risk of a wide range of adverse health effects. For example, non-smokers who are exposed to secondhand smoke may have as much as a 30 percent increase in their risk of lung cancer and heart disease. The 2014 U.S. Surgeon General's Report concluded that there is no established risk-free level of exposure to secondhand smoke.

Tobacco contains **nicotine,** which is a psychoactive drug. Although nicotine in tobacco smoke does not directly cause cancer or most of the other health risks of smoking, it is a highly addictive drug. In fact, nicotine is even more addictive than cocaine or heroin. The addictive nature of nicotine explains why it is so difficult for smokers to quit the habit even when they know the health risks and really want to stop smoking. The good news is that if someone does stop smoking, his or her risks of smoking-related diseases and death soon start to fall. For example, by one year after quitting, the risk of heart disease drops to only half of that of a continuing smoker.



Figure **12.1.4.2**: Smoking is known to cause many different cancers and chronic diseases such as stroke, blindness, gum infection, aortic rupture, heart disease, pneumonia, hardening of the arteries, chronic lung diseases, reduced fertility, and hip fracture.

SMOKING AND CANCER

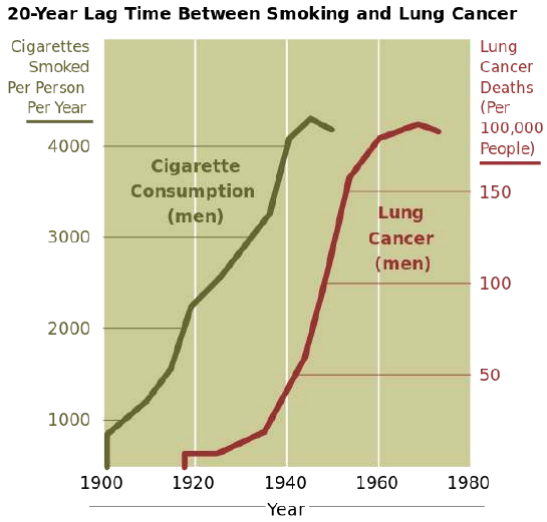


Figure **12.1.4.3**: Cigarette smoking by men in the U.S. began to decline in the 1950s, but it wasn't until the 1970s — roughly 20 years later — that this was reflected by a concomitant decline in lung cancer deaths in men.

One of the main health risks of smoking is cancer, particularly cancer of the lung. Because of the increased risk of lung cancer with

smoking, the risk of dying from lung cancer before age 85 is more than 20 times higher for a male smoker than for a male non-smoker. As the rate of smoking increases, so does the rate of lung cancer deaths, although the effects of smoking on lung cancer deaths can take up to 20 years to manifest themselves, as shown in Figure **12.1.4.3**.

Besides lung cancer, several other forms of cancer are also significantly more likely in smokers than non-smokers, including cancers of the kidney, larynx, mouth, lip, tongue, throat, bladder, esophagus, pancreas, and stomach. Unfortunately, many of these cancers have extremely low cure rates.

When you consider the composition of tobacco smoke, it's not surprising that it increases the risk of cancer. Tobacco smoke contains dozens of chemicals that have been proven to be carcinogens or causes of cancer. Many of these chemicals bind to DNA in a smoker's cells and may either kill the cells or cause mutations. If the mutations inhibit programmed cell death, the cells can survive to become cancer cells. Some of the most potent carcinogens in tobacco smoke include benzopyrene, acrolein, and nitrosamines. Other carcinogens in tobacco smoke are radioactive isotopes, including lead-210 and polonium-210.

RESPIRATORY EFFECTS OF SMOKING

Long-term exposure to the compounds found in cigarette smoke, such as carbon monoxide and cyanide, is thought to be responsible for much of the lung damage caused by smoking. These chemicals reduce the elasticity of alveoli, leading to chronic obstructive pulmonary disease (COPD). COPD is a permanent, incurable, and often fatal reduction in the capacity of the lungs, reducing the ability of the lungs to fully exhale air. The chronic inflammation that is also present in COPD is exacerbated by the tobacco smoke carcinogen acrolein and its derivatives. COPD is almost completely preventable simply by not smoking and by also avoiding secondhand smoke.

CARDIOVASCULAR EFFECTS OF SMOKING

Inhalation of tobacco smoke causes several immediate responses in the heart and blood vessels. Within one minute of inhalation of smoke, the heart rate begins to rise, increasing by as much as 30 percent during the first 10 minutes of smoking. Carbon monoxide in tobacco smoke binds with hemoglobin in red blood cells, thereby reducing the blood's ability to carry oxygen. Hemoglobin bound to carbon monoxide forms such a stable complex that it may result in a permanent loss of red blood cell function. Several other chemicals in tobacco smoke lead to the narrowing and weakening of blood vessels and an increase in substances that contribute to blood clotting. These changes increase blood pressure and the chances of a blood clot forming and blocking a vessel, thereby elevating the risk of heart attack and stroke. A recent study found that smokers are five times more likely than non-smokers to have a heart attack before the age of 40.

Smoking has also been shown to have a negative impact on the levels of blood lipids. Total cholesterol levels tend to be higher in smokers than non-smokers. Ratios of "good" cholesterol to "bad" cholesterol tend to be lower in smokers than in non-smokers.

ADDITIONAL ADVERSE HEALTH EFFECTS OF SMOKING

A wide diversity of additional adverse health effects are attributable to smoking. Here are just a few of them:

- Smokers are at a significantly increased risk of developing chronic kidney disease (in addition to kidney cancer). For example, smoking hastens the progression of kidney damage in people with diabetes.
- People who smoke, especially the elderly, have a greater risk of influenza and other infectious diseases than non-smokers. Smoking more than 20 cigarettes a day has been found to increase the risk of infectious diseases by as much as four times the risk in non-smokers. These effects occur because of damage to both the respiratory system and the immune system.
- In addition to oral cancer, smoking causes other oral problems including periodontitis (gum disease). Roughly half of the cases of gum inflammation are attributable to current or former smoking. Such inflammation increases the risk of tooth loss, which is also higher in smokers than non-smokers. In addition, smoking stains the teeth and causes halitosis (bad breath).
- Smoking is a key cause of erectile dysfunction (ED), probably because it leads to narrowing of arteries in the penis as it does elsewhere in the body. The incidence of ED is about 85 percent higher in males who smoke than it is in non-smokers.
- Smoking also has adverse effects on the female reproductive system, potentially causing infertility, in part because it interferes with the body's ability to produce estrogen. Female smokers are about 60 percent more likely to be infertile than non-smokers. Pregnant women who smoke or are exposed to secondhand smoke have a higher risk of miscarriages and low-birth-weight infants.
- Certain therapeutic drugs, including some antidepressants and anticonvulsants, are less effective in smokers than in non-smokers. This occurs because smoking increases levels of liver enzymes that break down the drugs.
- Smoking causes an estimated 10 percent of all deaths due to fires worldwide. Smokers are also at greater risk of dying in motor vehicle crashes and other accidents.
- Smoking leads to an increased risk of bone fractures, especially of the hip. It also leads to slower wound healing after surgery and an increased rate of postoperative complications.

FEATURE: HUMAN BIOLOGY IN THE NEWS

The item in Figure **12.1.4.4** looks like a regular cigarette, but it's actually an electronic cigarette or e-cigarette. E-cigarettes are battery-powered devices that change flavored liquids and nicotine into a vapor that is inhaled by the user. E-cigarettes are often promoted as being safer than traditional tobacco products and their use is touted as a good way to quit smoking. They are

often not banned in smoke-free areas where it is illegal to smoke tobacco cigarettes.



Figure **12.1.4.4**: e-cigarette

A study completed in 2015 by researchers at the Harvard School of Public Health and widely reported in the mass media found that e-cigarettes may in fact be very harmful to the user's health. E-cigarettes contain nicotine and cancer-causing chemicals such as formaldehyde. According to the study, about three-quarters of flavored e-cigarettes also contain a chemical named diacetyl that causes an incurable and potentially fatal disorder of the lungs, commonly called "popcorn lung" (bronchiolitis obliterans). In this disorder, the bronchioles compress and narrow due to the formation of scar tissue. This greatly diminishes the breathing capacity of people with the disorder. Popcorn lung gained its common name in 2004 when it was diagnosed in workers at popcorn factories. The buttery flavoring used in the factories contained diacetyl.

Some manufacturers of e-cigarettes and flavorings advertise that their products are now free of diacetyl. However, because e-cigarettes are not currently regulated by the FDA, there is no way of knowing for sure whether the products are actually safe. Equally disturbing is the appeal of flavored e-cigarettes to teens and the attempts of producers to specifically market their products to this age group. Flavors such as "cotton candy," "Katy Perry's cherry," and "alien blood" are obviously marketed to youth. Not surprisingly, the use of e-cigarettes is on the rise in middle and high school students, who are more likely to use them than regular cigarettes. Public health officials fear that e-cigarettes will be a gateway for teens to move on to smoking tobacco cigarettes. Some states have recently passed laws prohibiting minors from buying e-cigarettes. As more questions are raised about their potential negative health effects, it is likely that more laws will be passed to regulate them. Watch the news for updates on this issue.

REVIEW

1. What percentage of people who smoke are likely to die from it?
2. Contrast the life expectancy of long-term smokers and non-smokers.
3. What factors related to smoking determine how smoking affects a smoker's health?
4. What are the two sources of secondhand cigarette smoke? How does exposure to secondhand smoke affect non-smokers?
5. Why is it so difficult for smokers to quit the habit? How is their health likely to be affected by quitting?
6. List five types of cancer that are significantly more likely in smokers than non-smokers.
7. Why does smoking cause cancer?
8. Explain how smoking causes COPD.
9. Identify some of the adverse effects of smoking on the cardiovascular system.
10. Give three examples of additional adverse health effects that are more likely with smoking.
11. Do you think e-cigarettes can be addictive? Explain your reasoning.
12. People who smoke are more likely to get which of these than people who do not smoke.

    A. lung cancer
    B. influenza
    C. kidney disease
    D. All of the above

13. Name three toxic chemicals present in tobacco smoke.
14. *True or False.* Nicotine is more addictive than heroin.
15. *True or False.* Smoking has many negative effects on the respiratory and cardiovascular systems, but not on other systems of the body.

EXPLORE MORE

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SECTION OVERVIEW

12.2: URINARY SYSTEM

This chapter discusses the concept of excretion and explains the excretory functions of the skin, liver, large intestine, lungs, and kidneys. It also describes the other organs of the urinary system and several urinary system disorders.

12.2.1: INTRODUCTION TO THE URINARY SYSTEM

12.2.2: KIDNEYS

12.2.3: URETERS, URINARY BLADDER, AND URETHRA

12.2.4: DISORDERS OF THE URINARY SYSTEM

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12.2.1: INTRODUCTION TO THE URINARY SYSTEM

SCULPTURE GARDEN

In Figure **12.2.1.1**, this interesting outdoor art installation can be viewed at the Hague in the Netherlands. It's a colorful piece with an unusual subject. The wrinkled structures on each side of the sculpture represent the kidneys, and the striped structure in the distance represents the urinary bladder. The red and blue tubes are blood vessels, and the tan tubes are ureters. In short, the installation is a three-dimensional depiction of the human urinary system. Only one urinary system organ is not visible in the photo. Do you know what it is?



Figure **12.2.1.1**: Nier met blaas (Kidney with bladder)

The actual human **urinary system**, also known as the renal system, is shown in Figure **12.2.1.2**. The system consists of the kidneys, ureters, bladder, and urethra, which is the only structure not visible in the sculpture above. The main function of the urinary system is to eliminate the waste products of metabolism from the body by forming and excreting **urine.** Between 1 and 2 liters of urine are normally produced every day in a healthy individual.

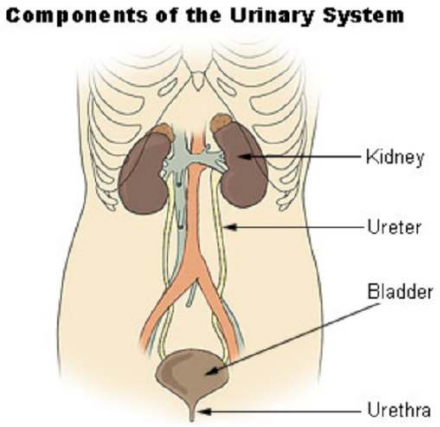


Figure **12.2.1.2**: The components of the urinary system include the two kidneys which lead to two tubes called ureters which lead to a holding structure called the bladder which leads to a tube called the urethra.

ORGANS OF THE URINARY SYSTEM

The urinary system is all about urine. It includes organs that form urine and also those that transport, store, or excrete urine.

KIDNEYS

Urine is formed by the kidneys, which filter many substances out of blood, allow the blood to reabsorb needed materials, and use the remaining materials to form urine. The human body normally has two paired kidneys, although it is possible to get by quite well with just one kidney. The anatomy and function of the kidney are discussed in detail in the next section.

URETERS, BLADDER, URETHRA

After urine forms in the kidneys, it is transported through the ureters (one per kidney) to the sac-like bladder, which stores the urine until urination. During urination, the urine is released from the bladder and transported by the urethra to be excreted outside the body through the external urethral opening.

FUNCTIONS OF THE URINARY SYSTEM

Waste products removed from the body with the formation and elimination of urine include many water-soluble metabolic products. The main waste products are urea, a by-product of protein catabolism, and uric acid, a by-product of nucleic acid catabolism. Excess water and mineral ions are also eliminated in urine.

Besides the elimination of waste products such as these, the urinary system has several other vital functions. These include:

- maintaining homeostasis of mineral ions in extracellular fluid. These ions are either excreted in urine or returned to the blood as needed to maintain the proper balance.
- regulating the acid-base balance in the body. For example, when pH is too low (blood is too acidic), the kidneys excrete less bicarbonate (which is basic) in the urine. When pH is too high (blood is too basic), the opposite occurs and more bicarbonate is excreted in the urine.
- controlling the volume of extracellular fluids, including the blood, which helps maintain blood pressure. The kidneys control fluid volume and blood pressure by excreting more or less salt and water in urine.

CONTROL OF THE URINARY SYSTEM

The formation of urine must be closely regulated to maintain body-wide homeostasis. Several endocrine hormones help control this function of the urinary system, including antidiuretic hormone, parathyroid hormone, and aldosterone.

- Antidiuretic hormone, also called vasopressin, is secreted by the hypothalamus. One of its main roles is conserving body water. It is released when the body is dehydrated and causes the kidneys to excrete less water in urine.
- Parathyroid hormone is secreted by the parathyroid glands. It works to regulate the balance of mineral ions in the body through its effects on several organs, including the kidneys. Parathyroid hormone stimulates the kidneys to excrete less calcium and more phosphorus in the urine.

- Aldosterone is secreted by the cortex of the adrenal glands, which rest atop the kidneys, as shown in Figure **12.2.1.3**. It plays a central role in regulating blood pressure through its effects on the kidneys. It causes the kidneys to excrete less sodium and water in urine.

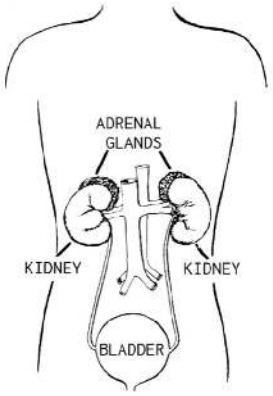


Figure **12.2.1.3**: The adrenal glands are located on top of the kidneys. They secrete aldosterone into the bloodstream, which carries it to the kidneys.

Once urine forms, it is excreted from the body in the process of urination. This process is controlled by both the autonomic and the somatic nervous systems. As the bladder fills with urine, it causes the autonomic nervous system to signal a muscle in the bladder wall to contract and the sphincter between the bladder and urethra to relax and open. This forces urine out of the bladder and through the urethra. Another sphincter at the distal end of the urethra is under voluntary control. When it relaxes under the influence of the somatic nervous system, it allows urine to leave the body through the external urethral opening.

REVIEW

1. What organs make up the urinary system?
2. State the main function of the urinary system.
3. What is the primary function of the kidneys?
4. Describe how blood enters and leaves the kidneys.
5. What are nephrons?
6. What happens to urine after it forms in the kidneys?
7. Identify the functions of the urinary system besides the elimination of waste products.
8. How is the formation of urine regulated?
9. Explain how the process of urination is controlled.
10. What function do the adrenal glands carry out that is related to urine?

    A. They form urine and transport it to the kidneys

    B. They excrete concentrated urine into the ureters

    C. They secrete a hormone that affects the composition of urine

    D. They store urine when water and salts need to be retained by the body
11. Explain why it is important to have voluntary control over the sphincter at the end of the urethra.
12. Compare the aldosterone to antidiuretic hormones in terms of how they affect the kidneys.
13. If your body needed to retain more calcium, which of the hormones described in this concept is the most likely to rise in the level? Explain your reasoning.
14. *True or False.* Urine is composed of water, urea, and minerals only.
15. *True or False.* The renal artery contains blood that was filtered by the kidney.

EXPLORE MORE

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12.2.2: KIDNEYS

KIDNEYS ON THE MENU

Pictured here amidst a bed of mixed veggies are a steak and kidney pudding. More often made into a pie, this savory dish is a British favorite. Kidneys on the menu typically come from sheep, pigs, or cows. In these animals as in the human animal, kidneys are the main organs of excretion.



Figure **12.2.2.1**: Steak and kidney pudding

LOCATION OF THE KIDNEYS

The two bean-shaped **kidneys** are located high in the back of the abdominal cavity, one on each side of the spine. Both kidneys sit just below the diaphragm, the large breathing muscle that separates the abdominal and thoracic cavities. As you can see in Figure **12.2.2.2**, the right kidney is slightly smaller and lower than the left kidney. The right kidney is behind the liver, and the left kidney is behind the spleen. The location of the liver explains why the right kidney is smaller and lower than the left.

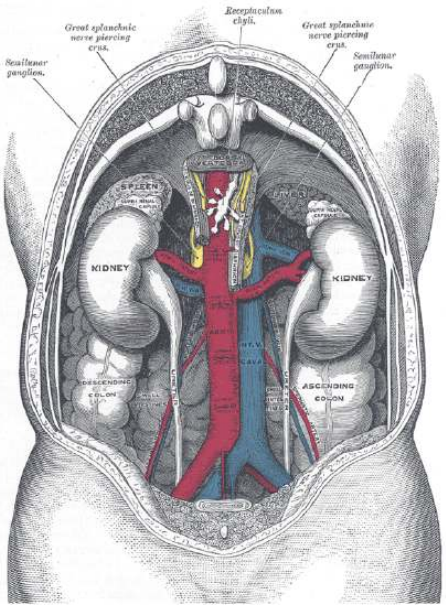


Figure **12.2.2.2**: This classic illustration of the abdominal cavity provides a view of the internal organs from the back of the body. It clearly shows the locations of the right and left kidney, as well as the large blood vessels that connect the kidneys to the body's main artery (aorta) and vein (inferior vena cava). The ureter exiting each kidney is also shown in the diagram.

KIDNEY ANATOMY

The shape of each kidney gives it a convex side and a concave side. You can see this clearly in the detailed diagram of kidney anatomy shown in Figure **12.2.2.3**. The concave side is where the renal artery enters the kidney and the renal vein and ureter leave the kidney. This area of the kidney is called the hilum. The entire kidney is surrounded by tough fibrous tissue, called the renal capsule, which in turn is surrounded by two layers of protective, cushioning fat.

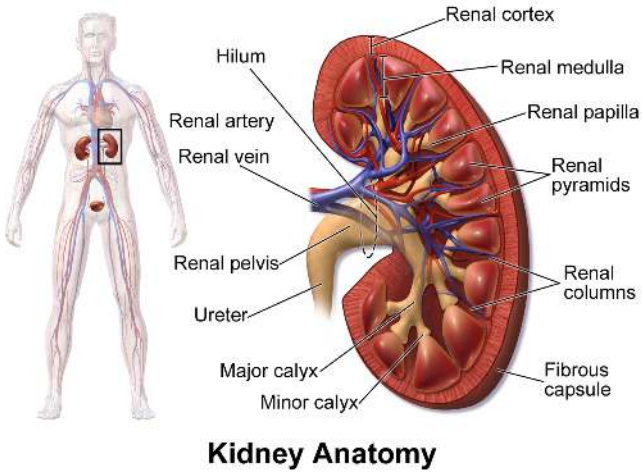


Figure **12.2.2.3**: This diagram shows the location and relative size of the two kidneys as well as the internal structure of each kidney.

Internally, each kidney is divided into two major layers: the outer renal cortex and the inner renal medulla (see Figure **12.2.2.3**). These layers take the shape of many cone-shaped renal lobules, each containing a renal cortex surrounding a portion of the medulla called a renal pyramid. Within the renal pyramids are the structural and functional units of the kidneys, the tiny nephrons. Between the renal pyramids are projections of cortex called renal columns. The tip or papilla of each pyramid empties urine into a minor calyx (chamber). Several minor calyces empty into a major calyx, and the latter empties into the funnel-shaped cavity called the renal pelvis, which becomes the ureter as it leaves the kidney.

RENAL CIRCULATION

The renal circulation is an important part of the kidney's main function of filtering waste products from the blood. Blood is supplied to the kidneys via the renal arteries. The right renal artery supplies the right kidney, and the left renal artery supplies the left kidney. These two arteries branch directly from the aorta, which is the largest artery in the body. Each kidney is only about 11 cm (4.4 in.) long and has a mass of just 150 grams (5.3 oz), yet it receives about 10 percent of the total output of blood from the heart. Blood is filtered through the kidneys about 20 times each hour, 24 hours a day, day after day.

As indicated in Figure **12.2.2.4**, each renal artery carries blood with waste products into the kidney. Within the kidney, the renal artery branches into increasingly smaller arteries that extend through the

renal columns between the renal pyramids. These arteries, in turn, branch into arterioles that penetrate the renal pyramids. Blood in the arterioles passes through nephrons, the structures that actually filter the blood. After blood passes through the nephrons and is filtered, the clean blood moves through a network of venules that converge into small veins. Small veins merge into increasingly larger ones and ultimately into the renal vein, which carries clean blood away from the kidney to the inferior *vena cava*.

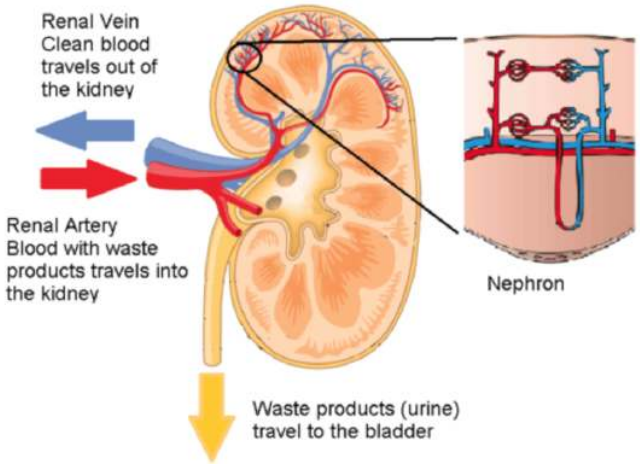


Figure **12.2.2.4**: The renal artery and renal vein carry blood to and from the kidney, respectively. As blood passes through the capillaries surrounding nephrons within the kidney, it is filtered and substances filtered from the blood are eventually excreted via ureter to the bladder.

NEPHRON STRUCTURE AND FUNCTION

The illustration above gives an indication of the complex structure of a nephron. The **nephron** is the basic structural and functional unit of the kidney, and each kidney typically contains at least a million of them. As blood flows through a nephron, many materials are filtered out of the blood, needed materials are returned to the blood, and the remaining materials form urine. Most of the waste products removed from the blood and excreted in the urine are byproducts of metabolism. At last half of the waste is urea, a waste product produced by protein catabolism. Another important waste is uric acid, produced in nucleic acid catabolism.

COMPONENTS OF A NEPHRON

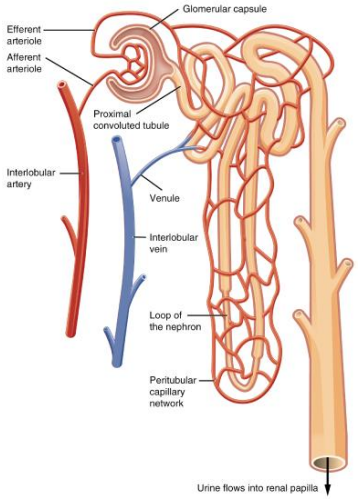


Figure **12.2.2.5**: This model of an individual nephron shows each of the structures that are involved in filtering blood, returning needed materials to blood, or excreting wastes that form urine. The arrows indicate the direction in which fluids flow through the nephron.

The diagram in Figure **12.2.2.5** shows in greater detail the components of a nephron. The renal corpuscle is a filtering structure that is consists of a network of capillaries called the glomerulus (plural, glomeruli) and the Bowman's capsule, a space surrounding the glomerulus. Bowman's capsule is the initial structure of a nephron. Extending from Bowman's capsule is the renal tubule. The proximal end (nearest Bowman's capsule) of the renal tubule is called the proximal convoluted (coiled) tubule. From here, the renal tubule continues as a loop (known as the loop of Henle), which in turn becomes the distal convoluted tubule. The latter finally joins with a collecting duct. As you can see in the diagram, peritubular capillaries surround the total length of the renal tubule.

THE FUNCTION OF A NEPHRON

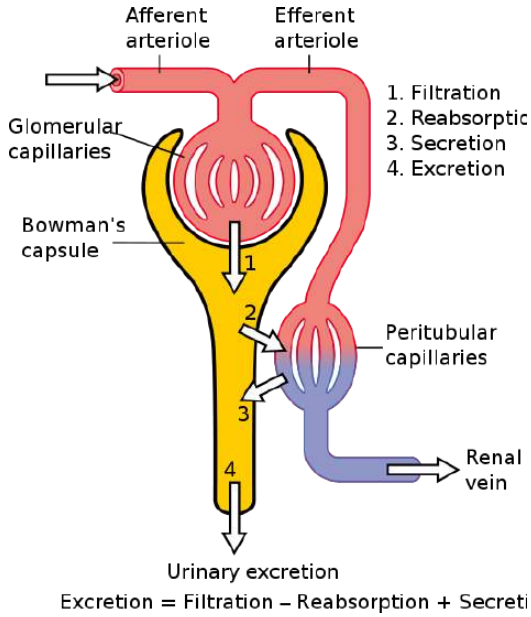


Figure **12.2.2.6**: This diagram of a nephron shows the parts of the nephron where different stages of nephron function take place. Filtration (1) occurs in the Renal corpuscle, Reabsorption (2) occurs in the proximal tubule, Secretion (3) occurs in the distal tubule, and Excretion (4) occurs in the collecting duct.

The simplified diagram of a nephron in Figure **12.2.2.6** shows how the nephron functions. Blood enters the nephron through an arteriole called the afferent arteriole. Some of the blood next passes through the capillaries of the glomerulus. Any blood that doesn't pass through the glomerulus, as well as blood after it passes through the glomerular capillaries, continues on through an arteriole called the efferent arteriole. The efferent arteriole follows the renal tubule of the nephron, where it continues to play roles in nephron functioning.

FILTRATION

As blood from the afferent arteriole flows through the glomerular capillaries, it is under pressure. Because of the pressure, water and solutes are filtered out of the blood and into the space made by Bowman's capsule. This is the filtration stage of nephron function. The filtered substances, called filtrate, pass into Bowman's capsule and from there into the proximal end of the renal tubule. At this stage, filtrate includes water, salts, organic solids such as nutrients, and waste products of metabolism such as urea.

REABSORPTION AND SECRETION

As filtrate moves through the renal tubule, some of the substances it contains are reabsorbed from the filtrate back into the blood in the efferent arteriole (via peritubular capillaries). This is the reabsorption stage of nephron function. About two-thirds of the filtered salts and water and all of the filtered organic solutes (mainly glucose and amino acids) are reabsorbed from the filtrate by the blood in the peritubular capillaries. Reabsorption occurs mainly in the proximal convoluted tubule and the loop of Henle.

At the distal end of the renal tubule, some additional reabsorption generally occurs. This is also the region of the tubule where other substances from the blood are added to the filtrate in the tubule. The addition of other substances to the filtrate from the blood is called secretion. Both reabsorption and secretion in the distal convoluted tubule are largely under the control of endocrine hormones that maintain homeostasis of water and mineral salts in the blood. These hormones work by controlling what is reabsorbed into the blood from the filtrate and what is secreted from the blood into the filtrate to become urine. For example, the parathyroid hormone causes more calcium to be reabsorbed into the blood and more phosphorus to be secreted into the filtrate.

COLLECTION OF URINE AND EXCRETION

By the time the filtrate has passed through the entire renal tubule, it has become the liquid waste known as urine. Urine empties from the distal end of the renal tubule into a **collecting duct**. From there, the urine flows into increasingly larger collecting ducts. As urine flows through the system of collecting ducts, more water may be reabsorbed from it. This will occur in the presence of antidiuretic hormone from the hypothalamus. This hormone makes the collecting ducts permeable to water, allowing water molecules to pass through them into capillaries by osmosis while preventing the passage of ions or other solutes. As much as three-fourths of the water may be reabsorbed from urine in the collecting ducts, making the urine more concentrated.

Urine finally exits the largest collecting ducts through the renal papillae. It empties into the renal calyces and finally into the renal pelvis (see Figure **12.2.2.3**. From there, it travels through the ureter to the urinary bladder for eventual excretion from the body. An average of about 1.5 liters of urine is excreted each day. Normally, urine is yellow or amber in color (Figure **12.2.2.7**). The darker the color, generally the more concentrated the urine is.



Figure **12.2.2.7**: Fresh urine is typically yellow or amber in color.

OTHER FUNCTIONS OF THE KIDNEYS

Besides filtering blood and forming urine for the excretion of soluble wastes, the kidneys have several vital functions in maintaining body-wide homeostasis. Most of these functions are related to the composition or volume of urine formed by the kidneys. These functions include maintaining the proper balance of water and salts in the body, normal blood pressure, and the correct range of blood pH. Through the processes of absorption and secretion by nephrons, more or less water, salt ions, acids, or bases are returned to the blood or excreted in urine as needed to maintain homeostasis.

KIDNEY HORMONES

- **Aldosterone** is secreted by the adrenal cortex. Aldosterone causes the kidneys to increase the reabsorption of sodium ions and water from the filtrate into the blood. This returns the

concentration of sodium ions in the blood to normal. The increased water in the blood also increases blood volume and blood pressure.

- **Calcitriol** is secreted by the kidneys in response to low levels of calcium in the blood. This hormone stimulates the uptake of calcium by the intestine, thus raising blood levels of calcium.
- **Erythropoietin** is secreted by the kidneys in response to low levels of oxygen in the blood. This hormone stimulates **erythropoiesis**, which is the production of red blood cells in the bone marrow. Extra red blood cells increase the level of oxygen carried in the blood.

FEATURE: HUMAN BIOLOGY IN THE NEWS

Kidney failure is a complication of common disorders including diabetes mellitus and hypertension. Almost half a million Americans have end-stage kidney disease and need to either receive a donated kidney or have frequent hemodialysis, a medical procedure in which the blood is artificially filtered through a machine. Transplant generally has better outcomes than hemodialysis but demand for organs far outstrips the supply. At any given time, more than 100,000 people in the U.S. are on a waiting list for a kidney transplant, but each year fewer than 20,000 receive them. Every day, 13 Americans die while waiting for a donor's kidney.

For the past decade, Dr. William Fissell, a kidney specialist at Vanderbilt University, has been working to create an implantable part-biological and part-artificial kidney. Using microchips like those used in computers, he has produced an artificial kidney small enough to implant in the patient's body in place of the failed kidney. According to Dr. Fissell, the artificial kidney is "... a bio-hybrid device that can mimic a kidney to remove enough waste products, salt, and water to keep a patient off [hemo]dialysis."

The filtration system in the artificial kidney consists of a stack of 15 microchips. Tiny pores in the microchips act as a scaffold for the growth of living kidney cells that can mimic the natural functions of the kidney. The living cells form a membrane to filter the patient's blood as a biological kidney would, but with less risk of rejection by the patient's immune system because they are embedded within the device. The new kidney doesn't need a power source because it uses the natural pressure of blood flowing through arteries to push the blood through the filtration system. A major part of the design of the artificial organ was devoted to fine-tuning the fluid dynamics so blood flows through the device without clotting.

The implantable kidney was given fast-track approval for testing in people by the U.S. Food and Drug Administration because of the potentially life-saving benefits of the device. The artificial kidney is expected to be tested in pilot trials by 2018. Dr. Fissell says he has a long list of patients eager to volunteer for the trials.

REVIEW

1. Where are the kidneys located?
2. Contrast the renal artery and renal vein.
3. Describe the structure of the kidney.
4. Identify the functions of a nephron.
5. Describe in detail what happens to fluids (blood, filtrate, and urine) as they pass through the parts of a nephron.
6. Use the example of the renin-angiotensin-aldosterone system to illustrate how the kidneys control homeostasis with the help of endocrine hormones.
7. Identify two endocrine hormones secreted by the kidneys and the functions they control.
8. Put the following structures in order of how urine flows out of the kidney, from the earliest to the latest:

   collecting ducts; renal tubule; renal pelvis; renal calyces
9. Name two regions in the kidney where water is reabsorbed.
10. *True or False.* Once the filtrate enters the renal tubule, no substances are added to it.
11. *True or False.* Some substances are reabsorbed in the distal end of the renal tubule.
12. Is the blood in the glomerular capillaries more or less filtered than the blood in the peritubular capillaries? Explain your answer.
13. How many nephrons are there per kidney?

    A. One

    B. Thirteen

    C. At least one thousand

    D. At least one million
14. If blood flow to the kidneys is blocked, what do you think would happen?
15. The loop of Henle is part of the:

    A. glomerulus

    B. renal tubule

    C. collecting duct

    D. ureter

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12.2.3: URETERS, URINARY BLADDER, AND URETHRA

COMMUNICATING WITH URINE

Why do dogs urinate on fire hydrants? Besides "having to go," they are marking their territory with chemicals called pheromones in their urine. It's a form of communication, in which they are "saying" with odors that the yard is theirs and other dogs should stay away. Dogs may urinate on fence posts, trees, car tires, and many other objects in addition to fire hydrants. Urination in dogs, as in people, is usually a voluntary process controlled by the brain. The process of forming urine, which occurs in the kidneys, occurs constantly and is not under voluntary control. What happens to all the urine that forms in the kidneys? It passes from the kidneys through the other organs of the urinary system, starting with the ureters.



Figure **12.2.3.1**: Dog urinating on hydrant

URETERS

As shown in Figure **12.2.3.2**, ureters are tube-like structures that connect the kidneys with the urinary bladder. They are paired structures, with one ureter for each kidney. In adults, ureters are between 25 and 30 cm (10 to 12 in.) long and about 3 to 4 mm (about 1/8 in.) in diameter.

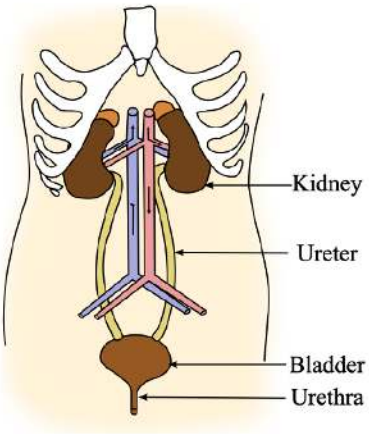


Figure **12.2.3.2**: Besides the kidneys, the urinary system includes two ureters, the urinary bladder, and the urethra.

Each ureter arises in the pelvis of a kidney (Figure **12.2.3.3**). It then passes down the side of the kidney and finally enters the back of the bladder.

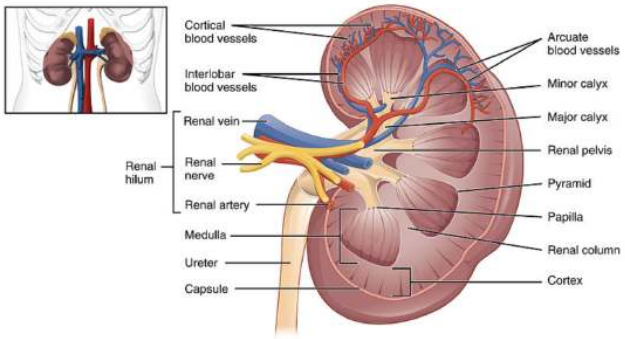


Figure **12.2.3.3**: Urine collects in the renal pelvis which is continuous with the ureter. The ureter then carries the urine from the kidney to the urinary bladder.

The walls of the ureters are composed of multiple layers of different types of tissues. You can see the layers in Figure **12.2.3.4**. The innermost layer is a special type of epithelium, called the transitional epithelium. Unlike the epithelium lining most organs, the transitional epithelium is capable of flattening and distending and does not produce mucus. It lines much of the urinary system, including the renal pelvis, bladder, and much of the urethra in addition to the ureters. Transitional epithelium allows these organs to stretch and expand as they fill with urine or allow urine to pass through. The next layer of the ureter walls is made up of loose connective tissue containing elastic fibers, nerves, and blood and lymphatic vessels. After this layer are two layers of smooth muscles, an inner circular layer, and an outer longitudinal layer. The smooth muscle layers can contract in waves of peristalsis to propel urine down the ureters from the kidneys to the urinary bladder. The outermost layer of the ureter walls consists of fibrous tissue.

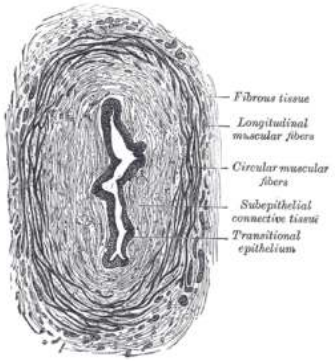


Figure **12.2.3.4**: This illustration shows a cross-section of a ureter. The white space inside is the lumen through which urine passes. From the lumen outward, the layers of the ureter wall include transitional epithelium, connective tissue, two layers of muscle fibers, and an outer layer of fibrous tissue.

URINARY BLADDER

The **urinary bladder** is a hollow, muscular, and stretchy organ that rests on the pelvic floor. It collects and stores urine from the kidneys before the urine is eliminated through urination. As shown in Figure **12.2.3.5**, urine enters the urinary bladder from the ureters through two ureteral openings on either side of the back wall of the bladder.

Urine leaves the bladder through a sphincter called the internal urethral sphincter. When the sphincter relaxes and opens, it allows urine to flow out of the bladder and into the urethra.

Like the ureters, the bladder is lined with transitional epithelium, which can flatten out and stretch as needed as the bladder fills with urine. The next layer (lamina propria) is a layer of loose connective tissue, nerves, and blood and lymphatic vessels. This is followed by a submucosa layer, which connects the lining of the bladder with the detrusor muscle in the walls of the bladder. The outer covering of the bladder is the peritoneum, which is a smooth layer of epithelial cells that lines the abdominal cavity and covers most abdominal organs.

The detrusor muscle in the wall of the bladder is made of smooth muscle fibers that are controlled by both the autonomic and somatic nervous systems. As the bladder fills, the detrusor muscle automatically relaxes to allow it to hold more urine. When the bladder is about half full, the stretching of the walls triggers the sensation of needing to urinate. When the individual is ready to void, conscious nervous signals cause the detrusor muscle to contract and the internal urethral sphincter to relax and open. As a result, urine is forcefully expelled out of the bladder and into the urethra.

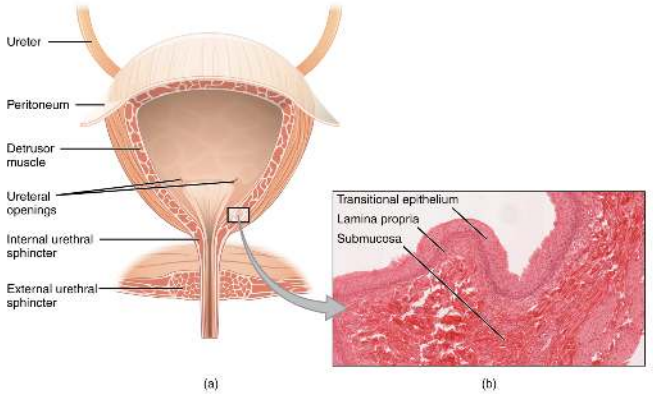


Figure **12.2.3.5**: This diagram of the urinary bladder shows (a) a cross-sectional drawing of the entire bladder and (b) a microscopic cross-section of the tissues in the wall of the bladder.

URETHRA

The **urethra** is a tube that connects the urinary bladder to the external urethral orifice, which is the opening of the urethra on the surface of the body. As shown in Figure **12.2.3.6**, the urethra in a person with XY chromosomes (anatomically male) travels through the penis, so it is much longer than the urethra in a person with XX chromosomes (anatomically female). In a genetically male person, the urethra averages about 20 cm (8 in.) long, whereas, in a genetically female individual, it averages only about 4.8 cm (1.9 in.) long. In an XY individual, the urethra carries semen as well as urine, but in the XX individual, it carries only urine.

Like the ureters and bladder, the proximal (closer to the bladder) two-thirds of the urethra are lined with transitional epithelium. The distal (farther from the bladder) third of the urethra is lined with mucus-secreting epithelium. The mucus helps protect the epithelium from urine, which is corrosive. Below the epithelium is loose connective tissue, and below that are layers of smooth muscle that are continuous with the muscle layers of the urinary bladder. When the bladder contracts to forcefully expel urine, the smooth muscle of the urethra relaxes to allow the urine to pass through.

In order for urine to leave the body through the external urethral orifice, the external urethral sphincter must relax and open. This sphincter is a striated muscle that is controlled by the somatic nervous system, so it is under conscious, voluntary control in most people (exceptions are infants, some elderly people, and patients with certain injuries or disorders). The muscle can be held in a contracted state and hold in the urine until the person is ready to urinate. Following urination, the smooth muscle lining the urethra automatically contracts to re-establish muscle tone, and the individual consciously contracts the external urethral sphincter to close the external urethral opening.

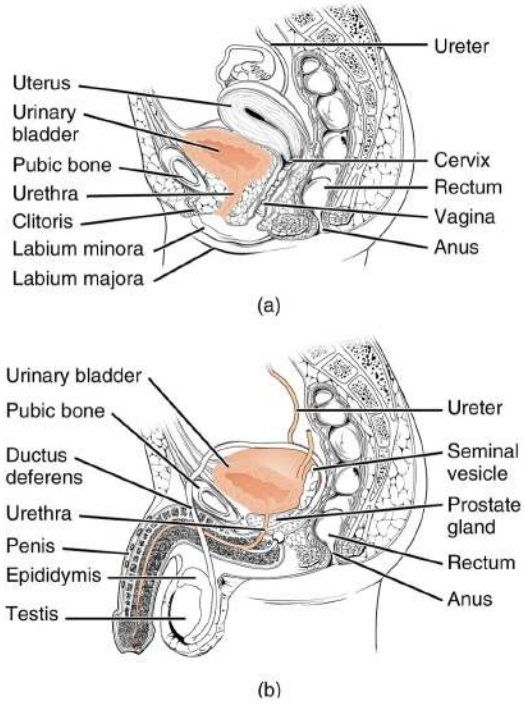


Figure **12.2.3.6**: The urinary bladder and urethra are colored brown to illustrate them in (a) female anatomy and (b) male anatomy. Notice how much longer the male urethra is because it travels through the length of the penis to reach the external urethral orifice.

REVIEW

1. What are ureters?
2. Describe the location of the ureters relative to other urinary tract organs.
3. Identify layers in the walls of a ureter and how they contribute to the ureter's function.
4. Describe the urinary bladder.
5. What is the function of the urinary bladder?
6. How does the nervous system control the urinary bladder?
7. What is the urethra?
8. How does the nervous system control urination?

9. Identify the sphincters that are located along the pathway from the ureters to the external urethral orifice.
10. What are two differences between the male and female urethra?
11. *True or False.* Urine travels through the urinary system due solely to the force of gravity.
12. *True or False.* Urination refers to the process that occurs from the formation of urine in the kidneys to the elimination of urine from the body.
13. When the bladder muscle contracts, the smooth muscle in the walls of the urethra _____ .
14. Transitional epithelium lines the:

    A. bladder

    B. ureters

    C. renal pelvis

    D. All of the above

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12.2.4: DISORDERS OF THE URINARY SYSTEM

AWARENESS RIBBON

Awareness ribbons are symbols meant to show support or raise consciousness for a cause. Different colors are associated with different issues, often relating to health problems. The first ribbon to gain familiarity for a health issue was the red ribbon for HIV/AIDS, created in 1991. The pink ribbon for breast cancer awareness is probably the best known today. Do you know what a green ribbon like the one pictured in Figure **12.2.4.1** represents? Among several other health problems, a green ribbon is meant to show support or raise awareness for kidney disorders.



Figure **12.2.4.1**: Kidney disorder awareness ribbon

The kidneys play such vital roles in eliminating wastes and toxins and maintaining body-wide homeostasis that disorders of the kidneys may be life-threatening. The gradual loss of normal kidney function commonly occurs with a number of disorders, including diabetes mellitus and high blood pressure. Other disorders of the kidneys are caused by faulty genes that are inherited. Loss of kidney function may eventually progress to kidney failure.

DIABETIC NEPHROPATHY

Diabetic nephropathy is a progressive kidney disease caused by damage to the capillaries in the glomeruli of the kidneys due to long-standing diabetes mellitus (see Figure **12.2.4.2**). It is not fully understood how diabetes leads to damage of glomerular capillaries, but it is thought that high levels of glucose in the blood are involved. In people with diabetes, nephropathy is more likely if their blood glucose is poorly controlled. Having high blood pressure, a history of cigarette smoking and a family history of kidney problems are additional risk factors. Diabetic nephropathy often has no symptoms at first. In fact, it may take up to a decade after kidney damage begins for symptoms to appear. When they do appear, they typically include severe tiredness, headaches, nausea, frequent urination, and itchy skin.

Proteins are large molecules that usually are not filtered out of blood in the glomeruli. When the glomerular capillaries are damaged, it allows proteins such as albumin to leak into the filtrate from the blood. As a result, albumin ends up being excreted in the urine. Finding a high level of albumin in the urine is one indicator of diabetic nephropathy and helps to diagnose the disorder. Drugs may be prescribed to reduce protein levels in the urine. Controlling high blood sugar levels and hypertension (high blood pressure) is also important to help slow kidney damage, as is a reduction of sodium intake.

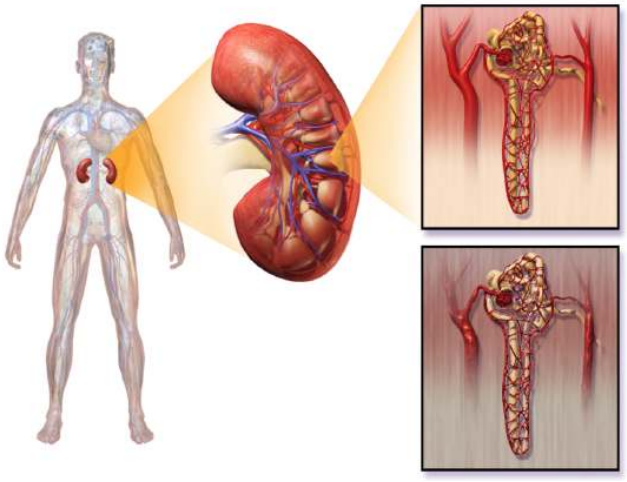


Figure **12.2.4.2**: Diabetic nephropathy is characterized by damage to the capillaries in the glomeruli of the kidneys, represented by the lower of the two inset diagrams.

POLYCYSTIC KIDNEY DISEASE

Polycystic kidney disease (PKD) is a genetic disorder in which multiple abnormal cysts develop and grow in the kidneys. Figure **12.2.4.3** shows a pair of kidneys that are riddled with cysts from PKD. In people who inherit PKD, the cysts may start to form at any point in life from infancy through adulthood. Typically, both kidneys are affected. Symptoms of the disorder may include high blood pressure, headaches, abdominal pain, blood in the urine, and excessive urination.



Figure **12.2.4.3**: In polycystic kidney disease, the kidneys are injured by the formation of multiple cysts, which may grow to be quite large.

There are two types of PKD. The more common type is caused by an autosomal dominant allele, and the less common type is caused by an autosomal recessive allele. Both types collectively make PKD one of the most common hereditary diseases in the United States, affecting more than half a million people. There is little or no difference in the rate of occurrence of PKD between genders or ethnic groups. There is no known cure for this disease other than a kidney transplant.

KIDNEY FAILURE

Both diabetic nephropathy and PKD may lead to **kidney** (or renal) **failure** (classified as end-stage kidney disease), in which the kidneys are no longer able to adequately filter metabolic wastes from the blood. Long-term, uncontrolled high blood pressure is another common cause of kidney failure. Symptoms of kidney failure may include nausea, more or less frequent urination, blood in the urine, muscle cramps, anemia, swelling of the extremities, and shortness of breath due to the accumulation of fluid in the lungs. If kidney function drops below the level needed to sustain life, then the only treatment option is kidney transplantation or some means of artificial filtration of the blood, such as by hemodialysis.

Hemodialysis is a medical procedure in which blood is filtered externally through a machine. You can see how it works in the simplified diagram in Figure **12.2.4.4**. During dialysis, waste products such as urea as well as excess water are removed from the patient's blood before the blood is returned to the patient. Hemodialysis is typically done on an outpatient basis in a hospital or special dialysis clinic. Less frequently, it is done in the patient's home. Depending on the patient's size, among other factors, the blood is filtered for 3 to 4 hours about 3 times a week. Because the treatment is needed so frequently, hemodialysis is one of the most common procedures performed in U.S. hospitals.

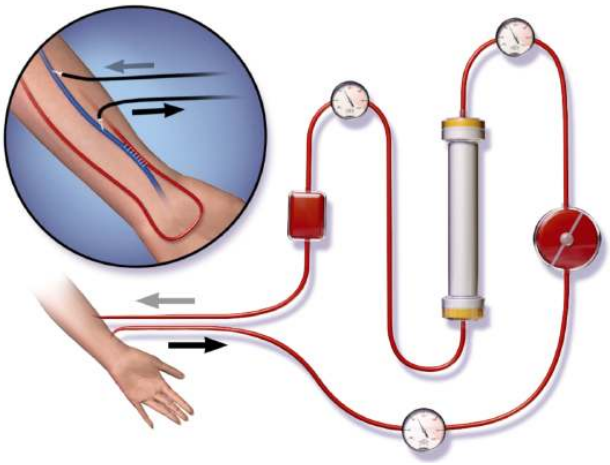


Figure **12.2.4.4**: This simple diagram shows the general process by which blood is filtered externally in the process of hemodialysis. Blood is taken from a patient, run through a filtration machine, and then returned.

KIDNEY STONES

A **kidney stone**, also known as a renal calculus, is a solid crystal that forms in a kidney from minerals in urine (see Figure **12.2.4.5**). The majority of kidney stones consist of crystals of calcium salts. Kidney stones typically leave the body in the urine stream. A small stone may pass through the ureters and other urinary tract organs without causing symptoms and go undetected. A larger stone may cause pain when it passes through the urinary tract. If a kidney stone grows large enough, it may block the ureter. Blockage of a ureter may cause a decrease in kidney function and damage to the kidney.

A kidney stone that causes pain is generally treated with pain medication until it passes through the urinary tract. A stone that causes a blockage may be treated with lithotripsy. This is a medical procedure in which high-intensity ultrasound pulses are applied externally to cause fragmentation of the stone into pieces small enough to pass easily through the urinary tract. Although lithotripsy is noninvasive, it can cause damage to the kidneys. An alternative treatment for a stone that blocks urine flow is to insert a stent into the ureter to expand it and allow both urine and the stone to pass. In some cases, surgery may be required to physically remove a large stone from the ureter.

A combination of lifestyle and genetic factors seem to predispose certain people to develop kidney stones. Risk factors include high consumption of cola soft drinks, eating a diet high in animal protein, being overweight, and not drinking enough fluids. Preventive measures are obvious. They include limiting cola consumption, eating less animal protein, losing weight, and increasing fluid intake.

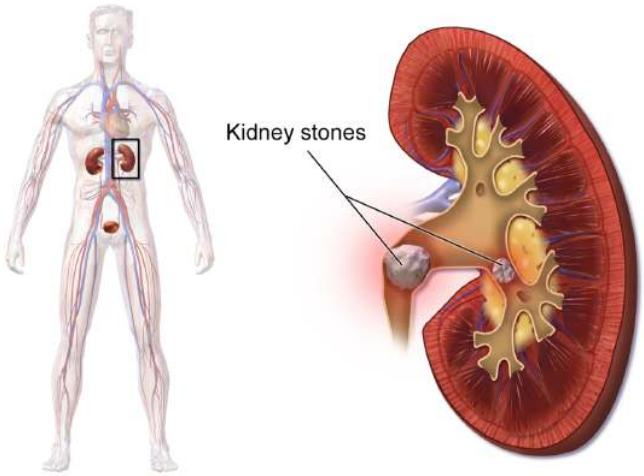


Figure **12.2.4.5**: Kidney stones form in the kidney and may grow large enough to block the major calyx or ureter.

OTHER URINARY SYSTEM DISORDERS

Although disorders of the kidneys are generally the most serious urinary system disorders, problems that affect other organs of the urinary tract are generally more common. They include bladder infections and urinary incontinence.

BLADDER INFECTION

A **bladder infection**, also called cystitis, is a very common type of urinary tract infection in which the urinary bladder becomes infected by bacteria (typically *Escherichia coli*), rarely by fungi. Symptoms of bladder infections may include pain with urination, frequent urination, and feeling the need to urinate despite having an empty bladder. In some cases, there may be blood in the urine. A much less common type of urinary tract infection is pyelonephritis, in which the kidney becomes infected. If a kidney infection occurs, it is generally because of an untreated bladder infection. Bladder infections are treated mainly with antibiotics.



Figure **12.2.4.6**: Using a diaphragm like this one as a barrier method of birth control may increase the risk of a woman developing a bladder infection following sexual intercourse

Risk factors for urinary bladder infections include sexual intercourse (especially when spermicide or a diaphragm, as shown in Figure **12.2.4.6**, is used for contraception), diabetes, obesity, and most importantly, female sex. Bladder infections are four times more common in women than in men. In fact, in women, they are the most common type of bacterial infection, and as many as 1 in 10 women has a bladder infection in any given year. Female anatomy explains the sex difference in the incidence of bladder infections. The urethra is much shorter and closer to the anus in females than in males, so contamination of the urethra and then the bladder with GI tract bacteria is more likely in females than in males. Once the bacteria reach the bladder, they can attach to the bladder wall and form a biofilm that resists the body's immune response.

URINARY INCONTINENCE

Urinary incontinence is a chronic problem of uncontrolled leakage of urine. It is very common, especially at older ages and especially in women. Sometimes urinary incontinence is a sign of another health problem, such as diabetes or obesity. Regardless of the underlying cause, the symptoms of urinary incontinence alone may have a large impact on the quality of life, frequently causing inconvenience, embarrassment, and distress.

In a person with male anatomy, urinary incontinence is most commonly caused by an enlarged prostate gland or treatment for prostate cancer. In genetically female individuals, there are two common types of urinary incontinence with different causes: stress incontinence and urge incontinence.

- Stress urinary incontinence is caused by loss of support of the urethra, usually due to stretching of pelvic floor muscles during childbirth. It is characterized by leakage of small amounts of urine with activities that increase abdominal pressure, such as coughing, sneezing, or lifting. Treatment of stress urinary incontinence may include Kegel exercises to strengthen the pelvic muscles (see Explore More below). More serious cases may call for surgery to improve support for the bladder.
- Urge urinary incontinence (commonly called "overactive bladder") is caused by uncontrolled contractions of the detrusor muscle in the wall of the bladder. This causes the bladder to empty unexpectedly. Urge incontinence is characterized by leakage of large amounts of urine in association with an insufficient warning to get to the bathroom in time. Treatment of urge incontinence may include taking medication to relax the detrusor muscle.

FEATURE: MY HUMAN BODY

You probably have had to "donate" a urine specimen for analysis in conjunction with a medical visit. A thorough medical exam often includes clinical tests for urine. Understanding what your urine may reveal about your health may help you appreciate the need for such tests.

The most common urine test is called a urinalysis. In a routine urinalysis, a urine sample may be analyzed by sight and smell and with simple urine test strips. If a particular disorder is suspected, urinalysis may be more extensive. For example, the urine may be analyzed with specific tests or viewed under a microscope to identify abnormal substances in the urine. If a bacterial infection is suspected, a sample of urine may be cultured in the lab to see if it grows bacteria and which type of bacteria grow. Knowing the type of bacteria is important for deciding which class of antibiotics is likely to be most effective in treating the infection.

The color and clarity of urine may be obvious first indicators of disorders or other abnormalities. Normal urine is yellow to amber in color and looks clear. If urine is nearly colorless, it could be a sign of excessive fluid intake, or it might be a sign of diabetes. Very dark urine may indicate dehydration, but it could also be caused by taking certain medications or ingesting some other substances. If the urine has a reddish tinge, it is often a sign of blood in the urine, which could be due to a urinary tract infection, kidney stone, or even cancer. If the urine appears cloudy instead of clear, it could be due to white blood cells in the urine, which may be another sign of a urinary tract infection.

Normal urine may have virtually no odor if it is very dilute. It will have a stronger odor if it is concentrated. Brief changes in the normal odor of urine often occur due to the ingestion of certain foods or medications. For example, after eating asparagus, urine may have a peculiar and distinctive odor for several hours. More significant is urine that has a sweet smell, because this may indicate sugar in the urine, which is a sign of diabetes.

Urine test strips, much like the familiar litmus test strips used to detect acids and bases in a chemistry lab, are used to identify abnormal levels of certain components in the urine. For example, urine test strips can detect and quantify the presence of nitrites in urine, which is usually a sign of infection with certain types of bacteria. Urine test strips can also be used to identify proteins such as albumin in urine, which may be a sign of a kidney infection or of kidney failure. Levels of sodium in urine can also be measured with test strips, and higher-than-normal levels may be another indication of kidney failure. In

addition, test strips can identify and quantify the presence of white blood cells and blood in a urine specimen, both of which are likely to be a sign of a urinary tract infection or some other urinary system disorder.

Besides the use of urine test strips, other simple urine tests that are often performed include Benedict's test, which is a test for the presence and quantity of glucose in urine. If the level is high, it is likely to indicate diabetes. The test is so simple that it may even be done in the home by the patient to monitor how well sugar levels are being controlled. Testing for some other substances in urine requires the patient to collect urine over a 24-hour period. This is the case, for example, when testing for the adrenal hormone cortisol in urine. When urine cortisol levels are higher than normal it may indicate Cushing's syndrome, and when the levels are lower than normal it may indicate Addison's disease.

REVIEW

1. What is diabetic nephropathy and what causes it?
2. Describe polycystic kidney disease (PKD).
3. Define kidney failure.
4. What are potential treatments for kidney failure when kidney function drops below the level needed to sustain life?
5. Describe hemodialysis.
6. What are kidney stones?
7. How may a large kidney stone be removed from the body?
8. How are bladder infections usually treated?
9. Why are bladder infections much more common in females than in males?
10. Define urinary incontinence.
11. Compare and contrast stress incontinence and urge incontinence.
12. Why is the presence of a protein such as albumin in the urine a cause for concern?
13. Patients undergoing hemodialysis usually have to do this procedure a few times a week. Why does it have to be done so frequently?
14. Which of the following is considered a genetic disorder?
    A. Polycystic kidney disease
    B. Diabetic nephropathy
    C. Kidney failure
    D. Urinary incontinence
15. What is the most common cause of a kidney infection?

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SECTION OVERVIEW

12.3: DIGESTIVE SYSTEM

This chapter outlines the structure and function of the gastrointestinal tract and accessory organs of digestion. It explains the processes of peristalsis, mechanical and chemical digestion of food, and absorption of nutrients. The chapter also describes several disorders of the gastrointestinal tract.

12.3.1: INTRODUCTION TO THE DIGESTIVE SYSTEM

12.3.2: DIGESTION AND ABSORPTION

12.3.3: UPPER GASTROINTESTINAL TRACT

12.3.4: LOWER GASTROINTESTINAL TRACT

12.3.5: ACCESSORY ORGANS OF DIGESTION

12.3.6: DISORDERS OF THE GASTROINTESTINAL TRACT

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12.3.1: INTRODUCTION TO THE DIGESTIVE SYSTEM

YUMMY!

If you're a dessert lover, then just the sight of this flan dish may make your mouth water. The "water" in your mouth is actually saliva, a fluid released by glands that are part of the digestive system. Saliva contains digestive enzymes among other substances important for digestion. When your mouth waters at the sight of a tasty treat, it's a sign that your digestive system is preparing to digest food.



Figure **12.3.1.1**: Caramel Cream Flan

WHAT IS THE DIGESTIVE SYSTEM?

The **digestive system** consists of organs that break down food, absorb its nutrients, and expel any remaining waste. Organs of the digestive system are shown in Figure **12.3.1.2**. Most of these organs make up the gastrointestinal (GI) tract. Food actually passes through these organs. The rest of the organs of the digestive system are called accessory organs. These organs secrete enzymes and other substances into the GI tract, but food does not actually pass through them.

FUNCTIONS OF THE DIGESTIVE SYSTEM

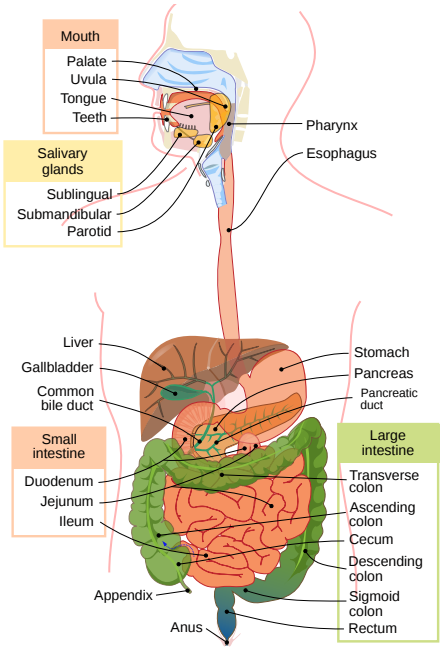


Figure **12.3.1.2**: The components of the digestive system include the gastrointestinal tract and accessory organs of digestion. The image has labeled parts of the mouth, salivary glands, liver, gallbladder and associated ducts, stomach, pancreas, and small and large intestine parts. Find the organs of the digestive system in this diagram as you read about them in the text.

The digestive system has three main functions relating to food: digestion of food, absorption of nutrients from food, and elimination of solid food waste. Digestion is the process of breaking down food into components the body can absorb. It consists of two types of processes: mechanical digestion and chemical digestion. Mechanical digestion is the physical breakdown of chunks of food into smaller pieces. This type of digestion takes place mainly in the mouth and stomach. Chemical digestion is the chemical breakdown (bonds are broken) of large, complex food molecules into smaller, simpler nutrient molecules that can be absorbed by body fluids (blood or lymph). This type of digestion begins in the mouth and continues in the stomach but occurs mainly in the small intestine.

After food is digested, the resulting nutrients are absorbed. Absorption is the process in which substances pass into the bloodstream or lymph system to circulate throughout the body. The absorption of nutrients occurs mainly in the small intestine. Any remaining matter from food that is not digested and absorbed passes out of the body through the anus in the process of elimination.

GASTROINTESTINAL TRACT

The **gastrointestinal (GI) tract** is basically a long, continuous tube that connects the mouth with the anus. If it were fully extended, it would be about 9 meters (30 feet) long in adults. It includes the mouth, pharynx, esophagus, stomach, and small and large intestines. Food enters the mouth and then passes through the other organs of the GI tract where it is digested and/or absorbed. Finally, any remaining food waste leaves the body through the anus at the end of the large intestine. It takes up to 50 hours for food or food waste to make the complete trip through the GI tract.

TISSUES OF THE GI TRACT

The walls of the organs of the GI tract consist of four different tissue layers, which are illustrated in Figure **12.3.1.3**: mucosa, submucosa, muscularis externa, and serosa.

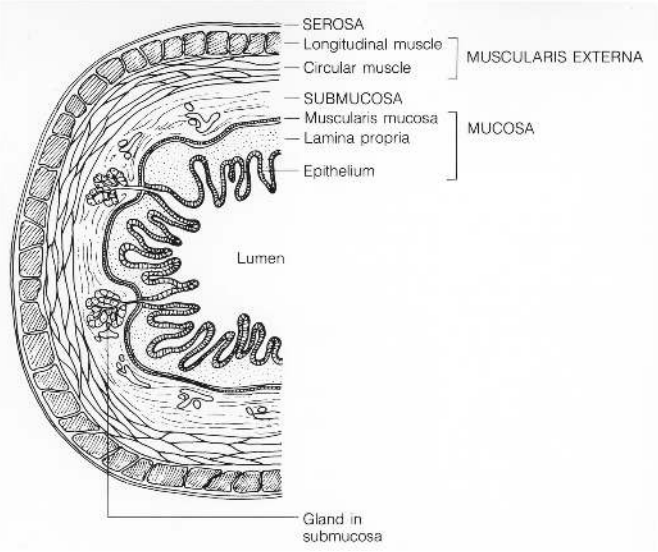


Figure **12.3.1.3**: This cross-sectional diagram of the wall of a typical GI tract organ shows the layers that comprise it.

1. The mucosa is the innermost layer surrounding the lumen, or open space within the organs of the GI tract. This layer consists mainly of the epithelium with the capacity to secrete and absorb substances. For example, the epithelium can secrete digestive enzymes and mucus, and it can absorb nutrients and water.
2. The submucosa layer consists of connective tissue that contains blood and lymph vessels and also nerves. The vessels are needed to absorb and carry away nutrients after food is digested, and nerves help control the muscles of the GI tract organs.
3. The muscularis externa layer contains two types of smooth muscle: longitudinal muscle and circular muscle. The longitudinal muscle runs the length of the GI tract organs and circular muscle encircles the organs. Both types of muscles contract to keep food moving through the track by the process of peristalsis (Figure **12.3.1.4**.
4. The serosa layer is the outermost layer of the walls of GI tract organs. This is a thin layer that consists of connective tissue and separates the organs from surrounding cavities and tissues.

PERISTALSIS IN THE GI TRACT

The muscles in the walls of GI tract organs enable peristalsis, which is illustrated in Figure **12.3.1.4**. Peristalsis is a continuous sequence of involuntary muscle contraction and relaxation that moves rapidly along an organ like a wave, similar to the way a wave moves through a spring toy. Peristalsis in organs of the GI tract propels food through the tract.

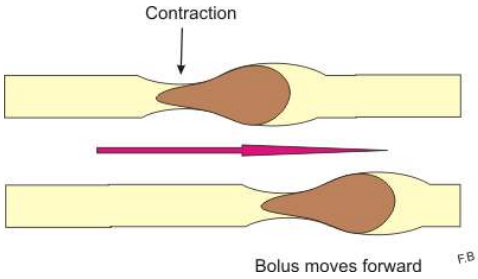


Figure **12.3.1.4**: Peristalsis pushes food through the GI tract.

DIVISIONS OF THE GI TRACT

The GI tract is often divided into an upper GI tract and a lower GI tract. For medical purposes, the upper GI tract is typically considered to include all the organs from the mouth through the first part of the small intestine, called the duodenum. For instructional purposes, it makes more sense to include the mouth through the stomach in the upper GI tract and all of the small intestine as well as the large intestine in the lower GI tract. The latter approach is followed here. All organs of GI which are discussed in the text are illustrated in Figure **12.3.1.2**.

UPPER GI TRACT

The mouth is the first digestive organ that food enters. The sight, smell, or taste of food stimulates the release of digestive enzymes and other secretions by salivary glands inside the mouth. The major salivary gland enzyme is amylase. It begins the chemical digestion of carbohydrates by breaking down starches into sugar. The mouth also begins the mechanical digestion of food. When you chew, your teeth break, crush, and grind food into increasingly smaller pieces. Your tongue helps to mix the food with saliva and also helps you swallow.

A lump of swallowed food is called a **bolus.** The bolus passes from the mouth into the pharynx and from the pharynx into the esophagus. The esophagus is a long, narrow tube that carries food from the pharynx to the stomach. It has no other digestive functions. Peristalsis starts at the top of the esophagus when food is swallowed and continues down the esophagus in a single wave, pushing the bolus of food ahead of it.

From the esophagus, food passes into the stomach, where both mechanical and chemical digestion continue. The muscular walls of the stomach churn and mix the food, thus completing mechanical digestion as well as mixing the food with digestive fluids secreted by the stomach. One of these fluids is hydrochloric acid. As well as killing pathogens in food, it gives the stomach the low pH needed by digestive enzymes that work in the stomach. One of these enzymes is pepsin, which chemically digests proteins. The stomach stores the partially digested food until the small intestine is ready to receive it. Food that enters the small intestine from the stomach is in the form of a thick slurry (semi-liquid) called **chyme.**

LOWER GI TRACT

The small intestine is a narrow but very long tubular organ. It may be almost 7 meters (23 feet) long in adults. It is the site of most chemical digestion and virtually all absorption of nutrients. Many digestive enzymes are active in the small intestine, some of which are produced by the small intestine itself, and some of which are produced by the pancreas, an accessory organ of the digestive system. Much of the inner lining of the small intestine is covered by tiny finger-like projections called **villi,** each of which in turn is covered by even tinier projections called **microvilli.** These projections, shown in Figure **12.3.1.5**, greatly increase the surface area through which nutrients can be absorbed from the small intestine.

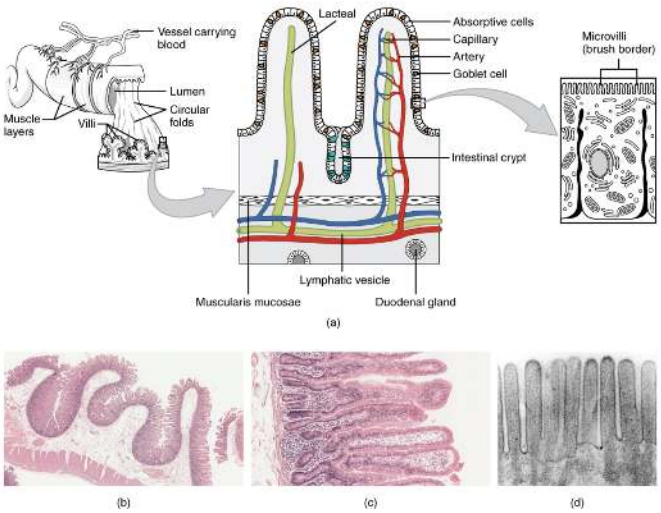


Figure **12.3.1.5**: The figure above shows three hierarchical small intestine wall modifications that increase the absorptive surface area. The broadest and most gross modification is the projection of mucosa and submucosa called circular folds (b); then, there are projections of mucosa called villi (c); and, finally, the projections of the plasma membrane of absorptive cells called microvilli (d). Microvilli are also referred to as brush border where enzymes reside.

The small intestine is made up of three parts:

1. The duodenum is the first part of the small intestine. It is also the shortest part. This is where most chemical digestion takes place.
2. The jejunum is the second part of the small intestine. This is where most nutrients are absorbed into the blood.
3. The ileum is the last part of the small intestine. A few remaining nutrients are absorbed in the ileum. From the ileum, any remaining food waste passes into the large intestine.

From the small intestine, any remaining nutrients and food waste pass into the large intestine. The large intestine is another tubular organ like the small intestine, but it is wider and shorter than the small intestine. It connects the small intestine and the anus. Waste that enters the large intestine is in a liquid state. As it passes through the large intestine, excess water is absorbed from it. The remaining solid waste, called feces, is eventually eliminated from the body through the anus.

ACCESSORY ORGANS OF THE DIGESTIVE SYSTEM

Accessory organs of the digestive system are not part of the GI tract, so they are not sites where digestion or absorption take place. Instead, these organs secrete or store substances that are needed for the chemical digestion of food. The accessory organs include the liver, gallbladder, and pancreas. They are shown in Figure **12.3.1.6** and described in the text:

- The liver is an organ that has a multitude of functions. Its main digestive function is producing and secreting a fluid called bile, which reaches the small intestine through a duct. Bile breaks down large globules of lipids into smaller ones that are easier for enzymes to chemically digest. Bile is also needed to reduce the acidity of food entering the small intestine from the highly acidic stomach because enzymes in the small intestine require a less acidic environment in order to work.
- The gallbladder is a small sac below the liver that stores some of the bile from the liver. The gallbladder also concentrates the bile by removing some of the water from it. It then secretes the concentrated bile into the small intestine as needed for fat digestion following a meal.
- The pancreas secretes many digestive enzymes and releases them into the small intestine for the chemical digestion of carbohydrates, proteins, and lipids. The pancreas also helps to lessen the acidity of the small intestine by secreting bicarbonate, a basic substance that neutralizes the acid.

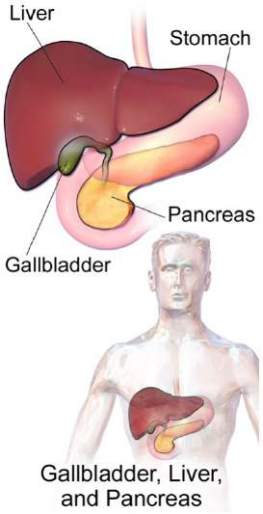


Figure **12.3.1.6**: This diagram shows the locations of the accessory organs of digestion: the liver, gallbladder, and pancreas.

REVIEW

1. What is the digestive system?
2. What are the three main functions of the digestive system? Define each function.
3. Describe the GI tract.
4. Distinguish between the upper and lower GI tracts.
5. Relate the tissues in the walls of GI tract organs to the functions the organs perform.
6. Identify accessory organs of digestion and their general function in digestion.
7. Identify the points in the GI tract where food becomes a bolus, chyme, and feces, respectively.
8. Does food pass through the pancreas? Why or why not?
9. *True or False.* Absorption mainly occurs in the stomach.
10. *True or False.* Some chemical digestion occurs in the mouth.
11. Most chemical digestion occurs in the _____ .

    A. Gall bladder

    B. Stomach

    C. Small intestine

    D. Large intestine

12. a. Describe one way in which proteins are at least partially chemically digested in the digestive system.

    b. Describe one way in which carbohydrates are at least partially chemically digested in the digestive system.

13. If the villi in your small intestine were damaged and could not function normally, what effect might this have on your body? Explain your reasoning.
14. The esophagus is considered:

    A. An accessory organ of the digestive system

    B. Part of the upper GI tract

    C. Part of the lower GI tract

    D. The longitudinal muscle

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12.3.2: DIGESTION AND ABSORPTION

INDIGESTION

The process of digestion does not always go as it should. Many people suffer from indigestion, or dyspepsia, a condition of impaired digestion. Symptoms may include upper abdominal fullness or pain, heartburn, nausea, belching, or some combination of these symptoms. The majority of cases of indigestion occur without evidence of an organic disease that is likely to explain the symptoms. Anxiety or certain foods or medications (such as aspirin) may be contributing factors in these cases. In other cases, indigestion is a symptom of an organic disease, most often gastroesophageal reflux disease (GERD) or gastritis. In a small minority of cases, indigestion is a symptom of a peptic ulcer of the stomach or duodenum, usually caused by a bacterial infection. Very rarely, indigestion is a sign of cancer.

An occasional bout of indigestion is usually nothing to worry about, especially in people less than 55 years of age. However, if you suffer frequent or chronic indigestion, it's a good idea to see a doctor. If an underlying disorder such as GERD or an ulcer is causing indigestion, this can and should be treated. If no organic disease is discovered, the doctor can recommend lifestyle changes or treatments to help prevent or soothe the symptoms of acute indigestion. Lifestyle changes might include modifications in eating habits, such as eating more slowly, eating smaller meals, or avoiding fatty foods. You also might be advised to refrain from taking certain medications, especially on an empty stomach. The use of antacids or other medications to relieve symptoms may also be recommended



Figure **12.3.2.1**: Add for heartburn medicine from 1882.

DIGESTION

Digestion of food is a form of catabolism, in which the food is broken down into small molecules that the body can absorb and use for energy, growth, and repair. Digestion occurs when food is moved through the digestive system. It begins in the mouth and ends in the small intestine. The final products of digestion are absorbed from the digestive tract, primarily in the small intestine. There are two different types of digestion that occur in the digestive system: mechanical digestion and chemical digestion. Figure **12.3.2.2** summarizes the roles played by different digestive organs in mechanical and chemical digestion, both of which are described in detail in the text.

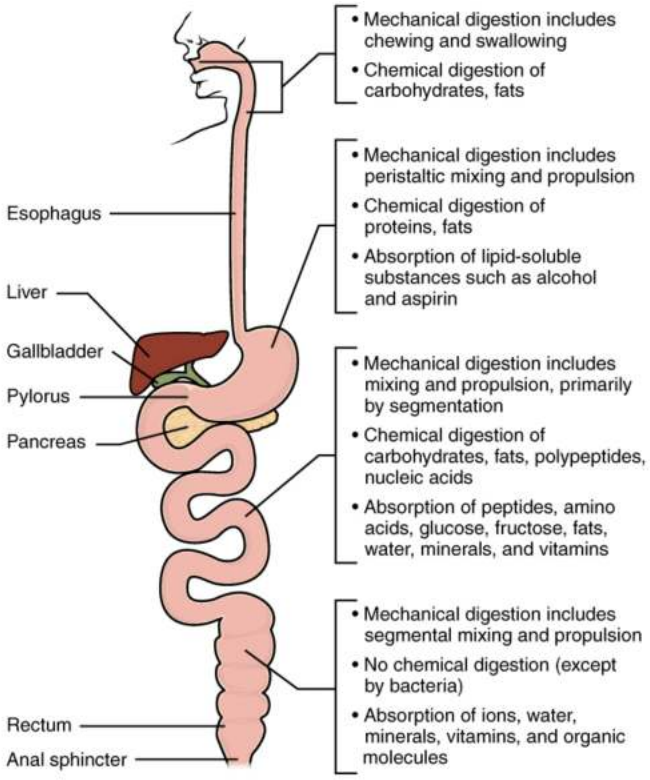


Figure **12.3.2.2**: Both, mechanical and chemical digestion take place throughout the gastrointestinal tract as indicated in this diagram, but absorption takes place only in the stomach and small and large intestines.

MECHANICAL DIGESTION

Mechanical digestion is a physical process in which food is broken into smaller pieces without becoming changed chemically. It begins with your first bite of food and continues as you chew food with your teeth into smaller pieces. The process of mechanical digestion continues in the stomach. This muscular organ churns and mixes the food it contains, an action that breaks any solid food into still smaller pieces.

Although some mechanical digestion also occurs in the intestines, it is mostly completed by the time food leaves the stomach. At that stage, food in the GI tract has been changed to the thick semi-fluid called chyme. Mechanical digestion is necessary so that chemical digestion can be effective. Mechanical digestion tremendously increases the surface area of food particles so they can be acted upon more effectively by digestive enzymes.

CHEMICAL DIGESTION

Chemical digestion is the biochemical process in which macromolecules in food are changed into smaller molecules that can be absorbed into body fluids and transported to cells throughout the body. Substances in food that must be chemically digested include carbohydrates, proteins, lipids, and nucleic acids. Carbohydrates

must be broken down into simple sugars, proteins into amino acids, lipids into fatty acids and glycerol, and nucleic acids into nitrogen bases and sugars. Some chemical digestion takes place in the mouth and stomach, but most of it occurs in the first part of the small intestine (duodenum).

DIGESTIVE ENZYMES

Chemical digestion could not occur without the help of many different digestive enzymes. Enzymes are proteins that catalyze or speed up biochemical reactions. Digestive enzymes are secreted by exocrine glands or by the mucosal layer of the epithelium lining the gastrointestinal tract. In the mouth, digestive enzymes are secreted by salivary glands. The lining of the stomach secretes enzymes, as does the lining of the small intestine. Many more digestive enzymes are secreted by exocrine cells in the pancreas and carried by ducts to the small intestine. Table **12.3.2.1** lists several important digestive enzymes, the organs and/or glands that secrete them, and the compounds they digest. You can read more about them in the text.

Table **12.3.2.1**: Digestive Enzymes

Digestive Enzyme	Organ, Glands That Secretes It	Compound It Digests
Amylase	Salivary Glands, Pancreas	Amylose (Polysaccharide)
Sucrase	Small Intestine	Sucrose (Disaccharide)
Lactase	Small Intestine	Lactose (Disaccharide)
Lipase	Salivary Glands, Pancreas	Lipid
Pepsin	Stomach	Protein
Trypsin	Pancreas	Protein
Chymotrypsin	Pancreas	Protein
Deoxyribonuclease	Pancreas	DNA
Ribonuclease	Pancreas	RNA
Nuclease	Small Intestine	Small Nucleic Acids

CHEMICAL DIGESTION OF CARBOHYDRATES

About 80 percent of digestible carbohydrates in a typical Western diet are in the form of the plant polysaccharide amylose, which consists mainly of long chains of glucose and is one of two major components of starch. Additional dietary carbohydrates include the animal polysaccharide glycogen, along with some sugars, which are mainly disaccharides.

To chemically digest amylose and glycogen, the enzyme amylase is required. The chemical digestion of these polysaccharides begins in the mouth, aided by amylase in saliva. Saliva also contains mucus, which lubricates the food, and hydrogen carbonate, which provides the ideal alkaline conditions for amylase to work. Carbohydrate digestion is completed in the small intestine, with the help of amylase secreted by the pancreas. In the digestive process, polysaccharides are reduced in length by the breaking of bonds between glucose monomers. The macromolecules are broken down to shorter polysaccharides and disaccharides, resulting in progressively shorter chains of glucose. The end result is molecules of the simple sugars glucose and maltose (which consists of two glucose molecules), both of which can be absorbed by the small intestine.

Other sugars are digested with the help of different enzymes produced by the small intestine. For example, sucrose, or table sugar, is a disaccharide that is broken down by the enzyme sucrase to form glucose and fructose, which are readily absorbed by the small intestine. Digestion of the sugar lactose, which is found in milk, requires the enzyme lactase, which breaks down lactose into glucose and galactose, which are then absorbed by the small intestine. Fewer than half of all adults produce sufficient lactase to be able to digest lactose. Those who cannot are said to be lactose intolerant.

CHEMICAL DIGESTION OF PROTEINS

Proteins consist of polypeptides, which must be broken down into their constituent amino acids before they can be absorbed. Protein digestion occurs in the stomach and small intestine through the action of three primary enzymes: pepsin, secreted by the stomach; and trypsin and chymotrypsin secreted by the pancreas. The stomach also secretes hydrochloric acid, making the contents highly acidic, which is required for pepsin to work. Trypsin and chymotrypsin in the small intestine require an alkaline environment to work. Bile from the liver and bicarbonate from the pancreas neutralize the acidic chyme as it empties into the small intestine. After pepsin, trypsin, and chymotrypsin break down proteins into peptides, these are further broken down into amino acids by other enzymes called peptidases, also secreted by the pancreas.

CHEMICAL DIGESTION OF LIPIDS

The chemical digestion of lipids begins in the mouth. The salivary glands secrete the digestive enzyme lipase, which breaks down short-chain lipids into molecules consisting of two fatty acids. A tiny amount of lipid digestion may take place in the stomach, but most lipid digestion occurs in the small intestine.

Digestion of lipids in the small intestine occurs with the help of another lipase enzyme from the pancreas as well as bile secreted by the liver. Bile is required for the digestion of lipids because lipids are oily and do not dissolve in the watery chyme. Bile emulsifies, or breaks up, large globules of food lipids into much smaller ones, called micelles, much as dish detergent breaks up grease. The micelles provide a great deal more surface area to be acted upon by lipase and also point the hydrophilic (“water-loving”) heads of the fatty acids outward into the watery chyme. Lipase can then access and break down the micelles into individual fatty acid molecules.

CHEMICAL DIGESTION OF NUCLEIC ACIDS

Nucleic acids (DNA and RNA) in foods are digested in the small intestine with the help of both pancreatic enzymes and enzymes produced by the small intestine itself. Pancreatic enzymes called ribonuclease and deoxyribonuclease break down RNA and DNA, respectively, into smaller nucleic acids. These, in turn, are further broken down into nitrogen bases and sugars by small intestine enzymes called nucleases.

CHEMICAL DIGESTION BY GUT FLORA

The human gastrointestinal tract is normally inhabited by trillions of bacteria, some of which contribute to digestion. Here are just two of

dozens of examples:

1. The most common carbohydrate in plants, which is cellulose, cannot be digested by the human digestive system. However, tiny amounts of cellulose are digested by bacteria in the large intestine.
2. Certain bacteria in the small intestine help digest lactose, which many adults cannot otherwise digest. As a byproduct of this process, the bacteria produce lactic acid, which increases the release of digestive enzymes and the absorption of minerals such as calcium and iron.

ABSORPTION

When digestion is finished, it results in many simple nutrient molecules that must go through the process of **absorption** from the GI tract by blood or lymph so they can be used by cells throughout the body. A few substances are absorbed in the stomach and large intestine. For example, water is absorbed in both of these organs, and some minerals and vitamins are also absorbed in the large intestine. However, about 95 percent of nutrient molecules are absorbed in the small intestine. The absorption of the majority of these molecules takes place in the second part of the small intestine, called the jejunum. However, there are a few exceptions. For example, iron is absorbed in the duodenum, and vitamin B12 is absorbed in the last part of the small intestine, called the ileum. After being absorbed in the small intestine, nutrient molecules are transported to other parts of the body for storage or further chemical modification. For example, amino acids are transported to the liver to be used for protein synthesis.

The epithelial tissue lining the small intestine is specialized for absorption. It has many wrinkles and is covered with villi and microvilli, creating an enormous surface area for absorption. As shown in Figure **12.3.2.3**, each villus also has a network of blood capillaries and fine lymphatic vessels called lacteals close to its surface. The thin surface layer of epithelial cells of the villi transports nutrients from the lumen of the small intestine into these capillaries and lacteals. Blood in the capillaries absorbs most of the molecules, including simple sugars, amino acids, glycerol, salts, and water-soluble vitamins (vitamin C and the many B vitamins). Lymph in the lacteals absorbs fatty acids and fat-soluble vitamins (vitamins A, D, E, and K).

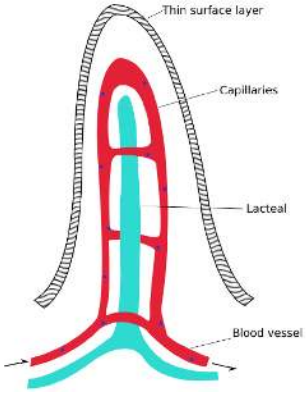


Figure **12.3.2.3**: This highly simplified drawing of an intestinal villus (plural villi) shows the capillaries and lacteals within it that carry away absorbed substances. Note that each cell in the thin surface layer of the villus is actually covered with microvilli that greatly increase the surface area for absorption.

FEATURE: MY HUMAN BODY

The process of digestion does not always go as it should. Many people suffer from indigestion, or dyspepsia, a condition of impaired digestion. Symptoms may include upper abdominal fullness or pain, heartburn, nausea, belching, or some combination of these symptoms. The majority of cases of indigestion occur without evidence of an organic disease that is likely to explain the symptoms. Anxiety or certain foods or medications (such as aspirin) may be contributing factors in these cases. In other cases, indigestion is a symptom of an organic disease, most often gastroesophageal reflux disease (GERD) or gastritis. In a small minority of cases, indigestion is a symptom of a peptic ulcer of the stomach or duodenum, usually caused by a bacterial infection. Very rarely, indigestion is a sign of cancer.

An occasional bout of indigestion is usually nothing to worry about, especially in people less than 55 years of age. However, if you suffer frequent or chronic indigestion, it's a good idea to see a doctor. If an underlying disorder such as GERD or an ulcer is causing indigestion, this can and should be treated. If no organic disease is discovered, the doctor can recommend lifestyle changes or treatments to help prevent or soothe the symptoms of acute indigestion. Lifestyle changes might include modifications in eating habits, such as eating more slowly, eating smaller meals, or avoiding fatty foods. You also might be advised to refrain from taking certain medications, especially on an empty stomach. The use of antacids or other medications to relieve symptoms may also be recommended.

REVIEW

1. Define digestion. Where does it occur?
2. Identify two organ systems that control the process of digestion by the digestive system.
3. What is mechanical digestion? Where does it occur?
4. Describe chemical digestion.

5. What is the role of enzymes in chemical digestion?
6. What is absorption? When does it occur?
7. a. Where does most absorption occur in the digestive system?

   b. Why does most of the absorption occur in this organ and not earlier in the GI tract?
8. Name two digestive enzymes found in saliva and identify which type of molecule they digest.
9. a. Where is bile produced?

   b. What are some functions of bile?
10. *True or False.* Pepsin digests cellulose.
11. *True or False.* Glucose can be absorbed by the body without being further broken down.
12. The pH of the stomach _____ .

    A. is neutral B. is alkaline

    C. is acidic D. depends only on what you eat
13. Lymph absorbs _____ .

    A. fatty acids B. sugars

    C. amino acids D. vitamin C

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12.3.3: UPPER GASTROINTESTINAL TRACT

HEAD STAND

Did you ever wonder what would happen if you tried to swallow food while standing on your head? Many people think that food travels down the gullet from the mouth by the force of gravity. If that were the case, then the food you swallowed would stay in your throat while you were standing on your head. In reality, your position doesn't have much to do with your ability to swallow. Food will travel from your mouth to your stomach whether you are standing upright or upside down. That's because the tube the food travels through — the esophagus — moves the food along by the muscular contractions is known as peristalsis. The esophagus is one of several organs that make up the upper gastrointestinal tract.



Figure **12.3.3.1**: Headstand

ORGANS OF THE UPPER GASTROINTESTINAL TRACT

Besides the esophagus, organs of the **upper gastrointestinal (GI) tract** include the mouth, pharynx, and stomach. These hollow organs are all connected to form a tube through which food passes during digestion. The only role in digestion played by the pharynx and esophagus is to move food through the GI tract. The mouth and stomach, in contrast, are organs where digestion, or the breakdown of food, also occurs. In both of these organs, food is broken into smaller pieces (mechanical digestion) as well as broken down chemically (chemical digestion). It should be noted that the first part of the small intestine (duodenum) is considered in some contexts to be part of the upper GI tract, but that practice is not followed here. You can read about the small intestine (and large intestine) in the concept Lower Gastrointestinal Tract.

MOUTH

The mouth is the first organ of the GI tract. Most of the oral cavity is lined with a mucous membrane. This tissue produces mucus, which helps to moisten, soften, and lubricate food. Underlying the mucous membrane is a thin layer of smooth muscle to which the mucous membrane is only loosely connected. This gives the mucous membrane considerable ability to stretch as you eat food. The roof of the mouth, called the palate, separates the oral cavity from the nasal cavity. The front part is the hard palate, consisting of a mucous membrane covering a plate of bone. The back part of the palate is softer and more pliable, consisting of mucous membrane over muscle and connective tissue. The hard surface of the front of the palate allows for the pressure needed in chewing and mixing food. The soft, pliable surface of the back of the palate can move to accommodate the passage of food while swallowing. Muscles at either side of the soft palate contract to create the swallowing action.

Several specific structures in the mouth are specialized for digestion. These include salivary glands, tongue, and teeth.

SALIVARY GLANDS

The mouth contains three pairs of major **salivary glands**, which are shown in Figure **12.3.3.2**. These three pairs are all exocrine glands that secrete **saliva** into the mouth through ducts.

1. The largest of the three major pairs of salivary glands are the parotid glands, which are located on either side of the mouth in front of the ears.
2. The next largest pair is the submandibular glands, located beneath the lower jaw.
3. The third pair is the sublingual glands, located underneath the tongue.

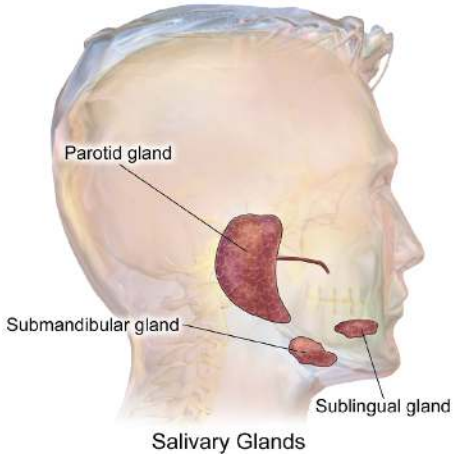


Figure **12.3.3.2**: Salivary glands in the mouth include the three major pairs of glands shown here. The sublingual gland is under the tongue. The submandibular gland is below the jaw. The parotid gland is the back of the mouth.

In addition to these three pairs of major salivary glands, there are also hundreds of minor salivary glands in the oral mucosa lining the mouth and on the tongue. Along with the major glands, most of the minor glands secrete the digestive enzyme amylase, which begins the chemical digestion of starch and glycogen (polysaccharides). However, the minor salivary glands on the tongue secrete the fat-digesting enzyme lipase, which in the mouth is called lingual lipase (to distinguish it from pancreatic lipase secreted by the pancreas).

The saliva secreted by the salivary glands mainly helps digestion, but it also plays other roles. It helps to maintain dental health by cleaning the teeth, and it contains antibodies that help protect against infection. By keeping the mouth lubricated, saliva also allows the mouth movements needed for speech.

TONGUE

The tongue is a fleshy, muscular organ that is attached to the floor of the mouth by a band of ligaments that gives it great mobility. This is necessary so the tongue can manipulate food for chewing and swallowing. Movements of the tongue are also necessary for speaking. The upper surface of the tongue is covered with tiny projections called papillae, which contain taste buds. The latter are collections of chemoreceptor cells. These sensory cells sense chemicals in food and send the information to the brain via cranial nerves, thus enabling the sense of taste.

TEETH

The teeth are complex structures made of a bone-like material called dentin and covered with enamel, which is the hardest tissue in the body. Adults normally have a total of 32 teeth, with 16 in each jaw. The right and left sides of each jaw are mirror images in terms of the numbers and types of teeth they contain. Teeth have different shapes to suit them for different aspects of mastication (chewing).

PHARYNX

The tube-like pharynx (Figure **12.3.3.3**) plays a dual role as an organ of both respiration and digestion. As part of the respiratory system, it conducts air between the nasal cavity and larynx. As part of the digestive system, it allows swallowed food to pass from the oral cavity to the esophagus. Anything swallowed has priority over inhaled air when passing through the pharynx. During swallowing, the backward motion of the tongue causes a flap of elastic cartilage, called the epiglottis, to close over the opening to the larynx. This prevents food or drinks from entering the larynx.

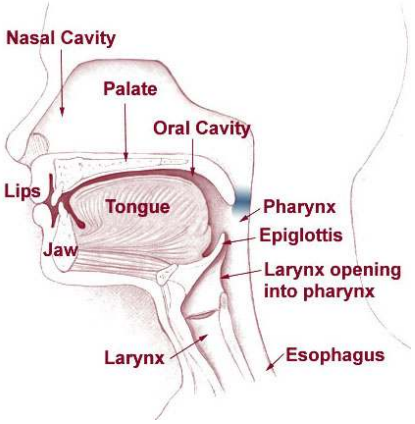


Figure **12.3.3.3**: The tongue moves backward during swallowing to cause the epiglottis to cover the opening to the larynx so food passes from the pharynx to the esophagus and not into the larynx.

ESOPHAGUS

The **esophagus,** which is shown in Figure **12.3.3.4**, is a muscular tube through which food is pushed from the pharynx to the stomach. The esophagus passes through an opening in the diaphragm (the large breathing muscle that separates the abdomen from the thorax) before reaching the stomach. In adults, the esophagus averages about 25 cm (10 in.) in length, depending on a person's height. The inner lining of the esophagus consists of a mucous membrane, which provides a smooth, slippery surface for the passage of food. The cells of this membrane are constantly being replaced as they are worn away from the frequent passage of food over them.

When food is not being swallowed, the esophagus is closed at both ends by upper and lower esophageal sphincters. **Sphincters** are rings of muscle that can contract to close off openings between structures. The upper esophageal sphincter is triggered to relax and open by the act of swallowing, allowing a bolus of food to enter the esophagus from the pharynx. Then the esophageal sphincter closes again to prevent food from moving back into the pharynx.

Once in the esophagus, the food bolus travels down to the stomach, pushed along by the rhythmic contraction and relaxation of muscles (peristalsis). The lower esophageal sphincter is located at the junction between the esophagus and the stomach. This sphincter opens when the bolus reaches it, allowing the food to enter the stomach. The sphincter normally remains closed at other times to prevent the contents of the stomach from entering the esophagus. Failure of this sphincter to remain completely closed can lead to heartburn. If it happens chronically, it can lead to gastroesophageal reflux disease (GERD), in which the mucous membrane of the esophagus may become damaged by the highly acidic contents of the stomach.

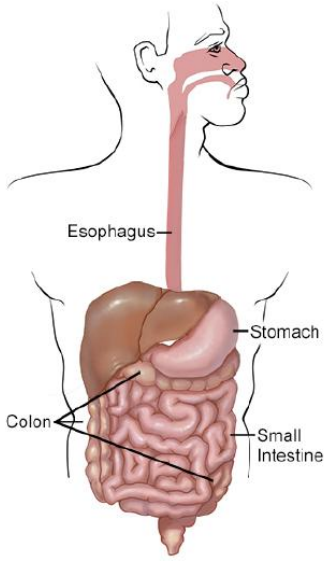


Figure **12.3.3.4**: The esophagus is located behind the trachea and it connects the pharynx to the stomach. The stomach is connected at the bottom to the small intestine.

STOMACH

The **stomach** (Figure **12.3.3.4** is a J-shaped organ that is joined to the esophagus at its upper end and to the first part of the small intestine (duodenum) at its lower end. When the stomach is empty of food, it normally has a volume of about 75 mL. However, it can expand to hold up to about a liter of food. Waves of muscle contractions (peristalsis) passing through the muscular walls of the stomach cause the food inside to be mixed and churned. The wall of the stomach has an extra layer of muscle tissue not found in other organs of the

GI tract that helps it squeeze and mix the food. These movements of the stomach wall contribute greatly to mechanical digestion by breaking the food into much smaller pieces. The churning also helps to mix the food with stomach secretions that aid in its chemical digestion.

Secretions of the stomach include gastric acid, which consists mainly of hydrochloric acid. This makes the stomach contents highly acidic, which is necessary so that the enzyme pepsin — also secreted by the stomach — can begin the digestion of protein. Mucus is secreted by the lining of the stomach to provide a slimy protective coating against the otherwise damaging effects of gastric acid. The fat-digesting enzyme lipase is secreted in small amounts in the stomach, but very little fat digestion occurs there.

By the time food has been in the stomach for about an hour, it has become the thick, semi-liquid chyme. When the small intestine is ready to receive chyme, a sphincter between the stomach and duodenum, called the pyloric sphincter, opens to allow the chyme to enter the small intestine for further digestion and absorption.

FEATURE: RELIABLE SOURCES

The ongoing epidemic of obesity has led to the development of several different bariatric surgeries that modify the stomach to help obese patients reduce their food intake and lose weight. Go online to learn more about bariatric surgery. Find sources you judge to be reliable that answer the following questions:

1. Who qualifies for bariatric surgery?
2. Describe the bariatric surgeries commonly called stomach stapling, lap band, and gastric sleeve. How does each type of surgery modify the stomach? How effective is each type in terms of weight loss?
3. What are the major potential risks of bariatric surgery?
4. Besides weight loss, what other benefits have been shown to result from bariatric surgery?

REVIEW

1. List organs of the upper gastrointestinal tract.
2. Identify structures in the mouth that are specialized for digestion.
3. Describe digestion in the mouth.
4. What general role do the pharynx and esophagus play in the digestion of food?
5. How does food travel through the esophagus?
6. Describe digestion in the stomach.
7. In which of the following structures does chemical digestion occur?

   A. Mouth

   B. Esophagus

   C. Stomach

   D. A and C

   E. A, B, and C
8. In which of the following structures does mechanical digestion occur?

   A. Mouth

   B. Pharynx

   C. Stomach

   D. A and C

   E. A, B, and C
9. Describe the differences between how air and food normally move past the pharynx.
10. Name two structures in the mouth that contribute to mechanical digestion.
11. What structure normally keeps stomach contents from backing up into the esophagus?
12. *True or False.* Peristalsis occurs in the esophagus, but not in the stomach.
13. *True or False.* The sense of taste is due to the detection of chemicals by the tongue.
14. Where is most of your food located thirty minutes after you eat a meal? Explain your answer.
15. What are the two roles of mucus in the upper GI tract?

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12.3.4: LOWER GASTROINTESTINAL TRACT

WHAT IS IT?

Figure **12.3.4.1** shows some of the cells of what has been called "the last human organ to be discovered." This "organ" weighs about 200 grams (0.44 lb.) and consists of a hundred trillion cells, yet scientists are only now beginning to learn everything it does and how it varies among individuals. What is it? It's the mass of bacteria that live in our lower gastrointestinal tract.



Figure **12.3.4.1**: Micrograph of *Bacteroides biacutis* - cultured in blood agar medium for 48 hours.

ORGANS OF THE LOWER GASTROINTESTINAL TRACT

Most of the bacteria that normally live in the **lower gastrointestinal (GI) tract** live in the large intestine. They have important and mutually beneficial relationships with the human organism. We provide them with a great place to live, and they provide us with many benefits, some of which you can read about below. Besides the large intestine and its complement of helpful bacteria, the lower GI tract also includes the small intestine. The latter is arguably the most important organ of the digestive system. It is where most chemical digestion and virtually all absorption of nutrients take place.

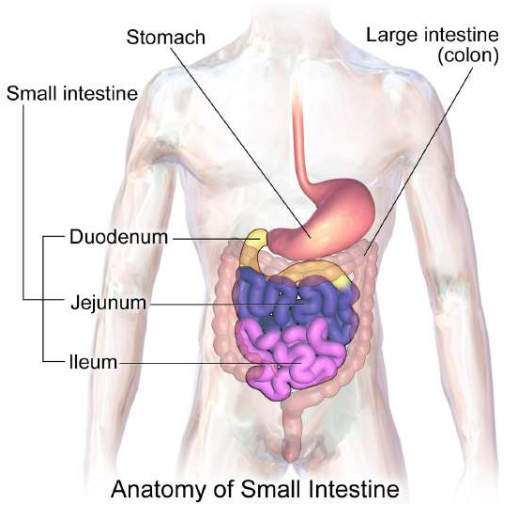


Figure **12.3.4.2**: The three parts of the small intestine are color-coded in this diagram, with yellow for the duodenum (the first part of the small intestines), blue for the jejunum (the middle), and pink for the ileum (the end of the small intestines).

SMALL INTESTINE

The **small intestine** (also called the small bowel or gut) is the part of the GI tract between the stomach and large intestine. Its average length in adults is 4.6 m (15 ft) in females and 6.9 m (22 ft 8 in.) in males. It is approximately 2.5 to 3.0 cm (1.0 to 1.2 in.) in diameter (it is called "small" because it is much smaller in diameter than the large intestine). The internal surface area of the small intestine totals an average of about 30 m^2 (323 ft^2). Structurally and functionally, the small intestine can be divided into three parts, called the duodenum, jejunum, and ileum, as shown in Figure **12.3.4.2** and described below.

The mucosa lining the small intestine is very wrinkled and covered with finger-like projections called villi. In fact, each square inch of mucosa contains around 20,000 villi. The individual cells on the surface of the villi also have many finger-like projections, the microvilli shown in Figure **12.3.4.3**. There are thought to be well over 100 billion microvilli per square inch of intestinal mucosa! All of these wrinkles, villi, and microvilli greatly increase the surface area for chyme to come into contact with digestive enzymes, which coat the microvilli, as well as forming a tremendous surface area for the absorption of nutrients. Inside each of the villi is a network of tiny blood and lymph vessels that receive the absorbed nutrients and carry them away in the blood or lymph circulation. The wrinkles and projections in the intestinal mucosa also slow down the passage of chyme so there is more time for digestion and absorption to take place.

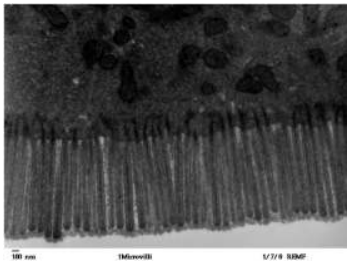


Figure **12.3.4.3**: The fringe-like structures in this photomicrograph are microvilli lining the inside of the small intestine.

DUODENUM

The **duodenum** is the first part of the small intestine, directly connected to the stomach. It is also the shortest part of the small intestine, averaging only about 25 cm (10 in.) in length in adults. Its main function is chemical digestion, and it is where most of the chemical digestion in the entire GI tract takes place.

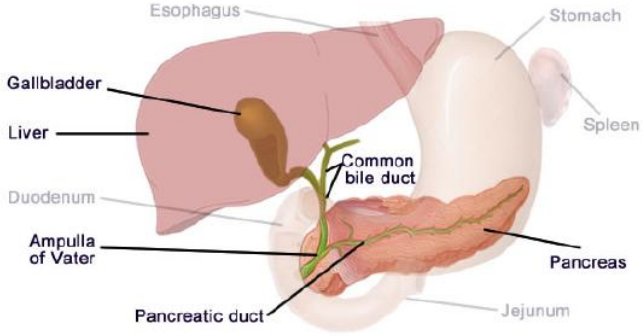


Figure **12.3.4.1**: This figure shows the liver, gallbladder, and pancreas, along with the ducts that carry their secretions to the duodenum

The duodenum receives partially digested, semi-liquid chyme from the stomach. It receives digestive enzymes and alkaline bicarbonate from the pancreas through the pancreatic duct, and it receives bile from the liver via the gallbladder through the common bile duct (Figure **12.3.4.4**). In addition, the lining of the duodenum secretes digestive enzymes and contains glands — called Brunner's glands — that secrete mucus and bicarbonate. The bicarbonate from the pancreas and Brunner's glands as well as bile from the liver neutralize the highly acidic chyme after it enters the duodenum from the stomach. This is necessary because the digestive enzymes in the duodenum require a nearly neutral environment in order to work. The three major classes of compounds that undergo chemical digestion in the duodenum are carbohydrates, proteins, and lipids.

DIGESTION OF CARBOHYDRATES IN THE DUODENUM

Complex carbohydrates such as starches are broken down by the digestive enzyme amylase from the pancreas to short-chain molecules consisting of just a few saccharides (that is, simple sugars). Disaccharides, including sucrose and lactose, are broken down into simple sugars by duodenal enzymes: sucrase breaks down sucrose, and lactase (if present) breaks down lactose. Some carbohydrates are not digested in the duodenum and ultimately pass undigested to the large intestine, where they may be digested by intestinal bacteria.

DIGESTION OF PROTEINS IN THE DUODENUM

In the duodenum, the pancreatic enzymes trypsin and chymotrypsin cleave proteins into peptides. Then, these smaller molecules are broken down into amino acids. Their digestion is catalyzed by pancreatic enzymes called peptidases.

DIGESTION OF LIPIDS IN THE DUODENUM

Pancreatic lipase breaks down triglycerides into fatty acids and glycerol. Lipase works with the help of bile secreted by the liver and stored in the gall bladder. Bile salts attach to triglycerides to help them emulsify or form smaller particles (called micelles) that can disperse through the watery contents of the duodenum. This increases the access to the molecules by pancreatic lipase.

JEJUNUM

The **jejunum** is the middle part of the small intestine, connecting the duodenum and the ileum. The jejunum is about 2.5 m (8.2 ft) long. Its main function is the absorption of the products of digestion, including sugars, amino acids, and fatty acids. Absorption occurs by simple diffusion (water and fatty acids), facilitated diffusion (the simple sugar fructose), or active transport (amino acids, small peptides, water-soluble vitamins, and most glucose). All nutrients are absorbed into the blood except for fatty acids and fat-soluble vitamins, which are absorbed into the lymph. Although most nutrients are absorbed in the jejunum, there are a few exceptions:

- Iron is absorbed in the duodenum.
- Vitamin B12 and bile salts are absorbed in the ileum.
- Water and lipids are absorbed throughout the small intestine, including the duodenum and ileum in addition to the jejunum.

ILEUM

The **ileum** is the third and final part of the small intestine, directly connected at its distal end to the large intestine. The ileum is about 3 m (9.8 ft) long. Some cells in the lining of the ileum secrete enzymes that catalyze the final stages of digestion of any undigested protein and carbohydrate molecules. However, the main function of the ileum is to absorb vitamin B12 and bile salts. It also absorbs any other remaining nutrients that were not absorbed in the jejunum. All substances in chyme that remain undigested or unabsorbed by the time they reach the distal end of the ileum pass into the large intestine.

LARGE INTESTINE

The **large intestine**, also called the large bowel, is the last organ of the GI tract. In adults, it averages about 1.5 m (5 ft) in length. It is shorter than the small intestine but at least twice as wide, averaging about 6.5 cm (2.5 in.) in diameter. Water is absorbed from the chyme as it passes through the large intestine, turning the chyme into solid feces. Feces is stored in the large intestine until it leaves the body during defecation.

PARTS OF THE LARGE INTESTINE

Like the small intestine, the large intestine can be divided into several parts, as shown in Figure **12.3.4.5**. The large intestine begins at the end of the small intestine, where a valve separates the small and large intestines and regulates the movement of chyme into the large intestine. The first part of the large intestine, where chyme enters from the small intestine, is called the cecum. From the cecum, the large intestine continues upward as the ascending colon, travels across the upper abdomen as the transverse colon, and then continues downward as the descending colon. It then becomes a V-shaped region called the sigmoid colon, which is attached to the rectum. The **rectum** stores feces until elimination occurs. It transitions to the final part of the large intestine, called the **anus,** which has an opening to the outside of the body for feces to pass through.

A projection from the cecum of the colon is known as the **appendix.** The function of the appendix is uncertain, but it does not seem to be involved in digestion or absorption. It may play a role in immunity, and in the fetus, it seems to have an endocrine function, releasing hormones needed for homeostasis. Some biologists speculate that the appendix may also store a sample of the colon's normal bacteria. If so, it may be able to repopulate the colon with the bacteria if illness or antibiotic medications deplete these microorganisms. Appendicitis, or infection and inflammation of the appendix, is a fairly common medical problem, typically resolved by surgical removal of the appendix (appendectomy). People who have had their appendix surgically removed do not seem to suffer any ill effects, so the organ is considered to be dispensable. As such, it is often referred to as a vestigial organ, which is a previously useful organ that has been retained over evolutionary time as part of the anatomy, even though it no longer has a function in the body.

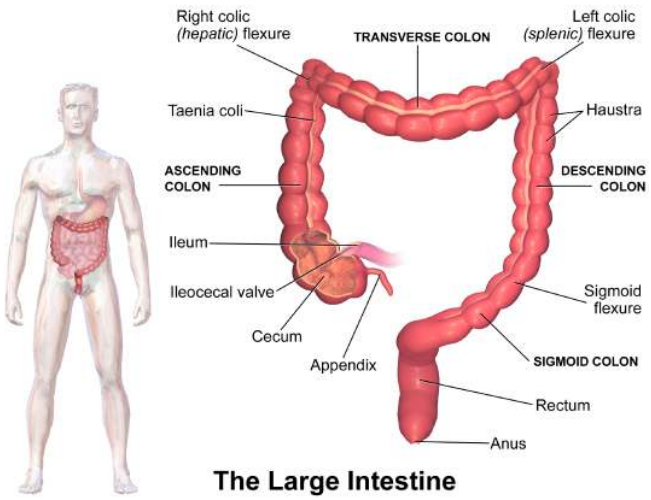


Figure **12.3.4.5**: The parts of the large intestine include the cecum (just after the small intestines), ascending colon (moving upward), transverse colon (moving across), descending colon (moving downward), sigmoid colon (small S-shaped segment), rectum (connecting to the anus), and anus.

FUNCTIONS OF THE LARGE INTESTINE

The removal of water from chyme to form feces starts in the ascending colon and continues throughout much of the length of the organ. Salts such as sodium are also removed from food wastes in the large intestine before the wastes are eliminated from the body. This allows salts as well as water to be recycled in the body.

The large intestine is also the site where huge numbers of beneficial bacteria ferment many unabsorbed materials in food waste. The bacterial breakdown of undigested polysaccharides produces nitrogen, carbon dioxide, methane, and other gases that are responsible for intestinal gas, or flatulence. These bacteria are particularly prevalent in the descending colon. Some of the bacteria also produce vitamins that are absorbed from the colon. The vitamins include vitamins B_1 (thiamine), B_2 (riboflavin), B_7 (biotin), B_{12}, and K. Another role of bacteria in the colon is immune function. The bacteria may stimulate the immune system to produce antibodies that are effective against similar, but pathogenic, bacteria, thereby preventing infections. Still, other roles played by bacteria in the large intestine include breaking down toxins before they can poison the body, producing substances that help prevent colon cancer, and inhibiting the growth of harmful bacteria.

FEATURE: MY HUMAN BODY

Colorectal cancer, or cancer of the colon or rectum, is the fourth most common cancer in the United States. It is also the second most common cause of cancer deaths in this country. Widespread screening of patients for signs of colorectal cancer has significantly lowered the death rate in recent years. Because early-stage colorectal cancer is usually asymptomatic, routine screening is important for identifying cancer early when chances of a cure are still high.

Screening for colorectal cancer has also become easier and less invasive in recent years. One way to test for colorectal cancer is to examine a sample of stool and look for occult (hidden from the unaided eye) blood in the stool. This test is based on the assumption that blood vessels in cancer are fragile and may be easily damaged by the passage of feces through the colon or rectum. The damaged vessels may bleed into the feces but rarely bleed enough for blood to be visible in the stool. Stool for the occult blood test can be collected by the patient at home with a test kit provided by a doctor. If occult blood is detected in the stool, a different type of follow-up test is generally needed to determine whether cancer is the cause of the bleeding.

A similarly simple and noninvasive but more definitive test for colorectal cancer looks for DNA from cancer cells in the stool. Again, the patient can collect the stool sample at home using a simple test kit and mail the specimen to a lab, which does the analysis. If the test comes back positive, then a direct visual examination of the colon and rectum by colonoscopy is required.

Colonoscopy is the gold standard for the diagnosis of colorectal cancer. Using a tiny camera at the end of a long tube inserted up into the colon, a doctor can directly visualize the lining of the large intestine and spot any suspicious areas that may be cancerous. While a colonoscopy is invasive and requires the patient to prepare for the test for a couple of days by changing his or her diet and drinking special fluids, it reveals more than just cancer. A colonoscopy also reveals any growths called polyps in the colon. Colon polyps are not cancer but often develop into cancerous lesions, so if they are found during a colonoscopy, a surgical instrument inserted with the scope is usually used to remove them. Therefore, a colonoscopy can not only detect cancer in its early stages, but it can even help prevent cancer by enabling the removal of potentially pre-cancerous polyps.

A test similar to colonoscopy may be done in some patients. Called a flexible sigmoidoscopy, it allows a doctor to use a small camera to inspect the rectum and lower third of the colon, where the majority of cases of colorectal cancer occur. However, the rest of the colon cannot be examined with a sigmoidoscopy. Another alternative to a full-blown colonoscopy is a virtual colonoscopy, in which a CT scan of the rectum and colon is used to make detailed cross-sectional images of the organs. The images can then be studied by a specialist to detect cancers or polyps. For both of these colonoscopy alternatives, a follow-up colonoscopy is required if polyps or potentially cancerous lesions are detected.

Unless you have a family history of colorectal cancer or certain other risk factors, you probably do not need to start routine screening for the disease until middle age. Your doctor can tell you the most appropriate starting age for your particular case, given your risk factors and current cancer guidelines. You may be able to be screened with one of the less invasive methods

rather than colonoscopy until you are somewhat older. Again, check with your doctor for specific recommendations. All of the testing methods have pros and cons that should be taken into consideration by a given patient and medical provider.

REVIEW

1. Which organs are included in the lower GI tract?
2. Name the parts of the small intestine.
3. How is the mucosa of the small intestine specialized for digestion and absorption?
4. What digestive substances are secreted into the duodenum, and what compounds in food do they help digest?
5. What is the main function of the jejunum?
6. What roles are played by the ileum?
7. Name the parts of the large intestine.
8. Identify the main functions of the large intestine.
9. How do beneficial bacteria in the large intestine help the human organism?
10. *True or False.* The first part of the large intestine is where most chemical digestion takes place.
11. *True or False.* The small intestine is actually longer than the large intestine.
12. When diarrhea occurs, feces leaves the body in a more liquid state than normal. What part of the digestive system do you think is involved in diarrhea? Explain your answer.
13. Arrange the following parts of the lower GI tract in order of how food passes through them, from earliest to latest. Note that not all parts are listed.

    cecum; duodenum; sigmoid colon; jejunum; rectum; ileum

14. Which enzyme digests proteins?

    A. trypsin

    B. amylase

    C. lipase

    D. lactase

15. What is intestinal gas, or flatulence, due to?

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ATTRIBUTIONS

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12.3.5: ACCESSORY ORGANS OF DIGESTION

JAUNDICED EYES

Did you ever hear of a person looking at something or someone with a “jaundiced eye”? It means to take a negative view, such as envy, maliciousness, or ill will. The expression may be based on the antiquated idea that liver bile is associated with such negative emotions as these, as well as the fact that excessive liver bile causes jaundice or yellowing of the eyes and skin. Jaundice is likely to be a sign of a liver disorder or blockage of the duct that carries bile away from the liver. Bile contains waste products, making the liver an organ of excretion. Bile also has an important role in digestion, making the liver an accessory organ of digestion.



Figure **12.3.5.1**: Jaundice Eyes

WHAT ARE ACCESSORY ORGANS OF DIGESTION?

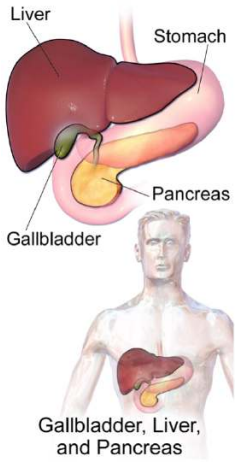


Figure **12.3.5.2**: The liver, gallbladder, and pancreas are the major accessory organs of digestion. In this figure, the pink tubular structure that starts at the lower stomach and wraps around the pancreas is the duodenum of the small intestine. This is where the accessory organs secrete their digestive substances. The pancreas is just behind the stomach. The liver is above on the right side and the gall bladder is just under the liver.

Accessory organs of digestion are organs that secrete substances needed for the chemical digestion of food but through which food does not actually pass as it is digested. Besides the liver, the major accessory organs of digestion are the gallbladder and pancreas. These organs secrete or store substances that are needed for digestion in the first part of the small intestine, the duodenum, where most chemical digestion takes place. You can see the three organs and their locations in Figure **12.3.5.2**.

LIVER

The **liver** is a vital organ located in the upper right part of the abdomen. It lies just below the diaphragm to the right of the stomach. The liver plays an important role in digestion by secreting bile. However, the liver has a wide range of additional functions unrelated to digestion. In fact, some estimates put the number of functions of the liver at about 500! A few of them are described below.

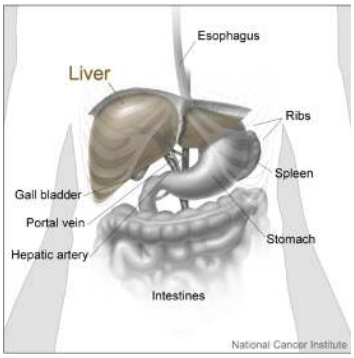


Figure **12.3.5.3**: The portal vein supplies the liver with wastes filtered out of the blood in the spleen as well as nutrients from the gastrointestinal tract. Oxygen-rich blood enters the liver via the hepatic artery.

STRUCTURE OF THE LIVER

The liver is a reddish-brown, wedge-shaped structure. In adults, the liver normally weighs about 1.5 kg (3.3 lb). It is both the heaviest internal organ and the largest gland in the human body. The liver is divided into four lobes of unequal size and shape. Each lobe, in turn, is made up of lobules, which are the functional units of the liver. Each lobule consists of millions of liver cells, called hepatic cells (or hepatocytes). They are the basic metabolic cells that carry out the various functions of the liver.

As shown in Figure **12.3.5.3**, the liver is connected to two large blood vessels: the hepatic artery and the portal vein. The hepatic artery carries oxygen-rich blood from the aorta, whereas the portal vein carries blood that is rich in digested nutrients from the GI tract and wastes filtered from the blood by the spleen. The blood vessels subdivide into smaller arteries and capillaries, which lead to the liver lobules. The nutrients from the GI tract are used to build many vital biochemical compounds, and the wastes from the spleen are degraded and excreted.

FUNCTIONS OF THE LIVER

The main digestive function of the liver is the production of bile. **Bile** is a yellowish alkaline liquid that consists of water, electrolytes, bile salts, and cholesterol, among other substances, many of which are waste products. Some of the components of bile are synthesized by hepatocytes; the rest are extracted from the blood.

As shown in the figure below, bile is secreted into small ducts that join together to form larger ducts, with just one large duct carrying bile out of the liver. If bile is needed to digest a meal, it goes directly

to the duodenum through the common bile duct. In the duodenum, the bile neutralizes acidic chyme from the stomach and emulsifies fat globules into smaller particles (called micelles) that are easier to digest chemically by the enzyme lipase. Bile also aids with the absorption of vitamin K. Bile that is secreted when digestion is not taking place goes to the gallbladder for storage until the next meal. In either case, the bile enters the duodenum through the common bile duct shown in Figure **12.3.5.4**

- The liver synthesizes glycogen from glucose and stores the glycogen as required to help regulate blood sugar levels. It also breaks down the stored glycogen to glucose and releases it back into the blood as needed.
- The liver stores many substances in addition to glycogen, including vitamins A, D, B12, and K. It also stores the minerals iron and copper.
- The liver synthesizes numerous proteins and many of the amino acids needed to make them. These proteins have a wide range of functions. They include fibrinogen, which is needed for blood clotting; insulin-like growth factor (IGF-1), which is important for childhood growth; and albumen, which is the most abundant protein in blood serum and functions to transport fatty acids and steroid hormones in the blood.
- The liver synthesizes many important lipids, including cholesterol, triglycerides, and lipoproteins.
- The liver is responsible for the breakdown of many waste products and toxic substances. The wastes are excreted in bile or travel to the kidneys, which excrete them in the urine.

The liver is clearly a vital organ that supports almost every other organ in the body. Because of its strategic location and diversity of functions, the liver is also prone to many diseases, some of which cause loss of liver function. There is currently no way to compensate for the absence of liver function in the long term, although liver dialysis techniques can be used in the short term. An artificial liver has not yet been developed, so liver transplantation may be the only option for people with liver failure.

GALLBLADDER

The **gallbladder** is a small, hollow, pouch-like organ that lies just under the right side of the liver (Figure **12.3.5.2** and Figure **12.3.5.3**). It is about 8 cm (3.1 in.) long and shaped like a tapered sac, with the open end continuous with the cystic duct. The gallbladder stores and concentrates bile from the liver until it is needed in the duodenum to help digest lipids. After the bile leaves the liver, it reaches the gallbladder through the cystic duct. At any given time, the gallbladder may store between 30 and 60 mL (1-2 oz) of bile. A hormone stimulated by the presence of fat in the duodenum signals the gallbladder to contract and force its contents back through the cystic duct and into the common bile duct to drain into the duodenum.

PANCREAS

The **pancreas** is a glandular organ that is part of both the digestive system and the endocrine system. As shown in Figure **12.3.5.4**, it is located in the abdomen behind the stomach, with the head of the pancreas surrounded by the duodenum of the small intestine. The pancreas is about 15 cm (6 in.) long, and it has two major ducts, the main pancreatic duct, and the accessory pancreatic duct. Both of these ducts drain into the duodenum.

As an endocrine gland, the pancreas secretes several hormones, including insulin and glucagon, which circulate in the blood. The endocrine hormones are secreted by clusters of cells called pancreatic islets (or islets of Langerhans). As a digestive organ, the pancreas secretes many digestive enzymes and also bicarbonate, which helps to neutralize acidic chyme after it enters the duodenum. The pancreas is stimulated to secrete its digestive substances when food in the stomach and duodenum triggers the release of endocrine hormones into the blood that reach the pancreas via the bloodstream. The pancreatic digestive enzymes are secreted by clusters of cells called acini, and they travel through the pancreatic ducts to the duodenum. In the duodenum, they help to chemically break down carbohydrates, proteins, lipids, and nucleic acids in chyme. The pancreatic digestive enzymes include:

- amylase, which helps to digest starch and other carbohydrates.
- trypsin and chymotrypsin, which help to digest proteins.
- lipase, which helps to digest lipids.
- deoxyribonucleases and ribonucleases, which help to digest nucleic acids.

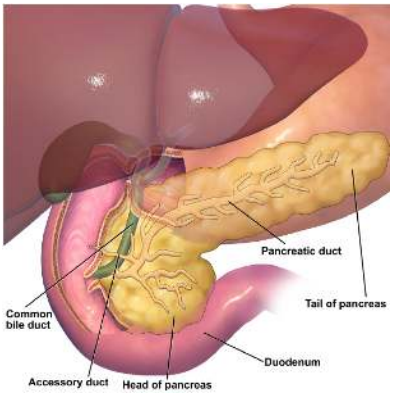


Figure **12.3.5.4**: Pancreatic digestive enzymes and bicarbonate travel to the duodenum through the pancreatic ducts. The main pancreatic duct joins with the common bile duct before the latter enters the duodenum

REVIEW

1. Name three accessory organs of digestion. How do these organs differ from digestive organs that are part of the GI tract?
2. Describe the liver and its blood supply.
3. Explain the main digestive function of the liver.
4. Besides its role as a digestive organ, what other vital functions does the liver have?
5. What is the gallbladder? How does it aid in digestion in the duodenum?

6. Which two body systems include the pancreas? What type of secretions does the pancreas release as part of each body system?
7. List pancreatic enzymes that work in the duodenum and the substances they help digest.
8. What are two substances produced by accessory organs of digestion that help neutralize chyme in the small intestine, and where are they produced?
9. People who have their gallbladder removed sometimes have digestive problems after eating high-fat meals. Why do you think this happens?
10. *True or False*. The liver is a gland.
11. *True or False*. Substances secreted by the pancreas enter into the duodenum from the common bile duct.
12. *True or False*. Bile contains wastes.
13. Which accessory organ of digestion synthesizes cholesterol?

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12.3.6: DISORDERS OF THE GASTROINTESTINAL TRACT

CROHN'S RASH

If you had a skin rash like the one in Figure **12.3.6.1**, you probably wouldn't assume that it was caused by a digestive system disease. However, that's exactly why the individual in the picture has a rash. He has a gastrointestinal (GI) tract disorder called Crohn's disease. This disease is one of a group of GI tract disorders that are known collectively as inflammatory bowel disease. Unlike other inflammatory bowel diseases, signs and symptoms of Crohn's disease may not be confined to the GI tract.

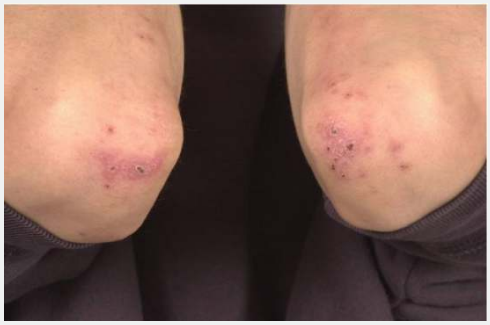


Figure **12.3.6.1**: Pustules and crusts around the elbows in a patient with Crohn's disease and bowel-associated dermatosis-arthritis syndrome (BADAS).

INFLAMMATORY BOWEL DISEASE

Inflammatory bowel disease is a collection of inflammatory conditions primarily affecting the intestines. The two principal inflammatory bowel diseases are Crohn's disease and ulcerative colitis. Unlike Crohn's disease, which may affect any part of the GI tract and the joints as well as the skin, ulcerative colitis mainly affects just the colon and rectum. Both diseases occur when the body's own immune system attacks the digestive system. Both diseases also typically first appear in the late teens or early twenties and occur equally in all sexes and genders.

CROHN'S DISEASE

Crohn's disease is a type of inflammatory bowel disease that may affect any part of the GI tract from the mouth to the anus, among other body tissues. The most commonly affected region is the ileum, which is the final part of the small intestine. Signs and symptoms of Crohn's disease typically include abdominal pain, diarrhea (with or without blood), fever, and weight loss. Malnutrition because of faulty absorption of nutrients may also occur. Potential complications of Crohn's disease include obstructions and abscesses of the bowel. People with Crohn's disease are also at a slightly greater risk than the general population of developing bowel cancer. Although there is a slight reduction in life expectancy in people with Crohn's disease, if the disease is well managed, affected people can live full and productive lives.

Crohn's disease is caused by a combination of genetic and environmental factors that lead to impairment of the generalized immune response (called innate immunity). The chronic inflammation of Crohn's disease is thought to be the result of the immune system "trying" to compensate for the impairment. Dozens of genes are likely to be involved, only a few of which have been identified. Because of the genetic component, close relatives such as siblings of people with Crohn's disease are many times more likely to develop the disease than people in the general population. Environmental factors that appear to increase the risk of the disease include smoking tobacco and eating a diet high in animal proteins. Crohn's disease is typically diagnosed on the basis of a colonoscopy, which provides a direct visual examination of the inside of the colon and the ileum of the small intestine.

People with Crohn's disease typically experience recurring periods of flare-ups followed by remission. There are no medications or surgical procedures that can cure Crohn's disease, although medications such as anti-inflammatory or immune-suppressing drugs may alleviate symptoms during flare-ups and help maintain remission. Lifestyle changes, such as dietary modifications and smoking cessation, may also help control symptoms and reduce the likelihood of flare-ups. Surgery may be needed to resolve bowel obstructions, abscesses, or other complications of the disease.

ULCERATIVE COLITIS

Ulcerative colitis is an inflammatory bowel disease that causes inflammation and ulcers (sores) in the colon and rectum. Unlike Crohn's disease, other parts of the GI tract are rarely affected in ulcerative colitis. The primary symptoms of the disease are lower abdominal pain and bloody diarrhea. Weight loss, fever, and anemia may also be present. Symptoms typically occur intermittently with periods of no symptoms between flare-ups. People with ulcerative colitis have a considerably increased risk of colon cancer and should be screened for colon cancer more frequently than the general population. However, ulcerative colitis seems to reduce primarily the quality of life and not the lifespan.

The exact cause of ulcerative colitis is not known. Theories about its cause involve immune system dysfunction, genetics, changes in normal gut bacteria, and lifestyle factors such as a diet high in animal protein and the consumption of alcoholic beverages. Genetic involvement is suspected in part because ulcerative colitis tends to "run" in families. It is likely that multiple genes are involved. Diagnosis is typically made on the basis of colonoscopy and tissue biopsies.

Lifestyle changes, such as reducing the consumption of animal protein and alcohol, may improve symptoms of ulcerative colitis. A number of medications are also available to treat symptoms and help prolong remission. These include anti-inflammatory drugs and drugs that suppress the immune system. In cases of severe disease, removal of the colon and rectum may be required and can cure the disease.

DIVERTICULITIS

Diverticulitis is a digestive disease in which tiny pouches in the wall of the large intestine become infected and inflamed. Symptoms typically include lower abdominal pain of sudden onset. There may also be fever, nausea, diarrhea or constipation, and blood in the stool. Having large intestine pouches called diverticula (Figure 12.3.6.2) that are not inflamed is called **diverticulosis.** Diverticulosis is thought to be due to a combination of genetic and environmental factors and is more common in people who are obese. Infection and inflammation of the pouches (diverticulitis) occur in about 10 to 25 percent of people with diverticulosis and is more common at older ages. The infection is generally caused by bacteria.



Figure **12.3.6.2**: Multiple pouches called diverticula in the wall of the large intestine

Diverticulitis can usually be diagnosed with a CT scan. Mild diverticulitis may be treated with oral antibiotics and a short-term liquid diet. For severe cases, intravenous antibiotics, hospitalization, and complete bowel rest (no nourishment via the mouth) may be recommended. Complications such as abscess formation or perforation of the colon require surgery.

PEPTIC ULCER

A **peptic ulcer** is a sore in the lining of the stomach or the duodenum (the first part of the small intestine). If the ulcer occurs in the stomach, it is called a gastric ulcer; if it occurs in the duodenum, it is called a duodenal ulcer. The most common symptoms of peptic ulcers are upper abdominal pain that often occurs at night and improves with eating. Other symptoms may include belching, vomiting, weight loss, and poor appetite. However, many people with peptic ulcers, particularly older people, have no symptoms. Peptic ulcers are relatively common, with about 10 percent of people developing a peptic ulcer at some point in their life.

The most common cause of peptic ulcers is infection with the bacterium *Helicobacter pylori*, which may be transmitted by food, contaminated water, or human saliva (for example, by kissing or sharing eating utensils). Surprisingly, the bacterial cause of peptic ulcers was not discovered until the 1980s. The scientists who made the discovery are Australians Robin Warren and Barry J. Marshall. Although the two scientists eventually won a Nobel Prize for their discovery, their hypothesis was poorly received at first. To demonstrate the validity of their discovery, Marshall used himself in an experiment. He drank a culture of bacteria from a peptic ulcer patient and developed symptoms of peptic ulcer in a matter of days. His symptoms resolved on their own within a couple of weeks, but he took antibiotics to kill any remaining bacteria at his wife's urging (apparently because bad breath is also one of the symptoms of *H. pylori* infection). Marshall's self-experiment was published in the Australian Medical Journal and is among the most cited articles ever published in the journal.

Another relatively common cause of peptic ulcers is the chronic use of non-steroidal anti-inflammatory drugs (NSAIDs), such as aspirin or ibuprofen. Additional contributing factors may include tobacco smoking and stress, although these factors have not been demonstrated conclusively to cause peptic ulcers independent of *H. pylori* infection. Contrary to popular belief, diet does not appear to play a role in either causing or preventing peptic ulcers. Eating spicy foods and drinking coffee and alcohol were once thought to cause peptic ulcers. These lifestyle choices are no longer thought to have much if any effect on the development of peptic ulcers.

Peptic ulcers are typically diagnosed on the basis of symptoms or the presence of *H. pylori* in the GI tract. However, endoscopy (Figure 12.3.6.3), which allows direct visualization of the stomach and duodenum with a camera, may be required for a definitive diagnosis. Peptic ulcers are usually treated with antibiotics to kill *H. pylori*, along with medications to temporarily decrease stomach acid and aid in healing. Unfortunately, *H. pylori* have developed resistance to commonly used antibiotics, so treatment is not always effective. If a peptic ulcer has penetrated so deep into the tissues that it causes perforation of the wall of the stomach or duodenum, then emergency surgery is needed to repair the damage.



Figure **12.3.6.3**: A doctor inserts a tiny camera through a tube (called an endoscope) to examine a patient's upper GI tract for peptic ulcers. He views the image created by the camera on a screen above the patient's head.

GASTROENTERITIS

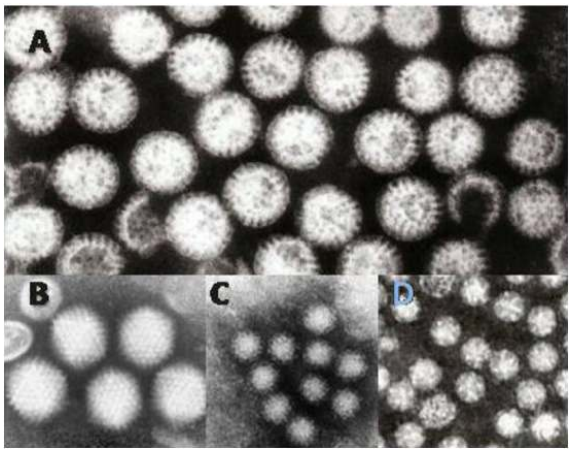


Figure **12.3.6.4**: These micrographs show four types of viruses that commonly cause gastroenteritis in humans: A. rotavirus, B. adenovirus, C. norovirus, and D. astrovirus.

Gastroenteritis, also known as infectious diarrhea, is an acute and usually self-limiting infection of the GI tract by pathogens. Symptoms typically include some combination of diarrhea, vomiting, and abdominal pain. Fever, lack of energy, and dehydration may also occur. The illness generally lasts less than two weeks, even without treatment, but in young children, it is potentially deadly. Gastroenteritis is very common, especially in poorer nations. Worldwide, up to five billion cases occur each year, resulting in about 1.4 million deaths. In the United States, infectious diarrhea is the second most common type of infection after the common cold.

Commonly called "stomach flu," gastroenteritis is unrelated to the influenza virus, although viruses are the most common cause of the disease (Figure **12.3.6.4**). In children, rotavirus is most often the cause, whereas norovirus is more likely to be the cause in adults. Besides viruses, other potential causes of gastroenteritis include fungi, protozoa (including *Giardia lamblia*, described below), and bacteria (most often *Escherichia coli* or *Campylobacter jejuni).* Transmission of pathogens may occur due to eating improperly prepared foods or foods left to stand at room temperature, drinking contaminated water, or having close contact with an infected individual.

Gastroenteritis is less common in adults than children, partly because adults have acquired immunity after repeated exposure to the most common infectious agents. Adults also tend to have better hygiene than children. If children have frequently repeated incidents of gastroenteritis, they may suffer from malnutrition, stunted growth, and developmental delays. Many cases of gastroenteritis in children can be avoided by giving them a rotavirus vaccine. Frequent and thorough hand washing can cut down on infections caused by other pathogens.

Treatment of gastroenteritis generally involves increasing fluid intake to replace fluids lost in vomitus or diarrhea. Oral rehydration solution, which is a combination of water, salts, and sugar, is often recommended. In severe cases, intravenous fluids may be needed. Antibiotics are not usually prescribed because they are ineffective against viruses that cause most cases of gastroenteritis.

GIARDIASIS



Figure **12.3.6.5**: Giardia lamblia is a single-celled organism that parasitizes the GI tract of humans as well as many other animal species. It is a eukaryotic cell with tentacle-like extensions.

Giardiasis, popularly known as beaver fever, is a type of gastroenteritis caused by a GI tract parasite, the single-celled protozoan *Giardia lamblia* (Figure **12.3.6.5**). The parasite inhabits the digestive tract of a wide variety of domestic and wild animal species in addition to human beings, including cows, rodents, and sheep as well as beavers (hence its popular name). Giardiasis is one of the most common parasitic infections in people the world over, with hundreds of millions of people infected worldwide each year.

Transmission of *G. lamblia* is via a fecal-oral route. Those at greatest risk include travelers to countries where giardiasis is common, people who work in child-care settings, backpackers and campers who drink untreated water from lakes or rivers, and people who have close contact with infected people or animals in other settings. In the United States, giardiasis occurs more often during the summer than in other seasons, probably because people spend more time outdoors and in wild settings at that time of year.

Symptoms of giardiasis can vary widely. About a third of people with the infection have no symptoms, whereas others have severe diarrhea with poor absorption of nutrients. Problems with absorption occur because the parasites inhibit intestinal digestive enzyme production, cause detrimental changes in microvilli lining the small intestine, and kill off small intestinal epithelial cells. The illness can result in weakness, loss of appetite, stomach cramps, vomiting, and excessive gas. Without treatment, symptoms may continue for several weeks. Treatment with an antibiotic may be needed if symptoms persist longer or are particularly severe.

REVIEW

1. What is inflammatory bowel disease?
2. Describe typical symptoms of inflammatory bowel disease.
3. Compare and contrast Crohn's disease and ulcerative colitis.
4. What is diverticulosis? How is it related to diverticulitis?
5. Identify the locations and causes of peptic ulcers.
6. Define and describe gastroenteritis.

7. Identify the cause of giardiasis. Why may it cause malabsorption?
8. Which of the following does not normally affect the small intestine?

   A. Peptic ulcers

   B. Crohn's disease

   C. Giardiasis

   D. Ulcerative colitis

9. Name three disorders of the GI tract that can be due to bacteria.
10. *True or False*. A colonoscopy can be used to examine the small intestine.
11. *True or False*. Peptic ulcers are mainly due to diet.
12. Name one disorder of the GI tract that can be *helped* by anti-inflammatory medications and one that can be *caused* by chronic use of anti-inflammatory medications.
13. People with ulcerative colitis should be frequently screened for _____ cancer.
14. Describe one reason why it can be dangerous to drink untreated water.
15. Do you think the “stomach flu” can be prevented by an influenza vaccine? Why or why not?

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SECTION OVERVIEW

12.4: NERVOUS SYSTEM

This chapter describes neurons and other cells of the nervous system and compares and contrasts divisions of the nervous system, including central, peripheral, somatic, and autonomic divisions. The chapter explains how nerve impulses occur and how we sense stimuli. It also describes disorders of the nervous system and the effects of psychoactive drugs on the nervous system.

12.4.1: INTRODUCTION TO THE NERVOUS SYSTEM

12.4.2: NEURONS

12.4.3: NERVE IMPULSES

12.4.4: CENTRAL NERVOUS SYSTEM

12.4.5: PERIPHERAL NERVOUS SYSTEM

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12.4.1: INTRODUCTION TO THE NERVOUS SYSTEM

IN THE BLINK OF AN EYE

As you drive into a parking lot, a skateboarder suddenly flies in front of your car across your field of vision. You see the skateboarder in the nick of time and react immediately. You slam on the brakes and steer sharply to the right — all in the blink of an eye. You avoid a collision, but just barely. You're shaken up but thankful that no one was hurt. How did you respond so quickly? Such rapid responses are controlled by your nervous system.



Figure **12.4.1.1**: Skateboarder

OVERVIEW OF THE NERVOUS SYSTEM

The **nervous system**, illustrated in Figure **12.4.1.2**, is the human organ system that coordinates all of the body's voluntary and involuntary actions by transmitting electrical signals to and from different parts of the body. Specifically, the nervous system extracts information from the internal and external environments using sensory receptors. It then usually sends signals encoding this information to the brain, which processes the information to determine an appropriate response. Finally, the brain sends signals to muscles, organs, or glands to bring about the response. In the example above, your eyes detected the skateboarder, the information traveled to your brain, and your brain instructed your body to act so as to avoid a collision.

SIGNALS OF THE NERVOUS SYSTEM

The signals sent by the nervous system are electrical signals called nerve impulses, and they are transmitted by special nervous system cells named neurons, or nerve cells, like the one in Figure **12.4.1.3** (all the parts of a neuron are explained in the next section). Dendrites of a neuron receive nerve impulses from other cells. Long projection (called axons) from neurons carries nerve impulses directly to specific target cells. Schwann cells wrapped around the axon are called **glial cells**. They create a myelin sheath which allows the nerve impulse to travel very rapidly through the axons. A cell that receives nerve impulses from a neuron may be excited to perform a function, inhibited from carrying out an action, or otherwise controlled. In this way, the information transmitted by the nervous system is specific to particular cells and is transmitted very rapidly.

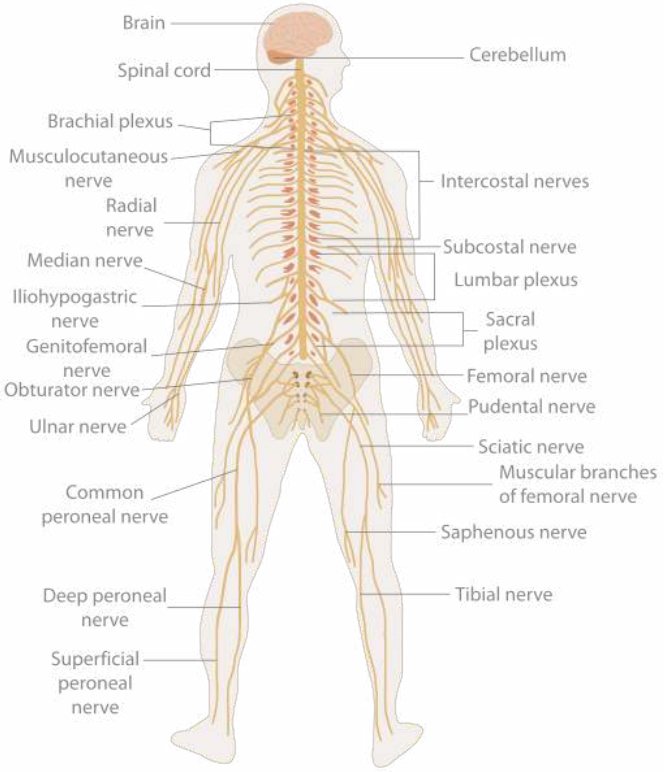


Figure **12.4.1.2**: The human nervous system consists of the brain and spinal cord (central nervous system) and a network of branching nerves that travel throughout the body (peripheral nervous system). Some of the major nerves in the peripheral system are identified in this drawing.

In fact, the fastest nerve impulses travel at speeds greater than 100 meters per second! Compare this to the chemical messages carried by the hormones that are secreted into the blood by endocrine glands. These hormonal messages are "broadcast" to all the cells of the body, and they can travel only as quickly as the blood flows through the cardiovascular system.

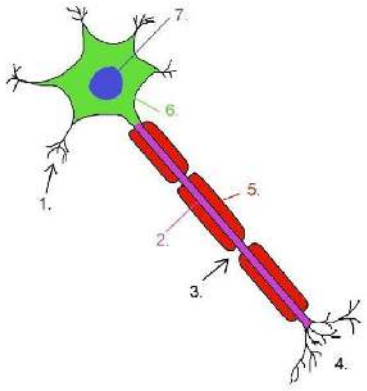


Figure **12.4.1.3**: This simple model of a neuron shows 1 Dendrite, 2 Axon, 3 Nodes of Ranvier, 4 Axon Terminals, 5 Schwann cell (Myelin Sheath), 6 Cell body, and 7 Nucleus

ORGANIZATION OF THE NERVOUS SYSTEM

As you might predict, the human nervous system is very complex. It has multiple divisions, beginning with its two main parts, the central nervous system (CNS) and the peripheral nervous system (PNS), as shown in Figure **12.4.1.4**. The CNS includes the brain and spinal cord, and the PNS consists mainly of nerves, which are bundles of axons from neurons. The nerves of the PNS connect the CNS to the rest of the body. You can learn much more about the CNS by reading the concept *Central Nervous System*.

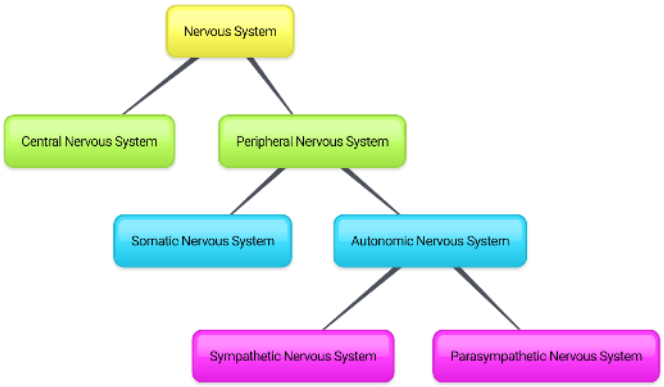


Figure **12.4.1.4**: The concept map illustrates that the nervous system is divided into the peripheral and central systems. The peripheral nervous system is divided into the autonomic and somatic systems. The autonomic nervous system is divided into the sympathetic and parasympathetic systems.

The PNS is divided into two major parts, called the autonomic and somatic nervous systems. The somatic nervous system controls activities that are under voluntary control, such as turning a steering wheel. The autonomic nervous system controls activities that are not under voluntary control, such as digesting a meal. The autonomic nervous system has two divisions: the sympathetic division, which controls the fight-or-flight response during emergencies, and the parasympathetic division, which controls the routine "housekeeping" functions of the body at other times. You can learn more about the PNS and its subdivisions by reading the concept *Peripheral Nervous System*.

REVIEW

1. List the general steps by which the nervous system generates an appropriate response to information from the internal and external environments.
2. What are neurons?
3. Compare and contrast the central and peripheral nervous systems.
4. Which major division of the peripheral nervous system allows you to walk to class? Which major division of the peripheral nervous system controls your heart rate?
5. Identify the functions of the three divisions of the autonomic nervous system.
6. What is an axon and what is its function?
7. *True or False*. A nerve impulse always causes the target cell to perform an action.
8. *True or False*. The spinal cord is not considered part of the peripheral nervous system.
9. Define nerve impulses.
10. Explain why signals in the nervous system are generally more targeted and specific than signals in the endocrine system.
11. Explain generally how the brain and spinal cord can interact with and control the rest of the body.
12. _____ actions are performed without the person thinking about them.
13. The fight-or-flight response is controlled by the:
    A. autonomic nervous system
    B. somatic nervous system
    C. central nervous system
    D. parasympathetic nervous system
14. How are nerves and neurons related?
15. What type of information from the outside environment do you think is detected by sensory receptors in your ears?

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12.4.2: NEURONS

LIFE AS ART

This colorful picture could be an abstract work of modern art. You might imagine it hanging in an art museum or art gallery. In fact, the picture illustrates real life rather than an artistic creation. It is a micrograph of human nervous tissue. The neon green structures in the picture are neurons. The neuron is one of two basic types of cells in the nervous system, the other type being the glial cell.

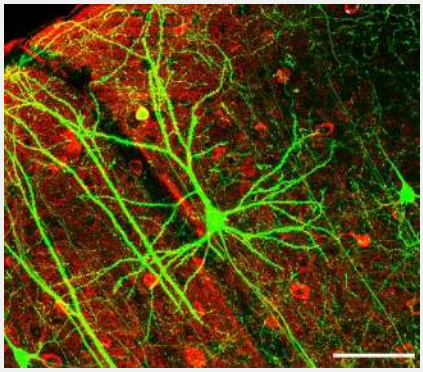


Figure **12.4.2.1**: Interneurons of Adult Visual Cortex

Neurons, also called nerve cells, are electrically excitable cells that are the main functional units of the nervous system. Their function is to transmit nerve impulses. They are the only type of human cells that can carry out this function.

NEURON STRUCTURE

Figure **12.4.2.2** shows the structure of a typical neuron. The main parts of a neuron are labeled in the figure and described below.

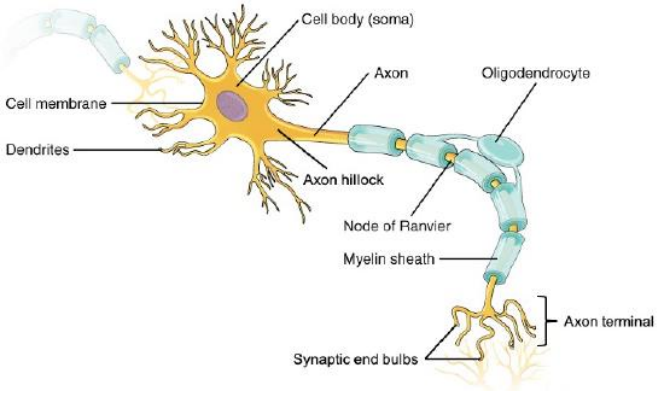


Figure **12.4.2.2**: Somatic Motor Neuron with cell body, axon, axon, myelin sheath, nodes of Ranvier, axon terminal, dendrites, synaptic end of the bulbs, and other associated structures.

- The **cell body** is the part of a neuron that contains the cell nucleus and other cell organelles. It is usually quite compact, and may not be much wider than the nucleus.
- **Dendrites** are thin structures that are extensions of the cell body. Their function is to receive nerve impulses from other cells and carry them to the cell body. A neuron may have many dendrites, and each dendrite may branch repeatedly to form a dendrite "tree" with more than 1,000 "branches." The end of each branch can receive nerve impulses from another cell, allowing a given neuron to communicate with tens of thousands of other cells.
- The **axon** is a long, thin extension of the cell body. It transmits nerve impulses away from the cell body and toward other cells. The axon branches at the end, forming multiple axon terminals. These are the points where nerve impulses are transmitted to other cells, often to the dendrites of other neurons. An area called a synapse occurs at each axon terminal. Synapses are complex membrane junctions that transmit signals to other cells. An axon may branch hundreds of times, but there is never more than one axon per neuron.
- Spread out along axons, especially the long axons of nerves, are many sections of the **myelin sheath.** These are lipid layers that cover sections of the axon. The myelin sheath is a very good electrical insulator, similar to the plastic or rubber that encases an electrical cord.
- Regularly spaced gaps between sections of myelin sheath occur along the axon. These gaps are called **nodes of Ranvier**, and they allow the transmission of nerve impulses along the axon. Nerve impulses skip from node to node, allowing nerve impulses to travel along the axon very rapidly.
- A Schwann cell (also on an axon) is a type of glial cell. Its function is to produce the myelin sheath that insulates axons in the peripheral nervous system. In the central nervous system, a different type of glial cell, called an oligodendrocyte, produces the myelin sheath.

NEUROGENESIS

Fully differentiated neurons, with all their special structures, cannot divide and form new daughter neurons. Until recently, scientists thought that new neurons could no longer be formed after the brain developed prenatally. In other words, they thought that people were born with all the brain neurons they would ever have, and as neurons died, they would not be replaced. However, new evidence shows that additional neurons can form in the brain, even in adults, from the division of undifferentiated neural stem cells that are found throughout the brain. The production of new neurons is called **neurogenesis.** The extent to which it can occur is not known, but it is not likely to be very great in humans.

NEURONS IN NERVOUS TISSUES

The nervous tissue in the brain and spinal cord consists of gray matter and white matter. Gray matter contains mainly the cell bodies of neurons. It is gray only in cadavers; living gray matter is actually more pink than gray (see image below). White matter consists mainly of axons covered with myelin sheath, which gives them their white color. White matter also makes up nerves of the peripheral nervous system. Nerves consist of long bundles of myelinated axons that extend to muscles, organs, or glands throughout the body. The axons in each nerve are bundled together like wires in a cable.

Axons in nerves may be more than a meter long in an adult. The longest nerve runs from the base of the spine to the toes.

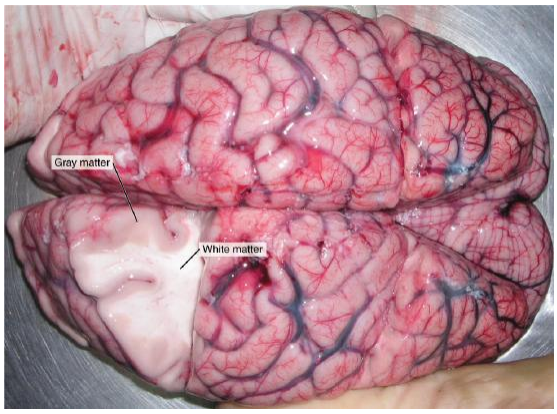


Figure 12.4.2.3: You can see the layers of (pinkish) gray matter and white matter in this photo of a brain from a recently deceased human patient

TYPES OF NEURONS

There are hundreds of different types of neurons in the human nervous system. These types exhibit a variety of structures and functions. Nonetheless, many neurons can be classified functionally based on the direction in which they carry nerve impulses.

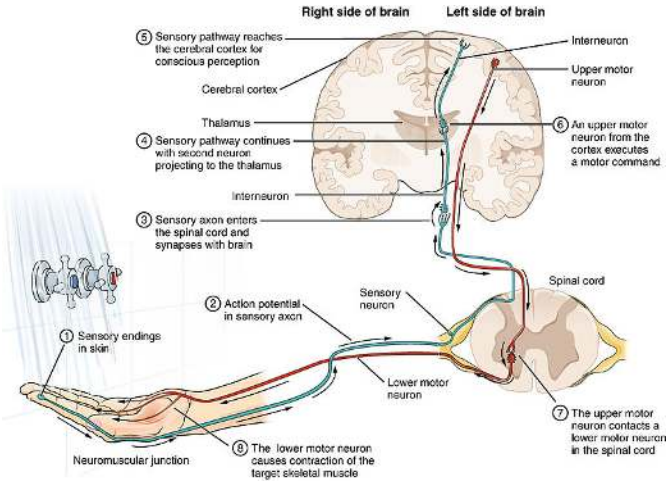


Figure 12.4.2.4: Sensory neurons carry information towards the CNS. Motor neurons carry information from the CNS. Interneurons carry information between sensory and motor neurons.

- **Sensory** (also called afferent) **neurons** carry nerve impulses from sensory receptors in tissues and organs to the central nervous system. They change physical stimuli such as touch, light, and sound into nerve impulses.
- **Motor** (also called efferent) **neurons,** like the one in figure 12.4.2.2, carry nerve impulses from the central nervous system to muscles and glands. They change nerve signals into the activation of these structures.
- **Interneurons** carry nerve impulses back and forth often between sensory and motor neurons within the spinal cord or brain.

GLIAL CELLS

Besides neurons, nervous tissues also consist of **glial cells** (also called neuroglia). They are now known to play many vital roles in the nervous system. There are several different types of glial cells, each with a different function. Schwann cells and Oligodendrocytes are glial cells that produce myelin sheath.

FEATURE: MY HUMAN BODY

Would you like your brain to make new neurons that could help you become a better learner? What college student wouldn't want a little more brainpower when it comes to learning new things? If research on rats applies to humans, then sustained aerobic exercise such as running can increase neurogenesis in the adult brain, and specifically in the hippocampus, a brain structure important for learning temporally and/or spatially complex tasks as well as memory. Although the research is still at the beginning stages, it suggests that exercise may actually lead to a "smarter" brain. However, even if the research results are not confirmed in the future for humans, it can't hurt to get more aerobic exercise, because it is certainly beneficial for your body if not for your brain.

REVIEW

1. Identify the three main parts of a neuron and their functions.
2. Describe the myelin sheath and nodes of Ranvier. How does their arrangement allow nerve impulses to travel very rapidly along axons?
3. What is a synapse?
4. Define neurogenesis. What is the potential for neurogenesis in the human brain?
5. Relate neurons to different types of nervous tissues.
6. Compare and contrast sensory and motor neurons.
7. Identify the role of interneurons.
8. For each type of neuron below, identify whether it is a sensory neuron, motor neuron, or interneuron.
   A. A neuron in the spinal cord receives touch information and then transmits that information to another spinal cord neuron that controls the movement of an arm muscle.
   B. A neuron that takes taste information from your tongue and sends it to your brain.
   C. A spinal cord neuron stimulates a muscle to contract.
9. The myelin sheath is made by:
   A. Sensory neurons
   B. White neurons
   C. Peripheral nervous system neurons
   D. Glial cells
10. *True or False.* Synapses often exist where a dendrite and an axon terminal meet.
11. *True or False.* There is only one axon terminal per neuron.

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12.4.3: NERVE IMPULSES

WHEN LIGHTNING STRIKES

This amazing cloud-to-surface lightning occurred when a difference in electrical charge built up in a cloud relative to the ground. When the buildup of charge was great enough, a sudden discharge of electricity occurred. A nerve impulse is similar to a lightning strike. Both a nerve impulse and a lightning strike occur because of differences in electrical charge, and both result in an electric current.



Figure **12.4.3.1**: Lightning

GENERATING NERVE IMPULSES

A **nerve impulse**, like a lightning strike, is an electrical phenomenon. A nerve impulse occurs because of a difference in electrical charge across the plasma membrane of a neuron. How does this difference in electrical charge come about? The answer involves ions, which are electrically charged atoms or molecules.

RESTING POTENTIAL

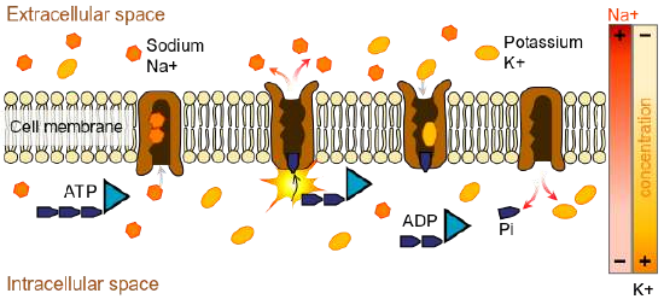


Figure **12.4.3.2**: The sodium-potassium pump maintains the resting potential of a neuron. There is more negative charge inside than outside the cell membrane. ATP is used to pump sodium out and potassium into the cell. There is more concentration of sodium outside the membrane and more concentration of potassium inside the cell due to the unequal movement of these ions by the pump

When a neuron is not actively transmitting a nerve impulse, it is in a resting state, ready to transmit a nerve impulse. During the resting state, the sodium-potassium pump maintains a difference in charge across the cell membrane of the neuron. The sodium-potassium pump is a mechanism of active transport that moves sodium ions out of cells and potassium ions into cells. The sodium-potassium pump moves both ions from areas of lower to higher concentration, using energy in ATP and carrier proteins in the cell membrane. Figure **12.4.3.3**shows in greater detail how the sodium-potassium pump works. Sodium is the principal ion in the fluid outside of cells, and potassium is the principal ion in the fluid inside of cells. These differences in concentration create an electrical gradient across the cell membrane, called **resting potential**. Tightly controlling membrane resting potential is critical for the transmission of nerve impulses.

ACTION POTENTIAL

An **action potential**, also called a nerve impulse, is an electrical charge that travels along the membrane of a neuron. It can be generated when a neuron's membrane potential is changed by chemical signals from a nearby cell. In an action potential, the cell membrane potential changes quickly from negative to positive as sodium ions flow into the cell through ion channels, while potassium ions flow out of the cell, as shown in Figure **12.4.3.3**.

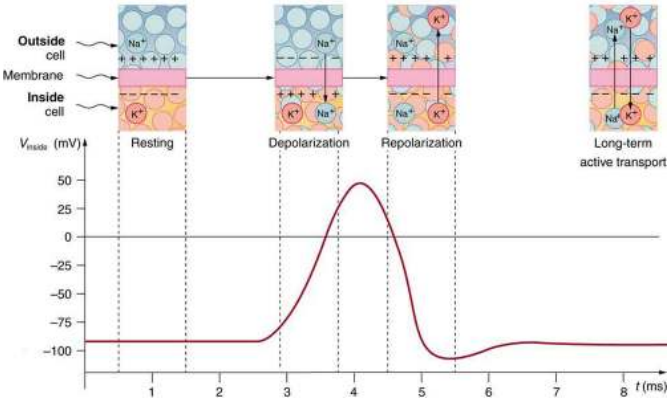


Figure **12.4.3.3**: An action potential speeds along an axon in milliseconds. Sodium ions flow in and cause the action potential, and then potassium ions flow out to reset the resting potential.

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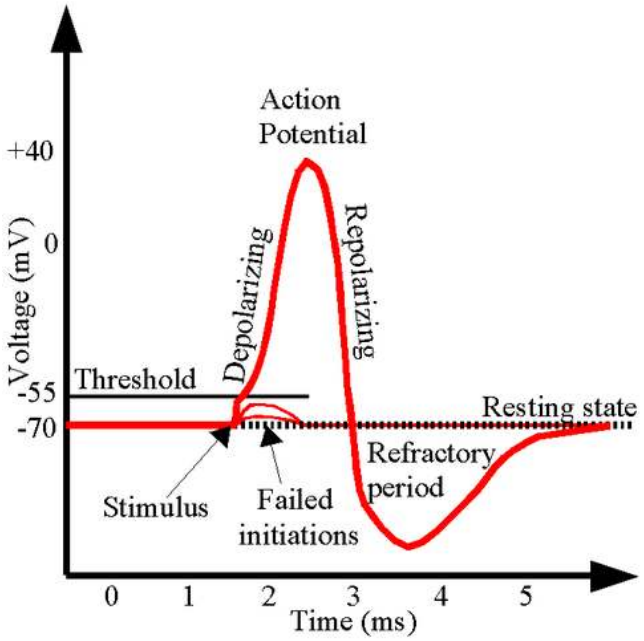


Figure **12.4.3.4**: An action potential graph of membrane potential over time. A neuron must reach a certain threshold in order to begin the depolarization step of reaching the action potential. The figure also shows the change in potential during the repolarization and refractory periods of the axon.

The change in membrane potential results in the cell becoming depolarized. An action potential works on an all-or-nothing basis. That is, the membrane potential has to reach a certain level of depolarization, called the threshold, otherwise, an action potential will not start. This threshold potential varies but is generally about 15 millivolts (mV) more positive than the cell's resting membrane potential. If a membrane depolarization does not reach the threshold level, an action potential will not happen. You can see in Figure **12.4.3.4** that two depolarizations did not reach the threshold level of -55mV.

The first channels to open are the sodium ion channels, which allow sodium ions to enter the cell. The resulting increase in positive charge inside the cell (up to about +40 mV) starts the action potential. This is called the depolarization of the membrane. Potassium ion channels then open, allowing potassium ions to flow out of the cell, which ends the action potential. The inside of the membrane becomes negative again. This is called repolarization of the membrane. Both of the ion channels then close, and the sodium-potassium pump restores the resting potential of -70 mV. The action potential will move down the axon toward the synapse like a wave would move along the surface of the water. Figure **12.4.3.4**shows the change in potential of the axon membrane during an action potential. The nerve goes through a brief refractory period before racing resting potential. During the refractory period, another action potential cannot be generated

In myelinated neurons, ion flows occur only at the nodes of Ranvier. As a result, the action potential signal "jumps" along the axon membrane from node to node rather than spreading smoothly along the membrane, as they do in axons that do not have a myelin sheath. This is due to a clustering of Na+ and K+ ion channels at the Nodes of Ranvier. Unmyelinated axons do not have nodes of Ranvier, and ion channels in these axons are spread over the entire membrane surface.

TRANSMITTING NERVE IMPULSES

The place where an axon terminal meets another cell is called a **synapse.** This is where the transmission of a nerve impulse to another cell occurs. The cell that sends the nerve impulse is called the presynaptic cell, and the cell that receives the nerve impulse is called the postsynaptic cell.

Some synapses are purely electrical and make direct electrical connections between neurons. However, most synapses are chemical synapses. The transmission of nerve impulses across chemical synapses is more complex.

CHEMICAL SYNAPSES

At a chemical synapse, both the presynaptic and postsynaptic areas of the cells are full of the molecular machinery that is involved in the transmission of nerve impulses. As shown in Figure **12.4.3.5**, the presynaptic area contains many tiny spherical vessels called synaptic vesicles that are packed with chemicals called **neurotransmitters**. When an action potential reaches the axon terminal of the presynaptic cell, it opens channels that allow calcium to enter the terminal. Calcium causes synaptic vesicles to fuse with the membrane, releasing their contents into the narrow space between the presynaptic and postsynaptic membranes. This area is called the synaptic cleft. The neurotransmitter molecules travel across the synaptic cleft and bind to **receptors**, which are proteins that are embedded in the membrane of the postsynaptic cell.

The effect of a neurotransmitter on a postsynaptic cell depends mainly on the type of receptors that it activates, making it possible for a particular neurotransmitter to have different effects on various target cells. A neurotransmitter might excite one set of target cells, inhibit others, and have complex modulatory effects on still others, depending on the type of receptors. However, some neurotransmitters have relatively consistent effects on other cells.

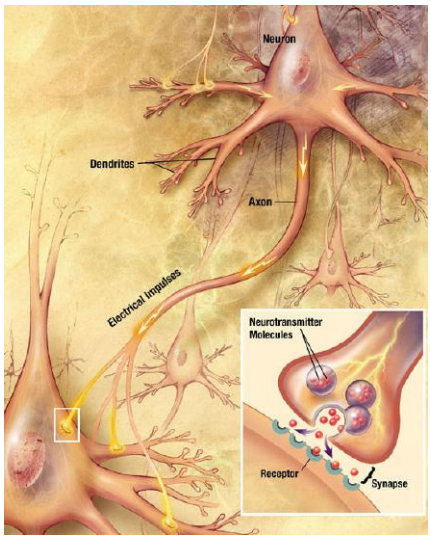


Figure **12.4.3.5**: This diagram shows how an action potential transmits a signal across a synapse to another cell by neurotransmitter molecules. The inset diagram shows the axon terminal, synapse, and receptor of the postsynaptic cell. The neurotransmitters are released from the axon terminal, travel in the synaptic cleft, and attach to the receptors.

REVIEW

1. Define nerve impulse.
2. What is the resting potential of a neuron, and how is it maintained?
3. Explain how and why an action potential occurs.
4. Outline how a signal is transmitted from a presynaptic cell to a postsynaptic cell at a chemical synapse.
5. What generally determines the effects of a neurotransmitter on a postsynaptic cell?
6. Identify three general types of effects neurotransmitters may have on postsynaptic cells.
7. Explain how an electrical signal in a presynaptic neuron causes the transmission of a chemical signal at the synapse.
8. The flow of which type of ion into the neuron results in an action potential?
   A. How do these ions get into the cell?
   B. What does this flow of ions do to the relative charge inside the neuron compared to the outside?
9. The sodium-potassium pump:
   A. is activated by an action potential
   B. requires energy
   C. does not require energy
   D. pumps potassium ions out of cells
10. *True or False.* Some action potentials are larger than others, depending on the amount of stimulation.
11. *True or False.* Synaptic vesicles from the presynaptic cell enter the postsynaptic cell.
12. *True or False.* An action potential in a presynaptic cell can ultimately cause the postsynaptic cell to become inhibited.
13. Name three neurotransmitters.

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12.4.4: CENTRAL NERVOUS SYSTEM

HOMUNCULUS

Figure **12.4.4.1** is a very odd-looking drawing and is called a homunculus. The mass represents a cross-sectional wedge of the human brain. The drawing shows some areas of the brain associated with different parts of the body. As you can see, larger areas of the brain in this region are associated with the hands, face, and tongue than the legs and feet. Given the importance of speech, manual dexterity, and face-to-face social interactions in human beings, it is not surprising that relatively large areas of the brain are needed to control these body parts. The brain is the most complex organ in the human body and part of the central nervous system.

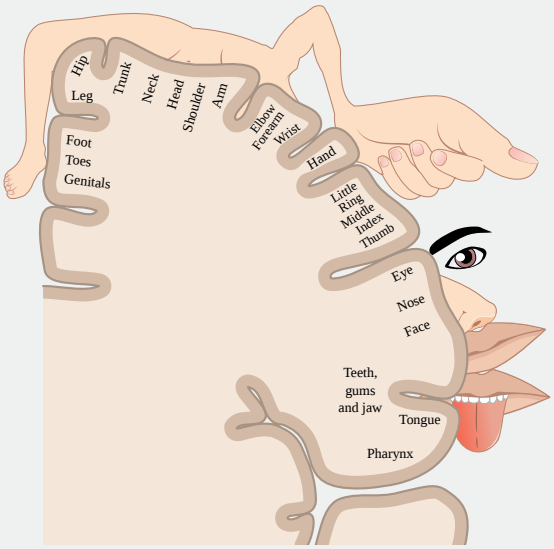


Figure **12.4.4.1**: Brain-Body Map. There's a map of your body on your brain's cortex, but the map is not proportional to actual space. Sensitive parts like the face and fingers are represented by more areas than less sensitive parts like the legs or back

WHAT IS THE CENTRAL NERVOUS SYSTEM?

The central nervous system (CNS) is the part of the nervous system that includes the brain and spinal cord. Figure **12.4.4.2** shows the central nervous system as one of the two main divisions of the total nervous system. The other main division is the peripheral nervous system (PNS). The CNS and PNS work together to control virtually all body functions. You can read much more about the PNS in the concept *Peripheral Nervous System*.

The delicate nervous tissues of the central nervous system are protected by major physical and chemical barriers. Physically, the brain and spinal cord are surrounded by tough meninges, a three-layer protective sheath that also contains cushioning cerebrospinal fluid. The bones of the skull and spinal vertebrae also contribute to physically protecting the brain and spinal cord. Chemically, the brain and spinal cord are isolated from the circulation — and most toxins or pathogens in the blood — by the **blood-brain barrier.** The blood-brain barrier is a highly selective membrane formed of endothelial cells (a type of glial cells) that separates the circulating blood from the extracellular fluid in the CNS. The barrier allows water, certain gases, glucose, and some other molecules needed by the brain and spinal cord to cross from the blood into the CNS while keeping out potentially harmful substances. These physical and chemical barriers make the CNS less susceptible to injury. However, damage to the CNS is likely to have more serious consequences.

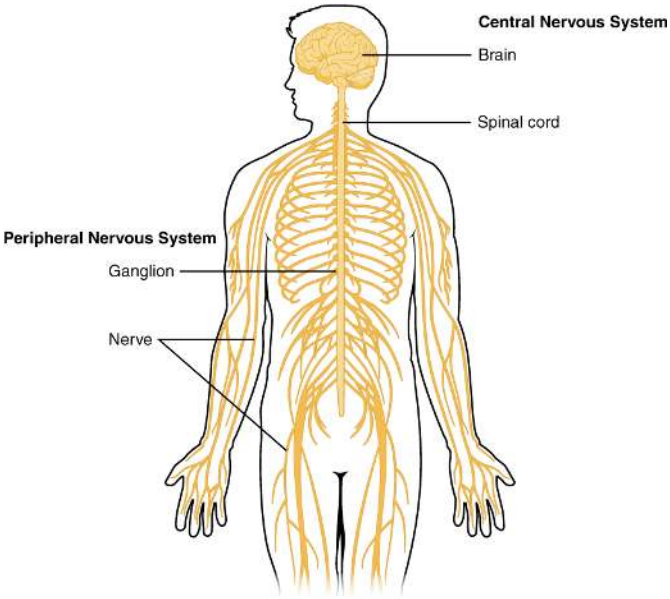


Figure **12.4.4.2**: The two main parts of the central nervous system are the brain and the spinal cord. Ganglions and nerves are part of the peripheral nerve system.

THE BRAIN

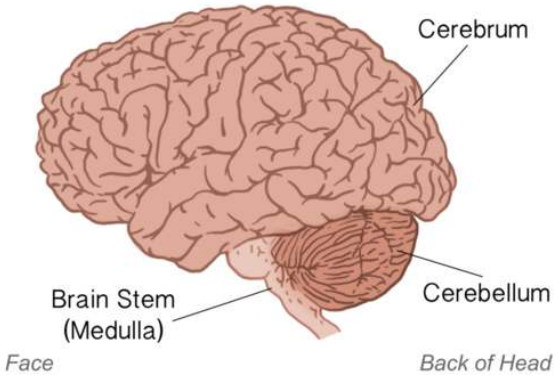


Figure **12.4.4.3**: Cerebrum, Cerebellum, and Brain Stem are the major parts of the brain. the medulla is part of the brain stem.

The **brain** is the control center not only of the rest of the nervous system but of the entire organism. The adult brain makes up only about 2 percent of the body's weight, but it uses about 20 percent of the body's total energy. The brain contains an estimated one hundred billion neurons, and each neuron has thousands of synaptic connections to other neurons. The brain also has about the same number of glial cells as neurons. No wonder the brain uses so much

energy! In addition, the brain uses mostly glucose for energy. As a result, if the brain is deprived of glucose, it can lead to unconsciousness. The brain is able to store some glucose in the form of glycogen, but in much smaller amounts than are found in the liver and skeletal muscles.

The brain controls such mental processes as reasoning, imagination, memory, and language. It also interprets information from the senses and commands the body how to respond. It controls basic physical processes such as breathing and heartbeat as well as voluntary activities such as walking and writing. The brain has three major parts: the cerebrum, cerebellum, and brain stem (Figure **12.4.4.3**). The figure shows the brain from the left side of the head. It shows how the brain would appear if the skull and meninges were removed. The brain stem via its medulla links to the spinal cord. The cerebellum is a small section at the back of the brain. The largest part of the brain is the cerebrum.

CEREBRUM

The **cerebrum** is the largest part of the brain. It controls conscious, intellectual functions. For example, it controls reasoning, language, memory, sight, touch, and hearing. When you read a book, play a video game, or recognize a classmate, you are using your cerebrum.

HEMISPHERES AND LATERALIZATION OF THE CEREBRUM

The cerebrum is divided from front to back into two halves called the left and right **hemispheres.** The two hemispheres are connected by a thick bundle of axons, known as the corpus callosum, which lies deep within the brain. The corpus callosum is the main avenue of communication between the two hemispheres. It connects each point in the cerebrum to the mirror-image point in the opposite hemisphere.

The right and left hemispheres of the cerebrum are similar in shape, and most areas of the cerebrum are found in both hemispheres. Some areas, however, show **lateralization,** or a concentration in one hemisphere or the other. For example, in most people, language functions are more concentrated in the left hemisphere, whereas abstract reasoning and visual-spatial abilities are more concentrated in the right hemisphere.

For reasons that are not yet clear, each hemisphere of the brain interacts primarily with the opposite side of the body. The left side of the brain receives messages from and sends commands to the right side of the body, and the right side of the brain receives messages from and sends commands to the left side of the body. Sensory nerves from the spinal cord to the brain and motor nerves from the brain to the spinal cord both cross the midline of the body at the level of the brain stem.

CEREBRAL CORTEX

Most of the information processing in the brain actually takes place in the **cerebral cortex.** This is a rind of gray matter and other tissues just a few millimeters thick that makes up the outer surface of the cerebrum in both hemispheres of the brain. The cerebral cortex has many folds in it that greatly increase the amount of surface area of the brain that can fit within the skull. Because of all the folds in the human cerebral cortex, it has a surface area of about 2,500 cm^2(2.5 ft^2). The size and importance of the cerebral cortex are far greater in the human brain than the brains of any other vertebrates including nonhuman primates.

LOBES OF THE CEREBRAL CORTEX

Each hemisphere of the cerebrum is further divided into the four lobes shown in Figure **12.4.4.4** and described below.

1. The **frontal lobes** are located at the front of the brain behind the forehead. The frontal lobes are associated with executive functions such as attention, self-control, planning, problem-solving, reasoning, abstract thought, language, and personality.

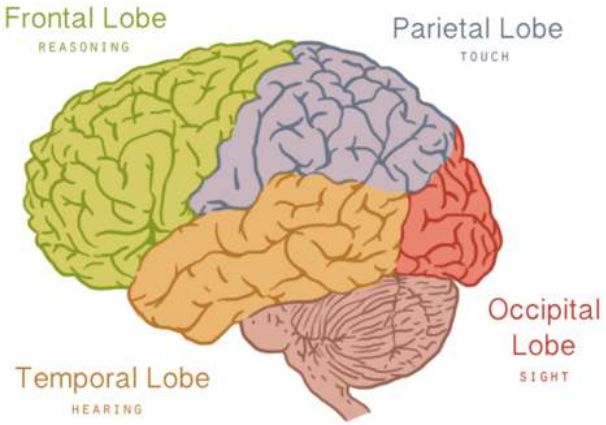


Figure **12.4.4.4**: Each hemisphere of the cerebrum consists of four parts, called lobes. The lobes are associated with multiple functions. The image shows one function of each lobe. Frontal, Parietal, Occipital, and Temporal lobes are associated with reasoning, touch, sight, and hearing, respectively.

2. The **parietal lobes** are located behind the frontal lobes at the top of the head. The parietal lobes are involved in sensation, including temperature, touch, and taste. Reading and arithmetic are also functions of the parietal lobes.

3. The **temporal lobes** are located at the sides of the head below the frontal and parietal lobes. The temporal lobes enable hearing, the formation and retrieval of memories, and the integration of memories and sensations.

4. The **occipital lobes** are located at the back of the head below the parietal lobes. The occipital lobes are the smallest of the four pairs of lobes. They are dedicated almost solely to vision.

INNER STRUCTURES OF THE BRAIN

Several structures are located deep within the brain and are important for communication between the brain and spinal cord or the rest of the body. These structures include the hypothalamus and thalamus. Figure **12.4.4.5** shows where these structures are located in the brain. The cerebrum, hypothalamus, and thalamus exist in two halves, one in each hemisphere.

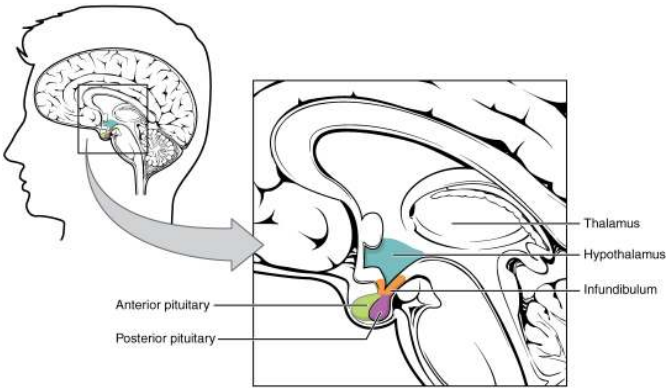


Figure **12.4.4.5**: Just below the cerebrum is the thalamus. Hypothalamus is located below the thalamus and a little to the anterior. The pituitary gland is attached to the hypothalamus via a tube called the infundibulum.

HYPOTHALAMUS

The **hypothalamus** is located just above the brain stem and is about the size of an almond. The hypothalamus is responsible for certain metabolic processes and other activities of the autonomic nervous system, including body temperature, heart rate, hunger, thirst, fatigue, sleep, wakefulness, and circadian (24-hour) rhythms. The hypothalamus is also an important emotional center of the brain. The hypothalamus can regulate so many body functions because it responds to many different internal and external signals, including messages from the brain, light, steroid hormones, stress, and invading pathogens, among others.

One way the hypothalamus influences body functions is by synthesizing hormones that directly influence body processes. For example, it synthesizes the hormone oxytocin, which stimulates uterine contractions during childbirth and the letdown of milk during lactation. It also synthesizes the hormone vasopressin (also called antidiuretic hormone), which stimulates the kidneys to reabsorb more water and excrete more concentrated urine. These two hormones are sent from the hypothalamus via a stalk-like structure called the infundibulum (see diagram above) directly to the posterior (back) portion of the pituitary gland, which secretes them into the blood.

The main way the hypothalamus influences body functions is by controlling the pituitary gland, known as the master gland of the endocrine system. The hypothalamus synthesizes neurohormones called releasing factors that travel through the infundibulum directly to the anterior (front) part of the pituitary gland. The releasing factors generally either stimulate or inhibit the secretion of anterior pituitary hormones, most of which control other glands of the endocrine system.

THALAMUS

The **thalamus,** which is located near the hypothalamus (Figure **12.4.4.5**), is a major hub for information traveling back and forth between the spinal cord and cerebrum. It filters sensory information traveling to the cerebrum. It relays sensory signals to the cerebral cortex and motor signals to the spinal cord. It is also involved in the regulation of consciousness, sleep, and alertness.

CEREBELLUM

The **cerebellum** is just below the cerebrum and at the back of the brain behind the brain stem (Figure **12.4.4.3**). It coordinates body movements and is involved in movements that are learned with repeated practice. For example, when you hit a softball with a bat or touch type on a keyboard you are using the cerebellum. Many nerve pathways link the cerebellum with motor neurons throughout the body.

BRAIN STEM

Sometimes called the “lower brain,” the **brain stem** is the lower part of the brain that is joined to the spinal cord. There are three parts to the brainstem: the midbrain, the pons, and the medulla oblongata, which are shown in Figure **12.4.4.6** below. The brain stem is primarily involved in the unconscious autonomic functions as well as several types of sensory information. It also helps coordinate large body movements such as walking and running. The **midbrain** deals with sight and sound information and translates these inputs before sending them to the forebrain. The **pons** relays messages to other parts of the brain (primarily the cerebrum and cerebellum) and helps regulate breathing. Some researchers have hypothesized that the pons plays a role in dreaming. Some of the functions of the Pons are shared by the **medulla oblongata,** also called the medulla. The medulla controls several subconscious homeostatic functions such as breathing, heart and blood vessel activity, swallowing, and digestion.

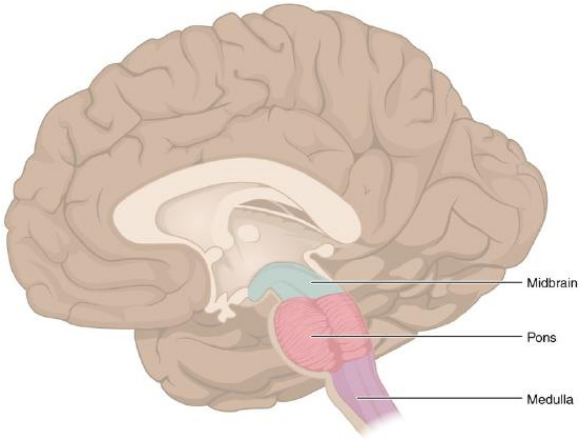


Figure **12.4.4.6**: Brain stem includes the midbrain, pons, and medulla oblongata

One of the brain stem’s most important roles is that of an “information highway.” That is, all of the information coming from the body to the brain and the information from the cerebrum to the body go through the brain stem. Sensory pathways for such things as pain, temperature, touch, and pressure sensation go upward to the cerebrum, and motor pathways for movement and other body processes go downward to the spinal cord. Most of the axons in the motor pathways cross from one side of the CNS to the other as they pass through the medulla oblongata. As a result, the right side of the brain controls much of the movement on the left side of the body,

and the left side of the brain controls much of the movement on the right side of the body.

SPINAL CORD



Figure 12.4.4.7: The spinal cord (yellow) runs from the bottom of the brain to the lower back

The **spinal cord** is a long, thin, tubular bundle of nervous tissues that extends from the brain stem and continues down the center of the back to the pelvis. It is highlighted in yellow in Figure 12.4.4.7. The spinal cord is enclosed within but is shorter than, the vertebral column.

STRUCTURE OF THE SPINAL CORD

The center of the spinal cord consists of gray matter, which is made up mainly of cell bodies of neurons, including interneurons and motor neurons. The gray matter is surrounded by white matter that consists mainly of myelinated axons of motor and sensory neurons. Spinal nerves, which connect the spinal cord to the PNS, exit from the spinal cord between vertebrae (Figure 12.4.4.8).

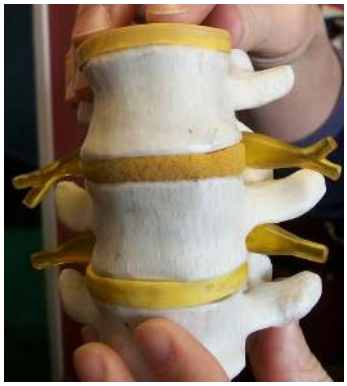


Figure 12.4.4.8: This model shows three vertebrae (white) with branching spinal nerves (yellow) emerging from either side of the spinal cord between vertebrae

FUNCTIONS OF THE SPINAL CORD

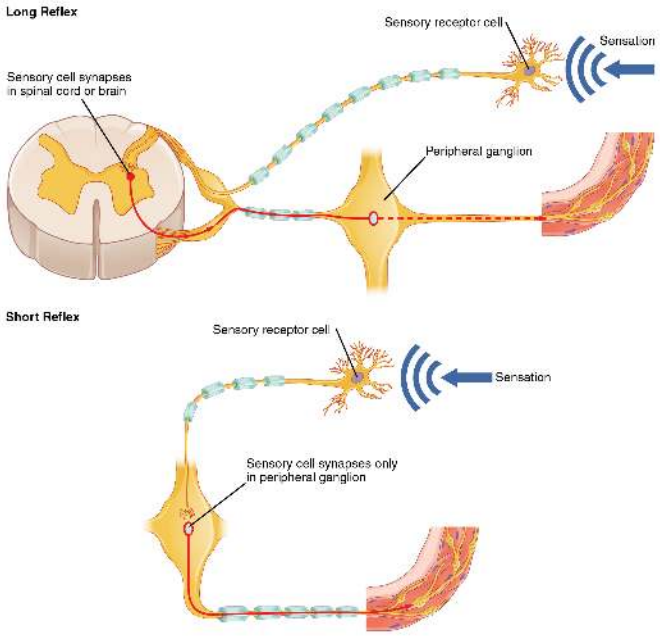


Figure 12.4.4.9: This diagram shows what happens in a long reflex (top), in which sensory nerves carry the message all the way to the spinal cord; and in a short reflex (bottom), in which sensory nerves travel only to a ganglion outside the spinal cord. Note that interneurons are involved in reflexes, connecting sensory and motor neurons, but they are not actually shown in the diagram.

The spinal cord serves as an information superhighway. It passes messages from the body to the brain and from the brain to the body. Sensory (afferent) nerves carry nerve impulses to the brain from sensory receptor cells everywhere in and on the body. Motor (efferent) nerves carry nerve impulses away from the brain to glands, organs, or muscles throughout the body.

The spinal cord also independently controls certain rapid responses called **reflexes** without any input from the brain. You can see how this may happen in Figure 12.4.4.9. A sensory receptor responds to a sensation and sends a nerve impulse along a sensory nerve to the spinal cord. In the spinal cord, the message passes to an interneuron and from the interneuron to a motor nerve, which carries the impulse to a muscle. The muscle contracts in response. These neuron connections form a reflex arc, which requires no input from the brain. No doubt you have experienced such reflex actions yourself. For example, you may have reached out to touch a pot on the stove, not realizing that it was very hot. Virtually at the same moment that you feel the burning heat, you jerk your arm back and remove your hand from the pot.

INJURIES TO THE SPINAL CORD

Physical damage to the spinal cord may result in **paralysis,** which is a loss of sensation and movement in part of the body. Paralysis generally affects all the areas of the body below the level of the injury because nerve impulses are interrupted and can no longer travel back and forth between the brain and body beyond that point. If an injury to the spinal cord produces nothing more than swelling, the symptoms may be transient. However, if nerve fibers (axons) in

the spinal cord are badly damaged, the loss of function may be permanent. Experimental studies have shown that spinal nerve fibers attempt to regrow, but tissue destruction usually produces scar tissue that cannot be penetrated by the regrowing nerves, as well as other factors that inhibit nerve fiber regrowth in the central nervous system.

FEATURE: MY HUMAN BODY

Each year, many millions of people have a stroke, and stroke is the second leading cause of death in adults. **Stroke,** also known as cerebrovascular accident, occurs when poor blood flow to the brain results in the death of brain cells. There are two main types of strokes:

- Ischemic strokes occur due to a lack of blood flow because of a blood clot in an artery going to the brain.
- Hemorrhagic strokes occur due to bleeding from a broken blood vessel in the brain.

Either type of stroke may result in paralysis, loss of the ability to speak or comprehend speech, loss of bladder control, personality changes, and many other potential effects, depending on the part of the brain that is injured. The effects of a stroke may be mild and transient or more severe and permanent. A stroke may even be fatal. It generally depends on the type of stroke and how extensive it is.

Are you at risk of stroke? The main risk factor for stroke is age: about two-thirds of strokes occur in people over the age of 65. There is nothing you can do about your age, but most other stroke risk factors can be reduced with lifestyle changes or medications. The risk factors include high blood pressure, tobacco smoking, obesity, high blood cholesterol, diabetes mellitus, and atrial fibrillation.

Chances are good that you or someone you know is at risk of a stroke, so it is important to recognize a stroke if one occurs. Stoke is a medical emergency, and the more quickly treatment is given, the better the outcome is likely to be. In the case of ischemic strokes, the use of clot-busting drugs may prevent permanent brain damage if administered within 3 or 4 hours of the stroke. Remembering the signs of a stroke is easy.

They are summed up by the acronym FAST, as explained in the chart below.



Figure **12.4.4.10**: The signs of stroke are abbreviated as FAST. Where F, A, S, and T stand for droopy face, arm weakness, slurry speech, and time to call 911, respectively.

REVIEW

1. What is the central nervous system?
2. How is the central nervous system protected?
3. What is the overall function of the brain?
4. Identify the three main parts of the brain and one function of each part.
5. Describe the hemispheres of the brain.
6. Explain and give examples of lateralization of the brain.
7. Identify one function of each of the four lobes of the cerebrum.
8. Summarize the structure and function of the cerebral cortex.
9. Explain how the hypothalamus controls the endocrine system.
10. Describe the spinal cord.
11. What is the main function of the spinal cord?
12. Explain how reflex actions occur.
13. Why do severe spinal cord injuries usually cause paralysis?
14. What do you think are some possible consequences of severe damage to the brain stem? How might this compare to the consequences of severe damage to the frontal lobe? Explain your answer.
15. Information travels very quickly in the nervous system, but generally, the longer the path between areas, the longer it takes. Based on this, explain why you think reflexes often occur at the spinal cord level and do not require input from the brain.

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12.4.5: PERIPHERAL NERVOUS SYSTEM

ONE PIANO, FOUR HANDS

Did you ever see two people play the same piano? How do they coordinate all the movements of their own fingers, let alone synchronize them with those of their partner? The peripheral nervous system plays an important part in this challenge.



Figure **12.4.5.1**: Two people playing piano together

WHAT IS THE PERIPHERAL NERVOUS SYSTEM?

The *peripheral nervous system (PNS)* consists of all the nervous tissue that lies outside of the central nervous system (CNS). The main function of the PNS is to connect the CNS to the rest of the organism. It serves as a communication relay, going back and forth between the CNS and muscles, organs, and glands throughout the body.

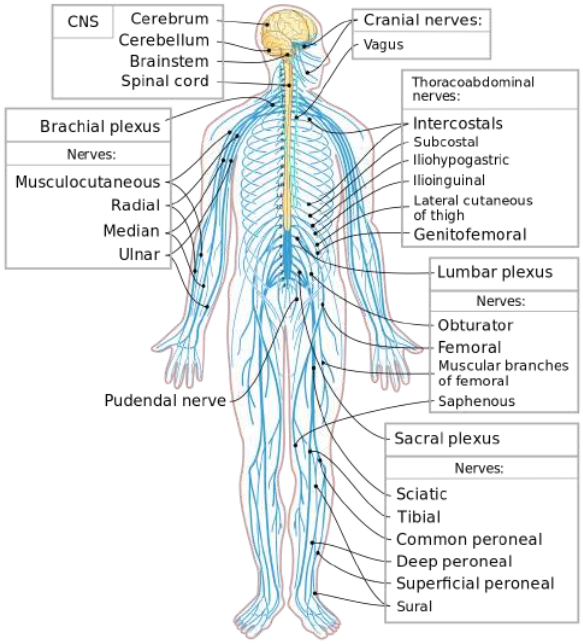


Figure **12.4.5.2**: The nerves of the peripheral nervous system are shown in blue in this figure.

TISSUES OF THE PERIPHERAL NERVOUS SYSTEM

The tissues that make up the PNS are nerves and ganglia. Ganglia are nervous tissues that act as relay points for messages transmitted through nerves of the PNS. Nerves are cable-like bundles of axons that make up the majority of PNS tissues. Nerves are generally classified on the basis of the direction in which they carry nerve impulses as sensory, motor, or mixed nerves. See examples of sensory and motor never in Figure **12.4.5.3**.

- **Sensory nerves** transmit information from sensory receptors in the body to the CNS. Sensory nerves are also called afferent nerves.
- **Motor nerves** transmit information from the CNS to muscles, organs, and glands. Motor nerves are also called efferent nerves.
- **Mixed nerves** contain both sensory and motor neurons, so they can transmit information in both directions. They have both afferent and efferent functions.

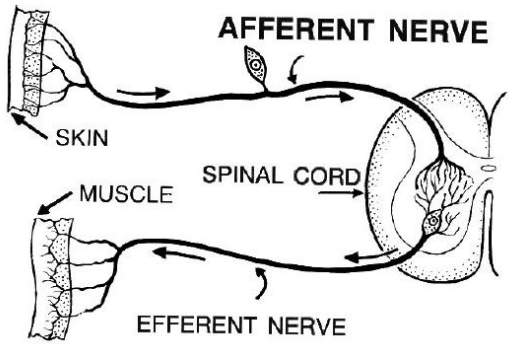


Figure **12.4.5.3**: An afferent nerve is a sensory nerve. The one pictured here sends nerve impulses from sensory cells in the skin to the CNS. An efferent nerve is a motor nerve. This one sends nerve impulses from the CNS to a muscle.

DIVISIONS OF THE PERIPHERAL NERVOUS SYSTEM

The PNS is divided into two major systems, called the autonomic nervous system and the somatic (or sensory-somatic) nervous system. Both systems of the PNS interact with the CNS and include sensory and motor neurons, but they use different circuits of nerves and ganglia.

SOMATIC NERVOUS SYSTEM

The **somatic nervous system** primarily senses the external environment and controls voluntary activities in which decisions and commands come from the cerebral cortex of the brain. For example, when you feel too warm, decide to turn on the air conditioner, and walk across the room to the thermostat, you are using your somatic nervous system. In general, the somatic nervous system is responsible for all of your conscious perceptions of the outside world and all of the voluntary motor activities you perform in response. Whether it's playing piano, driving a car, or playing basketball, you can thank your somatic nervous system for making it possible.

Structurally, the somatic nervous system consists of 12 pairs of cranial nerves and 31 pairs of spinal nerves (Figure **12.4.5.2**). Cranial nerves are in the head and neck and connect directly to the brain. Sensory cranial nerves sense smells, tastes, light, sounds, and body position. Motor cranial nerves control muscles of the face, tongue, eyeballs, throat, head, and shoulders. The motor nerves also control the salivary glands and swallowing. Four of the 12 cranial nerves participate in both sensory and motor functions as mixed nerves, having both sensory and motor neurons.

Spinal nerves of the somatic nervous system emanate from the spinal column between vertebrae. All of the spinal nerves are mixed nerves, containing both sensory and motor neurons. Spinal nerves also include motor nerves that stimulate skeletal muscle contraction, allowing for voluntary body movements.

AUTONOMIC NERVOUS SYSTEM

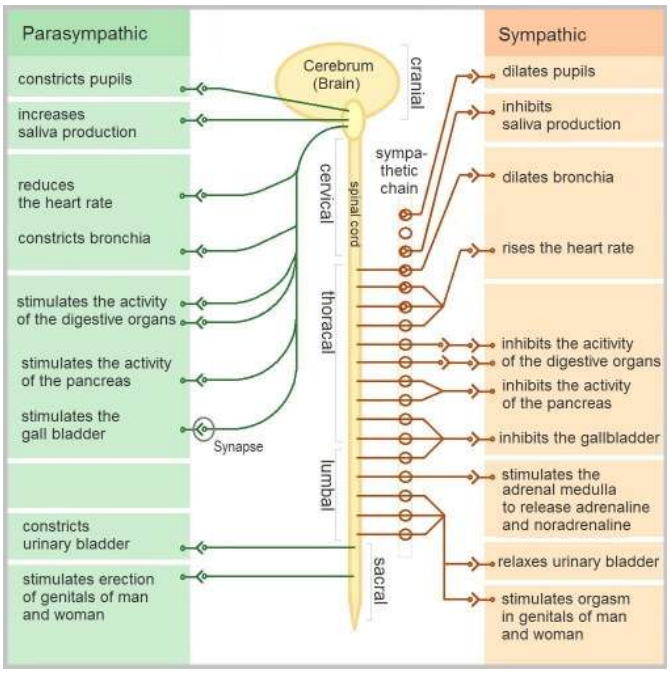


Figure **12.4.5.4**: This diagram summarizes the structures and functions controlled by the parasympathetic and sympathetic divisions of the autonomic nervous system. The images explained how eyes, salivary gland, bronchi, heart rate, digestive system, bladder, and genitalia are affected in opposite ways by the two systems.

The **autonomic nervous system** primarily senses the internal environment and controls involuntary activities. It is responsible for monitoring conditions in the internal environment and bringing about appropriate changes in them. In general, the autonomic nervous system is responsible for all the activities that go on inside your body without your conscious awareness or voluntary participation.

Structurally, the autonomic nervous system consists of sensory and motor nerves that run between the CNS (especially the hypothalamus in the brain) and internal organs (such as the heart, lungs, and digestive organs) and glands (such as the pancreas and sweat glands). Sensory neurons in the autonomic system detect internal body conditions and send messages to the brain. Motor nerves in the autonomic system function by controlling the contractions of smooth or cardiac muscle or glandular tissue. For example, when sensory nerves of the autonomic system detect a rise in body temperature, motor nerves signal smooth muscles in blood vessels near the body surface to undergo vasodilation, and the sweat glands in the skin secrete more sweat to cool the body.

The autonomic nervous system, in turn, has two subdivisions: the sympathetic division and parasympathetic division. The two subdivisions of the autonomic system are summarized in Figure **12.4.5.4**. Both affect the same organs and glands, but they generally do so in opposite ways.

- The **sympathetic division** controls the fight-or-flight response. Changes occur in organs and glands throughout the body that prepare the body to fight or flee in response to a perceived danger. For example, the heart rate speeds up, air passages in the

lungs become wider, more blood flows to the skeletal muscles, and the digestive system temporarily shuts down.

- The **parasympathetic division** returns the body to normal after the fight-or-flight response has occurred. For example, it slows down the heart rate, narrows air passages in the lungs, reduces blood flow to the skeletal muscles, and stimulates the digestive system to start working again. The parasympathetic division also maintains the internal homeostasis of the body at other times.

DISORDERS OF THE PERIPHERAL NERVOUS SYSTEM

Unlike the CNS, which is protected by bones, meninges, and cerebrospinal fluid, the PNS has no such protections. The PNS also has no blood-brain barrier to protect it from toxins and pathogens in the blood. Therefore, the PNS is more subject to injury and disease than is the CNS. Causes of nerve injury include diabetes, infectious diseases such as shingles, and poisoning by toxins such as heavy metals. Disorders of the PNS often have symptoms such as loss of feeling, tingling, burning sensations, or muscle weakness. If a traumatic injury results in a nerve being transacted (cut all the way through), it may regenerate, but this is a very slow process and may take many months.

REVIEW

1. Describe the general structure of the peripheral nervous system, and state its primary function.
2. What are ganglia?
3. Identify three types of nerves based on the direction in which they carry nerve impulses.
4. Outline all of the divisions of the peripheral nervous system.
5. Compare and contrast the somatic and autonomic nervous systems.
6. When and how does the sympathetic division of the autonomic nervous system affect the body?
7. What is the function of the parasympathetic division of the autonomic nervous system? What specific effects does it have on the body?
8. Name and describe two disorders of the peripheral nervous system.
9. Give one example of how the CNS interacts with the PNS to control a function in the body.
10. For each of the following types of information, identify whether the neuron carrying it is sensory or motor and whether it is most likely in the somatic or autonomic nervous system.
    A. Visual information
    B. Blood pressure information
    C. Information that causes muscle contraction in digestive organs after eating
    D. Information that causes muscle contraction in skeletal muscles based on the person's decision to make a movement
11. The cranial nerves:
    A. Carry sensory information
    B. Carry motor information
    C. Are part of the somatic nervous system
    D. All of the above
12. *True or False.* All of the spinal nerves carry both sensory and motor information.
13. *True or False.* The sympathetic nervous system enhances digestion to provide more energy for the body.

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A: The Periodic Table of Elements

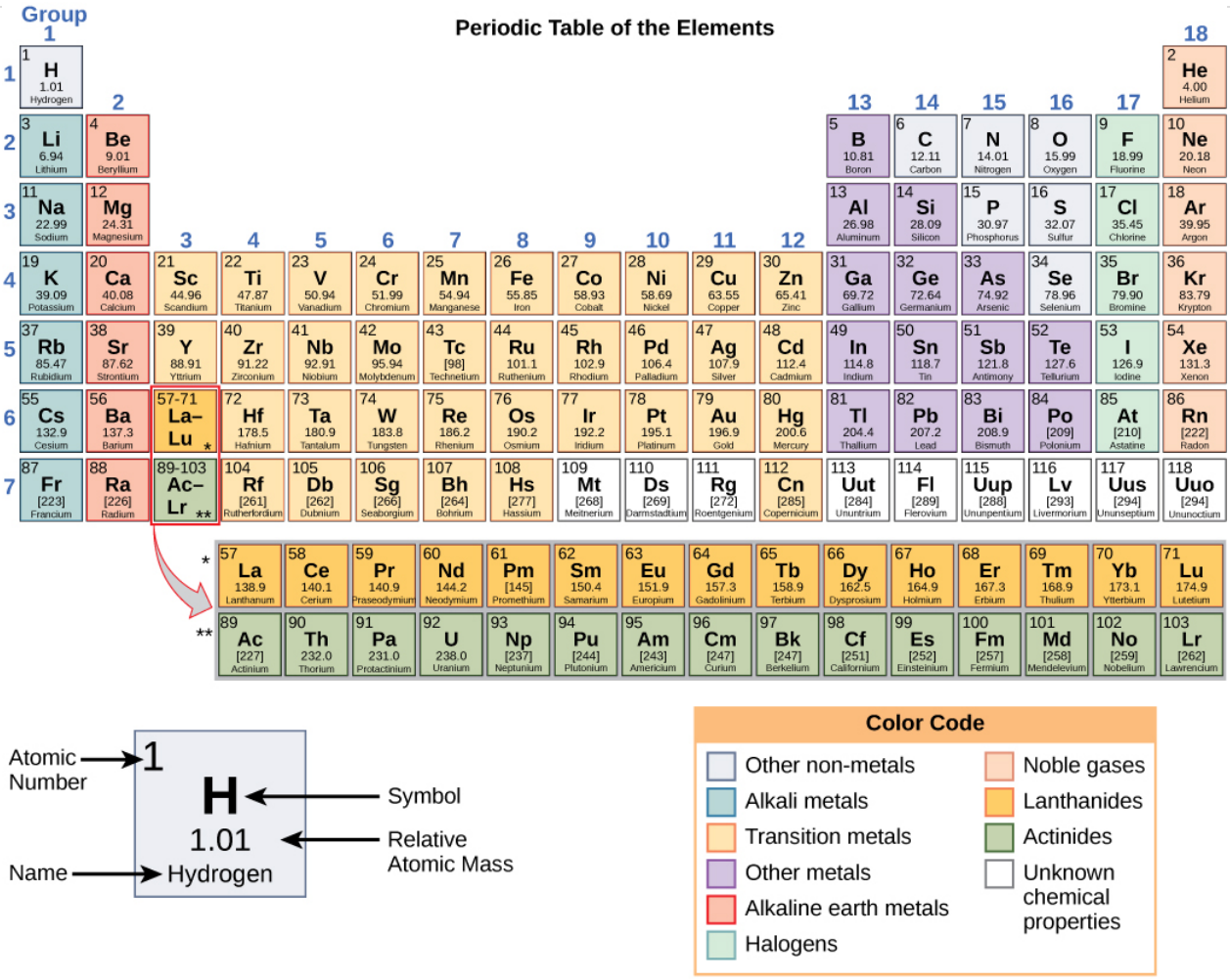


Figure *A.1*

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B: Geological Time

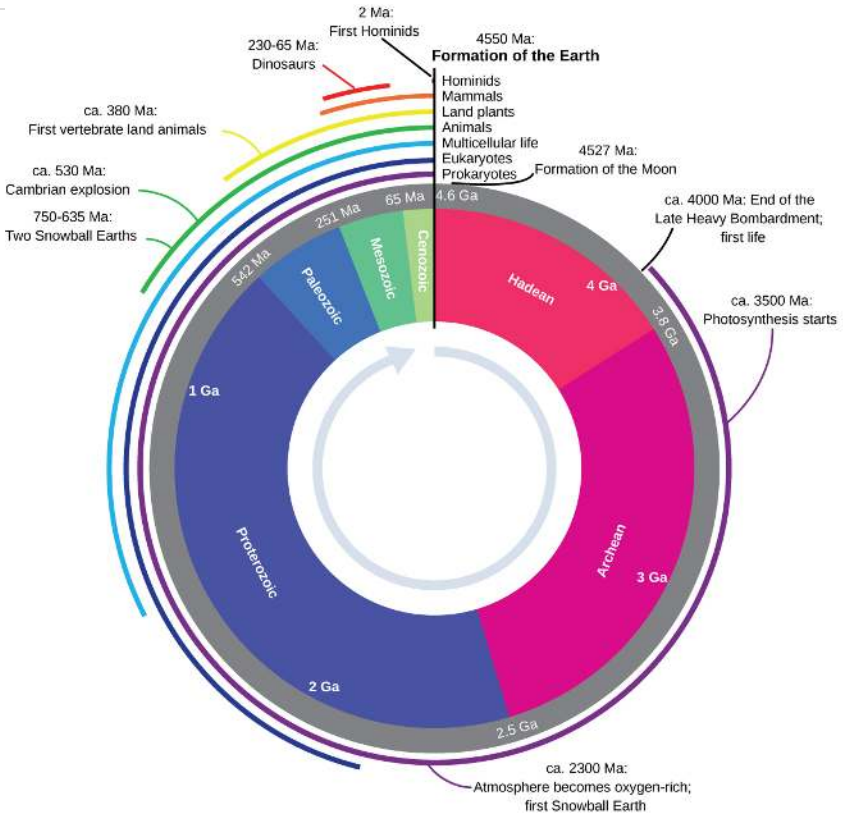


Figure *B.1*: Geological Time Clock

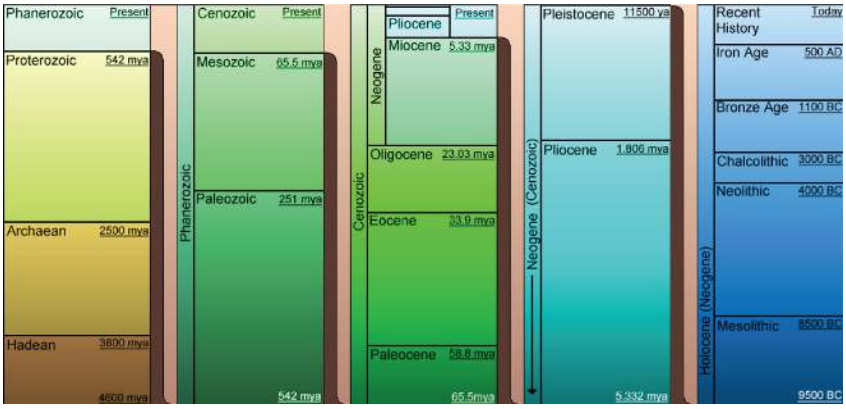


Figure *B.2*: Geological Time Chart (credit: Richard S. Murphy, Jr.)

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C: Measurements and the Metric System

Table $C.1$

Measurement	Unit	Abbreviation	Metric Equivalent	Approximate Standard Equivalent
Length	nanometer	nm	1 nm = 10^{-9} m	• 1 mm = 0.039 inch • 1 cm = 0.394 inch • 1 m = 39.37 inches • 1 m = 3.28 feet • 1 m = 1.093 yards • 1 km = 0.621 miles
	micrometer	µm	1 µm = 10^{-6} m	
	millimeter	mm	1 mm = 0.001 m	
	centimeter	cm	1 cm = 0.01 m	
	meter	m	• 1 m = 100 cm • 1 m = 1000 mm	
	kilometer	km	1 km = 1000 m	
Mass	microgram	µg	1 µg = 10^{-6} g	• 1 g = 0.035 ounce • 1 kg = 2.205 pounds
	milligram	mg	1 mg = 10^{-3} g	
	gram	g	1 g = 1000 mg	
	kilogram	kg	1 kg = 1000 g	
Volume	microliter	µl	1 µl = 10^{-6} l	• 1 ml = 0.034 fluid ounce • 1 l = 1.057 quarts • 1 kl = 264.172 gallons
	milliliter	ml	1 ml = 10^{-3} l	
	liter	l	1 l = 1000 ml	
	kiloliter	kl	1 kl = 1000 l	
Area	square centimeter	cm^2	1 cm^2 = 100 mm^2	• 1 cm^2 = 0.155 square inch • 1 m^2 = 10.764 square feet • 1 m^2 = 1.196 square yards • 1 ha = 2.471 acres
	square meter	m^2	1 m^2 = 10,000 cm^2	
	hectare	ha	1 ha = 10,000 m^2	
Temperature	Celsius	°C	—	1 °C = 5/9 × (°F − 32)

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