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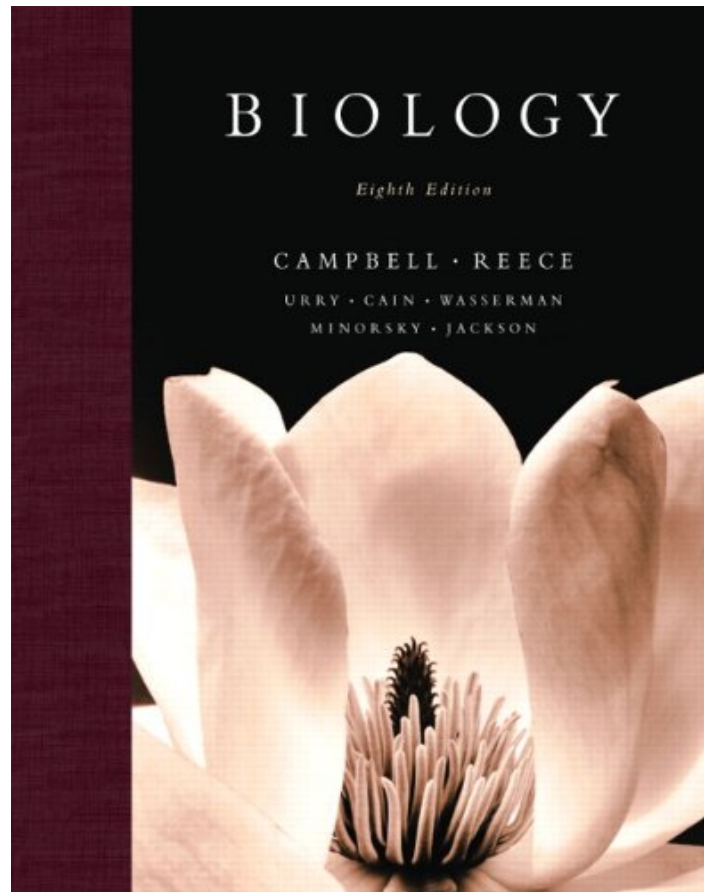
Biology, 8th Edition PDF

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Principles of Biology –
An Introduction to Biological Concepts

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Principles of Biology – An Introduction to Biological Concepts would not be possible without the work of the following College of Lake County faculty contributing authors and reviewers.

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Chapter 1: Introduction to Biology and the Process of Science

Figure 1.1 This NASA image is a composite of several satellite-based views of Earth. (credit: modification of work by NASA/Concepts of Biology OpenStax)

Viewed from space, Earth offers very few clues about the diversity of life forms that can be found there. The first forms of life on Earth are thought to have been microorganisms that existed for billions of years before plants and animals appeared. Mammals, birds, and flowers are all relatively recent additions to the planet, originating 130 to 200 million years ago. Humans have only inhabited this planet for the last 2.5 million years, and only in the last 200,000 years have humans started looking like we do today.

1.1 Themes and Concepts of Biology

Learning objectives

By the end of this section, you will be able to:

- *Identify and describe the properties of life*
- *Describe the levels of organization among living organisms*
- *Understand the role of evolution as a unifying principle of biology and how it contributes to species diversity*
- *Understand how life is classified*
- *Be able to define and explain all bolded terms*

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

earth has a diversity of life forms; how do we organize and classify these different organisms? Finally, 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 living organisms share the following key characteristics: order, response to stimuli, reproduction, adaptation, growth and development, homeostasis, and energy processing. These seven characteristics serve to define life. It is essential that students know these different properties of life and be able to explain each.

Order

Organisms are highly organized and consist of one or more cells. Even very simple, single-celled organisms are remarkably complex. Inside each cell, atoms come together through chemical bonding and form molecules. Molecules come together to form cell components or structures called organelles. Like the toad shown in Figure 1.2, multicellular organisms can consist of millions of cells. Different groups of cells then specialize in performing specific functions. Without order, specialization would not be possible.

Figure 1.2 A toad represents a highly organized individual. (credit: "Ivengo(RUS)"/Wikimedia Commons)

Response to Stimuli

Organisms respond to diverse stimuli. For example, plants can bend toward a source of light or respond to touch (Figure 1.3). Even tiny bacteria can move toward or away from chemicals, a process called chemotaxis. A movement toward a stimulus is considered a positive response, while movement away from a stimulus is regarded as a negative response.

Humans also respond to stimuli. For example, when we become warm on a hot sunny day, the body has tiny glands called sudoriferous, or sweat, glands that make and release sweat onto the skin's surface. The heat from the body can be transferred to the sweat, which acts as a cooling mechanism and helps to maintain constant body temperature.

Figure 1.3 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/Concepts of Biology OpenStax)

CONCEPTS IN ACTION- Watch this <u>video</u> to see how the sensitive plant responds to a touch stimulus.

Reproduction

Reproduction is necessary on both a cellular and organismal level. For a population to survive, some individuals within that population must reproduce. Organisms that are multicellular, such as plants and animals, also need to reproduce on a cellular level. As old cells become damaged or worn out, they must be replaced by new cells. For example, skin cells are damaged continuously and need to be replaced every two to three weeks; otherwise, the skin would lose its ability to provide protection.

Single-celled organisms must also reproduce. Reproduction begins by first duplicating their genetic material. Once the genetic material is duplicated, it is then divided equally into two new cells (Figure 1.4). The two new daughter cells should be identical to the parent cell.

Figure 1.4 Bacteria cell going through division. (credit: Pradana Aumars/<u>Wikimedia Commons</u>)

Adaptation

All living organisms exhibit a "fit" to their environment. Biologists refer to this fit as adaptation. Adaptations are a consequence of evolution by natural selection. Evolution has had some impact on every lineage of reproducing organisms. Examples of adaptations are diverse and unique. For example, some microorganisms live in boiling hot springs, whereas some moths have tongues the exact length of the flower from which they feed.

Adaptations are vital because they enhance an individual's ability to survive and reproduce; however, adaptations are not constant. As an environment changes, natural selection causes the individuals in a population to adapt to those changes.

For example, imagine that there is a population of finches living on an island. An environmental event has resulted in two main food sources: soft insects and hard seeds. Not all finches within the population have the same beak length or size. Finches in the population that have long, skinny beaks begin to feed on soft insects because they are easy for those birds to catch and eat. Finches with large, more dense beaks feed on hard seeds because their dense beaks allow them to

crush and open the hard seeds. Unfortunately, finches that have beaks that are neither long nor dense may slowly begin to decline in number because they are limited in their ability to obtain nutrients. Finches that obtain food can put energy into reproduction and survival needs. When those finches reproduce, they pass along those adaptations that allow them to be successful in their respective feeding environments. Over time two distinct groups may arise, those with thick, dense beaks and those with longer skinnier beaks (Figure 1.5). If these individuals genetically change in such a way that they no longer can interbreed with one another, a speciation event will have occurred.
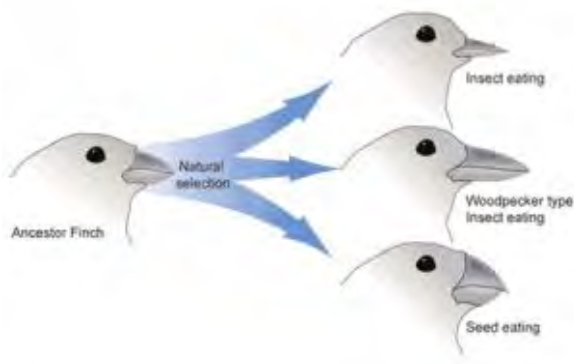
Figure 1.5 Different finch phenotype variations due to environmental changes. (credit: National Human Genome Research Institute's Talking Glossary/Wikimedia Commons)

Growth and Development

Development is often described as the processes that an individual goes through as it grows and matures. For example, in humans, development begins once the sperm fertilizes the egg. Human development can be broken down into different stages including embryonic development, fetal development, infancy, childhood, puberty, and adulthood. Development can also be observed in many other organisms. For example, butterflies go through a developmental process called metamorphosis that begins at the egg stage and then proceeds to the larva, pupa, and adult stages.

Both multicellular and single-celled organisms grow and develop according to specific instructions encoded in their DNA. DNA is organized into genes that provide information for cellular growth and development. An individual's DNA ensures that a species' young (Figure 1.6) will grow up to exhibit many of the same traits as its parents.

Figure 1.6 Although no two looks alike, these kittens have inherited genes from both parents and share many of the same characteristics. (credit: Pieter & Renée Lanser/ Concepts of Biology OpenStax)

Homeostasis

Even the smallest organisms are complex and require multiple regulatory mechanisms to coordinate internal functions, such as the transport of nutrients (Figure 1.7), response to stimuli, and coping with environmental stresses. **Homeostasis** or "steady state" is the ability of an organism to regulate and maintain constant internal conditions.
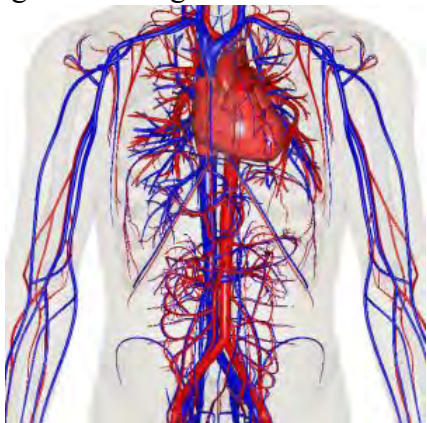
Figure 1.7 Human circulatory system plays an important role in transporting oxygen, removal of waste, and delivering nutrients to every cell. (credit: Public domain/Wikimedia Commons)

Cells require appropriate conditions such as proper temperature, pH, and concentrations of nutrients to function correctly. Although these conditions may change, organisms can maintain internal conditions within a narrow range. 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 1.8), have body structures such as thick layers of fur or fat, which help them withstand low temperatures and conserve body heat. In hot climates, plants carry out unique versions of photosynthesis to reduce water loss and optimize their potential of making sugar.

a

b

Figure 1.8a. Polar bears and other mammals living in ice-covered regions keep their body temperature relatively constant, even though the environment can be very hot during the day and cold at night. (credit: "longhorndave"/Flickr) b. Polar bear maintain their body temperature by generating heat and reducing heat loss through thick fur and a dense layer of fat under their skin. In this infrared image the polar bear's body heat hardly registers; only the uninsulated eyes and mouth show temperatures significantly warmer than the environment. (credit: Arno/Coen/Wikimedia Commons)

Organisms like humans (Figure 1.9), use their skeletal muscles to generate heat. The contraction of skeletal muscles helps humans maintain stable internal body temperature as environmental conditions fluctuate. If body temperature drops below a certain point, metabolism begins to slow and may even stop, leading to death. Conversely, if body temperature rises above a certain point, it can lead to the destruction of key molecules called proteins. Students that continue and take Anatomy and Physiology classes will spend time discussing how the body works to maintain homeostasis. Students will also look at what occurs when the body loses its ability to maintain stable internal conditions, otherwise referred to as a homeostatic imbalance.
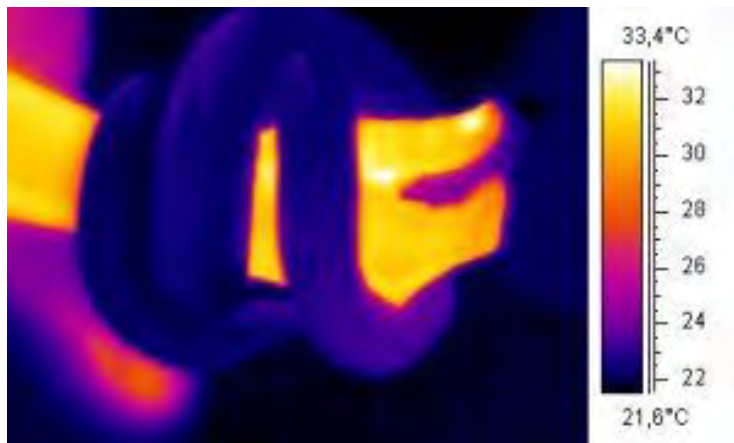
Figure 1.9 Thermogram of a snake wrapped around a human arm. (credit: Arno/Coen/Wikimedia Commons)

Energy Processing

All organisms, including the California condor shown in Figure 1.10, use a source of energy for their metabolic activities. Some organisms can obtain energy through metabolic pathways such as photosynthesis. Photosynthesis is a process where light energy can be captured and converted into chemical energy. Organisms that are capable of making their own chemical energy are referred to as **autotrophs**. Others must obtain their chemical energy by consuming other organisms. These individuals are referred to as **heterotrophs**. Regardless of whether an organism is an autotroph or a heterotroph, all living cells must have energy to drive metabolism.

Figure 1.10 A lot of energy is required for a California condor to fly. (credit: Pacific Southwest Region U.S. Fish and Wildlife/ Concepts of Biology OpenStax)

Levels of Organization of Living Things

Living things are highly organized and structured. 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 biologically important molecules are macromolecules. A **macromolecule** is a large molecule that is typically formed by combining smaller molecules. For example, nucleotides are small molecules linked together to form the macromolecule, DNA (deoxyribonucleic acid) (Figure 1.11). DNA contains the instructions necessary for cells and organisms to maintain homeostasis.

Figure 1.11 A molecule, like this large DNA molecule, is composed of atoms. (credit: "Brian0918"/Wikimedia Commons)

CONCEPTS IN ACTION- To see an animation of this DNA molecule, click here.

Some cells contain collections of macromolecules surrounded by membranes; these are called organelles. **Organelles** are small structures that exist within cells and perform specialized functions. For example, in some cells, DNA is enclosed within a membrane-bound organelle called the nucleus (plural: nuclei). All living things are made of cells; the **cell** is the smallest fundamental unit found in living organisms. Cells exhibit all of the properties of life discussed above. Viruses are often not considered living because they are not made of cells, nor are they capable of reproducing on their own. To make new viruses, they must invade and take over a living cell.

Some **organisms** consist of a single cell, while others are multicellular. 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 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; 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.
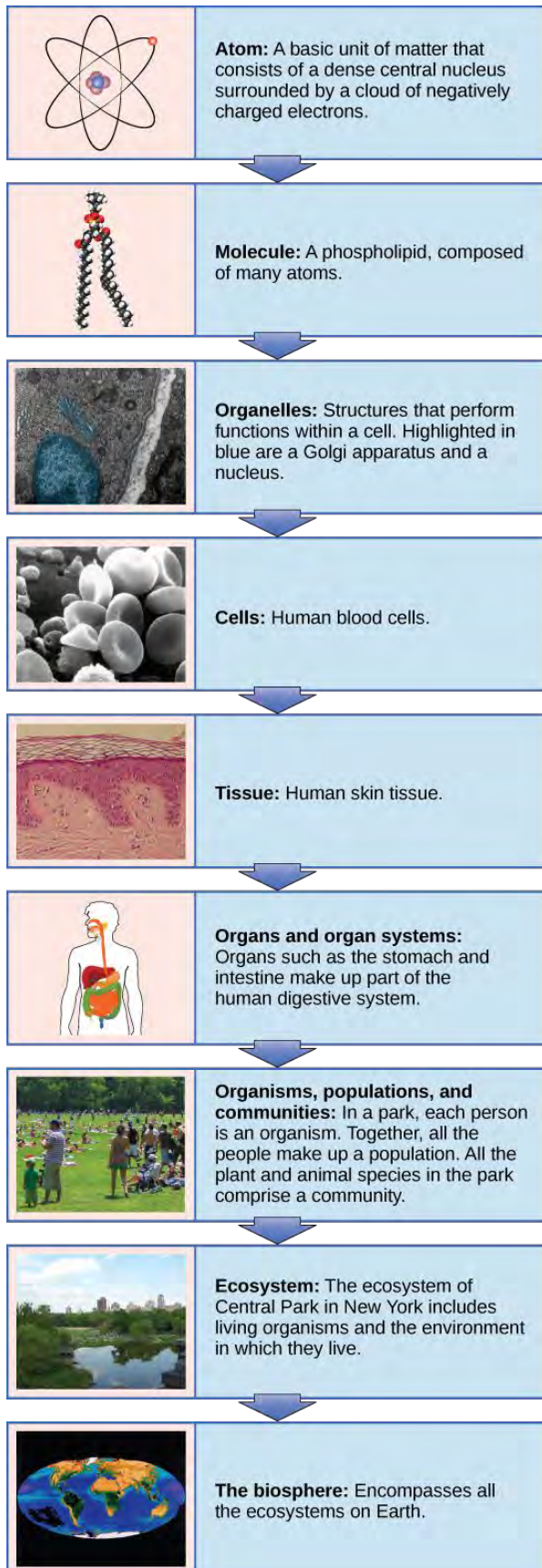
Figure 1.12 From an atom to the entire Earth, biology examines all aspects of life. (credit "molecule": modification of work by Jane Whitney; credit "organelles": modification of work by Louisa Howard; credit "cells": modification of work by Bruce Wetzel, Harry Schaefer, National Cancer Institute; credit "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/ Concepts of Biology OpenStax)

All the individuals living within a specific area are collectively called a **population**. For example, a forest may include many white pine trees. All these pine trees represent the population of white pine trees in this forest. Different populations may live in the same area. The forest with the pine trees includes populations of flowering plants, insects, and microbial populations. A **community** is the set of populations inhabiting a particular area. For instance, all 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 1.12), the **biosphere** is the collection of all ecosystems on planet Earth. It includes land, water, and portions of the atmosphere.

Check your knowledge

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)

The Diversity of Life

The science of biology is very broad because there is a tremendous diversity of life on Earth. The source of this diversity is evolution. **Evolution** is the process of genetic change in a population. Evolution helps explain how new species can arise from older species. Speciation events can occur when individuals within a population are separated and begin to change or evolve independently of one another. If the individuals change to the point where they can no longer interbreed, a speciation event has occurred, and species diversity has increased. Evolution will be discussed in much greater detail in chapter 11.

In the 18th century, a Swedish scientist named Carl Linnaeus first proposed organizing living 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, and domain (Figure 1.13).

DOMAIN Eukarya	Dog	Wolf	Coyote	Fox	Lion Seal	Mouse Human	Whale Bat	Fish Snake	Earthworm Moth	Paramecium Tree
KINGDOM Animalia	Dog	Wolf	Coyote	Fox	Lion Seal	Mouse Human	Whale Bat	Fish Snake	Earthworm Moth	
PHYLUM Chordata	Dog	Wolf	Coyote	Fox	Lion Seal	Mouse Human	Whale Bat	Fish Snake		
CLASS Mammalia	Dog	Wolf	Coyote	Fox	Lion Seal	Mouse Human	Whale Bat			
ORDER Carnivora	Dog	Wolf	Coyote	Fox	Lion Seal					
FAMILY Canidae	Dog	Wolf	Coyote	Fox						
GENUS Canis	Dog	Wolf	Coyote							
SPECIES Canis lupus	Dog	Wolf								

Figure 1.13 This diagram shows the levels of taxonomic hierarchy for a dog, from the broadest category—domain—to the most specific—species. (credit: Fowler et al./Concepts of Biology OpenStax)

The highest taxonomy level, **domain**, is a relatively new addition (1990's) to the system. Scientists now recognize three domains of life: the Eukarya, the Archaea, and the Bacteria. The domain Eukarya is very diverse and includes the kingdoms of fungi, plants, animals, and several kingdoms of protists. Humans, plants, yeast, and mushrooms are just a few representatives of the domain Eukarya. These organisms are classified as **eukaryotes** because they have nuclei and other membrane-bound organelles. Both the Archaea and Bacteria are single-celled organisms classified as prokaryotes (Figure 1.14). **Prokaryotes** are organisms that lack nuclei and other membrane-bound organelles. Prokaryotes, like eukaryotes, are very diverse and can be subdivided into phyla, class, order, etc.
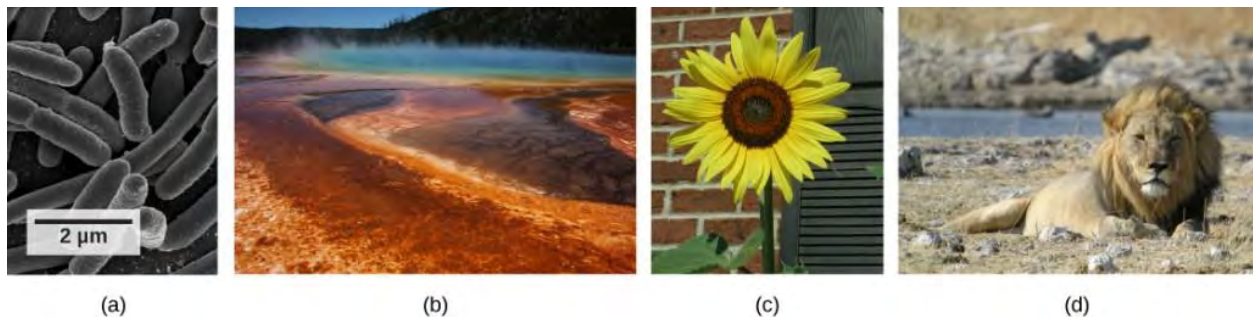
Figure 1.14 These images represent different domains. The scanning electron micrograph shows (a) bacterial cells belong to the domain Bacteria, while the (b) extremophiles, seen all together as colored mats in this hot spring, belong to domain Archaea. Both the (c) sunflower and (d) lion are part of the 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 / Concepts of Biology OpenStax)

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.

The pioneering research of American microbiologist Carl Woese at the University of Illinois has shown that life on Earth has evolved along three lineages, now called domains. The phylogenic tree in Figure 1.15 can be used to show the separation of living organisms into those three domains: Bacteria, Archaea, and Eukarya.
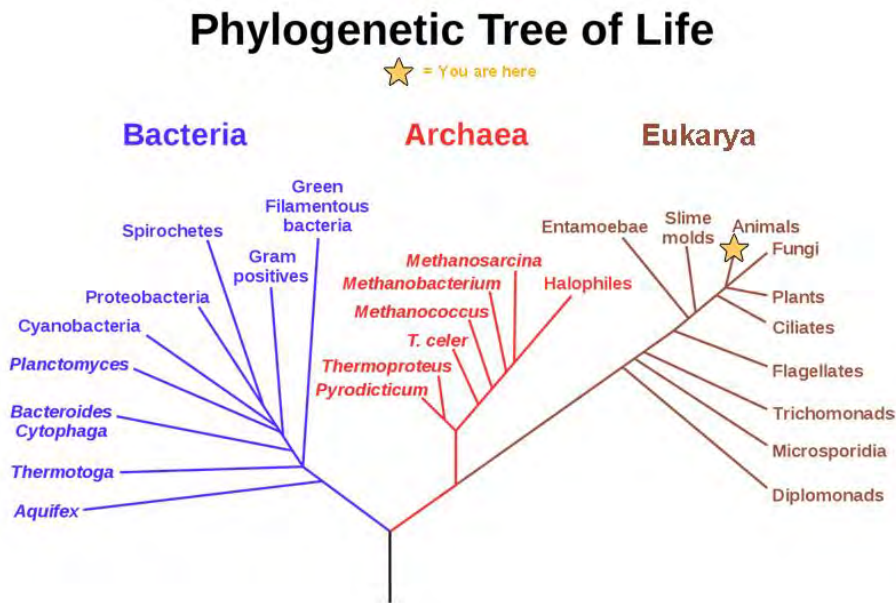
Figure 1.15 This phylogenetic tree was constructed by microbiologist Carl Woese using genetic relationships. (credit: modification of work by Eric Gaba/ Concepts of Biology OpenStax)

Branches of Biological Study

The scope of biology is broad and therefore contains many branches and sub-disciplines. For instance, molecular biology studies biological processes at the molecular level, including interactions among molecules such as DNA, RNA, and proteins. 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.

Paleontology, another branch of biology, uses fossils to study life's history (Figure 1.16). 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 exist within biology.

Figure 1.16 Researchers work on excavating dinosaur fossils at a site in Castellón, Spain. (credit: Mario Modesto/ Concepts of Biology OpenStax)

CAREER CONNECTION - 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 materials 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.

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 processing DNA (Figure 1.17a) found in many different environments and materials. Forensic scientists also analyze biological evidence left at crime scenes, such as insect parts or pollen grains (Figure 1.17b). 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 1.17a This forensic scientist works in a DNA extraction lab. (credit: U.S. Army CID Command Public Affairs/ Concepts of Biology OpenStax) b. This scientist uses microscopy for sample analysis. (credit: National Cancer Institute /Public Domain)

Section Summary

Biology is the science of life. All living organisms share several key properties such as order, response to stimuli, reproduction, adaptation, growth and development, homeostasis, and energy processing. Living things are highly organized following a hierarchy that includes atoms, molecules, organelles, cells, tissues, organs, and organ systems. Organisms 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, and ecology, among others.

Exercises

1. 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.

2. The smallest unit of biological structure that meets the functional requirements of "living" is the _____.
    a. organ
    b. organelle
    c. cell
    d. macromolecule

3. 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

4. Briefly explain how evolution is a source of species diversity.

Answers

1. (b)
2. (c)
3. (d)
4. Evolution leads to genetic changes in a population. For example, if you had a population of insects that live on a maple tree, some insects may begin to feed selectively on the bark of the tree, while others may selectively feed on the leaves. Over time, genetic changes can occur that may prevent these two groups from breeding with one another. In this case, a speciation event has occurred, increasing species diversity.

Glossary

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

autotroph: an organism that can make its own food from materials in its environment

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

domain: the highest level of the taxonomic hierarchy; includes the Eukarya, Archaea, and Bacteria

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

heterotroph: an organism that cannot make its own food and must consume other organisms to obtain its energy

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

1.2 The Process of Science
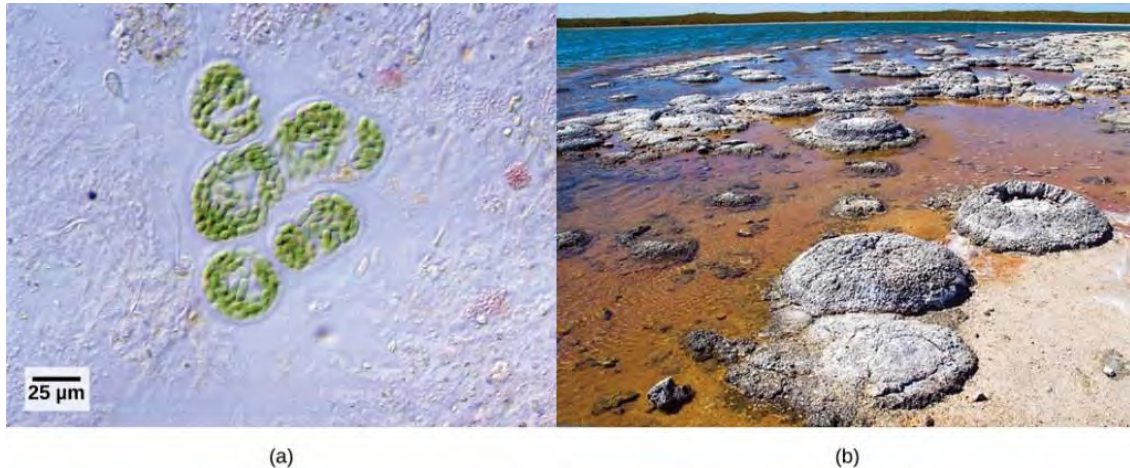
Figure 1.18 (a) cyanobacteria seen through a light microscope are some of Earth's oldest life forms (b) stromatolites along the shores of Lake Thetis in Western Australia are ancient structures formed by the layering of cyanobacteria in shallow waters. (credit a: modification of work by NASA; scale-bar data from Matt Russell; credit b: modification of work by Ruth Ellison / Concepts of Biology OpenStax)

Learning objectives

By the end of this section, you will be able to:

- *Understand the process of scientific inquiry*
- *Know the steps of the scientific method and be able to apply it*
- *Be prepared to explain how a hypothesis is different than a theory*
- *Compare inductive reasoning with deductive reasoning*
- *Describe the goals of basic science and applied science*
- *Be prepared to define and explain all bolded terms*

Biology is a science that gathers knowledge about the natural world (Figure 1.18). Specifically, **biology** is the study of life. Biological discoveries are made by a community of researchers who work both individually and together using agreed-on methods. 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. Science has significant practical implications and applications, for example, in the prevention of disease (Figure 1.19). Other types of science are 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 1.19 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 / Concepts of Biology OpenStax)

The Nature of Science

Science can be defined as knowledge about the natural world. It is a precise way of learning about the world and is largely responsible for the technological revolutions that have taken place. There are, however, areas of knowledge and human experience that the methods of science cannot be applied to. These include such things as answering moral questions, aesthetic questions, or spiritual questions. Science cannot investigate these areas because they are outside the realm of natural phenomena and cannot be observed and measured.

The **scientific method** is a method of research with defined steps that includes careful observation and experiments. The steps of the scientific method will be examined in greater detail later, but one of the most important aspects of the scientific method is the testing of hypotheses. A **hypothesis** (plural hypotheses) is a suggested explanation for a scientific question or an observation, which can be tested. A good hypothesis should be clear and concise. It should also lead to **predictions,** which are statements that describe what should happen if the hypothesis is correct and supported. A hypothesis should also be **falsifiable**, meaning the hypothesis can be incorrect if data that is collected refutes the hypothesis. An example of a hypothesis that is not falsifiable is, "Chicago is the most beautiful city in the world." There is no experiment that might show this statement is false. Once a hypothesis has undergone rigorous testing, and large amounts of data have been collected by multiple research groups who have drawn the same or similar conclusions, the hypothesis is referred to as a theory. In science, a **theory** is a confirmed explanation for a set of observations or phenomena that has been thoroughly tested and supported with substantial amounts of data. In this way, it is very different than a hypothesis. However, like hypotheses, theories are testable, falsifiable, and lead to predictions. A scientific theory is the foundation of scientific knowledge. Also, in many scientific disciplines (less so in biology), there are scientific laws, often expressed in mathematical formulas. Scientific laws describe how elements of nature will behave under certain specific conditions. There is not a strict process that a hypothesis must go through to become a theory or a law. 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

Those fields of science related to the physical world and its phenomena and processes are considered natural sciences. There is no complete agreement when it comes to defining what the natural sciences include (Figure 1.20). For some experts, the natural sciences are astronomy, biology, chemistry, earth science, and physics. Other scholars choose to divide natural sciences into life sciences and physical sciences. Life sciences study living things and include biology. Physical sciences study nonliving matter and include astronomy, physics, and chemistry. Some disciplines, such as biophysics and biochemistry, build on two sciences, and are interdisciplinary.
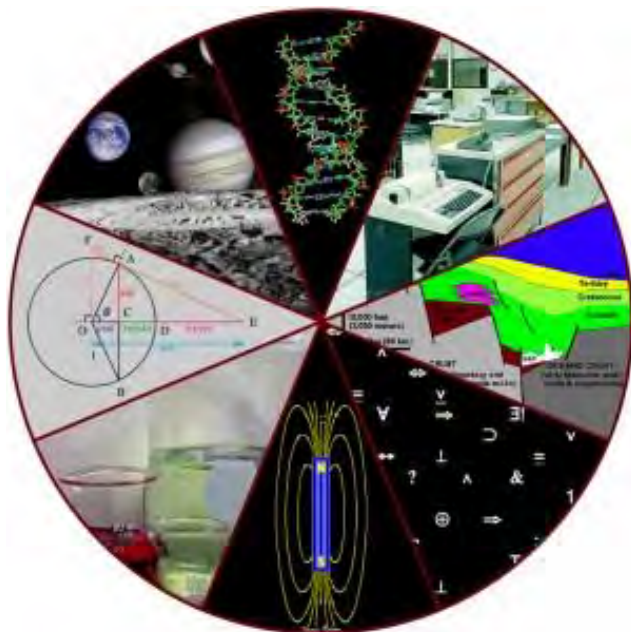
Figure 1.20 Some fields of science include astronomy, biology, computer science, geology, logic, physics, chemistry, and mathematics. (credit: "Image Editor" Flickr / Concepts of Biology OpenStax)

Scientific Inquiry

One thing is common to all forms of science: the ultimate goal is to obtain knowledge. 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**, which is descriptive or categorical, or they can be **quantitative**, consisting of numbers. 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 predict specific results. From those general principles, a scientist can extrapolate and predict the specific results that would be valid so 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 valid.

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. 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 typically starts with an observation that leads to a question. Observations can be made using any or all of an individual's general senses such as touch and/or their special senses such as vision. (Students planning to take Anatomy and Physiology will learn more about your different senses.) Let's think about a scenario that starts with an observation and apply the scientific method to address the observation. One Monday morning, a student arrives in 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 arm?"

Recall that a hypothesis is a testable explanation to the question. 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 formulated, a prediction can 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. 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 shown to be false or eliminated, but it can never be proven true. Science does not deal with proof, like mathematics. If an experiment supports the hypothesis, this is not to say that down the road, a better explanation will not be found, which is why the word "prove" is not used when a hypothesis is supported.

Each experiment will have variables, controls, and experimental groups. A variable is any part of the experiment that can vary or change during the experiment. There are typically three kinds of variables: independent, dependent, and standardized. The **independent variable** is the variable that is being altered or changed by the researcher. It is the variable whose effect is being tested. The **dependent variable** is the variable that may change when the independent variable is applied. This is what the researcher will observe, measure, and record during the experiment. The **standardized variables** are variables that must be kept consistent among all test groups; otherwise, they can affect the outcome or results of the experiment. The **experimental groups** in an experiment receive varying types or amounts of the independent variable. A control group is usually included as a basis of comparison for the experimental groups. For the **control group** the independent variable is absent or set to some predetermined standard. Look for the variables, controls, and experimental group(s) in the following example.

An experiment is conducted to test the hypothesis that phosphate availability 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 is treated by adding salt. Salt is a known substance that is not used by algae. The independent variable here is the phosphate. The experimental groups are the ponds to which phosphate was added, and the control group is the ponds to which the salt was added. Adding the salt is a control against the possibility that adding extra matter to the pond influences algae growth. Some factors must be standardized in both the control and experimental ponds. For example, both the temperature and pH of the water should be standardized. If the water in the control ponds has a significantly higher temperature or pH compared to the water used in the experimental ponds, this could influence the growth of algae. These factors need to be measured and kept relatively constant between the two groups. These are examples of standardized variables. If the ponds treated with phosphate show more algae growth than the control ponds, then we have found support for our hypothesis. If they do not, then we reject our hypothesis. Be aware that rejecting a hypothesis does not determine whether or not the other hypotheses can be accepted; it simply eliminates one hypothesis that is not valid (Figure 1.21).
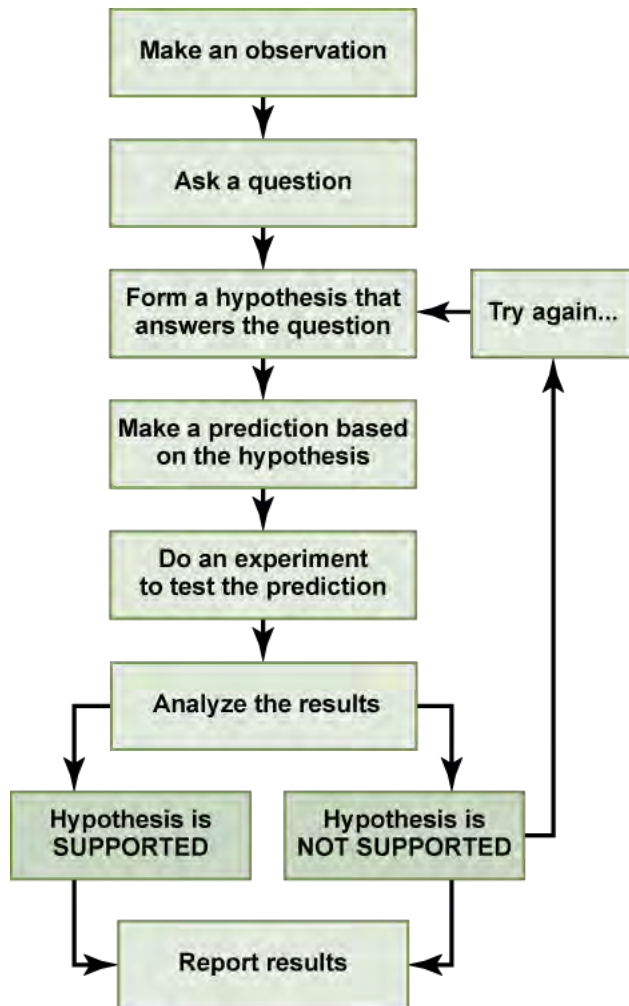
Figure 1.21 The scientific method is a series of defined steps that include experiments and careful observation. (credit: Fowler et al. / Concepts of Biology OpenStax)

In the example below, the scientific method is used to solve an everyday problem.

Check your knowledge

Which option 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, then my coffeemaker also won't work when plugged in.
5. I plug my coffeemaker into the outlet.
6. My coffeemaker works.

Answers: (3) hypothesis; (4) prediction; The hypothesis would be rejected.
Hypothesis 2: The toaster has a loose wire and is broken.

The scientific method is not as rigid and structured as it might first appear. Sometimes an experiment leads to conclusions that favor a change in approach. Often, experiments bring about entirely new scientific questions. Many times, science does not operate linearly; 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 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 by the researcher.

One example of how basic and applied science can work together occurred with the discovery of the DNA structure. This discovery then led to the understanding of the molecular mechanisms that control DNA replication. Every human has unique chromosomes, strands of DNA wrapped around proteins, found in their cells. DNA provides the instructions necessary for life. During cell division, new copies of DNA must be made before a cell divides to form two new cells (Figure 1.22). 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.
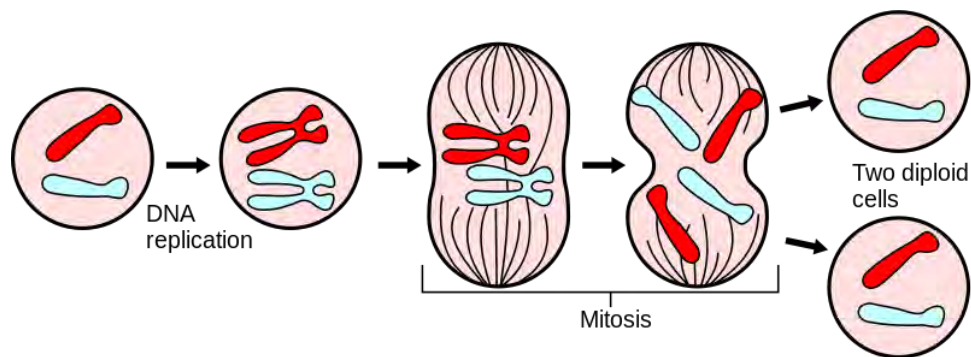
Figure 1.22 Shows DNA replication and cell division by the process of mitosis. Note: diploid means each cell has pairs of chromosomes. (credit: Mysid / Wikimedia Commons)

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 essential 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 a few individuals 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 the scientist's work is suitable for publication. The process of peer review helps to ensure that the research described in a scientific paper is original, significant, logical, and thorough.

There are many journals and the popular press that do not use a peer-review system. Results of any studies published in non-peer reviewed forums are not always reliable, and caution should be used when examining the validity of the work. Sometimes information can be portrayed as scientific fact but lack objective, repeatable data. **Pseudoscience** is claims or beliefs that are represented as scientific fact but cannot be evaluated using the scientific method. For example, astrology is based on a set of beliefs that connect an individual's personality traits with their astrological sign. Scientists using the scientific method have not been able to generate any data that supports these claims and connections. As a result, astrology can be used as an example of pseudoscience.

Today, data and information are readily accessible online through the internet. The internet offers a unique platform to share information across the world, which can help advance both scientific discovery and knowledge. However, it is always important to consider when looking at information online, where the data is coming from, and how valid this information is.

Section 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, testable explanation for an observation or question. A scientific theory is a well-tested and consistently verified explanation for a set of observations or phenomena that has been universally accepted by the scientific community. A scientific law is a description, often in the form of a mathematical formula. 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.

Exercises

1. In the example below, the scientific method is used to solve an everyday problem. Which part of 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.   Jose notices that all the trees in his backyard are dying. They are having a usual dry summer with very little rainfall. His mom also applied fertilizer to the lawn in the early spring. Jose is curious, "why are the trees are all dying?" Jose thinks that because there has been very little rainfall that explains why the trees are dying. If he waters the trees, then they should begin to grow and stop dying. After watering the trees every day for two months, Jose notices that the trees still seem to be dying.
2. _____claims or beliefs that are portrayed as scientific fact but cannot be evaluated using the scientific method.
    a. Hypothesis
    b. Variable
    c. Pseudoscience
    d. Theory
3. 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
4. Explain the difference between a hypothesis and a theory.

Glossary

biology: the study of life

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 results

dependent variable: the variable that will change when the independent variable is altered; this is what the researcher will measure or observe during the experiment

experimental group: the group where the independent variable is applied

falsifiable: it can be shown to be false by experimental results

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

independent variable: is the variable that is being altered or changed by the researcher; it is the variable being tested

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

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

predictions: statements that describe what should happen if the hypothesis is supported

pseudoscience: claims or beliefs that are portrayed as scientific fact but cannot be evaluated using the scientific method

qualitative data: data that is descriptive

quantitative data: data that is numerical

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

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

standardized variable: variables that must be kept consistent otherwise they can affect the outcome or results of the experiment

Chapter 2: Introduction to the Chemistry of Life
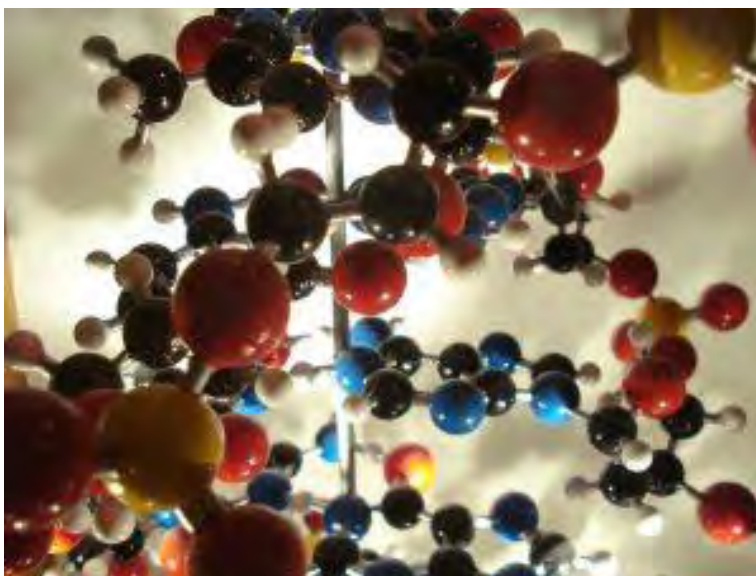
Figure 2.1 Atoms are the building blocks that come together through chemical bonding to form molecules in the universe. In this model of a molecule, the atoms of carbon (black), hydrogen (white), nitrogen (blue), oxygen (red), and sulfur (yellow) are in proportional atomic size. The silver rods indicate chemical bonds that hold the atoms together in a specific three-dimensional shape. (credit: modification of work by Christian Guthier)

The elements carbon, hydrogen, nitrogen, oxygen, sulfur, and phosphorus are the key building blocks found in all living things. Elements are unique forms of matter with specific chemical and physical properties that cannot be broken down into simpler substances by ordinary chemical processes. They form the carbohydrates, lipids, proteins, and nucleic acids which are the fundamental components of all organisms. In this chapter, we will discuss how the unique properties of atoms allow them to interact and form the molecules of life.

2.1 The Building Blocks of Molecules

Learning objectives

By the end of this section, you will be able to:

- *Describe matter, elements, and compounds*
- *Describe the interrelationship between protons, neutrons, and electrons*
- *Be able to use the number of electrons an element has to determine its reactivity*
- *Be able to define and explain all bolded terms*

At its most fundamental level, life is made up of matter. **Matter** is any substance that occupies space and has mass. **Elements** are unique forms of matter with specific chemical and physical

properties that cannot be broken down into simpler substances by ordinary chemical reactions. There are 118 elements, but only 98 occur naturally. The remaining elements are unstable and require scientists to synthesize them in laboratories.

Each element is typically designated by a single capital letter, or two letters if the first letter is already "taken" (Figure 2.2). Some elements follow the English term for the element, such as C for carbon and Ca for calcium. Other elements' chemical symbols are derived from their Latin names. For example, the symbol for sodium is Na, referring to *natrium*, the Latin word for sodium.

Figure 2.2a The element of hydrogen as designated on a periodic table (credit: Science Activist/Flickr) b. The element of helium as designated on a periodic table (credit: Science Activist/Flickr)

The four elements common to all living organisms are oxygen (O), carbon (C), hydrogen (H), and nitrogen (N). Some elements common to all living organisms are relatively rare on the earth as a whole, as Table 2.1 shows. For example, the atmosphere is rich in nitrogen and oxygen but contains very little carbon and hydrogen. The earth's crust contains oxygen and a small amount of hydrogen but has little nitrogen and carbon. In spite of their differences in abundance, all elements obey the same chemical and physical laws.

Approximate Percentage of Elements in Living Organisms (Humans) Compared to the Nonliving World

Element	Life (Humans)	Atmosphere	Earth's Crust
Oxygen (O)	65%	21%	46%
Carbon (C)	18%	trace	trace
Hydrogen (H)	10%	trace	0.1%
Nitrogen (N)	3%	78%	trace

Table 2.1 Approximate Percentage of Elements in Living Organisms (Humans) Compared to the Nonliving World (credit: Clark et al./Biology 2E OpenStax)

Organisms cannot make elements; they must come from the environment. An example of an element that humans must take in is calcium (Ca). When you consume dairy products, calcium is absorbed and used for many processes, including strengthening bones, cell division, muscle contraction, and nervous system function. The elements in the human body are shown in Figure 2.3, beginning with the most abundant: oxygen (O), carbon (C), hydrogen (H), and nitrogen (N). Trace elements are also important to the body but in much lower quantities. Iodine, which is a trace element, is required to make thyroid hormone, an important hormone that regulates body metabolism. Trace element deficiencies will lead to homeostatic imbalances within the body.

Element	Symbol	Percentage in Body
Oxygen	O	65.0
Carbon	C	18.5
Hydrogen	H	9.5
Nitrogen	N	3.2
Calcium	Ca	1.5
Phosphorus	P	1.0
Potassium	K	0.4
Sulfur	S	0.3
Sodium	Na	0.2
Chlorine	Cl	0.2
Magnesium	Mg	0.1
Trace elements include boron (B), chromium (Cr), cobalt (Co), copper (Cu), fluorine (F), iodine (I), iron (Fe), manganese (Mn), molybdenum (Mo), selenium (Se), silicon (Si), tin (Sn), vanadium (V), and zinc (Zn).		less than 1.0
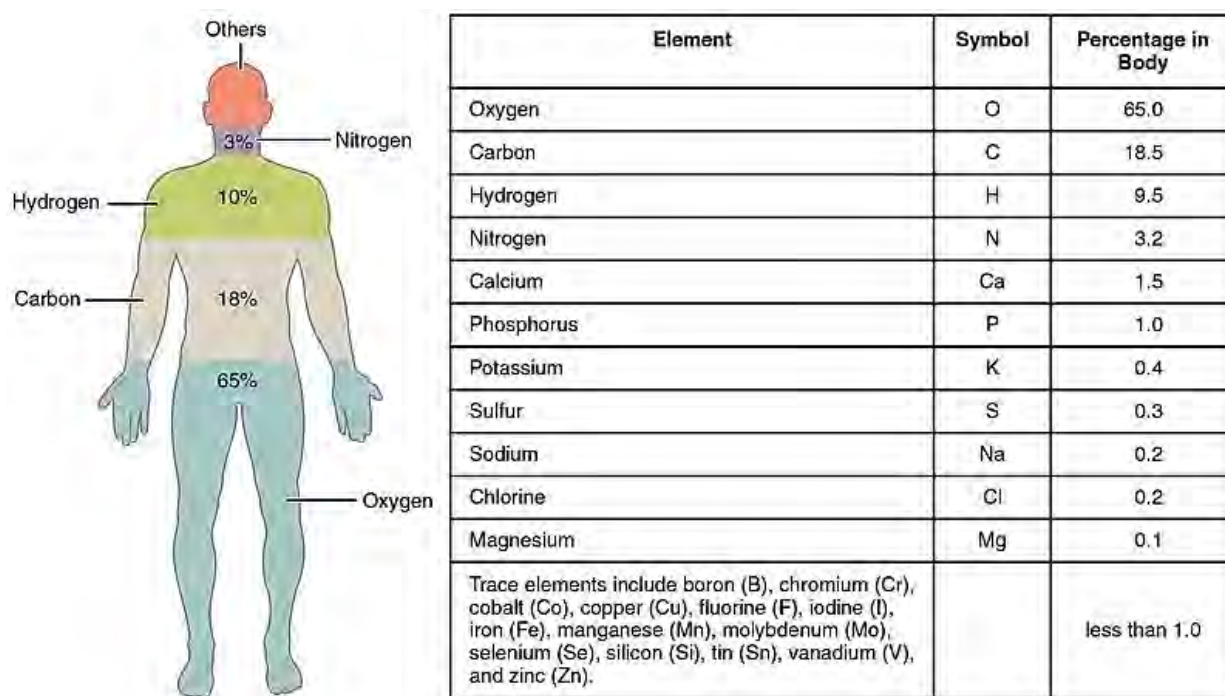
Figure 2.3 Elements of the Human Body - The main elements that compose the human body are shown from most abundant to least abundant. (credit: Betts et al./Anatomy and Physiology OpenStax)

The Structure of the Atom

To understand how elements come together, we must first discuss the element's smallest component or building block, the atom. An **atom** is the smallest unit of matter that retains all the chemical properties of the element. For example, one gold atom has all the properties of gold, such as being a solid metal at room temperature. A gold coin is simply a very large number of gold atoms molded into the shape of a coin and contains small amounts of other elements known as impurities. We cannot break gold atoms down into anything smaller while still retaining the properties of gold.

An atom is composed of two regions. The center of the atom, which is called the **nucleus,** contains subatomic particles called **protons** and **neutrons**. The atom's outermost region holds subatomic particles known as **electrons**. Electrons orbit around the nucleus, as Figure 2.4. illustrates. All atoms, except hydrogen, contain protons, electrons, and neutrons. Most hydrogen atoms contain only one proton and one electron and have no neutrons.
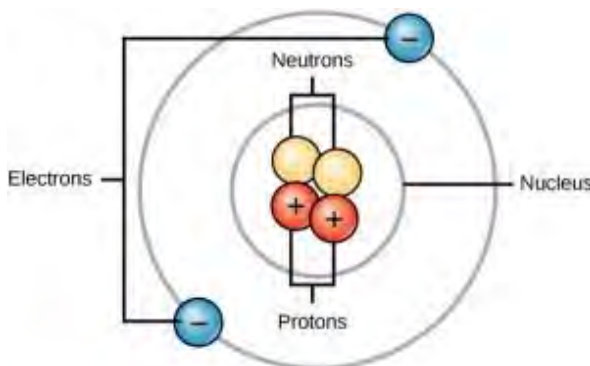
Figure 2.4 Atoms are made up of protons and neutrons located within the nucleus, and electrons surrounding the nucleus. (credit: Clark et al./Biology 2E OpenStax)

Protons and neutrons have approximately the same mass, about 1.67×10^{-24} grams. Scientists arbitrarily define this amount of mass as one atomic mass unit (amu). Although similar in mass, protons and neutrons differ in their electrical charge. A proton is positively charged; whereas, a neutron is uncharged (Table 2.2). The number of neutrons in an atom contributes significantly to its mass, but not to its charge. Electrons are much smaller in mass than protons or neutrons, weighing only 9.11×10^{-28} grams. As a result, electrons do not contribute significantly to an element's overall atomic mass. When calculating atomic mass, it is customary to ignore the mass of any electrons and calculate the atom's mass based on the number of protons and neutrons alone.

Each electron has a negative charge equal to the positive charge of a proton. In uncharged, neutral atoms, the number of electrons orbiting the nucleus is equal to the number of protons inside the nucleus. The atom will have no charge because the positive and negative charges cancel each other out.

Protons, Neutrons, and Electrons

	Charge	Mass (amu)	Location
Proton	+	1	nucleus
Neutron	0	1	nucleus
Electron	–	0	orbitals

Table 2.2 shows the characteristics of the three subatomic particles. (credit: Clark et al./Biology 2E OpenStax)

Most of an atom's volume, greater than 99 percent, is empty space. With all this empty space, one might ask why solid objects do not just pass through one another. The reason this does not occur is due to the electrons that surround all atoms. Electrons are negatively charged, and negative charges of different objects repel one another, preventing this from occurring.

Atomic Number and Mass

Atoms of each element contain a unique number of protons and electrons. The number of protons determines an element's **atomic number**, which scientists use to distinguish one element from another. For example, hydrogen has an atomic number of 1, meaning it has one proton. Helium has an atomic number of 2, meaning it has two protons in its nucleus (Figure 2.2). All atoms of a particular element will have the same number of protons. The number of neutrons an atom has is variable. **Isotopes** are different atoms of the same element that vary only in their number of neutrons. Together, the number of protons and neutrons determines an element's **atomic mass number** (Figure 2.5). Note that we disregard the small contribution of mass from electrons in calculating the mass number. We can use this approximation of mass to easily calculate how many neutrons an element has by subtracting the number of protons from the mass number.

An element's isotopes will all have slightly different mass numbers. When scientists determine the atomic mass of an element, they take the mean of the mass numbers for all its naturally occurring isotopes. Often, the resulting number contains a fraction. For example, the atomic mass of chlorine (Cl) is 35.45 because chlorine is composed of several isotopes, most with atomic mass 35 (17 protons and 18 neutrons) and some with atomic mass 37 (17 protons and 20 neutrons).
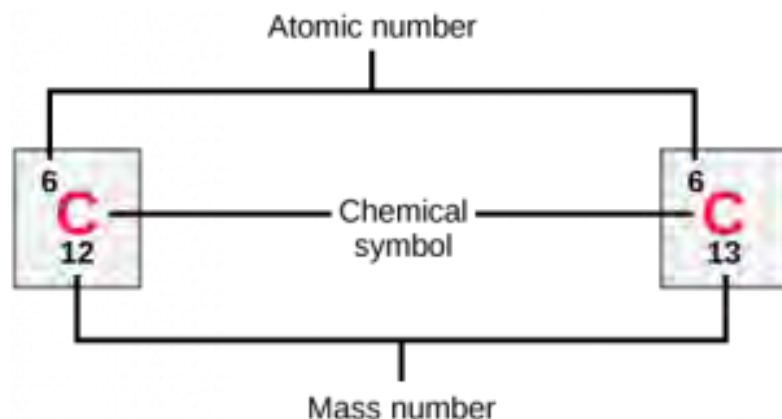
Figure 2.5 Carbon has an atomic number of six, and two stable isotopes with mass numbers of twelve and thirteen, respectively. Its relative atomic mass is 12.011 (credit: Clark et al./Biology 2E OpenStax)

Check your knowledge

How many neutrons does carbon-12 have?

How many neutrons does carbon-13 have?

If an atom has 13 electrons, 13 protons, and 13 neutrons, what is its atomic mass?

Answer: C-12 (6 neutrons); C-13 (7 neutrons)
Atomic mass of 26 amu.

Isotopes

As mentioned above, isotopes are different forms of an element that have the same number of protons but a different number of neutrons. Hydrogen-1 contains one proton, zero neutrons, and one electron. Hydrogen-2, also called deuterium, has one proton, one neutron, and one electron (Figure 2.6). These two alternate forms of hydrogen are isotopes. Some elements, such as carbon, potassium, and uranium, have naturally occurring isotopes. Carbon-12 contains six protons, six neutrons, and six electrons; therefore, it has a mass number of 12. Carbon-14 contains six protons, eight neutrons, and six electrons; its atomic mass is 14. Some isotopes are unstable and will lose neutrons, other subatomic particles, or energy to form more stable atoms. These are called **radioactive isotopes** or radioisotopes.

Protium (^1H)   Deuterium (^2H)   Tritium (^3H)
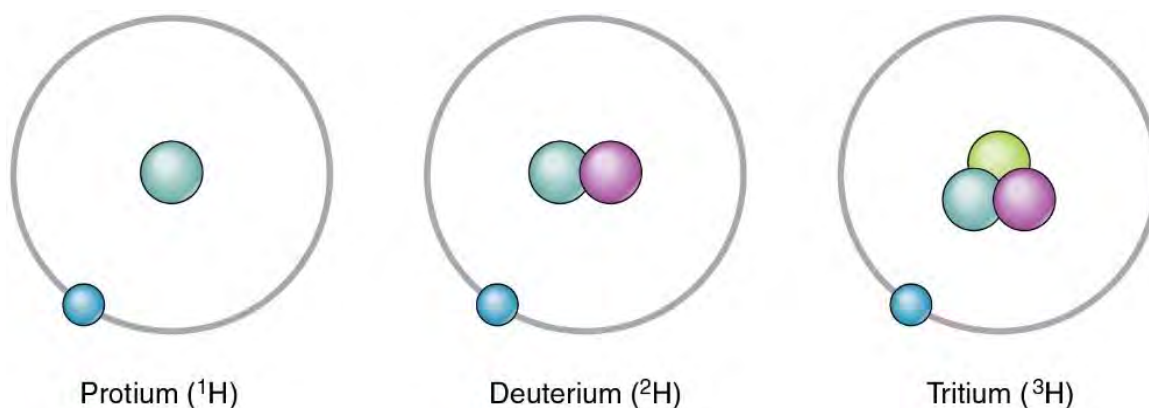
Figure 2.6 Isotopes of Hydrogen. (credit: Betts et al./Anatomy and Physiology OpenStax)

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 a relatively slow process (Figure 2.7).

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 dead organisms or objects, such as fossils.

Figure 2.7 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/Biology 2E OpenStax)

CAREER CONNECTION - Interventional Radiologist

The controlled use of radioisotopes has advanced medical diagnosis and treatment of disease. Interventional radiologists are physicians who treat disease by using minimally invasive techniques involving radiation. Many conditions that could once only be treated with a lengthy and traumatic operation can now be treated non-surgically, reducing the cost, pain, length of hospital stay, and recovery time for patients. For example, in the past, the only options for a patient with one or more tumors in the liver were surgery and chemotherapy. Some liver tumors, however, are difficult to access surgically, and others could require the surgeon to remove too much of the liver. Chemotherapy is also highly toxic to the liver, and certain tumors do not respond well. In some cases, an interventional radiologist can treat the tumors by disrupting the patient's blood supply. In this procedure, called radioembolization, the radiologist accesses the liver with a fine needle, threaded through one of the patient's blood vessels. The radiologist then inserts tiny radioactive "seeds" into the blood vessels that supply the tumors. In the days and weeks following the procedure, the radiation emitted from the seeds destroys the vessels and directly kills the tumor cells in the vicinity of the treatment.

Radioisotopes emit subatomic particles that can be detected and tracked by imaging technologies. One of the most advanced uses of radioisotopes in medicine is the positron emission tomography (PET) scanner. The procedure begins with administering a very small dose of radioactive glucose, the simple sugar that cells use for energy. The PET camera shows the medical team, which of the patient's tissues are taking up the most glucose. Thus, the most metabolically active tissues show up as bright "hot spots" on the images (Figure 2.8). PET can reveal some cancerous masses because cancer cells consume glucose at a high rate to fuel their rapid reproduction.
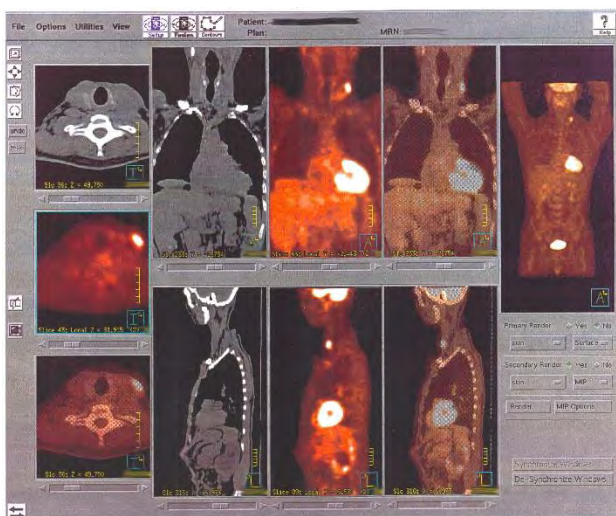
Figure 2.8 PET Scan PET highlights areas in the body where there is relatively high glucose use, which is characteristic of cancerous tissue. This PET scan shows sites of the spread of a large primary tumor to other sites. (credit: Betts et al./Anatomy and Physiology OpenStax)[/caption]

CONCEPTS 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.

The Periodic Table

The **periodic table** organizes and displays different elements. Created by a Russian chemist, Dmitri Mendeleev (1834–1907), in 1869, the table groups elements that, although unique, share certain chemical properties with each other. The properties of elements are responsible for their physical state at room temperature; they may be gases, solids, or liquids. Elements also have specific chemical reactivity. **Reactivity** is the ability of elements to combine and chemically bond with each other.

In the periodic table in Figure 2.9, the elements are organized and displayed according to their atomic number and are arranged in a series of rows and columns based on shared chemical and physical properties. In addition to providing the atomic number for each element, the periodic table also displays the element's atomic mass. Looking at carbon, for example, its symbol (C) and name appear. Its atomic number of six is shown in the upper left-hand corner and its atomic mass of 12.11.

Figure 2.9 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. (credit: Concepts of Biology 1st Canadian Edition)

Check your knowledge

How many neutrons do potassium (K) and oxygen (O) have, respectively?

Answer: potassium - (20 neutrons) and oxygen - (8 neutrons)

The periodic table groups elements according to chemical properties. Scientists base the differences in chemical reactivity between the elements on the number and spatial distribution of an atom's electrons. Atoms that chemically react and bond with each other form molecules. **Molecules** are simply two or more neutral atoms chemically bonded together. The atoms that chemically bond may be identical, or they may be different from one another. Chemical **compounds** differ from molecules in that they are always made up of different types of atoms held together by chemical bonds. Logically, when two atoms chemically bond to form a molecule or compound, their electrons, which form the outermost region of each atom come together first.

Electron Shells and the Bohr Model

There is a connection between the number of protons in an element, the atomic number, and the number of electrons it has. In all electrically neutral atoms, the number of electrons is the same as the number of protons. Each element, at least when electrically neutral, has a characteristic number of electrons equal to its atomic number.

In 1913, Danish scientist Niels Bohr (1885–1962) developed an early model of the atom. The Bohr model describes an atom as having a central nucleus containing protons and neutrons. The

electrons orbit the nucleus at specific distances (Figure 2.10). These orbits form electron shells or energy levels, which are a way of visualizing the number of electrons in the outermost shells. These energy levels are designated by a number and the symbol "n." For example, 1n represents the first energy level located closest to the nucleus.
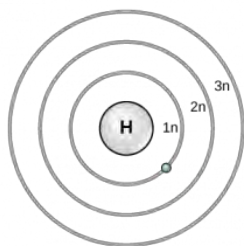
Figure 2.10 Bohr model. (credit: Clark et al./Biology 2E OpenStax)

Electrons fill orbitals in a consistent order. First, they fill the orbitals closest to the nucleus. Once the closest orbitals are filled, electrons fill orbitals of increasing energy further from the nucleus. The number of electrons in the outermost energy level determines the atom's energetic stability, how reactive or nonreactive an atom is. These electrons determine the tendency of an atom to form chemical bonds with other atoms. Remember, when atoms form chemical bonds with one another, molecules are formed.

Under standard conditions, atoms fill the inner shells first, often resulting in a variable number of electrons in the outermost shell. The innermost shell has a maximum of two electrons, but the next electron shell can hold up to eight electrons. This is known as the octet rule, which states, except for the innermost shell, that atoms are more stable energetically when they have eight electrons in their **valence shell**, the outermost electron shell. Figure 2.11 shows examples of some neutral atoms and their electron configurations. Notice that in Figure 2.11, helium has a complete outer electron shell, with two electrons filling its first and only shell. Similarly, neon has a complete outer 2n shell containing eight electrons. Because these atoms have full outer shells, they are considered stable or non-reactive. In contrast, chlorine has seven and sodium one electron in their outer shells, and therefore they are unstable and more likely to react and form chemical bonds with other atoms. An atom's reactivity is governed by its need to be more energetically stable, which results if their valence shells are full.
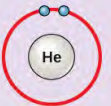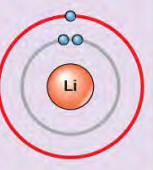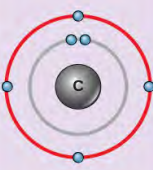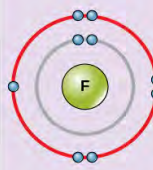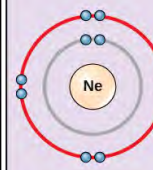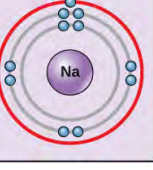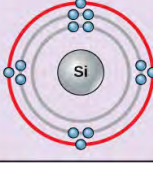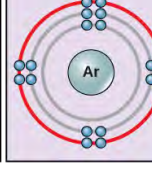
Figure 2.11 Bohr diagrams indicate how many electrons fill each principal shell. Group 18 elements (helium, neon, and argon) have a full outer or valence shell. A full valence shell is the most stable electron configuration. Elements in other groups have partially filled valence shells and gain or lose electrons to achieve a stable electron configuration. (credit: Clark et al./Biology 2E OpenStax)

Check your knowledge

An atom may give, take, or share electrons with another atom to achieve a full valence shell. Looking at the above figure, how many electrons do elements in group 1 need to lose in order to achieve a stable electron configuration?
How many electrons do elements in groups 14 need to gain in order to achieve a stable configuration?

Answers: (1), (4)

Electron Orbitals

Although useful to explain the reactivity and chemical bonding of certain elements, the Bohr model does not accurately reflect how electrons spatially distribute themselves around the nucleus. They do not circle the nucleus like the earth orbits the sun, but we find them in electron orbitals. Scientists call the area where an electron is most likely to be found its **orbital**. While the concepts of electron shells and orbitals are closely related, orbitals provide a more accurate depiction of an atom's electron configuration.

Section Summary

Matter is anything that occupies space and has mass. It is made up of atoms of different elements. All the 98 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.

Exercises

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

2. 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.

3. Oxygen has an atomic number of 8. How many electrons would oxygen need to obtain to be considered stable?
    a. 1
    b. 2
    c. 4
    d. 8

4. An isotope of sodium (Na) has an atomic mass number of 22. How many neutrons does it have?
    a. 11
    b. 12
    c. 22
    d. 44

5. Compare and contrast protons neutrons and electrons.

Answer

1. Potassium-39 has twenty neutrons. Potassium-40 has twenty-one neutrons.
2. (a)
3. (b)
4. (a)
5. Protons, neutrons, and electrons are all subatomic particles that make up an atom. Protons, which have a positive charge, and neutrons that are electrically neutral, can be found in a defined space called the nucleus. Electrons that are negatively charged are found in orbitals that are arranged in discrete energy levels.

Glossary

atom: an element's smallest component or building block

atomic number: the number of protons in an atom

compound: are made up of different types of atoms held together by chemical bonds

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

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

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

molecules: two or more neutral atoms chemically bonded together

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

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

orbital: an area where an electron is most likely to be found its

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

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

reactivity: the ability of elements to combine and chemically bond with each other

valence shell: the outermost electron shell

2.2 Chemical Bonds

Learning objectives

By the end of this section, you will be able to:

- *Understand how electrons can be donated, accepted, or shared between atoms to form chemical bonds*
- *Understand chemical bond strength; which bonds are stronger vs. which bonds are weaker*
- *Understand why chemical bonds differ in strength*
- *Describe the differences between polar covalent and nonpolar covalent bonds. Be able to give examples.*
- *Be able to define and explain all bolded terms*

Chemical Reactions and Molecules

According to the octet rule, all elements are most stable when their outermost shell is filled with electrons. This is because it is energetically favorable for atoms to be in that configuration, and it makes them stable. Since not all elements have enough electrons to fill their outermost shells, atoms form chemical bonds with other atoms. Forming chemical bonds allows atoms to obtain the electrons they need to achieve a stable electron configuration. When two or more atoms chemically bond with each other, a molecule is formed. The familiar water molecule, H_2O, consists of two hydrogen atoms and one oxygen atom. These atoms bond together by sharing electrons to form the water molecule, as Figure 2.12 illustrates. Atoms can form molecules by donating, accepting, or sharing electrons to fill their outer shells.
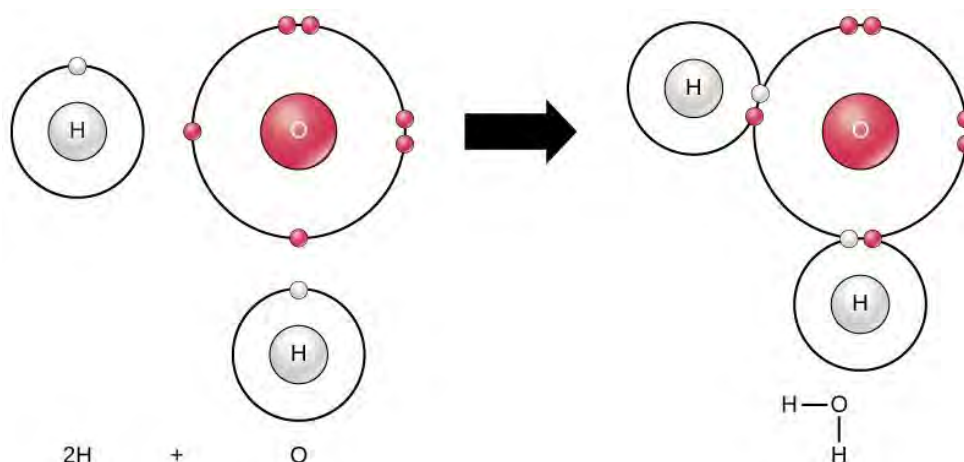
Figure 2.12 When two hydrogens and an oxygen share pairs of electrons via covalent bonds it forms a water molecule. (credit: Clark et al./Biology 2E OpenStax)

Chemical reactions occur when two or more atoms bond together to form molecules or when bonded molecules break apart. We usually call the substances used at the beginning of a chemical reaction **reactants**, and the substances at the end of the reaction **products**. We typically draw an arrow between the reactants and products to indicate the chemical reaction's direction. To create a water molecule, the chemical equation would be:

$$2H + O \rightarrow H_2O$$
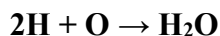
An example of a simple chemical reaction is breaking down hydrogen peroxide molecules. Each hydrogen peroxide molecule consists of two hydrogen atoms bonded to two oxygen atoms (H_2O_2). H_2O_2 is the chemical formula for hydrogen peroxide. A **chemical formula** is a way to show how many and which atoms make up a molecule.

The reactant hydrogen peroxide breaks down into water (H_2O), and an oxygen molecule (O_2). In the equation below, the reaction includes two hydrogen peroxide molecules and two water molecules. This is an example of a balanced chemical equation. Each element's number of atoms is the same on each side of the equation. According to the law of conservation of matter, the number of atoms before and after a chemical reaction should be equal. Under normal circumstances, atoms cannot be created or destroyed.

$$2H_2O_2 \text{ (hydrogen peroxide)} \rightarrow 2H_2O \text{ (water)} + O_2 \text{ (oxygen)}$$
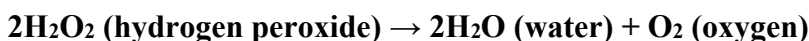
All the reactants and products of this reaction are molecules. However, in this reaction, only hydrogen peroxide and water are chemical **compounds** meaning they contain atoms of more than one type of atom. Molecular oxygen, as Figure 2.13 shows, consists of two oxygen atoms double-bonded together and is not classified as a compound but as a molecule.
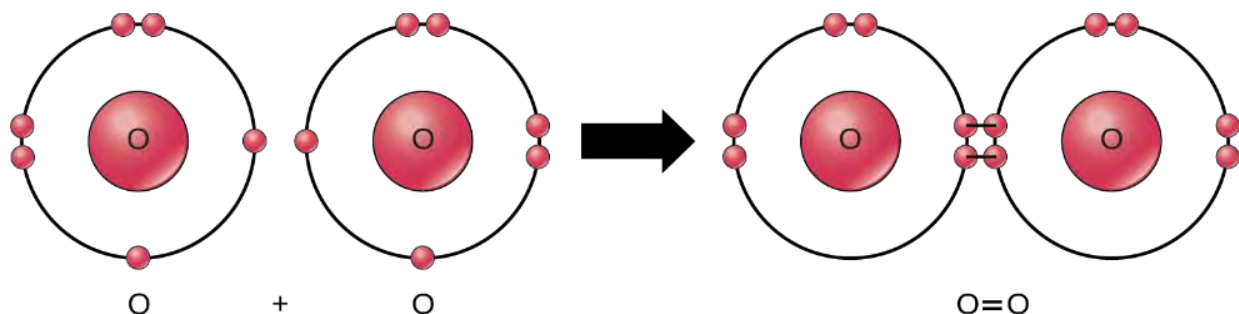
Figure 2.13 A double bond joins the oxygen atoms in an O_2 molecule. (credit: Clark et al./Biology 2E OpenStax)

Reversible reactions are those that can go in either direction. In reversible reactions, reactants turn into products, but when the product's concentration goes beyond a certain threshold, some of these products convert back into reactants. This back and forth continues until a certain relative balance between reactants and products occur, a state called equilibrium. A chemical equation with a double-headed arrow pointing towards both the reactants and products often denote these reversible reaction situations.

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

$$HCO_3^- + H^+ \leftrightarrow H_2CO_3$$

Chemical Bonds

Chemical bonds are interactions between two or more atoms that result in the formation of molecules. An atom can donate, accept, or share electrons with other atoms to fill its outer shell and satisfy the octet rule.

There are three types of bonds or interactions that will be discussed: ionic, covalent, and hydrogen bonds. Ionic and covalent bonds are strong interactions that require a large input of energy to break the bonds apart. Hydrogen bonds are considered weak bonds because they require less energy to break them apart.

Ions and Ionic Bonds

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 outermost 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, Na^{+1} (Figure 2.14a and b).

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, Cl^{-1} (Figure 2.14a and b). This movement of electrons from one element to another is referred to as **electron transfer**.

As Figure 2.14 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 (Figure 2.14a). 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.
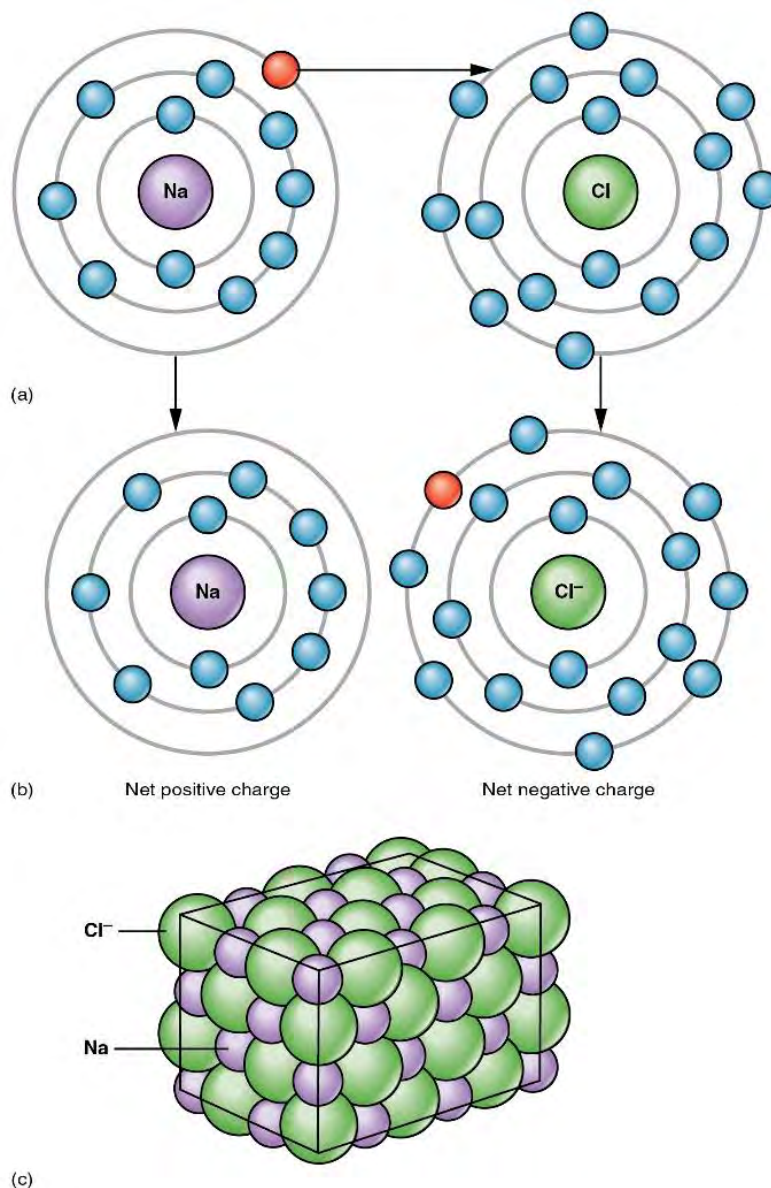
Figure 2.14 Ionic Bonding (a) Sodium donates the electron in its valence shell to chlorine, which needs only one electron to have a full valence shell. (b) The opposite electrical charges of the resulting sodium cation and chloride anion result in the formation of an ionic bond. (c) The attraction of many sodium and chloride ions results in the formation of large groupings called crystals. (credit: Betts et al./Anatomy and Physiology OpenStax)

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 cations and anions are attracted to one another, these ions stay together and form an **ionic bond** or a bond between ions. When proportional amounts of Na^+ and Cl^- ions combine they produce the ionic compound, NaCl, in a crystallized form (Figure 2.14c). The sodium and chloride ions attract each other in a lattice of ions with a net-zero charge forming what is commonly known as table salt Figure 2.15.

Figure 2.15 Edible salt. (credit: Miansari66 / Public Domain)

Covalent Bonds

A covalent bond is another example of a strong chemical bond that can occur between two or more atoms. A **covalent bond** forms when one or more pairs of electrons are shared between atoms. These are some of the strongest and most commonly formed chemical bonds in living organisms. Their strength is greatly attributed to the fact that large amounts of energy are required to break these bonds apart.

For example, the hydrogen atoms and oxygen atom that combine to form water molecules are bound together by covalent bonds. Each atom participating in a covalent bond must share at least one electron. The electron shared by the hydrogen atom divides its time between the outer shell of the hydrogen atom and the outer shell of the oxygen atom. To fill the outer shell of an oxygen atom, two electrons from two hydrogen atoms are needed, hence the subscript "2" in H_2O.

There are two types of covalent bonds: polar and nonpolar. **Nonpolar covalent bonds** form between two atoms that share the electrons equally. For example, an oxygen atom can bond with another oxygen atom to fill their outer shells. This bond is nonpolar because the electrons will be equally distributed between each of the oxygen atoms. Two covalent bonds form between two oxygen atoms because oxygen requires two shared electrons to fill its outermost shell (Figure 2.16).

O + O → O=O
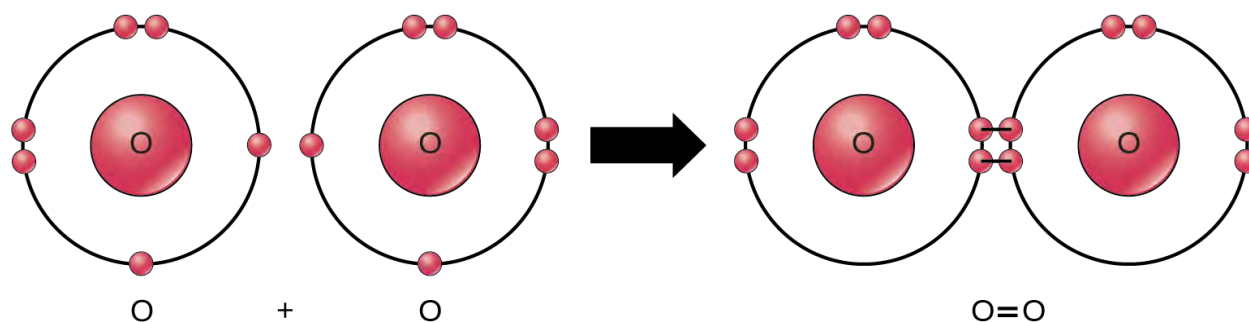
Figure 2.16 A nonpolar covalent bond joins the oxygen atoms in an O_2 molecule. (credit: Clark et al./Biology 2E OpenStax)

Another example of a nonpolar covalent bond is methane (CH_4) (Figure 2.17). Carbon has four electrons in its outermost shell and needs four more to fill it. With methane, (CH_4), it obtains these four electrons from four hydrogen atoms. Each hydrogen atom shares one electron, making a stable outer shell. Hydrogen also now has a full outer shell because it only needs to acquire one additional electron to fill its valence shell. Carbon and hydrogen do not have the same electronegativity but are similar enough that the bonds that form are nonpolar. **Electronegativity** can be thought of as an atom's ability to attract a shared pair of electrons more closely to its own nucleus. If two atoms have the same or similar electronegativities then they will share the pair of electrons equally and partial charges on the atoms participating in the bond will not occur or will be minimal. In the case of methane (CH_4), because the electronegativity of hydrogen and carbon are similar, they share the electrons in a way that creates a nonpolar covalent bond.
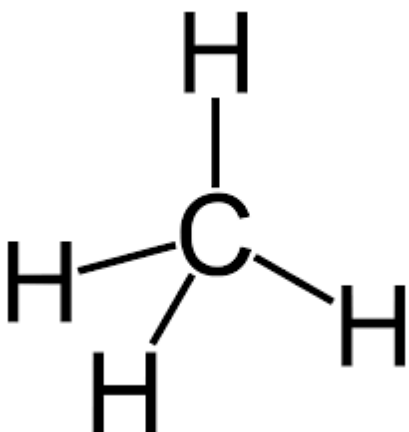
Figure 2.17 A molecule of methane is held together with nonpolar covalent bonds. (credit: Benjah-bmm27/Public Domain)

In a **polar covalent bond**, the shared pair of electrons spend more time closer to one atom's nucleus than to the other atom's nucleus. Because of the unequal distribution of electrons between the different nuclei, a slightly positive ($\delta+$) or slightly negative ($\delta-$) charge develops. The bonds between hydrogen and oxygen atoms in water are polar covalent bonds (Figure 2.18). The shared electrons spend more time near the oxygen nucleus than they spend near the hydrogen nuclei. This results in the oxygen atom having a small negative charge, and the hydrogen atoms having a small positive charge.

Figure 2.18 Polar Covalent Bonds in a Water Molecule (credit: Betts et al./Anatomy and Physiology OpenStax)
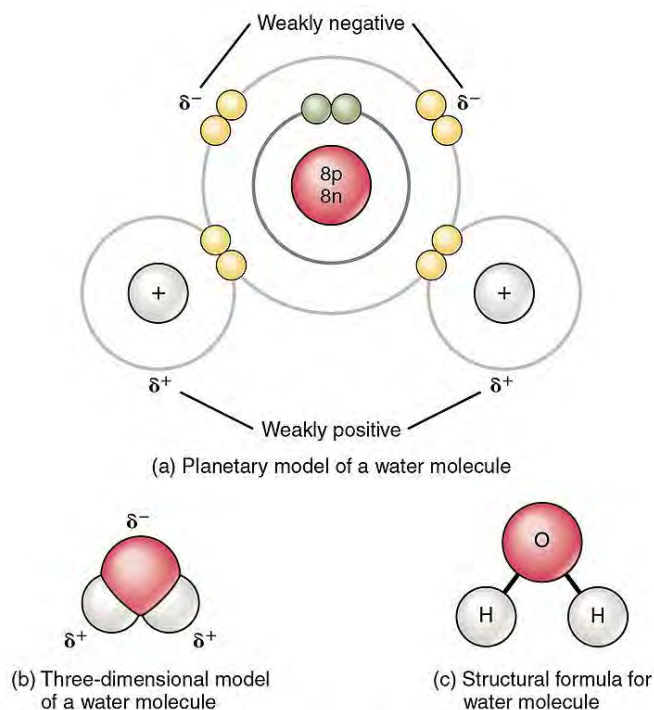
The hydrogen atoms' partial positive charge and the oxygen atom's partial negative charge can be explained by looking at the different electronegativities of these two atoms. The nucleus of an oxygen atom is more attractive to the shared pair of electrons than the hydrogen's nucleus. Thus, oxygen has a higher **electronegativity** than hydrogen and the shared electrons spend more time near the oxygen nucleus than the hydrogen atoms' nucleus (Figure 2.18).

The atom's relative electronegativity contributes to developing partial charges whenever one atom is significantly more electronegative than the other (Figure 2.19). The charges that these polar bonds generate may then be used to form hydrogen bonds. Hydrogen bonds are weak bonds between slightly positively charged hydrogen atoms to slightly negatively charged atoms in other molecules.
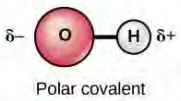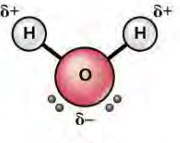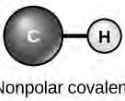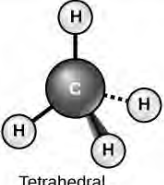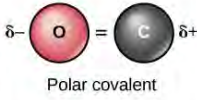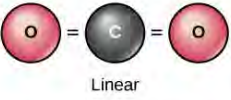
Bond type	Molecular shape	Molecular type
Water $\delta-$ O H $\delta+$ Polar covalent	$\delta+$ H H $\delta+$ O $\delta-$ Bent	Polar
Methane C H Nonpolar covalent	H C H H H Tetrahedral	Nonpolar
Carbon dioxide $\delta-$ O = C $\delta+$ Polar covalent	O = C = O Linear	Nonpolar

Figure 2.19 Whether a molecule is polar or nonpolar depends both on bond type and molecular shape. (credit: Clark et al./Biology 2E OpenStax)

Hydrogen Bonds

Ionic and covalent bonds are strong bonds. As a result, they require large amounts of energy to break. However, not all bonds between elements are ionic or covalent. Weaker bonds can also form. These bonds occur between positive and negative charges that do not require much energy to break. **Hydrogen bonds** are weak bonds but are important because they allow three-dimensional molecules to fold into their appropriate shapes and contribute to the unique properties of water (Figure 2.20).

When polar covalent bonds containing a hydrogen atom form, the hydrogen atom in the bond has a slightly positive charge. Because the hydrogen atom is slightly positive ($\delta+$), it will be attracted to neighboring negative partial charges ($\delta-$). When this happens, a weak interaction occurs between the $\delta+$ charge of the hydrogen atom of one molecule and the $\delta-$ charge of the other molecule. This interaction is called a hydrogen bond (Figure 2.20). For example, the liquid nature of water is caused by the hydrogen bonds between water molecules. 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.
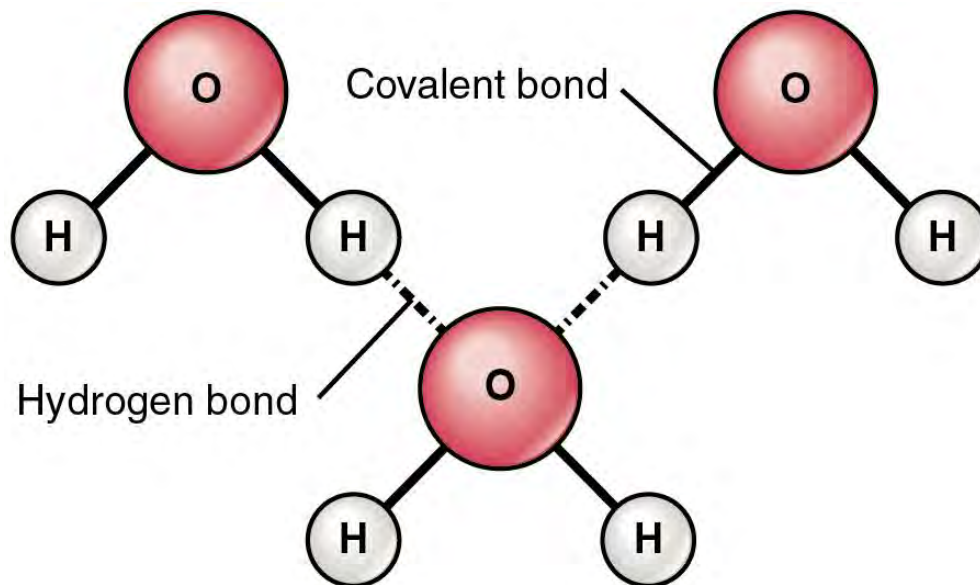
Figure 2.20 Hydrogen bonds form between slightly positive (δ+) and slightly negative (δ–) charges of polar covalent molecules, such as water. (credit: Betts et al. / Anatomy and Physiology)

Hydrogen bonds form between many different molecules not just water. For example, hydrogen bonds hold together two long strands of DNA to give the DNA molecule its characteristic double-stranded structure (Figure 2.21). Hydrogen bonds also cause some proteins to fold into their three-dimensional shapes.
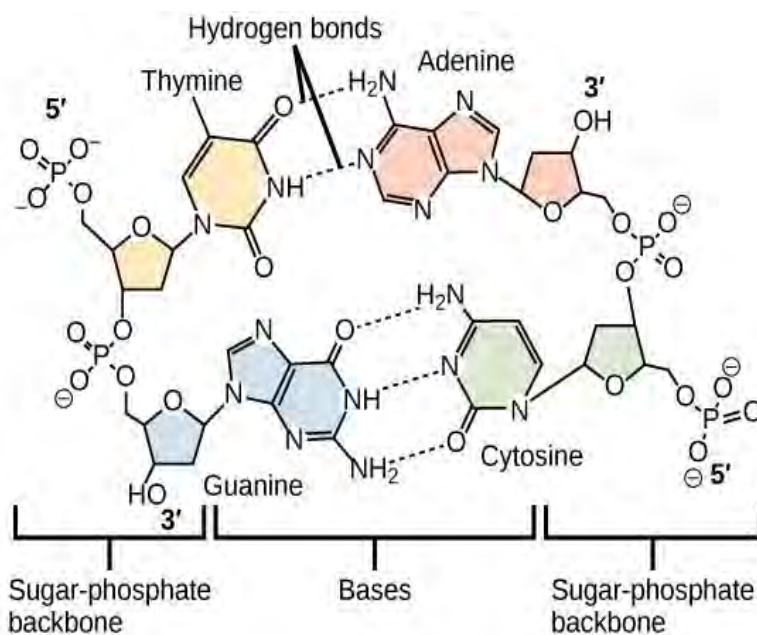
Figure 2.21 Hydrogen bonds connect two strands of DNA to create the double-helix structure. (credit: Clark et al./ Biology 2E OpenStax)

Section Summary

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. Chemical bonds differ in their strengths and lead to the formation of molecules. Hydrogen bonds give water the unique properties that sustain life.

Exercises

1. In the below reaction what is the reactant?

   $2H_2O_2$ (hydrogen peroxide) → $2H_2O$ (water) + O_2 (oxygen)
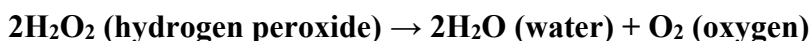
2. Positive ions are formed by losing electrons and are called:
   a. anions
   b. polar molecules
   c. water
   d. cations

3. Which type of bond represents a strong chemical bond where electrons are shared unequally?
   a. hydrogen bond
   b. ionic bond
   c. polar covalent bond
   d. nonpolar covalent bond

4. Compare and contrast ionic and covalent bonds.

5. Hydrogen bonds are weak bonds yet they play an important role in holding the two strands of DNA together. Hypothesize why it would be important that a weak bond is used in this example vs. a strong bond.

Answer

1. Hydrogen peroxide
2. (d)
3. (c)
4. Ionic and covalent bonds both allow for atoms to become more stable and result in the synthesis of molecules and/or chemical compounds. Ionic bonds are chemical bonds that form between ions of opposite charges whereas covalent bonds are a result of atoms sharing pairs of electrons.
5. Hydrogen bonds form weak bonds between different molecules. Before a cell can reproduce it must make a copy of its DNA. If strong bonds were used to hold the two strands together, instead of the weaker hydrogen bonds, the cell would need to invest a lot more energy into reproduction order to first break these bonds.

Glossary

anion: a negative ion formed by gaining electrons

cation: a positive ion formed by losing electrons

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

chemical formula: shows how many and which atoms make up a molecule

compound: are made up of different types of atoms held together by chemical bonds

chemical reactions: occur when two or more atoms bond together to form molecules or when bonded atoms break apart

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

electronegativity: an atom's ability to attract a shared pair of electrons more closely to its own nucleus

electron transfer: the movement of electrons from one element to another

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

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

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

products: the substances that are formed at the end of a chemical reaction (usually on the right side of a chemical equation

reactants: the substances used at the beginning of a chemical reaction (usually on the left side of a chemical equation)

2.3 Water

Do you ever wonder why scientists spend time looking for water on other planets? The reason is simple; water is essential to life. Even minute traces of water 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 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.
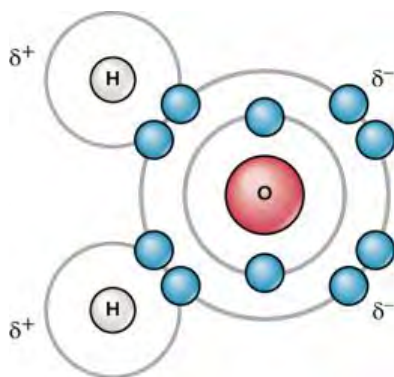
Figure 2.22 The water molecule depicts a polar covalent bond. (credit: modified from Parker et al./Microbiology OpenStax)

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 (Figure 2.22). Because of these charges, the slightly positive hydrogen atoms repel each other and form a unique shape. Each water molecule attracts other water molecules because of the positive and negative charges in the different parts of the water molecule (Figure 2.23).
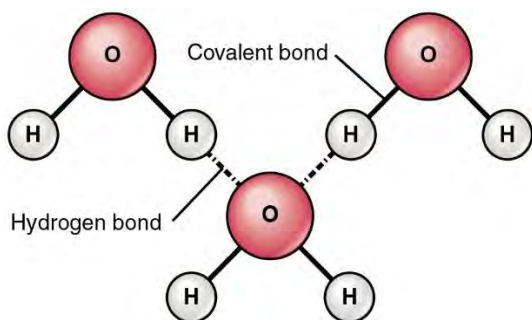
Figure 2.23 Hydrogen bonds form between slightly positive ($\delta+$) and slightly negative ($\delta-$) charges of polar covalent molecules, such as water. (credit: Betts et al. / Anatomy and Physiology OpenStax)

Water also attracts other polar molecules, such as sugars or ions, by forming hydrogen bonds. We call a polar substance that interacts readily with or dissolves in water **hydrophilic** (hydro- = "water"; -philic = "loving"). In contrast, nonpolar molecules such as oils and fats do not interact or dissolve well with water, as shown in Figure 2.24. A good example of this is vegetable oil poured into a glass of water (Figure 2.25). We call such nonpolar substances **hydrophobic** (hydro- = "water"; -phobic = "fearing").

Hydrophobic molecules readily dissolve or interact with other molecules that are also hydrophobic. Some molecules have both hydrophobic and hydrophilic regions as a result of the atoms that make the molecule up. Phospholipids, the major component of the cell membrane, have both a hydrophilic and a hydrophobic region. Phospholipids will be discussed more in chapter 3.

Figure 2.24 As this macroscopic image of oil and water shows, oil is a nonpolar compound and, hence, will not dissolve in water. (credit: Gautam Dogra/ Biology 2E OpenStax)

Figure 2.25 Oil and water separate due to their inability to chemically interact. (credit: Victor Blacus/ Wikimedia Commons)

Water Stabilizes Temperature

The hydrogen bonds in water allow it to absorb and release heat energy more slowly than many other liquids and substances. **Temperature** measures the motion of molecules. As the motion increases, energy is higher, and therefore the temperature is higher. Water can absorb a great deal of energy before its temperature rises due to a large number of hydrogen bonds that hold water

molecules together. This means that water can moderate temperature changes both within organisms and within different 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, and individual water molecules can be released. The release of individual water molecules at the surface of a liquid (such as a body of water, the leaves of a plant, or the skin of an organism) is known as the process of **evaporation**. For example, when humans exercise, their skeletal muscles generate a considerable amount of heat energy. One way humans maintain their temperature homeostasis is by producing sweat using their sudoriferous glands. Sweat, which is 90 percent water, allows for the cooling of an organism because breaking hydrogen bonds in liquid sweat requires a large input of heat energy. Once the sweat begins to evaporate, it takes the heat energy away from the body, which results in a cooling effect.

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 2.26a). When frozen, ice is less dense than liquid water, meaning it floats (Figure 2.26b). This can be explained by the fact that when the temperature is cool, water molecules can form the maximum amount of hydrogen bonds, and the individual water molecules are spaced farther apart. In lakes, ponds, and oceans, ice will form on the surface of the water, creating an insulating barrier which protects the animal and plant life that lives beneath the surface of the water. If this did not happen, plants and animals living in the water would freeze into a block of ice and would not be able to move around freely, making life in cold temperatures difficult, if not impossible.
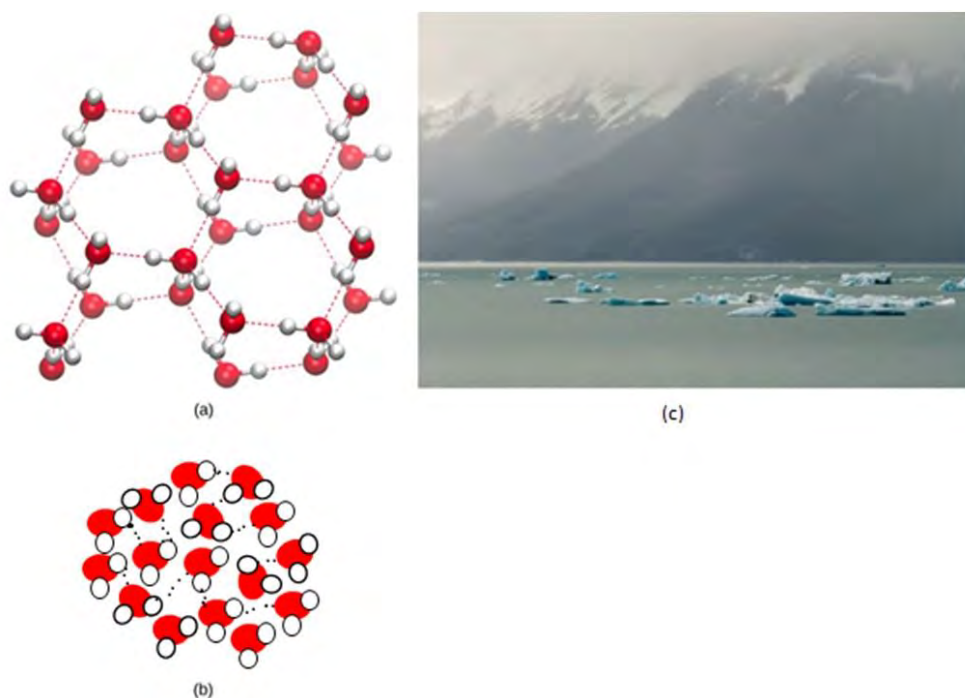
Figure 2.26 (a) Shows the lattice-like molecular structure of ice. (b) In liquid form water molecules pack tightly making it denser c) Shows ice (a) as it floats on liquid water (b). (credit a: modification of work by Jane Whitney; credit b: Elizabeth O'Grady c: modification of work by Carlos Ponte/ Biology 2E OpenStax)

Water Is an Excellent Solvent

Because water is polar, with slightly positive and negative charges, ionic compounds and polar molecules can readily dissolve in it. Water is, therefore, referred to as a **solvent,** a substance capable of dissolving another substance. The **solute** is defined as the substance being dissolved. Together the solute and the solvent make up a **solution**.

In the case of table salt, NaCl, mixed in water, the sodium and chloride ions separate, or dissociate, in the water. The ions remain separated because each independently forms hydrogen bonds with the surrounding water molecules (Figure 2.27). 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. If the water is removed, for example, by boiling the solution, the sodium and chloride ions will once again form ionic bonds, and salt crystals will reform.
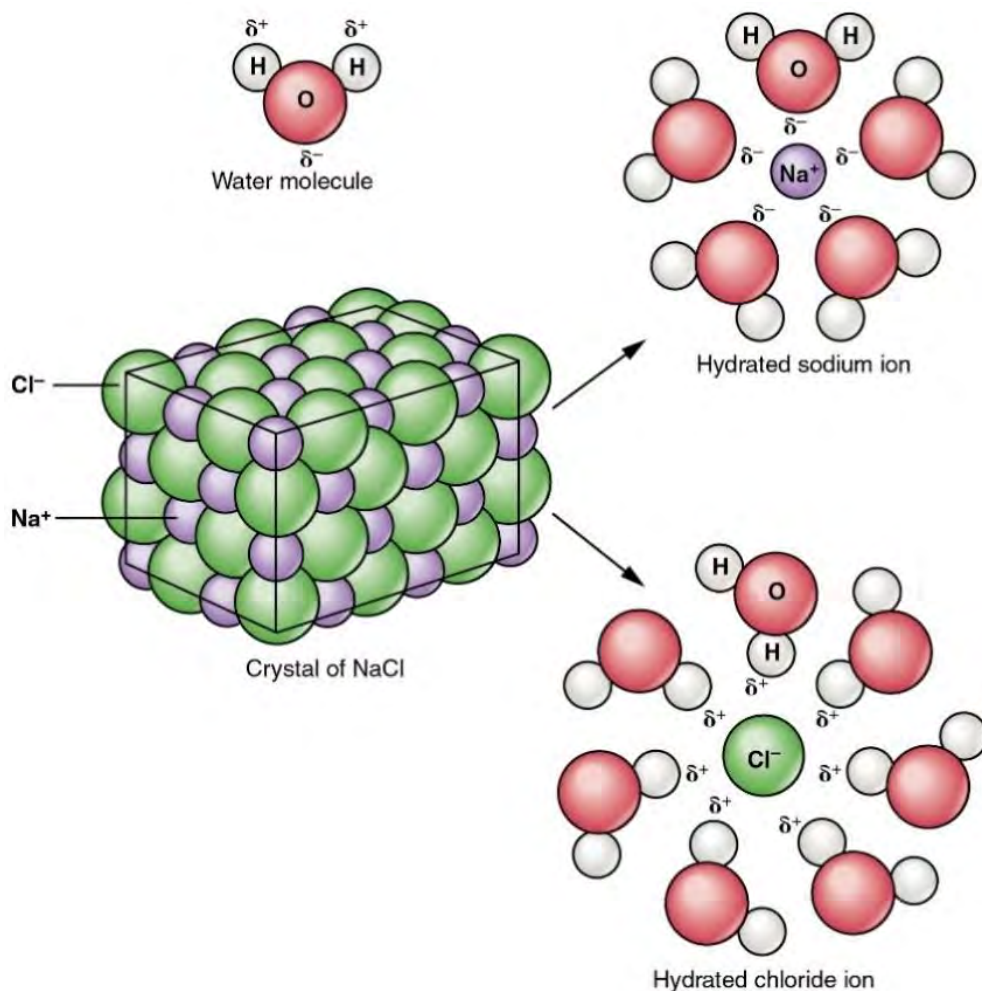
Figure 2.27 Dissociation of Sodium Chloride in Water. Notice that the crystals of sodium chloride dissociate not into molecules of NaCl, but into Na+ cations and Cl– anions, each surrounded by water molecules. (credit: Betts et al./Anatomy and Physiology OpenStax)

Water Is Cohesive and Adhesive

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 forms a dome-like shape above the rim of the glass. 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. 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. The paper floats even though 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 of the water's surface. 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 2.28).

Figure 2.28 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 water, and keeping it from sinking. (credit: Cory Zanker/ Biology 2E OpenStax)

Water is also said to be **adhesive**, meaning that there is an attraction between water molecules and other types of molecules. This is observed when water "climbs" up a straw placed in a glass of water (Figure 2.29). 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.
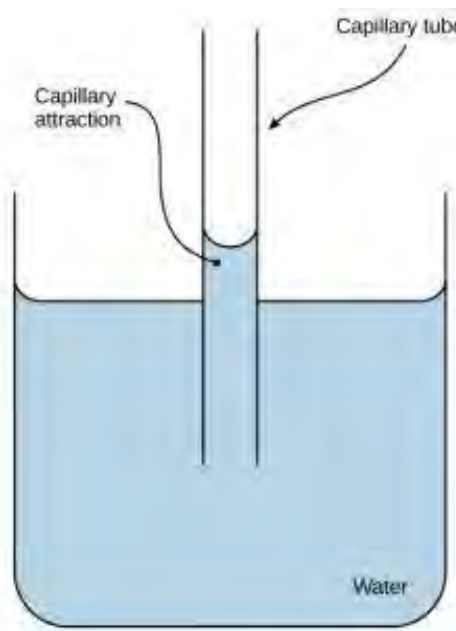
Figure 2.29 shows a straw submerged in water, demonstrating adhesion. (credit: modification of work by Pearson-Scott Foresman, donated to the Wikimedia Foundation/ Biology 2E OpenStax)

Cohesive and adhesive forces are important for sustaining life. For example, because of these forces, water can flow up from the roots of plants to the leaves where photosynthesis occurs. If plants cannot access water via their roots, they cannot make their food and, therefore, cannot survive. In another example, insects such as the water strider (Figure 2.30) use the water's surface tension to stay afloat on the water's surface where they will mate. Without water's unique properties, these individuals would not survive.

Figure 2.30 Water's cohesive and adhesive properties allow this water strider (Gerris sp.) to stay afloat. (credit: Tim Vickers/ Biology 2E OpenStax)

CONCEPTS IN ACTION- To learn more about water, visit the U.S. Geological Survey Water Science for Schools: All About Water! Website

Section Summary

Water has many properties that are critical to maintaining life. Water 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. This allows 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 for the survival of living organisms.

Exercises

1. 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.

2. Water can absorb a large amount of heat energy before the temperature rises due to large amounts of:
   a. polar covalent bonds
   b. hydrogen bonds
   c. its cohesive properties
   d. its adhesive properties

3. Which of the following would be hydrophobic?
   a. NaCl (table salt)
   b. Sugar
   c. Oil
   d. Water

4. Why can some insects walk on water?

5. Explain why water is an excellent solvent.

Answers
1. (d)
2. (b)
3. (c)
4. 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].
5. Water molecules are polar, meaning they have separated partial positive and negative charges. Because of these charges, water molecules can 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.

Glossary

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

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

solution: a homogeneous mixture made of two or more components

solute: the substance being dissolved

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

Footnotes

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/

2.4 pH and Buffers

pH

The pH of a solution is a measure of its acidity or alkalinity. You may have used **litmus paper**, a paper that can be used as a pH indicator, to test how much acid or base exists in a solution. You might have even used litmus paper to make sure the water in an outdoor swimming pool is treated correctly. In both cases, this pH test measures the amount of hydrogen ions that exist in a given solution.

$$H_2O(l) \leftrightarrow H^+(aq) + OH^-(aq)$$
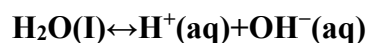
*(aq) means water is the solvent that dissolves the ions

Hydrogen ions spontaneously generate in pure water by the dissociation, ionization, of a small percentage of water molecules. While the hydroxide ions (OH^-) are kept in solution by their hydrogen bonding with other water molecules, the hydrogen ions (H^+), consisting of only a single proton, immediately bond to water molecules forming hydronium ions. For simplicity, scientists still refer to hydrogen ions and their concentration as if they were free in liquid water and not as being bound to water.

Acids

An acid is a substance that releases hydrogen ions (H^+) in solution (Figure 2.31a). Because an atom of hydrogen has just one proton and one electron, a positively charged hydrogen ion is simply a proton. This solitary proton is highly likely to participate in chemical reactions. Strong acids are compounds that release all their H^+ in solution; that is, they ionize completely. Hydrochloric acid (HCl), which is released from cells in the lining of the stomach, is a strong acid because it releases all its H^+ ions in the stomach's watery environment. This strong acid aids in digestion and kills ingested microbes. Weak acids do not ionize completely; that is, some of their hydrogen ions remain bonded within a compound in solution. An example of a weak acid is vinegar or acetic acid.
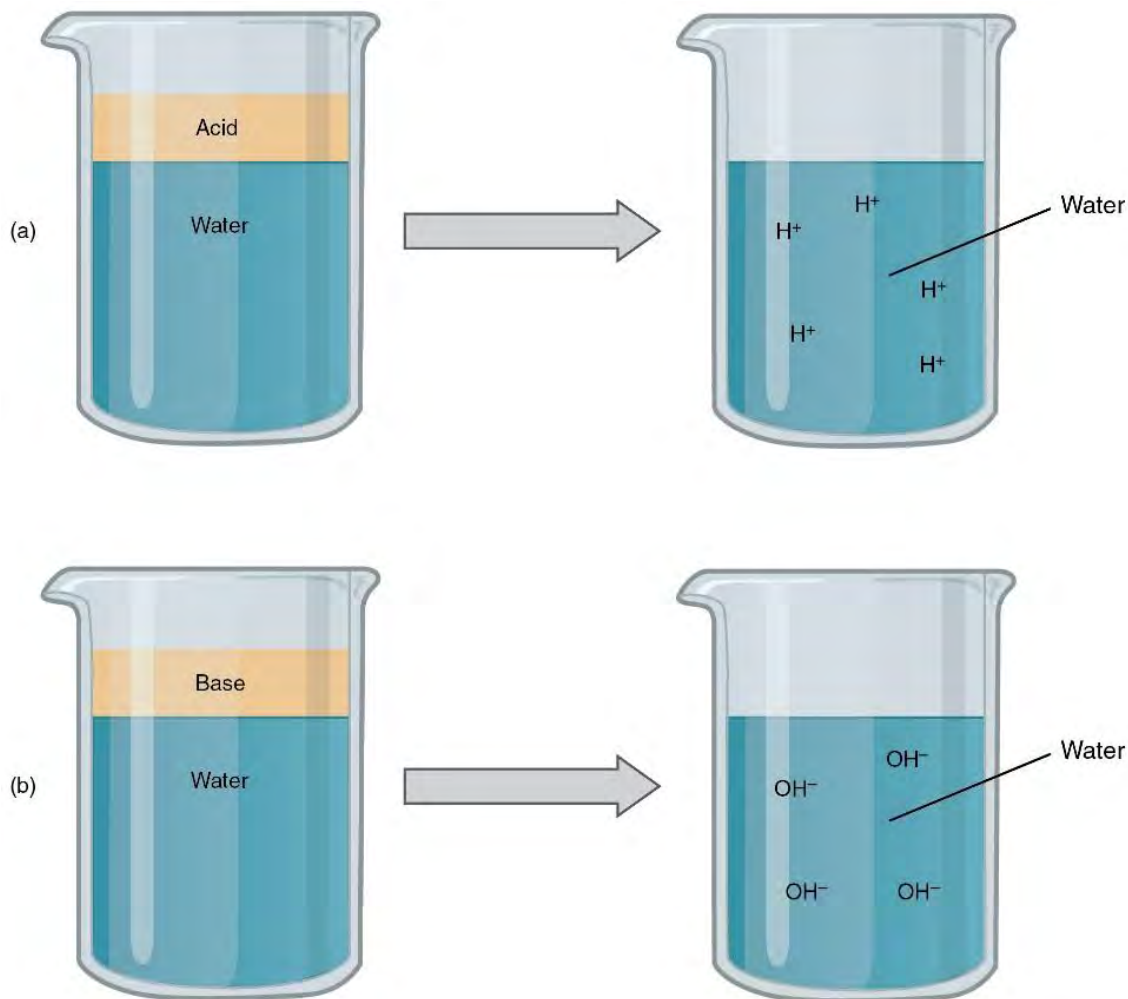
Figure 2.31 Acids and Bases (a) In aqueous solution, an acid dissociates into hydrogen ions (H+) and anions. (b) In aqueous solution, a base dissociates into hydroxyl ions (OH^-) and cations. (credit: Betts et al./Anatomy and Physiology OpenStax)[/caption]

Bases

A base is a substance that releases hydroxide ions (OH^-) in solution, or one that accepts H^+ already present in solution (Figure 2.31b). The hydroxide ions combine with H^+ present to form water molecules, thereby removing H^+ and reducing the solution's acidity. Strong bases release most or all their hydroxide ions; weak bases release only some hydroxide ions or absorb only a few H^+. Food mixed with hydrochloric acid (HCl) from the stomach would burn the cells that make up the small intestine if it were not for the release of bicarbonate (HCO_3^-), a weak base that attracts H^+. Bicarbonate accepts some of the H^+, thereby reducing the acidity of the solution.

The Concept of pH

The relative acidity or alkalinity of a solution can be indicated by its pH. A solution's pH is the negative, base-10 logarithm of the hydrogen ion (H^+) concentration of the solution. As an example, a pH four solution has a H^+ concentration that is ten times greater than that of a pH five solution. That is, a solution with a pH of 4 is ten times more acidic than a solution with a pH of 5. The concept of pH will begin to make more sense when you study the pH scale shown in Figure 2.32. The scale consists of a series of increments ranging from 0 to 14. A solution with a pH of 7 is considered neutral, neither acidic nor basic. Pure water has a pH of 7. The lower the number below 7, the more acidic the solution, or the greater the concentration of H^+. The higher the number above 7, the more basic (alkaline) the solution, or the lower the concentration of H^+. Human urine, for example, is ten times more acidic than pure water, and HCl is 10,000,000 times more acidic than water.

Most cells operate within a very narrow pH range. For example, the pH of human blood typically ranges from 7.2 to 7.6. If the pH fluctuates outside of this range, several organ systems in the body can malfunction. Cells that make up plants also function within specific pH limits. Corn, for example, often grows best when the pH is between 5.5-7. If the pH varies too high or too low, cells no longer function properly, and proteins will break down. Deviation outside of the pH range can even result in death.
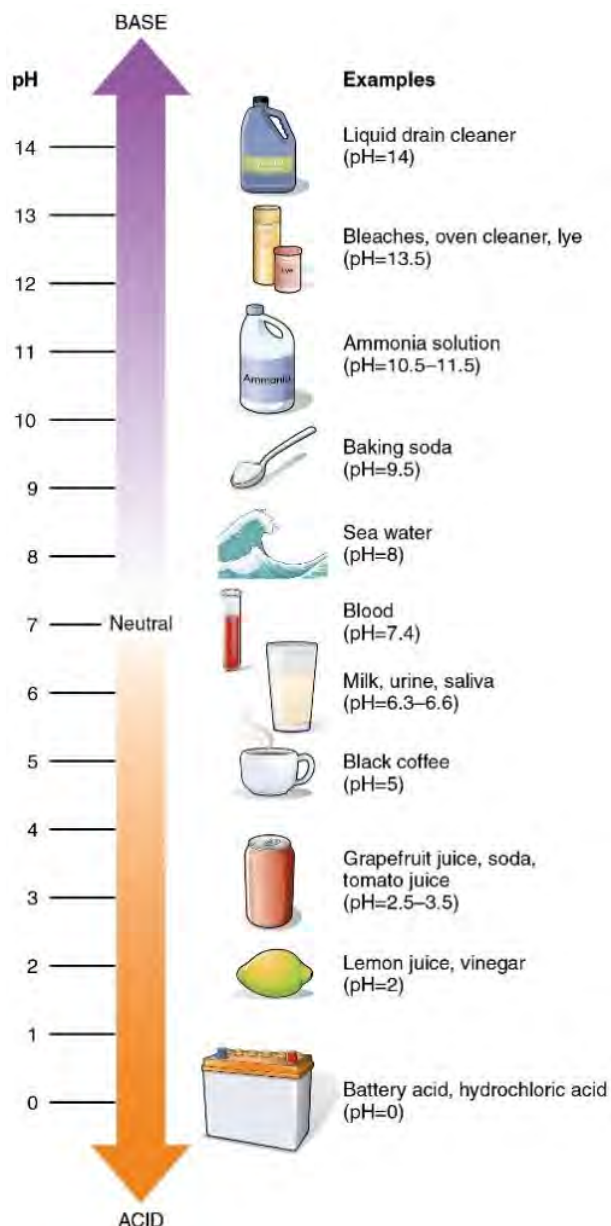
Figure 2.32 The pH Scale (credit: Betts et al./Anatomy and Physiology OpenStax)

So how is it that organisms deal with changes in pH? How is it that we can ingest or inhale acidic or basic substances and not die? For example, how is that we can drink orange juice, an acidic solution, and yet survive? The body has several mechanisms for regulation, involving breathing, the excretion of chemicals in urine, and the internal release of chemicals called buffers into body fluids. **Buffers** readily absorb excess H^+ or OH^-, keeping the pH of the body carefully maintained within a narrow range. Carbon dioxide is part of a prominent buffer system in the human body; it keeps the blood pH within the proper range of approximately 7.4. This buffer

system involves carbonic acid (H_2CO_3) and bicarbonate (HCO_3^-) anion (Figure 2.33). 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. Without this buffer system, the pH in our bodies would fluctuate too much, and we would fail to survive.
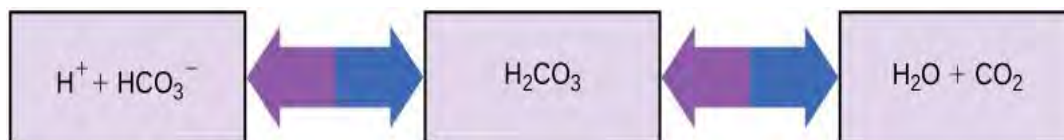
Figure 2.33 This diagram shows the body's buffering of blood pH levels. The blue arrows show the process of raising pH as more CO2 is made. The purple arrows indicate the reverse process: the lowering of pH as more bicarbonate is created. (credit: Clark et. al / Biology 2E OpenStax)

Antacids are another example of buffers that people sometimes use to deal with excess stomach acid. Many of these over-the-counter medications work in the same way as blood buffers, usually with at least one ion capable of absorbing hydrogen ions. This results in an increase of pH, bringing relief to those who suffer "heartburn" after eating.

HOMEOSTATIC IMBALANCES - Acids and Bases

Excessive acidity of the blood and other body fluids is known as acidosis. Common causes of acidosis are situations and disorders that reduce the effectiveness of breathing, especially the person's ability to exhale fully, which causes a buildup of CO_2 and H^+ in the bloodstream. Acidosis can also be caused by metabolic problems that reduce the level or function of buffers that act as bases or promote the production of acids. For instance, with severe diarrhea, too much bicarbonate can be lost from the body, allowing acids to build up in body fluids. In people with poorly managed diabetes ineffective regulation of blood sugar, acids called ketones are produced as a form of energy to fuel the body. These can build up in the blood, causing a serious condition called diabetic ketoacidosis. Kidney failure, liver failure, heart failure, cancer, and other disorders also can prompt metabolic acidosis.

In contrast, alkalosis is a condition in which the blood and other body fluids are too alkaline (basic). As with acidosis, respiratory disorders are a major cause. In respiratory alkalosis, carbon dioxide levels fall too low. Lung disease, aspirin overdose, shock, and ordinary anxiety can cause respiratory alkalosis, which reduces the normal concentration of H^+.

Metabolic alkalosis often results from prolonged, severe vomiting, which causes a loss of hydrogen and chloride ions. Medications can also prompt alkalosis. These include diuretics that cause the body to lose potassium ions, as well as antacids when taken in excessive amounts.

Section Summary

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.

Exercises

1. Acids:
   a. Increase OH^- ions in solution
   b. Decrease OH^- ions in solution
   c. Decrease H^+ ions in solution
   d. Increase H^+ ions in solution

2. 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

3. 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

4. Explain why buffers are biologically important.

Answers

1. (d)
2. (c)
3. (c)
4. Buffers readily absorb excess H^+ or OH^-, keeping the pH of the body carefully maintained within a specific range. If the pH deviates outside of this range, body systems can malfunction. Cells no longer function properly, and proteins will break down.

Glossary

acid: a substance that donates hydrogen ions and therefore lowers pH

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

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

Chapter 3 Biologically Important Molecules
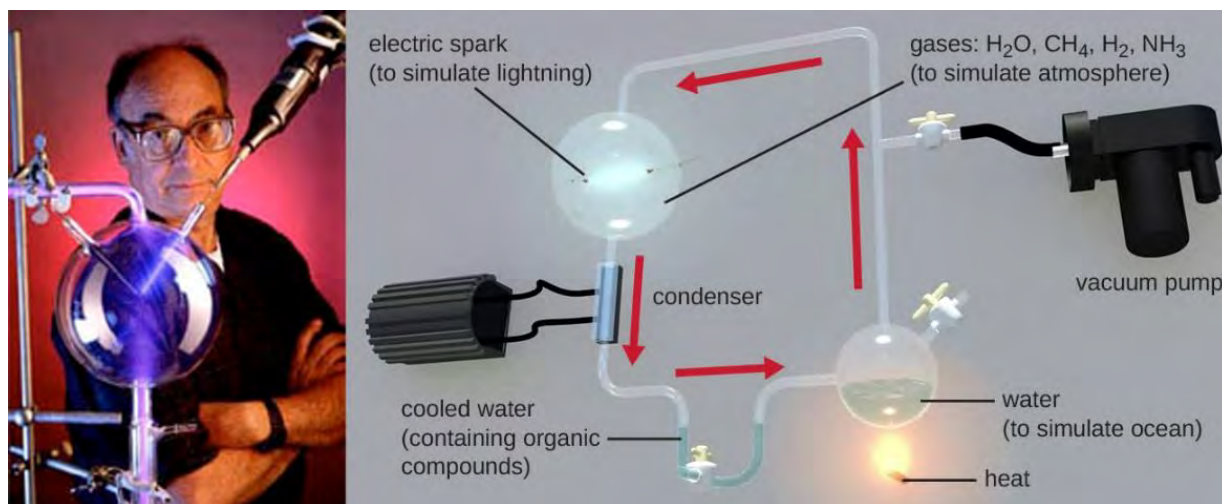
Figure 3.1 Scientist Stanley Miller (pictured) and Harold Urey demonstrated that organic compounds might have originated naturally from inorganic matter. (credit: "photo": modification of work by NASA; credit "illustration": modification of work by Courtney Harrington / Microbiology OpenStax)

The earth is estimated to be 4.6 billion years old, but for the first 2 billion years the atmosphere lacked oxygen. Without oxygen, the planet could not support life. One hypothesis about how life emerged on earth involves the concept of "primordial soup." This hypothesis proposes that life began in a body of water when metals and gases from the atmosphere combined with a source of energy, such as lightning or ultraviolet light. These interactions formed carbon compounds, the first chemical building blocks of life. In 1952, Stanley Miller (1930–2007), a graduate student at the University of Chicago, and his professor Harold Urey (1893–1981) set out to confirm this hypothesis. Miller and Urey combined what they believed to be the significant components of the earth's early atmosphere—water (H_2O), methane (CH_4), hydrogen (H_2), and ammonia (NH_3)— in a sealed, sterile flask. Next, they heated the flask to produce water vapor and passed electric sparks through the mixture to mimic lightning in the atmosphere (Figure 3.1). When they analyzed the contents of the flask a week later, they found amino acids. Amino acids are carbon compounds that make up proteins. Proteins are essential for life. Their data provided evidence that supported the "primordial soup" hypothesis.

In this chapter, students will look at the atom carbon and the role it plays in making up the four major classes of carbon-based molecules: carbohydrates, lipids, proteins, and nucleic acids. Students will also learn to identify and describe the functions of different macromolecules.

3.1 Carbon

Cells contain many complex molecules called macromolecules. Carbohydrates, lipids, proteins, and nucleic acids are all examples of large molecules necessary for life. There has been some discussion on what constitutes a macromolecule. For example, carbohydrates, proteins, and nucleic acid are all significantly larger in molecular size when compared to lipids. Some suggest because of this they should not be called a macromolecule. On the other hand, lipids are made up of many atoms and are significantly larger than, for example, a molecule of water. Whether lipids are classified as a macromolecule or not, one fact holds true, lipids are important cell components that perform a wide array of functions allowing living organisms to maintain homeostasis.

Carbohydrates, lipids, proteins, and nucleic acids are all organic molecules. **Organic molecules** generally refer to those molecules that have carbon as the principal element, bonded to hydrogen and other carbon atoms. Some carbon-containing compounds are *not* classified as organic, such as CO and CO_2. Molecules that do not contain carbon and hydrogen, such as water, are classified as inorganic.

Carbon atoms are the fundamental components for all carbohydrates, lipids, proteins, and nucleic acids. Because carbon does not have a full valence electron shell, it is incredibly reactive. Carbon has an atomic number of 6 and is in group six on the periodic table. Therefore, elemental carbon has 6 protons and 6 electrons. Carbon atoms can form up to four covalent bonds with other atoms to satisfy the octet rule. The methane molecule provides an excellent example. In methane, the carbon atom forms four separate covalent bonds with four different hydrogen atoms (Figure 3.2). The valence shells for both hydrogen and carbon are now satisfied, thus creating a relatively stable molecule.

Figure 3.2 Methane has a tetrahedral geometry, with each of the four hydrogen atoms spaced 109.5° apart. (credit: Clark et al./ Biology 2E OpenStax)
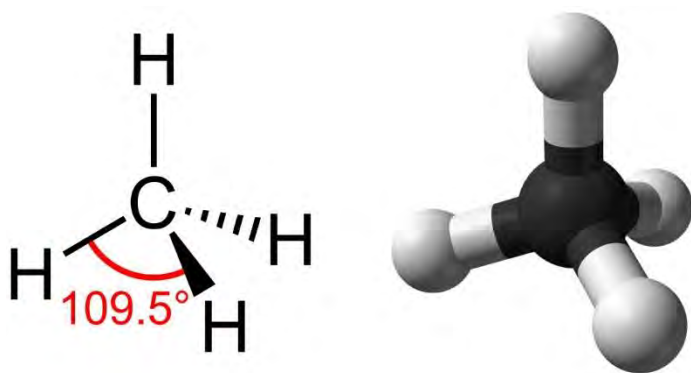
Hydrocarbons

Hydrocarbons are organic molecules consisting entirely of carbon and hydrogen, such as methane described above. We often use hydrocarbons in our daily lives. Fuels like the propane in a gas grill, or the butane in a lighter, are classified as hydrocarbons. The atoms in hydrocarbons form many covalent bonds which store large amounts of energy. This energy is released when these molecules burn (oxidize). For this reason, hydrocarbon molecules make excellent fuel sources.

Hydrocarbons form the backbones of large macromolecules and may be linear chains, carbon rings, or a combination of both. Furthermore, carbon-carbon bonds may be single, double, or triple bonds, with each type of bond affecting the molecule's three-dimensional shape in a specific way (Figure 3.3). The three-dimensional shape or conformation of a molecule is critical to determining its function.

Methane (CH_4)	Ethane (C_2H_6)	Ethene (C_2H_4)
Tetrahedral (single bond)	Tetrahedral (single bond)	Planar (double bond)
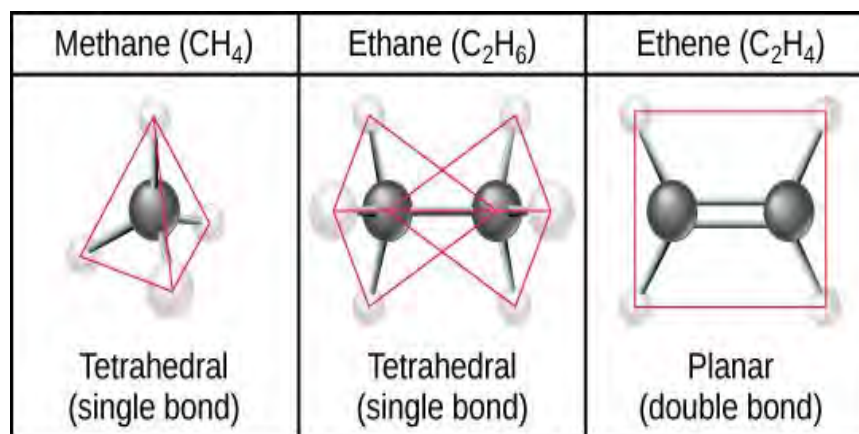
Figure 3.3 When carbon forms single bonds with other atoms, the shape is tetrahedral. When two carbon atoms form a double bond, the shape is planar, or flat. Single bonds, like those in ethane, can rotate. Double bonds, like those in ethene, cannot rotate. (credit: Clark et al./ Biology 2E OpenStax)

Isomers

The bonds that hold a molecule together help dictate its three-dimensional shape. Isomers are molecules that have the same chemical formula but differ from one another in the arrangement of their atoms and or chemical bonds. Structural isomers like butane and isobutane (Figure 3.4) differ in the placement of their covalent bonds. Both molecules have four carbons and ten hydrogen atoms (C_4H_{10}), but they differ from one another in the arrangement of their atoms. Structural differences lead to differences in chemical properties which will cause the isomers to function differently. For example, butane is used as a fuel source for lighters and torches, whereas isobutane is used as a coolant in refrigeration units and a propellant in spray cans.

(a) Structural isomers
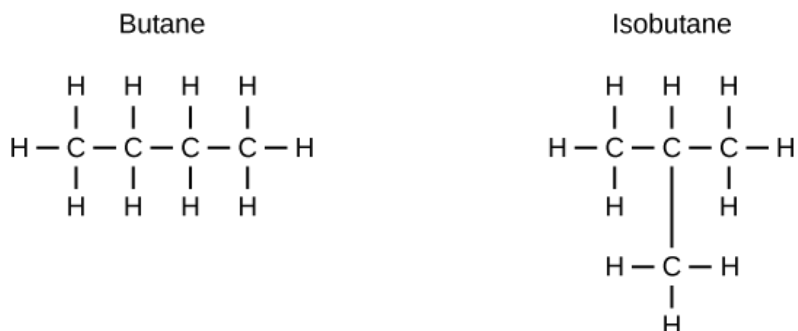
Butane

Isobutane

Figure 3.4 a. Structural butane and isobutane isomers have a different covalent arrangement of atoms. (credit: Modified by Elizabeth O'Grady original work of Clark et al./ Biology 2E OpenStax)

Functional Groups

Functional groups are groups of atoms that are found within macromolecules and confer specific chemical properties to those molecules. The functional groups in a macromolecule are usually attached to the carbon backbone at one or several different places along its chain and or ring structure. Carbohydrates, lipids, proteins, and nucleic acids each have their own characteristic set of functional groups that contributes significantly to its differing chemical properties and its function in living organisms. For example, proteins are unique from other biologically important molecules in that their building blocks, amino acids, have both a carboxyl and amino functional group. Nucleic acids in comparison are made of building blocks called nucleotides, that always contain a phosphate functional group.

Figure 3.5 shows some of the important functional groups in biological macromolecules. They include hydroxyl, methyl, carbonyl, carboxyl, amino, phosphate, and sulfhydryl groups. We usually classify functional groups as **hydrophobic** or **hydrophilic** depending on their charge or polarity. An example of a hydrophobic group is the nonpolar methyl molecule, which is hugely prevalent in lipids. The carboxyl group is hydrophilic and found in amino acids, the building blocks of proteins.

Figure 3.5 These functional groups are in many different biological molecules. (credit: Clark et al./ Biology 2E OpenStax)

Functional Group	Structure	Properties
Hydroxyl	O—H, R	Polar
Methyl	R—CH_3	Nonpolar
Carbonyl	R—C(=O)—R'	Polar
Carboxyl	C(=O), R, OH	Charged, ionizes to release H^+. Since carboxyl groups can release H^+ ions into solution, they are considered acidic.
Amino	R—N with H, H	Charged, accepts H^+ to form NH_3^+. Since amino groups can remove H^+ from solution, they are considered basic.
Phosphate	O, R, P—OH, O, OH	Charged, ionizes to release H^+. Since phosphate groups can release H^+ ions into solution, they are considered acidic.
Sulfhydryl	R—S, H	Polar

Section Summary

Living things are made of different carbon-based macromolecules. 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. Functional groups help explain why different macromolecules have different chemical properties.

Exercises

1. Each carbon molecule can bond with as many as_____ other atom(s) or molecule(s).
    a. one
    b. two
    c. three
    d. four

2. Which of the following would be hydrophobic?
    a. methyl group
    b. carbonyl group
    c. hydroxyl group
    d. carboxyl group

3. Explain what a functional group is and why they are important.

Answers

1. (d)
2. (a)
3. Functional groups are groups of atoms that occur within molecules and confer specific chemical properties to those molecules. They usually attach to the carbon backbones of macromolecules via chemical bonding. Each of the four types of macromolecules, proteins, lipids, carbohydrates, and nucleic acids, has its own characteristic set of functional groups. These functional groups contribute significantly to their differing chemical properties and functions in living organisms.

Glossary

hydrocarbon: organic molecules consisting entirely of carbon and hydrogen

functional group: groups of atoms that occur within molecules and confer specific chemical properties to those molecules

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

hydrophobic: describes a material that does not dissolve in water; "water-fearing"

isomers: molecules that share the same chemical formula but differ in the placement (structure) of their atoms and/or chemical bonds

organic molecule: any carbon-containing liquid, solid, or gas

3.2 Synthesis and Breakdown of Macromolecules

Learning objectives

By the end of this section, you will be able to:

- *Understand how macromolecules are synthesized (dehydration synthesis)*
- *Understand how macromolecules are broken down (hydrolysis reactions)*
- *Explain the difference between a monomer and a polymer*
- *Be able to define and explain all bolded terms*

As you've learned, biological important molecules are relatively large molecules that are necessary for life. Each biological important molecule is built from smaller organic molecules. There are four major biological important molecule classes (carbohydrates, lipids, proteins, and nucleic acids). Each is an important cell component and performs a wide variety of functions. Biological important molecules are organic, meaning they contain carbon. They often also contain hydrogen, oxygen, nitrogen, and additional minor elements.

Most biologically important molecules are made from single subunits, or building blocks, called **monomers**. The monomers combine using covalent bonds to form larger molecules known as **polymers**. When monomers combine, water is released as a by-product. This type of reaction is called a **dehydration synthesis**, a condensation reaction, which means "to put together while losing water" (Figure 3.6a). Conversely, the covalent bonds that hold the polymer together can also be broken if need be. When a **hydrolysis reaction** occurs, a water molecule is used to break a chemical bond (Figure 3.6b). We will look more closely at each type of reaction below.

(a) Dehydration synthesis

Monomers are joined by removal of OH from one monomer and removal of H from the other at the site of bond formation.
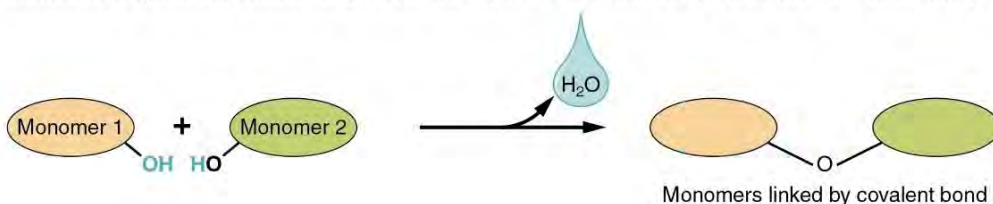
(b) Hydrolysis

Monomers are released by the addition of a water molecule, adding OH to one monomer and H to the other.
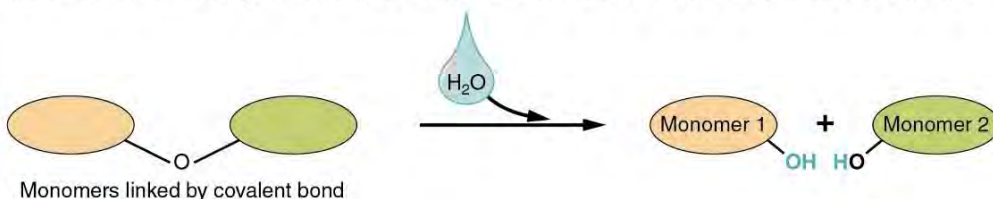
Figure 3.6 (a) In dehydration synthesis, two monomers are covalently bonded. (b) In a hydrolysis reaction, the covalent bond between two monomers is split apart. (credit: Betts et al./Anatomy and Physiology OpenStax)

Dehydration Synthesis

In a dehydration synthesis (Figure 3.7), the hydrogen of one monomer combines with the hydroxyl group of another monomer, forming a water molecule. At the same time, the monomers then come together and share electrons resulting in the formation of a covalent bond. As additional monomers are added, this growing chain forms a polymer. Different monomer types can combine in many configurations, giving rise to a diverse group of macromolecules. Alternatively, the same kind of monomers can also come together and form different polymers. For example, glucose monomers are the significant components of starch, glycogen, and cellulose.
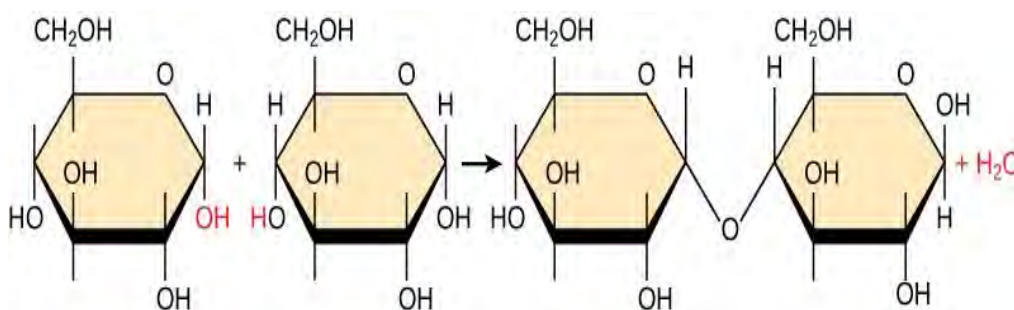
Figure 3.7 In the dehydration synthesis reaction above, two glucose molecules link to form the disaccharide maltose. In the process, it forms a water molecule. (credit: Clark et al./ Biology 2E OpenStax)

Hydrolysis

Polymers can be broken down into monomers during hydrolysis reactions. Hydrolysis reactions occur when a water molecule is used to break a chemical bond (Figure 3.8). During these reactions, the polymer breaks into two components: one part gains a hydrogen atom (H+), and the other gains a hydroxyl molecule (OH–). Both the hydrogen and hydroxyl ions are a result of splitting a water molecule.
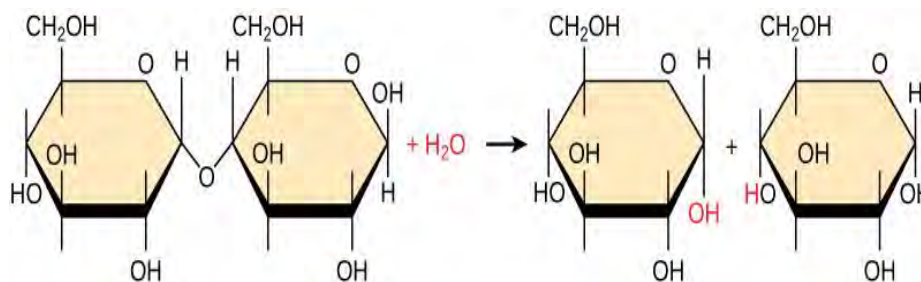
Figure 3.8 In the hydrolysis reaction above, the disaccharide maltose breaks down to form two glucose monomers by adding a water molecule. (credit: Clark et al./ Biology 2E OpenStax)

Dehydration synthesis and hydrolysis reactions can occur quickly with the help of molecules called enzymes. In dehydration reactions, enzymes help with the formation of new bonds, while enzymes used in hydrolysis reactions break bonds apart.

In both cases, enzymes speed up reactions. However, each macromolecule usually has its own specific enzymes. For example, lactase is used to break down the carbohydrate lactose, whereas glycogen synthase is used to make the carbohydrate glycogen. Enzymes called proteases, such as pepsin and peptidase, break down proteins, whereas enzymes called lipases break down lipids. We will take a closer look at how enzymes function later when we discuss proteins.

CONCEPTS IN ACTION - Visit this site to see visual representations of dehydration synthesis and hydrolysis.

Check your knowledge

Hydrolysis reactions result in _____.
    a. polymers
    b. monomers
    c. water molecules
    d. oxygen molecules

Answer: b

Section Summary

Carbohydrates, lipids, proteins, and nucleic acids are the four major classes of biological important molecules. Most biologically important molecules are comprised of single units called monomers that are joined by covalent bonds to form larger polymers. When a monomer forms a covalent bond with another monomer as a result of a water molecule being released, this reaction is called dehydration synthesis. Hydrolysis reactions occur when polymers break down into smaller units (monomers) with the help of a water molecule. Dehydration synthesis and hydrolysis reactions are similar for all macromolecules, but each monomer and polymer reaction is specific to its class. Dehydration synthesis reactions and hydrolysis reactions typically require the help of enzymes to speed up the rate of the chemical reactions.

Exercises

1. What is released when monomers are joined together in a dehydration synthesis reaction?
    a. water
    b. oxygen
    c. monomers
    d. none of the above

2. Which of the statements below is correct?
    a. During dehydration synthesis, macromolecules are broken down.
    b. Water is involved in hydrolysis reactions but not dehydration synthesis.
    c. Hydrolysis reactions build macromolecules.
    d. Enzymes are used in both dehydration synthesis and hydrolysis reactions.

3. What role do electrons play in dehydration synthesis?

Answers

1. (a)
2. (d)
3. During a dehydration synthesis, the monomers share electrons and form covalent bonds.

Glossary

dehydration synthesis: a reaction where monomers combine with the help of water (and often an enzyme) to form polymers

hydrolysis reactions: a reaction where a water molecule (and usually an enzyme) is used to break a chemical bond within a polymer

monomers: the single subunits, or building blocks that make up polymers

polymers: larger molecules that are formed by combining monomers using covalent bonds

3.3 Biological Molecules – Carbohydrates

<u>**Learning objectives**</u>
By the end of this section, you will be able to:

- *Identify the four major classes of biologically important molecules found in cells*
- *Recognize monomers and polymers for carbohydrates*
- *Understand the functions of different types of carbohydrates*
- *Be able to define and explain all bolded terms*

There are four major biological macromolecule classes (carbohydrates, lipids, proteins, and nucleic acids). Each is important for cell homeostasis and performs a wide variety of functions. We will take a closer look at each of these biologically important molecules starting first with carbohydrates.

Carbohydrates

Carbohydrates are macromolecules that students may be familiar with. To lose weight, some individuals adhere to "low-carb" diets. Athletes, in contrast, often "carb-load" before competitions to ensure that they have sufficient energy to compete at a high level. Carbohydrates are an essential part of our diet. Grains, fruits, and vegetables are all-natural sources of carbohydrates. Carbohydrates provide energy for the body, mainly through glucose, a simple sugar. Carbohydrates also have other essential functions. For example, in plants, the carbohydrate cellulose provides structural support, whereas, in some insects, their hard-outer shell is composed of a different carbohydrate called chitin. We will explore various functions of carbohydrates later in this section.

Carbohydrates are represented by the formula $(C_nH_{2n}O_n)$, where n is the number of carbon and oxygen atoms in the molecule. In other words, the ratio of carbon to hydrogen to oxygen is 1:2:1 in carbohydrate molecules. For example, the chemical formula for glucose is $C_6H_{12}O_6$. Carbohydrates are classified into three subtypes: monosaccharides, disaccharides, and polysaccharides.

Monosaccharides

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 monosaccharides have names ending with the suffix -ose, such as glucose, galactose, and fructose (Figure 3.9).

In most living species, glucose is an essential source of energy. During cellular respiration, glucose is used as a source of energy, when its covalent bonds are broken. The energy released is used to make adenosine triphosphate (ATP), an energy-rich molecule that powers most cellular activity. Plants can synthesize their glucose using light energy, carbon dioxide, and water through the process of photosynthesis. Animal cells cannot perform photosynthesis, so they must

consume other organisms as an energy source. Plants store excess glucose as starch, a complex polysaccharide. Polysaccharides will be discussed in more detail later in this section. When organisms consume plants, they hydrolyze (verb form of hydrolysis reactions) the starch molecules into monosaccharides. These monosaccharides are then used to generate their ATP.

Galactose (part of lactose, or milk sugar) and fructose (found in fruit) are other common monosaccharides. Glucose, galactose, and fructose are all **isomers** meaning they have the same chemical formula ($C_6H_{12}O_6$) but differ structurally. Because of these structural differences, each molecule has different chemical properties. For example, the sugar fructose is sweeter than the sugar glucose.

Figure 3.9 Glucose, galactose, and fructose are isomeric monosaccharides. (credit: Fowler et al. / Concepts of Biology OpenStax)
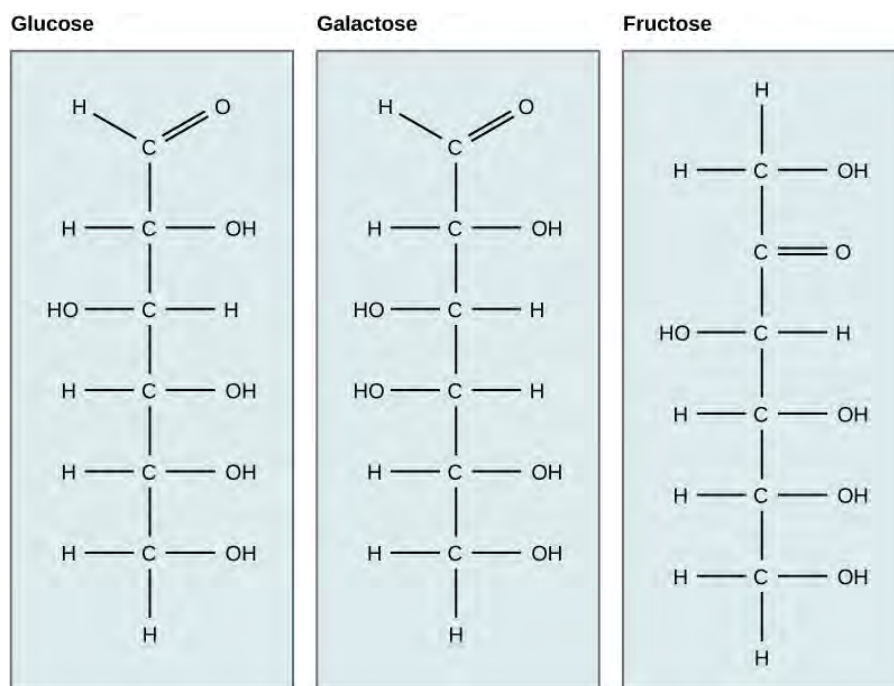
Disaccharides

Disaccharides (di- = "two") form when two monosaccharides undergo a dehydration synthesis. During this process, the hydroxyl group (–OH) of one monosaccharide combines with a hydrogen atom of another monosaccharide, releasing a water molecule (H_2O). A covalent bond forms between the atoms in the two sugar molecules (Figure 3.10).
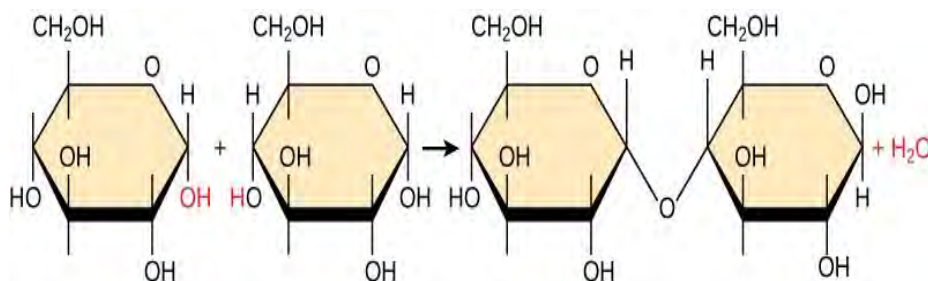
Figure 3.10 In the dehydration synthesis reaction above, two glucose molecules link to form the disaccharide maltose. In the process, a water molecule formed. (credit: Clark et al./ Biology 2E OpenStax)

Many disaccharide names also end with the suffix -ose. Lactose is a disaccharide made up of the monomers glucose and galactose. It is found naturally in milk. Maltose, or malt sugar, is a disaccharide formed from a dehydration synthesis between two glucose molecules. The most common disaccharide is sucrose, more commonly known as table sugar. Sucrose is composed of the monomers glucose and fructose (Figure 3.11).

Figure 3.11 A lump of sucrose, commonly called table sugar. (credit: Uwe Hermann/ Flickr)

Polysaccharides

A **polysaccharide** (poly- = "many") is a chain of three or more monosaccharides linked together by covalent bonds. The chain may be branched or unbranched and is typically very large (i.e. thousands of monosaccharides). Starch, glycogen, cellulose, and chitin are all examples of polysaccharides (Figure 3.12).
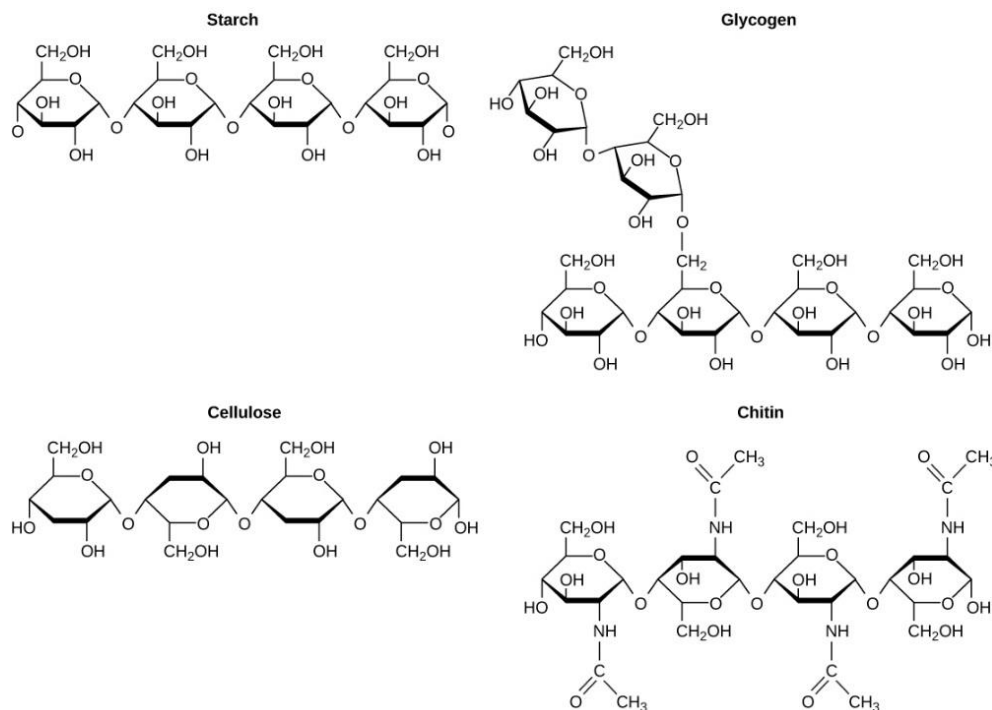
Figure 3.12 Although their structures and functions differ, all polysaccharide carbohydrates are made up of monosaccharides. (credit: Fowler et al. / Concepts of Biology OpenStax)

Starch

Plants can synthesize glucose through the process of photosynthesis. Any excess glucose that is not used to make ATP is stored as **starch** in different parts of the plant, including its roots and seeds. The potato in Figure 3.13 is an excellent example of a plant root that is rich in starch, storing glucose that was produced in the leaves of the potato plant. When animals consume potatoes, the starch is broken down through hydrolysis reactions into monomers of glucose. Cells can then absorb the glucose and use it to generate their form of energy, ATP.

a.

b.
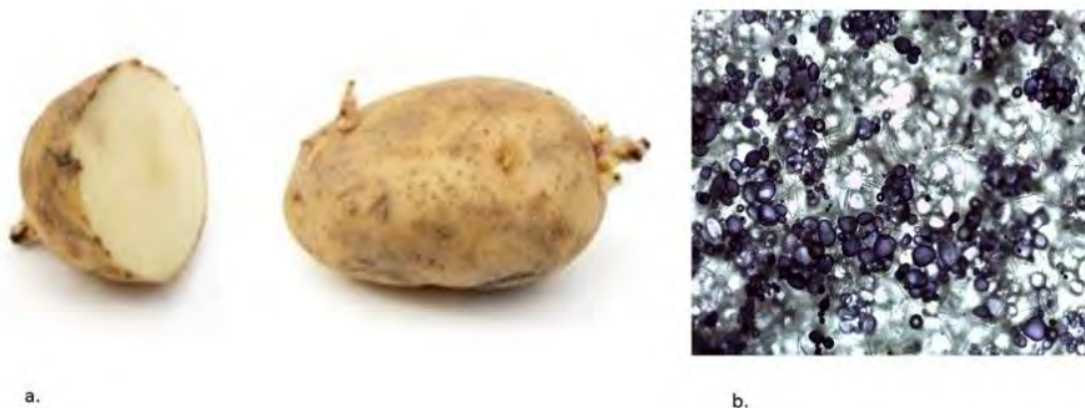
Figure 3.13 a. A potato represents the root of a plant that stores the plant's starch. b. Potato cells stained with iodine. Starch stains purple in specialized organelles called amyloplasts (10x magnification). (credit: a. ZooFari / Wikimedia b. Elizabeth O'Grady)

Glycogen

Humans and many other vertebrates store their excess glucose as **glycogen**. Glycogen is made up of glucose monomers and is the animal equivalent of starch. It is a highly branched molecule and most often stored in liver cells (Figure 3.14). Whenever glucose levels in the body decrease, glycogen in the liver can be broken down into glucose molecules with the help of enzymes. When glucose levels in the body are elevated, liver cells can take up excess glucose. Excess glucose is converted to glycogen in a dehydration synthesis reaction with the help of the enzyme, glycogen synthase. In humans, two important hormones, insulin and glucagon, govern these two processes of glycogen formation and glycogen breakdown.
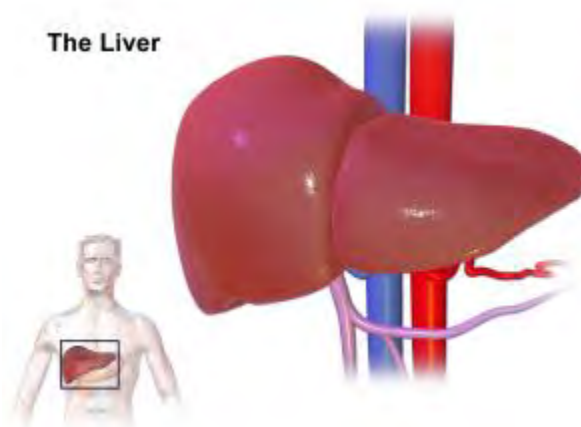
Figure 3.14 The human liver contains stored glycogen. (credit: BruceBlaus / Wikimedia)

Cellulose

Cellulose is one of the most abundant natural polysaccharides. The cell walls of plants are mostly made of cellulose, which provides structural support for the cell (Figure 3.15). Wood and paper are also mostly cellulose in nature. Glucose monomers in cellulose are held together by covalent bonds and pack tightly into long extended chains. Tightly packed chains of glucose give cellulose its rigidity and high tensile strength, which is very important to plant cells.

Figure 3.15 Plants, which are composed of plant cells, have rigid cell walls that contain cellulose. (credit: Yash Deshpande / Wikimedia)

Cellulose passing through the human digestive system is called dietary fiber. The glucose-glucose bonds in cellulose cannot be broken down by human digestive enzymes. Humans rely on dietary fiber to help maintain the consistency of their stools rather than providing a source of energy. Diets that lack dietary fiber may result in stools becoming hard and difficult to pass, a condition referred to as constipation. Herbivores such as cows, buffalos, and horses can digest cellulose found in plant matter and use it as a food source. These animals and certain species of bacteria that reside in their rumen, part of the digestive system of herbivores, secrete the enzyme cellulase. Cellulase can break cellulose down into glucose monomers that are then used to synthesize ATP.

Chitin

Insects, spiders, and crabs are arthropods that protect their internal organs with hard outer shells, called the exoskeletons (Figure 3.16). Exoskeletons are made of a polysaccharide called **chitin**. Chitin is also found in the scales of fish and the cell walls of fungi.
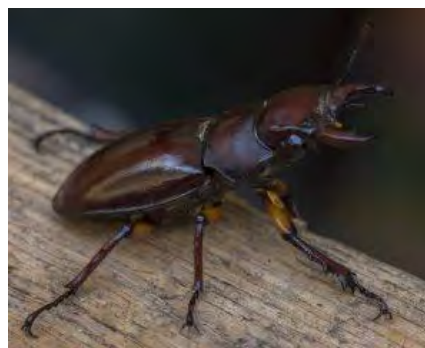
Figure 3.16 Stag Beetle (*Lucanus capreolus*) with its hard exoskeleton made of chitin. (credit: Dr. Bob Remedi)

CONCEPTS IN ACTION - For an additional perspective on carbohydrates, explore "Biomolecules: the Carbohydrates" through this interactive animation.

CAREER CONNECTION - Registered Dietitian

Obesity is a worldwide health concern. It has been linked with diseases such as diabetes, atherosclerosis, and hypertension. As a result, 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.

Section Summary

Carbohydrates are classified as monosaccharides, disaccharides, and polysaccharides. The classification depends on the number of monomers in the molecule. Carbohydrates are a group of macromolecules that are a vital energy source for cells and provide structural support to many organisms.

Exercises

1. An example of a monosaccharide is _____.
    a. fructose
    b. maltose
    c. starch
    d. glycogen

2. Glycogen and chitin are examples of _____.
    a. monosaccharides
    b. disaccharides
    c. lipids
    d. polysaccharides

3. Plant cell walls contain which of the following in abundance _____.
    a. starch
    b. cellulose
    c. glycogen
    d. lactose

4. Compare and contrast starch and glycogen.

Glossary

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

dehydration synthesis: a reaction where monomers combine with the help of water (and often an enzyme) to form polymers

disaccharide: two sugar monomers that are linked together by a peptide bond

glycogen: a storage carbohydrate in animals

monosaccharide: a single unit or monomer of carbohydrates

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

starch: a storage carbohydrate in plants

3.4 Biological Molecules – Lipids

Lipids

Lipids include a diverse group of compounds. All lipids share one major characteristic: they are all hydrophobic (or at least have a hydrophobic region, as in phospholipids). Lipids are mostly hydrocarbons, meaning they have large proportions of nonpolar carbon-carbon or carbon-hydrogen bonds. As a result, they do not interact well with water. Because lipids are very structurally diverse and are not made from a single subunit, the terms monomer and polymer may not be applied when discussing lipids. Lipids are also smaller in molecular size when compared to polymers of carbohydrates, proteins, and nucleic acids and therefore some sources do not consider them large macromolecules.

Lipids perform many different functions. For example, they can be used for long-term energy storage, provide insulation from the environment, and act as a water-proofing material (Figure 3.17). Lipids are used as the building blocks for many hormones that help organisms regulate different physiological processes within the body. They are also an essential component of the plasma membrane. Lipids include fats, phospholipids, steroids, and waxes.

Figure 3.17 Hydrophobic lipids in the fur of aquatic mammals, such as this river otter, protect them from the elements. (credit: Ken Bosma / Concepts of Biology OpenStax)

Fats

Many cells store energy for long-term use in the form of **fats. Triglycerides**, an example of a fat molecule, is a naturally occurring fat that can be found in many of the foods we consume. Humans and other animals store most fat in our bodies as triglycerides (Figure 3.18). A glycerol molecule is an organic compound with three carbon atoms, five hydrogen atoms, and three hydroxyl (–OH) groups. Each fatty acid consists of a long chain of hydrocarbons with an attached acidic carboxyl group, hence the name "fatty acid."
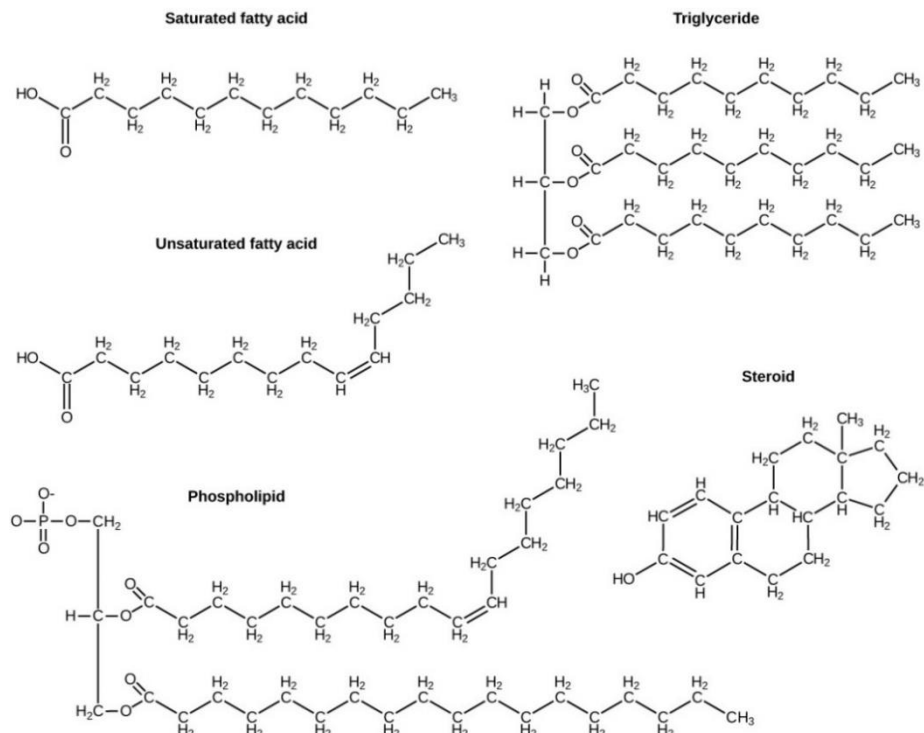
Figure 3.18 Lipids include fats, such as triglycerides, which are made up of fatty acids and glycerol; other examples of lipids are phospholipids and steroids. (credit: Fowler et al. / Concepts of Biology OpenStax)

Fatty acids may be saturated or unsaturated (Figure 3.18 and 3.19). If there are only single bonds between neighboring carbon atoms, 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, it is called an **unsaturated fatty acid** (Figure 3.18 and 3.19). They are called unsaturated fatty acids because when carbon atoms form double bonds between them, the two carbon atoms in that bond each has one less hydrogen atom attached to it. Therefore, it is said to be "unsaturated."

Figure 3.19 Fatty acids: Saturated vs. Unsaturated (credit: Betts et al./ Anatomy and Physiology OpenStax)
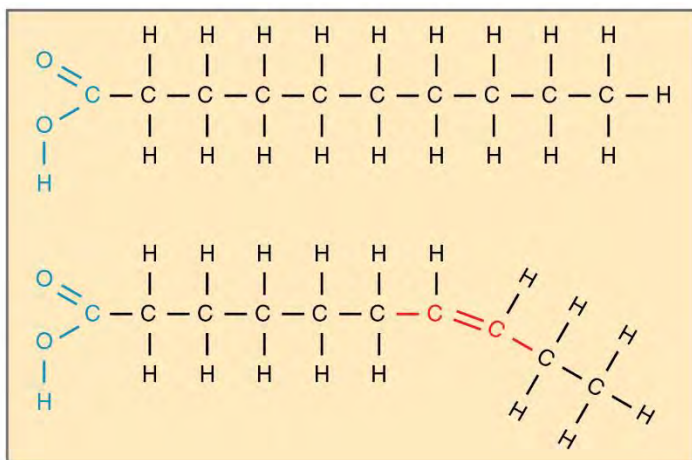
Most unsaturated fats are liquid at room temperature and are called **oils**. Examples of unsaturated fats include olive oil and canola oil. Saturated fats tend to get packed tightly together and are solid at room temperature. Examples of saturated fats include palmitic acid, which can be found in meat, and butyric acid, which is found in butter. Unsaturated fats help to improve blood cholesterol levels, whereas saturated fats contribute to plaque formation in blood vessels, which increases the risk of a heart attack.

Mammals store fats in specialized cells called adipocytes, where globules of fat occupy most of the space in the cell. In plants, fats or oils are stored in seeds and used as sources of energy during embryonic development.
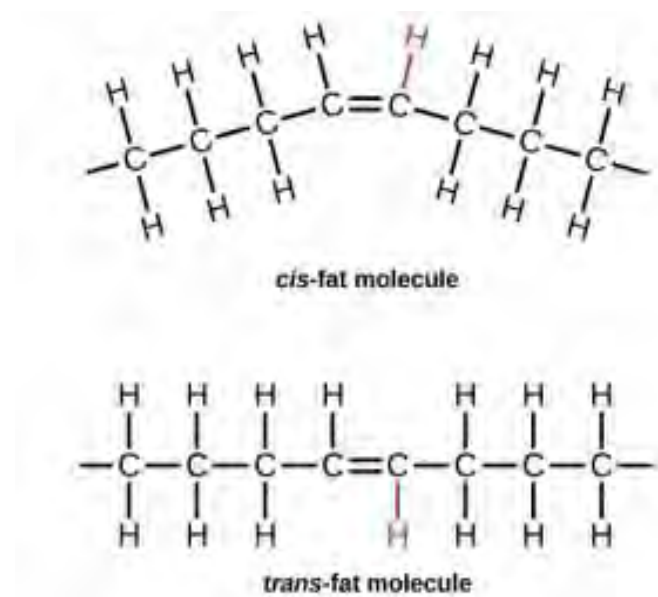
In the food industry, oils can be artificially hydrogenated to make them semi-solid. Hydrogenation leads to less spoilage and increases its shelf life. During the hydrogenation process the orientation around the double bonds is changed, which changes the chemical properties of the molecule. This forms a ***trans*-fat** (Figure 3.20).

Figure 3.20 A trans-fat is made from changing the chemical properties of a cis-fat. (credit: Fowler et al. / Concepts of Biology OpenStax)

Some types of margarine, 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 increased levels of low-density lipoprotein (LDL), or "bad" cholesterol. High levels of LDL can lead to plaque formation in the blood vessels, resulting in heart disease. Many fast-food restaurants have recently eliminated the use of *trans*-fats. In the U.S., food labels are now required to list their *trans*-fat content.

Fats are often perceived as being bad. It is true that eating an excess of fried foods, and other "fatty" foods lead to weight gain. However, fats do have essential functions. Omega-3 fatty acids are essential in brain function and healthy growth and development. They also may prevent heart disease and reduce the risk of cancer. Fats also serve as long-term energy storage and provide insulation for the body. "Healthy" unsaturated fats in moderate amounts should be consumed regularly.

Phospholipids

Like fats, **phospholipids** (Figure 3.18) are composed of fatty acid chains attached to a glycerol molecule. Unlike a triglyceride, a phospholipid only has two fatty acid chains instead of three. The third carbon of the glycerol backbone is bound to a phosphate group (Figure 3.21). The addition of alcohol modifies the phosphate group. Because of this arrangement, a phospholipid has both hydrophobic and hydrophilic regions. The fatty acid chains are hydrophobic and exclude themselves from water, whereas the phosphate "head" is hydrophilic and interacts with water.
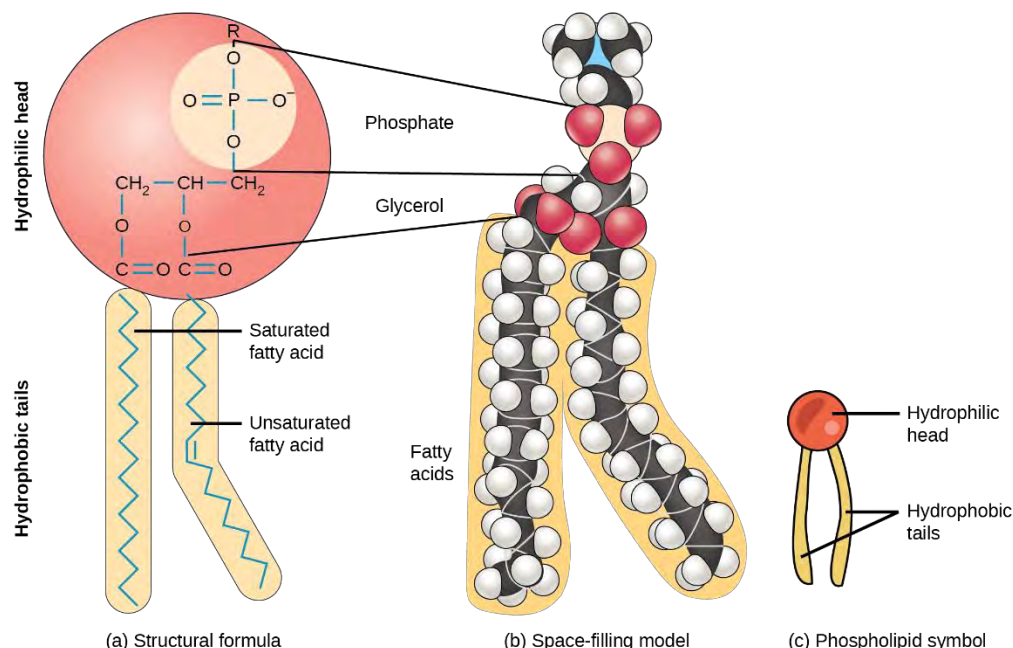
Figure 3.21 The molecular structure of a phospholipid. (Credit: Clark et al. / Biology 2E OpenStax)

Phospholipids are the major component of the plasma membrane. They come together and organize themselves in what is called a phospholipid bilayer (Figure 3.22). The phospholipid bilayer consists of two adjacent layers of phospholipids arranged tail to tail. The hydrophobic tails associate with one another, forming the interior of the cell membrane. The polar heads interact with the fluid inside and outside of the cell.

Figure 3.22 The cell membrane is composed in part of a phospholipid bilayer (credit: Betts et al./ Anatomy and Physiology OpenStax)
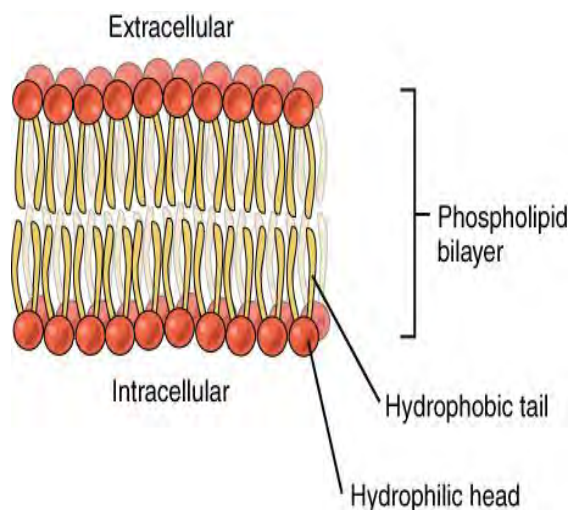
Steroids

Unlike the phospholipids and fats discussed earlier, **steroids** have a ring structure. Steroids do not structurally resemble other lipids; however, they are all hydrophobic. All steroids have four linked carbon rings (Figure 3.23). Some steroids, like cholesterol, have a short tail.
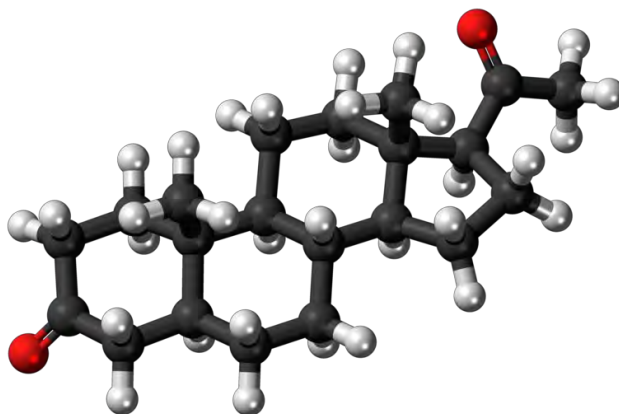
Figure 3.23 Ball-and-stick model of the 5α-Dihydroprogesterone molecule, a steroid hormone. (credit: Jynto/ Wikimedia)

Cholesterol is the most common steroid. In animals, the liver synthesizes cholesterol, which acts as the precursor for many steroid hormones, including testosterone and estradiol. Testosterone and estradiol are crucial hormones that lead to the sexual maturation and secondary sex characteristics of males and females. A **hormone** is a chemical signaling molecule, usually a protein or steroid, secreted by an endocrine gland or group of endocrine cells. It acts to control or regulate specific physiological processes. Another example of a steroid hormone is cortisol. Cortisol is released by the adrenal gland and can affect glucose regulation and inflammation (Figure 3.24).

Cholesterol is also the precursor of bile salts, which help emulsifying (breakdown) fats. Although cholesterol is often spoken of in negative terms, it is necessary for the body to function properly. It is also a key component of an animal cell's plasma membrane, which will be discussed in Chapter 4.
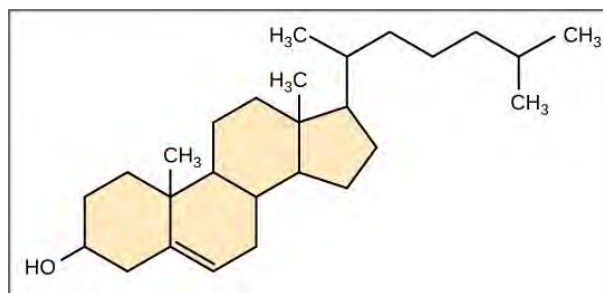
Cholesterol
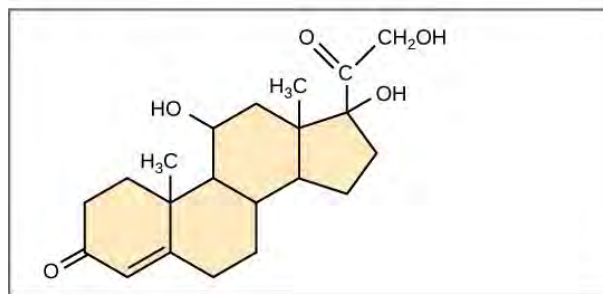
Cortisol

Figure 3.24 Four fused hydrocarbon rings comprise steroids such as cholesterol and cortisol (credit: Clark et al. / Biology 2E OpenStax)

Waxes

Waxes are also classified as lipids. They are composed of a hydrocarbon molecule with an alcohol (–OH) group and a fatty acid chain. Examples of animal waxes include beeswax and lanolin, both of which can be used to prevent and treat dry skin. Plants also have waxes. The superficial waxy cuticle that covers leaves helps prevent plants from drying out (Figure 3.25).

Figure 3.25 Plant leaves have a superficial waxy cuticle, which often gives them their shiny appearance. (credit: Yash Deshpande [/ Wikimedia](#))

CONCEPTS IN ACTION- For an additional perspective on lipids, explore "Biomolecules: The Lipids" through this interactive [animation](#).

Check your knowledge

Which type of lipid makes up the superficial cuticle found on plant leaves?
   a. Phospholipids
   b. Cholesterol
   c. Steroids
   d. Waxes

Answer: d

Section Summary

Lipids are a class of biological molecules that are nonpolar and hydrophobic. Major types include fats, waxes, phospholipids, and steroids. Fats and oils are a stored form of energy. Phospholipids are the major component of the cell membrane. Steroids are the precursor molecules important in forming cholesterol and many required hormones. Waxes are generated by both plants and animals and are essential in both waterproofing and preventing organisms from drying out.

Exercises

1. 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

2. Which lipids are made up of a hydrocarbon chain with an alcohol (–OH) group and form the cuticle of plants?
   a. saturated fats
   b. triglycerides
   c. waxes
   d. phospholipids

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

4. Compare and contrast unsaturated fat and saturated fats.

Answers

1. (a)
2. (c)
3. Fat serves as a valuable way for animals to store energy. It can also provide insulation. Phospholipids and steroids are essential components of cell membranes. Lipids also form hormones that control or regulate different physiological processes.
4. Both are types of lipids and are hydrophobic. Unsaturated fats are fats with at least one double bond, in a specific configuration, between carbon atoms. This results in a bend in the chain's carbon backbone, preventing triglyceride molecules from packing too tightly together and results in them being in a liquid form at room temperature. In contrast to unsaturated fats, saturated fats do not have double bonds between carbon atoms saturated fats. Saturated fats are solid at room temperature and usually of animal origin.

Glossary

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

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

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

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

lipids: a class of macromolecules that are nonpolar and insoluble in water

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

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

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

waxes: a type of lipid made up of a hydrocarbon chain with an alcohol (–OH) group and a fatty acid

3.5 Biological Molecules – Proteins

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 they may be used as toxins or enzymes. Each cell in a living system may contain thousands of different proteins, each with a unique function. The structures of proteins, like their functions, vary greatly. All proteins, however, are polymers made up of amino acids arranged in a linear sequence.

Types and Functions of Proteins

Enzymes are proteins that speed up the rate of chemical reactions. Enzymes do this by decreasing the amount of activation energy needed to start the chemical reaction. Enzymes are usually complex proteins. Each enzyme has a specific **substrate,** a reactant that binds to the enzyme. An enzyme may assist in hydrolysis reactions or dehydration synthesis reactions. Enzymes that break down their substrates are called catabolic enzymes, whereas those that build more complex molecules are called anabolic enzymes. Salivary amylase is an example of a catabolic enzyme. Salivary amylase hydrolyzes starch into simple sugars like glucose. An example of an anabolic enzyme is rubisco, which plants use during photosynthesis to make sugar from carbon dioxide.

Some enzymes function as hormones. **Hormones** are molecules that are important for chemical signaling between cells. Hormones regulate specific physiological processes, including growth, development, metabolism, and reproduction. For example, insulin is a protein hormone that helps regulate blood glucose levels. Not all hormones are protein-based. Some hormones, such as estradiol and testosterone, are made of lipids.

Proteins also provide structural support for many cells. Plants have several different structural proteins found in their rigid cell walls. Cell wall structural proteins offer support and protection for the plant. Actin is a structural protein found in muscle cells that allows for muscle contraction. Keratin, another critical protein in mammals, is the major component of skin and hair. Hair provides physical protection from damaging UV rays and helps organisms maintain stable body temperatures.

Proteins play many additional roles that are important in sustaining life. Table 3.1 lists several different types of proteins, provides examples, and gives a brief description of their functions.

Protein Types and Functions

Type	Examples	Functions
Digestive Enzymes	Amylase, lipase, pepsin, trypsin	Help in food by catabolizing nutrients into monomeric units
Transport	Hemoglobin, albumin	Carry substances in the blood or lymph throughout the body
Structural	Actin, tubulin, keratin	Construct different structures, like the cytoskeleton
Hormones	Insulin, thyroxine	Coordinate different body systems' activity
Defense	Immunoglobulins	Protect the body from foreign pathogens
Contractile	Actin, myosin	Effect muscle contraction
Storage	Legume storage proteins, egg white (albumin)	Provide nourishment in early embryo development and the seedling

Table 3.1 lists the primary types and functions of proteins. (credit : Clark et al. / Biology 2E OpenStax)

Protein Shape

Proteins have different shapes. For example, hemoglobin is a globular protein, meaning it is shaped kind of like a globe. Its shape is important because it allows hemoglobin to attach and release oxygen molecules easily. Oxygen molecules are needed by all of the cells that make up the human body. Collagen, located in the skin, is a fibrous protein. Fibrous proteins tend to be long and sometimes cylindrical. In our skin, collagen plays an essential protective function and helps hold the skin together.

Twenty types of amino acids are used to make all proteins. Different proteins have different types and different arrangements of their amino acids, which results in each protein being unique. We will now take a closer look at the chemical make-up of an amino acid.

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 has a side chain called the R group (Figure 3.26). The R group is a side chain that can be made up of several different atoms. The R groups are very diverse and ultimately give each amino acid its defining characteristics (Figure 3.27).

Figure 3.26 Amino acids have a central asymmetric carbon to which an amino group, a carboxyl group, a hydrogen atom, and a side chain (R group) are attached. (credit : Clark et al. / Biology 2E OpenStax)

Figure 3.27 There are 20 common amino acids commonly found in proteins, each with a different R group (variant group) that determines its chemical nature. (credit : Clark et al. / Biology 2E OpenStax)

The chemical nature of the side chain determines the amino acid's nature (that is, whether it is acidic, basic, polar, or nonpolar). For example, the amino acids valine, methionine, and alanine are nonpolar or **hydrophobic** (Figure 3.27). Note that these R groups are mostly hydrocarbons, which consist of nonpolar covalent bonds. Amino acids such as serine, threonine, and cysteine, are polar and have **hydrophilic** side chains. The side chains of lysine and arginine are positively charged, and therefore these amino acids have a basic pH. (Figure 3.28). By understanding the chemical nature of each amino acid, it is easier to understand why proteins function the way they do.

The sequence and the number of amino acids ultimately determine the protein's shape, size, and function. Amino acids can be linked together using a dehydration synthesis reaction. One amino acid's carboxyl group and the incoming amino acid's amino group combine, releasing a water molecule. The resulting bond that forms is covalent and called a **peptide bond** (Figure 3.28).

Figure 3.28 Peptide bond formation is a dehydration synthesis reaction. (credit : Clark et al. / Biology 2E OpenStax)

As two amino acids are linked together they form a peptide chain. As more amino acids are added it is called a polypeptide chain. A polypeptide chain is technically a polymer of amino acids. However, the term protein is not usually used until the polypeptide chain(s) have folded into their distinct three-dimensional shape and can carry out their unique function(s). After a polypeptide chain is made, most are modified. Parts of the polypeptide chain may be removed, or other chemical groups may be added. Only after these modifications are made is the protein completely functional.

CONCEPTS IN ACTION - Click through the steps of protein synthesis in this interactive tutorial.

Check your knowledge

What type of bond is a peptide bond?

True or False: All amino acids are polar.

Answers: Peptides bonds are covalent bonds between amino acids.
Amino acids are both polar and non-polar.

Protein Structure

As we discussed earlier, a protein's shape is critical to its function. For example, an enzyme can bind to a specific substrate at an active site. If this active site is altered because of changes in the protein shape, the enzyme may be unable to attach to the substrate. 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 3.29).
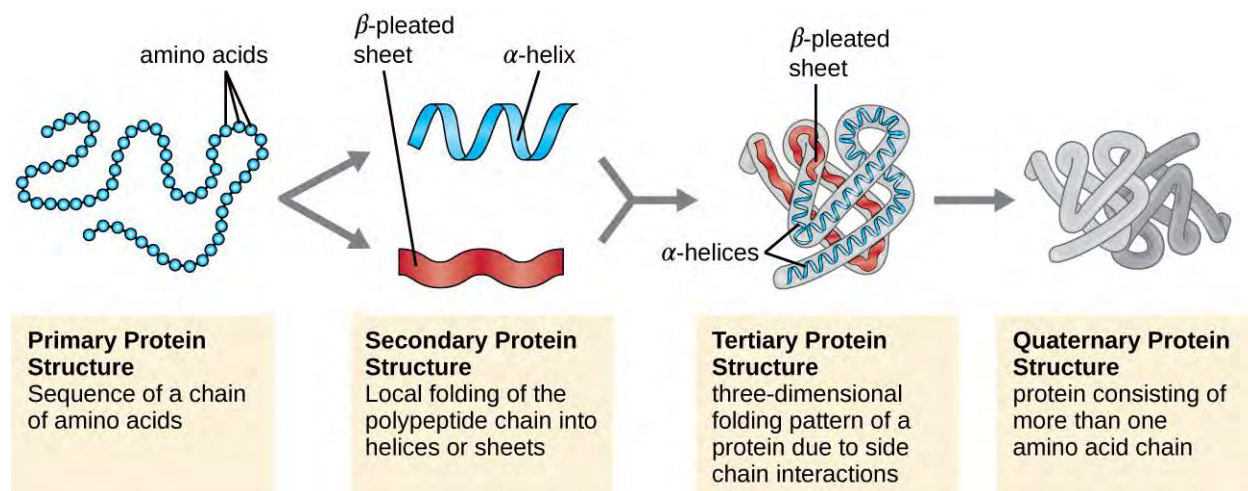
Figure 3.29 illustrates the four levels of protein structure (primary, secondary, tertiary, and quaternary). (credit: Parker et al. / Microbiology OpenStax)

Primary Structure

The **primary structure** is simply the polypeptide chain--the sequence of amino acids bonded together via peptide bonds. Figure 3.30 depicts the primary structure of a protein. A protein's primary structure is not rigid, but rather is flexible because of the nature of the bonds that hold the amino acids together.
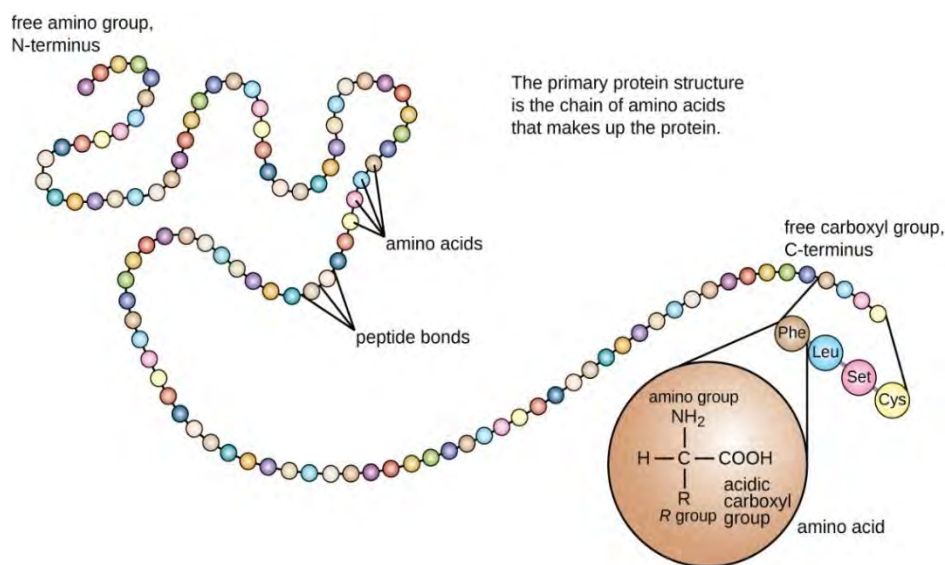
Figure 3.30 The primary structure of a protein is the polypeptide chain. (credit: modification of work by National Human Genome Research Institute / Microbiology OpenStax)

Secondary Structure

Due to chemical bonding, the polypeptide chain begins to fold in some regions giving rise to the **secondary structure** of the protein. The most common secondary structures are the α-helix and β-pleated sheet structures (Figure 3.31). Folding occurs because of hydrogen bonds that form between different amino acids within the chain.

Figure 3.31 The secondary structure of a protein may be an α-helix or a β-pleated sheet, or both. (credit: Parker et al. / Microbiology OpenStax)
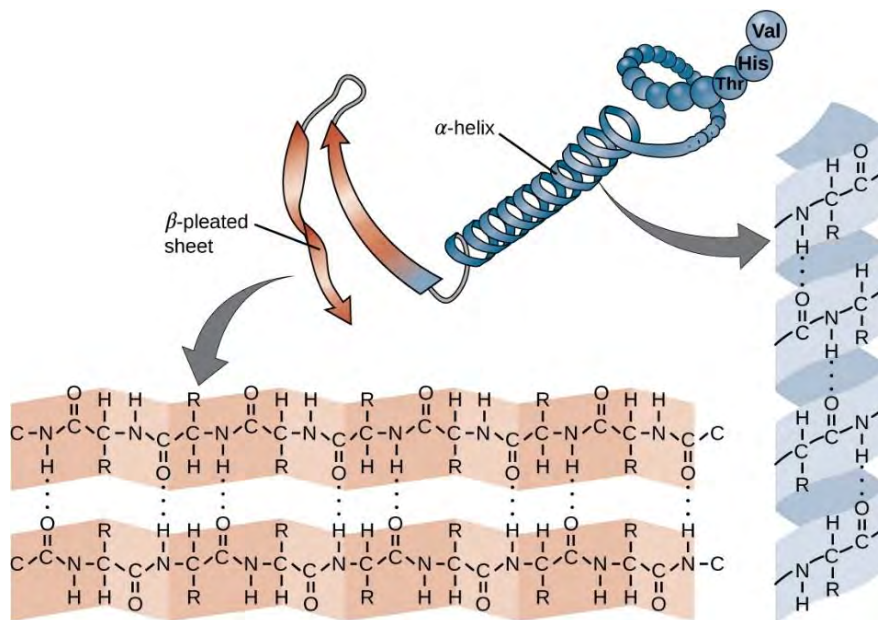
Tertiary Structure

The polypeptide's unique three-dimensional shape is its **tertiary structure** (Figure 3.32). This structure is in part due to chemical interactions within the polypeptide chain. Primarily, interactions among different R groups create the protein's complex three-dimensional shape. It is only when the protein has folded into its three-dimensional shape is it considered to be functional. This assumes no additional modifications need to be made. When a protein loses its three-dimensional shape, it may no longer function properly.
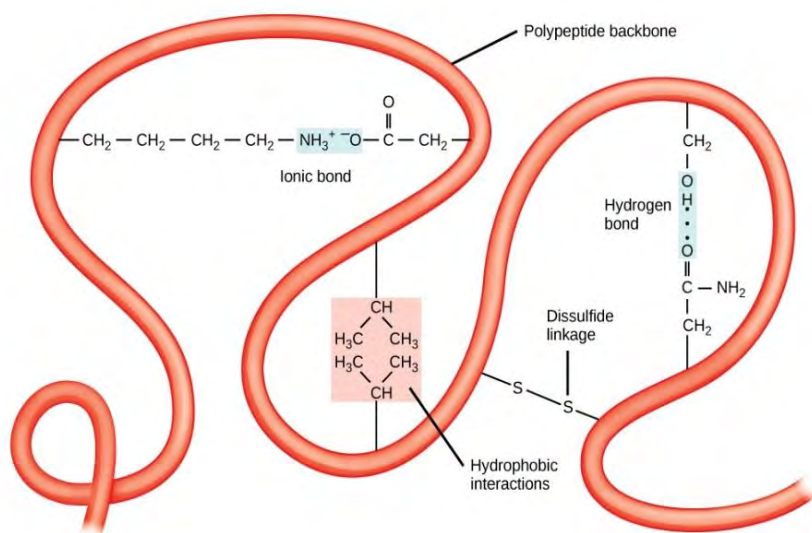
Figure 3.32 A variety of chemical interactions determine the proteins' tertiary structure. (credit: Parker et al. / Microbiology OpenStax)

Quaternary Structure

Some proteins consist of several separate polypeptide chains. These proteins function only when all polypeptide chains are present and appropriately configured. The interactions that hold these subunits together leads to what is referred to as the **quaternary structure** of the protein.
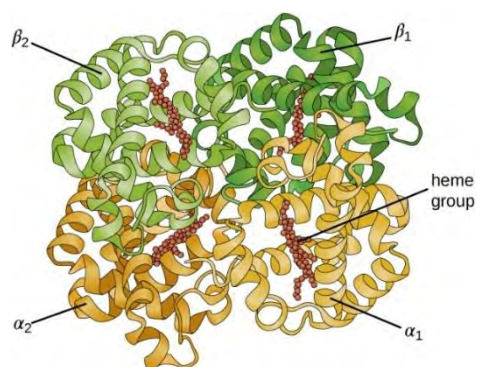
Relatively weak interactions stabilize the overall quaternary structure. Hemoglobin, for example, has a quaternary structure of four globular protein subunits: two α and two β polypeptides. Each subunit contains an iron-based heme that will bond to an oxygen molecule (Figure 3.33).

Figure 3.33 A hemoglobin molecule has two α and two β polypeptides together with four heme groups. (credit: Parker et al. / Microbiology OpenStax)

Denaturation and Protein Folding

Each protein has a unique sequence and is held together by chemical interactions. These chemical interactions result in unique three-dimensional shapes that allow proteins to function. If the protein is subjected to changes in temperature, pH, salinity, harsh chemicals, etc. the protein shape may change. When a protein loses its three-dimensional shape and is no longer functional, the protein is said to be **denatured**. Denaturation is often reversible because the polypeptide's primary structure may be conserved during the process. If the denaturing agent is removed, and the primary structure was preserved, the protein can refold and resume its normal function.

Sometimes denaturation is irreversible. One example of irreversible denaturation is frying an egg. Liquid egg whites are rich in the protein albumin. When the liquid egg white is placed in a hot pan, the heat denatures the protein. As the protein is denatured, there is a structural change from the liquid clear egg into a semi-solid white substance. Once the semi-solid white substance has formed, it cannot revert to its original state.

It is important to keep in mind that each protein has its own optimal conditions under which it functions best. For example, not all proteins denature at high temperatures. Some bacteria that survive in hot springs have proteins that function at temperatures closer to boiling. Proteins that are produced and used in the stomach can tolerate and work under acidic conditions, whereas proteins that function in the blood operate at a pH closer to neutral.

Folding is critical to a protein's overall function. Scientists initially thought proteins themselves were responsible for the folding process. Recently researchers have discovered that often proteins receive assistance in the folding process from protein helpers, or chaperones (or chaperonins). These discoveries lead scientists to believe that there are still more exciting details to be learned on the process of protein folding.

CONCEPTS IN ACTION - For an additional perspective on proteins, view this animation called "Biomolecules: The Proteins."

MICRO CONNECTIONS - Primary Structure, Dysfunctional Proteins, and Cystic Fibrosis

Proteins associated with the plasma membranes of cells are classified as peripheral or integral. Peripheral proteins are associated with one side of the membrane, whereas integral proteins are embedded in the membrane. Integral proteins can allow specific materials to move into or out of the cell. Cystic fibrosis (CF) is a human genetic disorder caused by a change in an integral membrane protein. It affects mostly the lungs but may also affect the pancreas, liver, kidneys, and intestine. Individuals who have CF are unable to make a transmembrane (integral) protein (CFTR) that usually helps transport salt and water into and out of cells (Figure 3.34). Because of a mutation in the DNA, one amino acid, phenylalanine, is left out when the integral transport protein is made. The loss of one amino acid changes the primary structure of the protein.
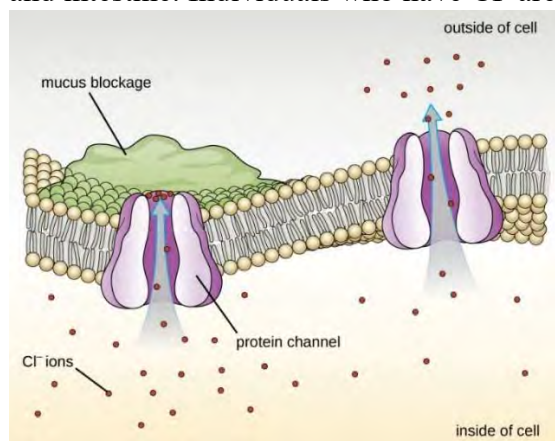
Figure 3.34 The normal CFTR protein is a channel protein that helps salt (sodium chloride) move in and out of cells. (credit: Parker et al. / Microbiology OpenStax)

The change in the primary structure prevents the protein from functioning correctly, which causes the body to produce unusually thick mucus that clogs the lungs and leads to the accumulation of sticky mucus. The mucus obstructs the pancreas and stops natural enzymes from helping the body break down food and absorb vital nutrients.

In the lungs, the altered mucus provides an environment where bacteria can thrive. This colonization leads to the formation of biofilms in the small airways of the lungs. The most common pathogens found in the lungs of patients with cystic fibrosis are *Pseudomonas aeruginosa* (Figure 3.35) and *Burkholderia cepacia*. *Pseudomonas* differentiates within the biofilm in the lung and forms large colonies, called "mucoid" *Pseudomonas*. The colonies have a unique pigmentation that shows up in laboratory tests (Figure 3.35) and provides physicians with the first clue that the patient has CF. Such colonies are rare in healthy individuals.

Figure 3.35 (a) A scanning electron micrograph shows the opportunistic bacterium Pseudomonas aeruginosa. (b) Pigment-producing P. aeruginosa on cetrimide agar shows the green pigment called pyocyanin. (credit a: modification of work by the Centers for Disease Control and Prevention / Microbiology OpenStax)
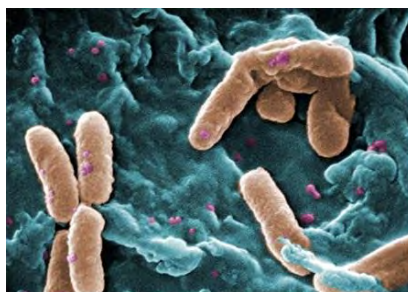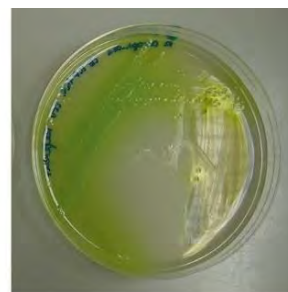
CONCEPTS IN ACTION - For more information about cystic fibrosis, visit the Cystic Fibrosis Foundation website.

Section Summary

Proteins are a class of macromolecules that can perform a diverse range of functions for the cell. They help in metabolism, provide structural support, speed up the rate of chemical reactions, transport materials, and function as hormones. The building blocks of proteins are amino acids. Proteins have four structures: primary, secondary, tertiary, and quaternary. Protein shape and function are intricately linked. Any change in shape caused by changes in temperature, pH, salinity, or chemical exposure may lead to protein denaturation and a loss of function.

Exercises

1. A _____ bond forms between the carboxyl group of one amino acid and the amino group of another amino acid.
    a. hydrogen
    b. ionic
    c. peptide
    d. all of the above

2. Enzymes speed up chemical reactions by _____ the energy needed to start the reaction.
    a. increasing
    b. decreasing

3. Denaturation can sometimes be reversed.
    a. True
    b. False

4. The monomers that make up proteins are called _____.
    a. nucleotides
    b. disaccharides
    c. amino acids
    d. chaperones

5. Explain what happens if even one amino acid is substituted for another in a polypeptide chain.
6. A mysterious disease results in the unfolding of proteins. This disease effects which protein structure?

Answers

1. (c)
2. (b)
3. (a)
4. (c)
5. This causes a change in protein structure and function.
6. Tertiary structure is affected when proteins unfold. This will also affect the quaternary structure.

Glossary

amino acid: a monomer of a protein

denaturation: loss of shape in a protein that may be a result of changes in temperature, pH, or chemical exposure

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

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

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

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

peptide bond: a covalent bond that forms between one amino acids carboxyl group and another amino acids amino group

polypeptide chain: a long chain of amino acids linked by peptide bonds

primary structure: a linear sequence of amino acids in a protein

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

quaternary structure: association of different polypeptide chains in a protein

secondary structure: structure that proteins form by hydrogen bonding between the oxygen atom of one amino acid and the hydrogen attached to the nitrogen atom of another amino acid

substrate: a reactant that binds to a specific enzyme

tertiary structure: a protein's three-dimensional conformation, including interactions between secondary structural elements

3.6 Biological Molecules - Nucleic Acids

Nucleic acids are essential macromolecules that allow cells to survive. They carry the cell's genetic blueprint and contain instructions that allow cells to function properly.

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. DNA contains the "instructions" on how the cell makes different proteins necessary for maintaining homeostasis. DNA is located in the nucleus of eukaryotes and in two eukaryotic organelles, chloroplasts and mitochondria. Prokaryotes also possess DNA, however it is not enclosed in a membrane-bound organelle.

The second type of nucleic acid, RNA, is mostly involved in protein synthesis and regulation. In eukaryotic cells, DNA never leaves the nucleus, so a specific type of RNA, messenger RNA (mRNA), helps to relay information from the nucleus to other parts of the cell. Transfer RNA (tRNA) and ribosomal RNA (rRNA) are essential in protein synthesis and will be discussed in chapter 10.

DNA and RNA are polymers made up of monomers called **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. Each nitrogenous base in a nucleotide is attached to a sugar molecule, which is attached to a phosphate group (Figure 3.36).

Figure 3.36 A nucleotide is made up of three components: a nitrogenous base, a pentose sugar, and a phosphate group. (credit: Fowler et al. / Concepts of Biology OpenStax)
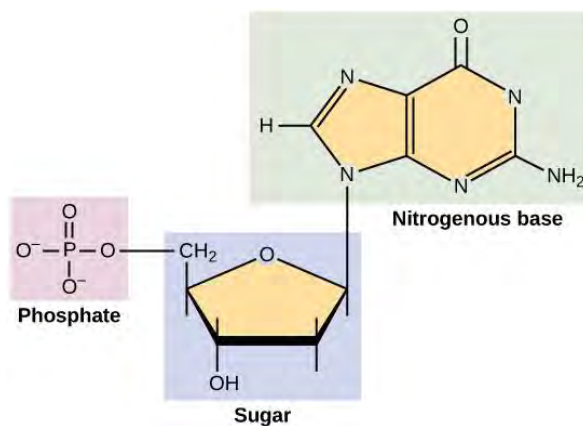
Although both DNA and RNA are made of nucleotides, there are distinct differences. First, DNA and RNA are made up of different types of pentose sugars. DNA contains the sugar deoxyribose (so-called because it has one less oxygen atom), whereas RNA is made using the sugar ribose. Each DNA nucleotide contains one of the following nitrogenous bases: adenine, cytosine,

guanine, and thymine. RNA nucleotides also use the bases: adenine, cytosine, guanine, however, instead of the base thymine, RNA uses the base uracil. Notice that the nucleotides that makeup DNA never contain the nitrogenous base uracil, and nucleotides that makeup RNA never contain the base thymine. The nitrogen-containing bases adenine and guanine are classified as purines. The bases cytosine, thymine and uracil are pyrimidines (Figure 3.37).

Structurally, DNA is shaped like a double helix, which we will discuss later. RNA is usually singled stranded and performs several different roles important for generating proteins. Take some time to review Table 3.2 which shows the features of both DNA and RNA.

DNA and RNA Features

	DNA	RNA
Function	Carries genetic information	Involved in protein synthesis
Location	Remains in the nucleus of eukaryotes	Leaves the nucleus in eukaryotes
Structure	Double helix	Usually single-stranded
Sugar	Deoxyribose	Ribose
Pyrimidines	Cytosine, thymine	Cytosine, uracil
Purines	Adenine, guanine	Adenine, guanine

Table 3.2 shows the features of both DNA and RNA. (credit: Clark et al./ Biology 2E OpenStax)
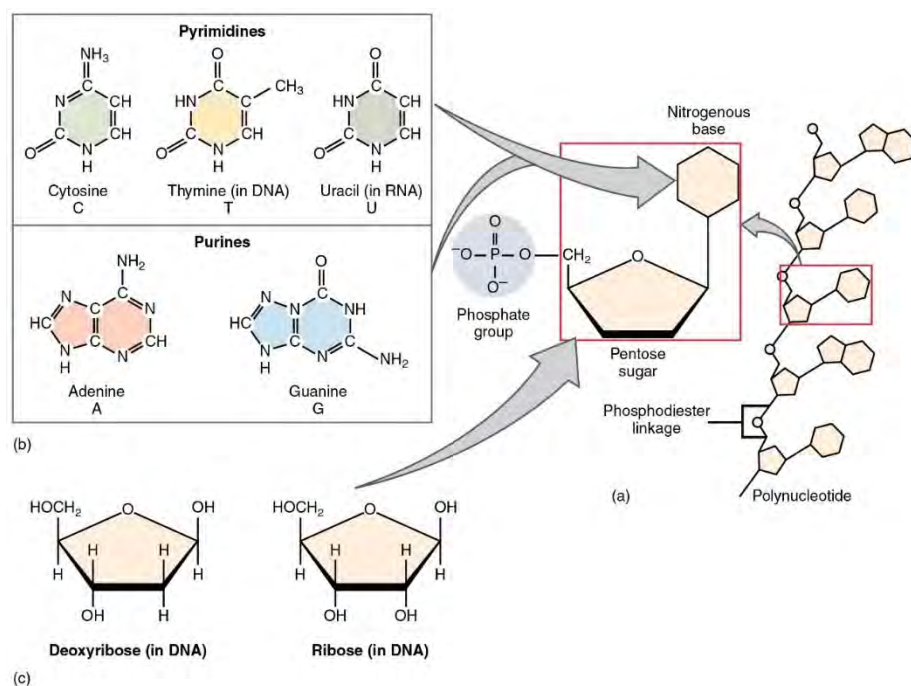
Figure 3.37 (a) A nucleotide. (b) The nitrogen-containing bases of nucleotides. (c) The two pentose sugars of DNA and RNA (credit: Betts et al. / Anatomy and Physiology OpenStax)

DNA Double-Helical Structure

DNA is shaped like a double helix (Figure 3.38). It is composed of two strands of nucleotides. Each DNA strand is formed with covalent bonds between the phosphate and sugar groups of adjacent nucleotides. The bonds between the sugar and phosphate make up the "sugar-phosphate backbone." The two separate DNA strands are held together by hydrogen bonds between nitrogenous bases (Figure 3.38). The strands usually coil, hence the "double helix" description.
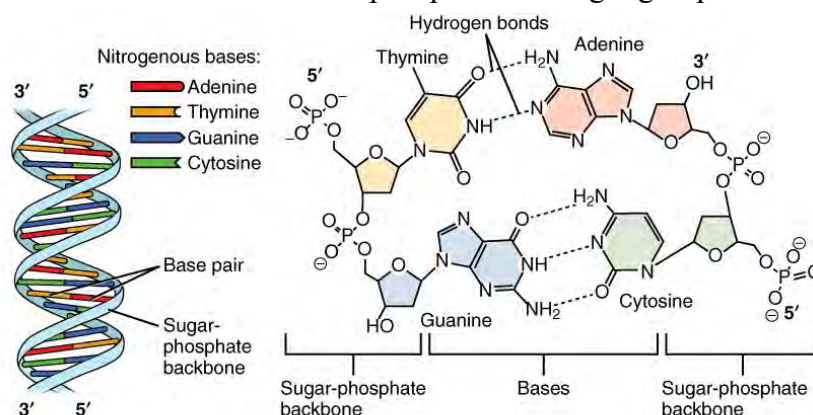
Figure 3.38 Molecular Structure of DNA. The DNA double helix is composed of two complementary strands. The strands are bonded together via their nitrogenous base pairs using hydrogen bonds. (credit: Betts et al. / Anatomy and Physiology OpenStax)
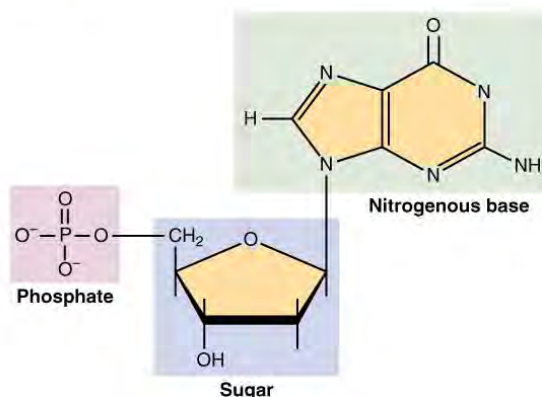
DNA and RNA are both examples of nucleic acids that perform unique functions that allow cells to survive. The flow of information within a cell or organism usually begins with DNA, which is used to make RNA, which is necessary to synthesize protein. DNA dictates the structure of mRNA in a process called **transcription**, and RNA dictates the protein's structure in a process called **translation**. This is the Central Dogma of Life, which holds true for many organisms (Figure 3.39). However, exceptions to the rule occur with some viral infections. The flow of information will be examined in chapter 10.
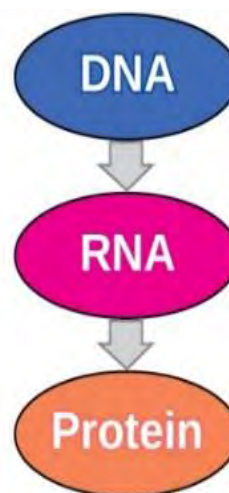
Figure 3.39 The central dogma states that DNA encodes RNA, which in turn encodes protein. (credit: Fowler et al. / Concepts of Biology OpenStax)

Section Summary

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. DNA and RNA have both similarities and differences. They both perform unique functions that allow cells to survive.

Exercises

1. The two strands of DNA are held together by what type of bond?
    a. hydrogen
    b. polar covalent
    c. nonpolar covalent
    d. ionic

2. The building blocks of nucleic acids are _____.
    a. monosaccharides
    b. amino acids
    c. lipids
    d. nucleotides

3. A nucleotide of DNA may contain _____.
    a. ribose, uracil, and a phosphate group
    b. deoxyribose, uracil, and a phosphate group
    c. deoxyribose, thymine, and a phosphate group
    d. ribose, thymine, and a phosphate group

4. What are the structural differences between RNA and DNA?

Answers

1. (a)
2. (d)
3. (c)
4. DNA forms a double helix, whereas RNA is single-stranded. DNA uses the nitrogenous base thymine, and RNA uses the nitrogenous base uracil. DNA is composed of the sugar deoxyribose, and RNA uses the sugar ribose.

Glossary

deoxyribonucleic acid (DNA): a double-stranded polymer of nucleotides that carries the hereditary information of the cell

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

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

transcription: the process of making RNA from DNA

translation: the process of making protein from mRNA

Chapter 4: Introduction to Cell Structure and Function
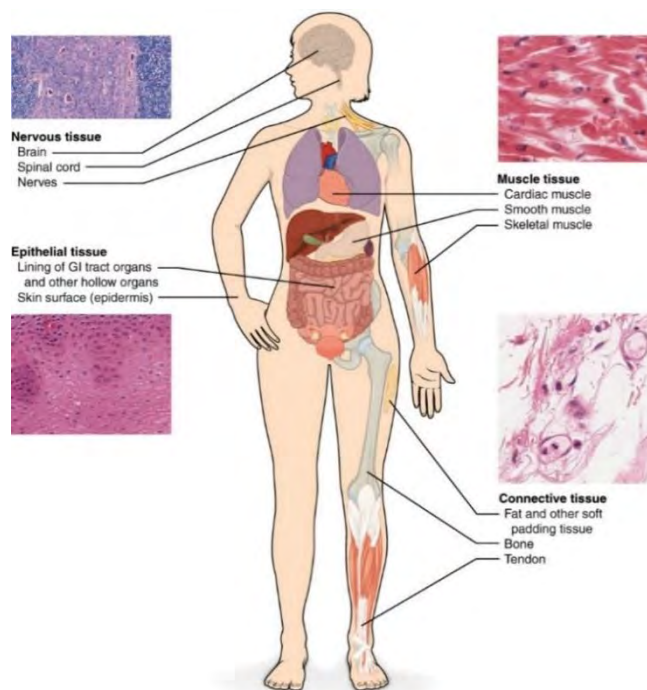
Figure 4.1 The body is made up of cells organized into four tissue types. Clockwise from from top left: nervous tissue, muscle tissue, connective tissue, and epithelial tissue LM × 872, LM × 282, LM × 460, LM × 800. (Micrographs provided by the Regents of University of Michigan Medical School © 2012 / Anatomy and Physiology OpenStax)

Close your eyes and picture a brick wall. What is the basic building block of that wall? Most would answer, it is a single brick. Like a brick wall, multicellular organisms are composed of basic building blocks, called cells. In multicellular organisms, several cells of one particular kind interconnect with each other and perform shared functions to form tissues. For example, the muscle tissue in animals or mesophyll tissue in plants. 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).

An average human is thought to have 37.2 trillion cells. All cells that make up your body are classified as eukaryotic animal cells. However, the cells of the body are not uniform. Each population of cells is specialized for a specific purpose. For example, epithelial cells protect the surface of the body and line internal organs and body cavities (Figure 4.1). These cells are very flat and fried egg-shaped. Muscle cells help physically move the body from one location to the next and allow movement of materials within the body. These cells are very long and cylindrical. Each of these cell types plays a vital role during the growth, development, and day-to-day maintenance of the body.

Despite the enormous variations, all cells share certain fundamental characteristics. In this chapter you will learn about the similarities and differences amongst cell types.

4.1 How Microorganisms Are Studied

Learning objectives

By the end of this section, you will be able to:

- *Describe the roles of cells in organisms*
- *Understand the importance of the microscope*
- *Summarize the cell theory*

Microorganisms, as the name implies, are tiny in size and often cannot be seen without some magnification. They differ from each other not only in size but also in structure, habitat, metabolism, and many other characteristics.

The **cell** is the smallest unit of life that makes up a living organism. Cells are found in each of the three domains of life: Bacteria, Archaea, and Eukarya. Cells within the domains Bacteria and Archaea are all **prokaryotes**; their cells lack a nucleus. Cells in the domain Eukarya are classified as **eukaryotes**; their cells do contain a nucleus. It is important to mention that there are other microorganisms besides cells, such as viruses, that do not fall within the domains of life. We will briefly discuss viruses, before focusing our attention on cells.

Viruses are acellular, meaning they are not composed of cells. Essentially, a virus consists of proteins and genetic material. The genetic material can be either DNA or RNA. Viruses are inactive outside of a host organism. Therefore, they do not grow and develop, nor can they reproduce on their own. However, by incorporating themselves into a host cell, viruses can utilize the host's cellular mechanisms to multiply and infect other hosts. Viruses can infect all types of cells, from human eukaryotic cells (Figure 4.2) to the cells of other microorganisms, including prokaryotic bacteria. A key take-away message is that viruses are dependent on the host cells. Viruses themselves do not display all the properties of life.
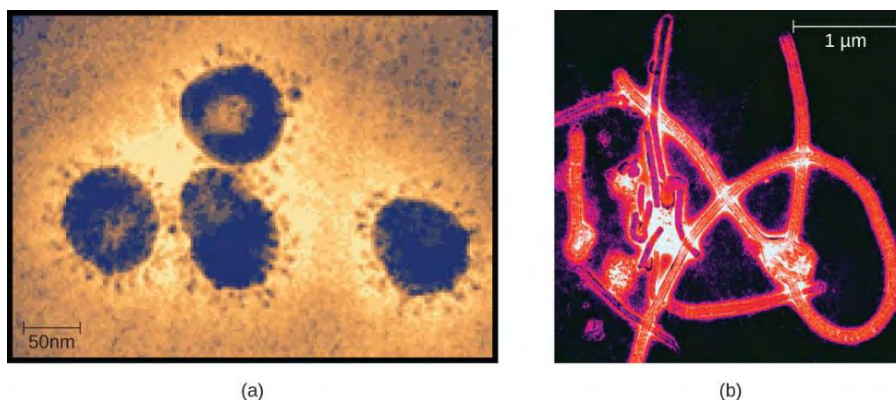
Figure 4.2 (a) Members of the Coronavirus family can cause respiratory infections like the COVID-19, common cold, severe acute respiratory syndrome (SARS), and Middle East respiratory syndrome (MERS). (b) Ebolavirus, a member of the Filovirus family. (credit a: modification of work by Centers for Disease Control and Prevention; credit b: modification of work by Thomas W. Geisbert / Microbiology OpenStax)

Microscopy

We will now turn our attention to how cells are studied. Cells vary in size, and with few exceptions, cannot be seen with the naked eye (Figure 4.3). In order to study cells, scientists use microscopes (micro- = "small"; -scope = "to look at"). A **microscope** is an instrument that magnifies an object.

Figure 4.3 Onion cells (eukaryotic plant cells) stained to show the cell walls and nuclei. (credit: Elizabeth O'Grady)
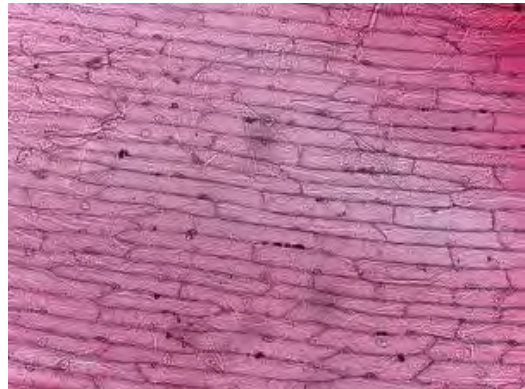
Light Microscopes

In the lab, you will become proficient using a compound light microscope (Figure 4.4a). Visible light passes and bends through the lens system, which enables the user to see the specimen. Light microscopes are advantageous for viewing living organisms. However, since individual cells are generally transparent, their components are not distinguishable unless they are colored with special stains. Staining, however, usually kills the cells. In the lab, you will learn how to stain specimens and make slides.
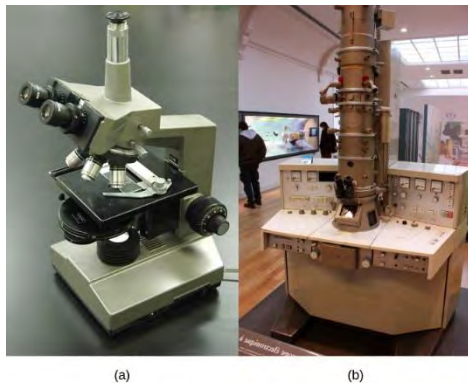
Figure 4.4 (a) A standard light microscope. (b) An electron microscope provides significantly more magnification than a light microscope. (credit a: modification of work by "GcG"/Wikimedia Commons; credit b: modification of work by Evan Bench / Biology 2E OpenStax)

Cell Theory

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

By the late 1830s, botanist Matthias Schleiden and zoologist Theodor Schwann were studying tissues and proposed that all living things are composed of one or more cells. They also suggested that the cell is the smallest and most basic unit of life and that all new cells arise from existing cells. Many scientists, including Louis Pasteur, famous for his discovery of the process of pasteurization, confirmed these same conclusions through their experimentation. Their work, along with many others, is why these principles still stand today and are considered the **cell theory**.

CAREER CONNECTION - Cytotechnologist

Have you ever heard of a medical test called a Pap smear (Figure 4.5)? In this test, a doctor takes a small sample of cells from the patient's uterine cervix and sends it to a medical lab. 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. They are trained to determine which cellular changes are normal and which are abnormal. Their focus is not limited to cervical cells. They examine cellular specimens that come from all organs. When they notice abnormalities, they consult a pathologist, a medical doctor who interprets and diagnoses changes in the body caused by disease.

Cytotechnologists play a vital role in saving people's lives. When doctors discover abnormalities early, a patient's treatment can begin sooner, which usually increases the chances of a successful outcome.
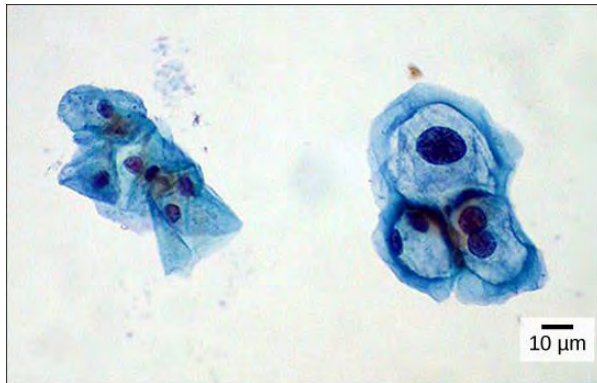
Figure 4.5 Uterine cervix cells, viewed through a light microscope, are from a Pap smear. Healthy cells are on the left. The cells on the right are infected with human papillomavirus (HPV). Notice that the infected cells are larger. (credit: modification of work by Ed Uthman, MD; scale-bar data from Matt Russell / Biology 2E OpenStax)

Check your knowledge

There are many different types of microscopes. Which type of microscope will you be using in the laboratory for this course?

Answer: Compound light microscope

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. The 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.

Exercises

1. Which of the following statements is NOT correct?
    a. Viruses display all the properties of life outside of a host cell.
    b. New cells arise from existing cells.
    c. Cytotechnologists study cells.
    d. All organisms are composed of one or more cells.

2. The _____ is the basic unit of life.
    a. organism
    b. cell
    c. tissue
    d. organ

3. In your own words, briefly describe the cell theory.

Answers

1. (a)
2. (b)
3. The cell theory states that all living organisms are made of living cells and living cells come from other living cells. Cells are thought to be the most basic unit of life.

Glossary

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

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

microscope: the instrument that magnifies an object

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

4.2 Comparing Prokaryotic and Eukaryotic Cells

Learning objectives

By the end of this section, you will be able to:

- Compare and contrast prokaryotic cells and eukaryotic cells
- Name examples of prokaryotic and eukaryotic organisms
- Describe the relative sizes of different kinds of cells
- Be able to define and explain all bolded terms

All cells share four common characteristics. First, all cells are enclosed within a plasma membrane, an outer layer that separates the cell's interior from its surrounding environment. Second, all cells contain cytoplasm, a jelly-like region within the cell where proteins and cell structures are found. Third, all cells have genetic material, such as DNA, which provides information necessary for the cell to remain alive. Finally, all cells have ribosomes, a non-membrane bound organelle, used to synthesize proteins. All cells also display the properties of life: order, response to stimuli, reproduction, evolution, growth and development, homeostasis, and energy processing.

Cells fall into one of two broad categories: prokaryotic cells or eukaryotic cells. Organisms in the domains Bacteria and Archaea are classified as prokaryotes (pro- = "before"; -kary- = "nucleus") whereas cells of animals, plants, fungi, and protists are all eukaryotes (eu- = "true"). Although all prokaryotic and eukaryotic cells share the similarities discussed above, they also differ in several ways. Below, we will take a closer look at just how prokaryotic cells and eukaryotic cells differ from one another.

Components of Prokaryotic Cells

A **prokaryotic cell** is a simple, single-celled (unicellular) organism that lacks a nucleus or any other membrane-bound organelle. Like all cells, prokaryotes do contain DNA, which is usually organized in chromosomes. Prokaryotic chromosomes are typically circular and unpaired. Prokaryotic DNA is found in the central part of the cell: a darkened region called the **nucleoid** (Figure 4.6).

Figure 4.6 This figure shows the generalized structure of a prokaryotic cell. (credit: Parker et al. / Microbiology OpenStax)
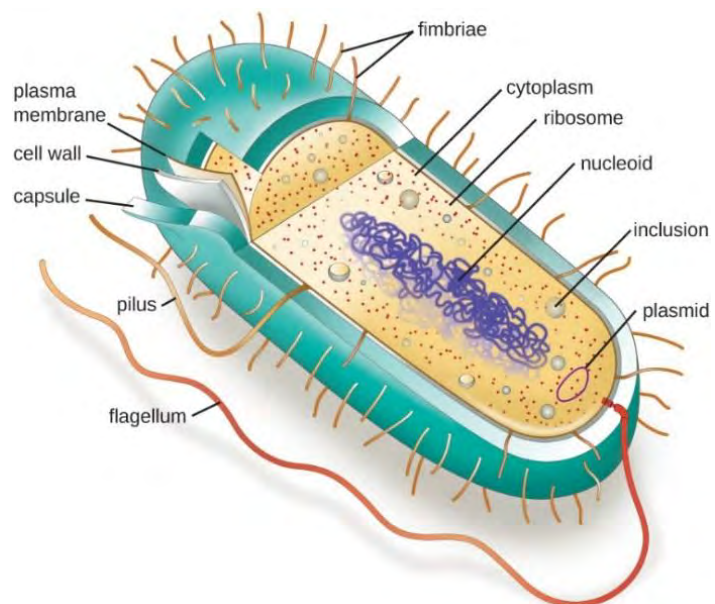
The domains of Bacteria and Archaea are both classified as prokaryotic cells, however there are significant differences between them. Unlike Archaea, bacteria have a cell wall made of peptidoglycan, and many have a polysaccharide capsule (Figure 4.6). The cell wall acts as an extra layer of protection, 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 or pili. Flagella are used for locomotion, while most pili are used to exchange genetic material during a process called conjugation.

Unlike most bacteria, archaeal cell walls do not contain peptidoglycan, but their cell walls are often composed of a similar substance called pseudopeptidoglycan. Like bacteria, archaea are found in nearly every habitat on earth, even extreme environments that are very cold, very hot, very basic, or very acidic (Figure 4.7). Some archaea live in the human body, but none have been shown to be human pathogens.

Figure 4.7 Some archaea live in extreme environments, such as the Morning Glory Pool, a hot spring in Yellowstone National Park. The color differences in the pool result from the different communities of microbes that can thrive at various water temperatures. (credit: Parker et al. / Microbiology OpenStax)

Eukaryotic Cells
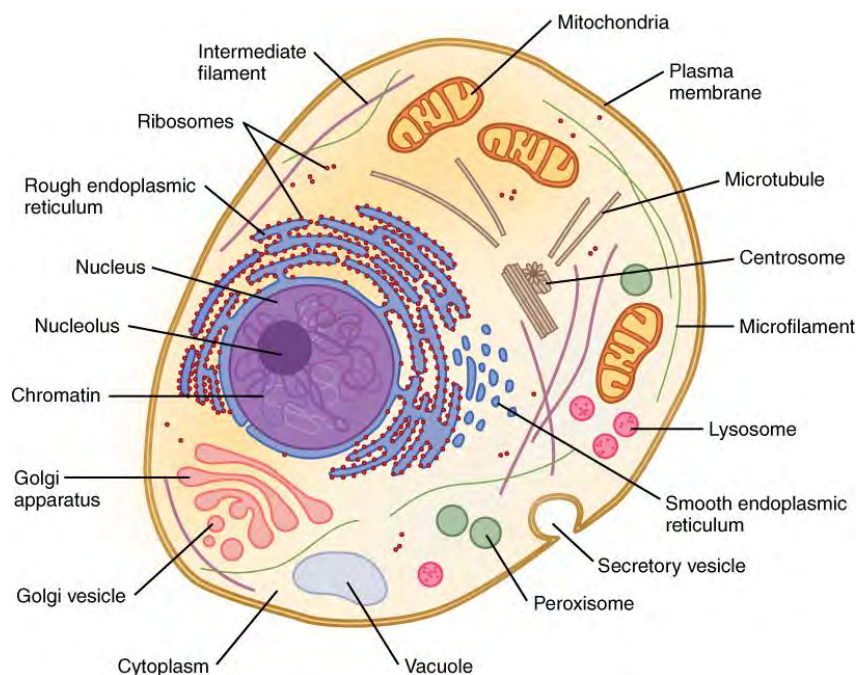
Eukaryotic cells are cells that contain a membrane-bound nucleus and other membrane-bound compartments or sacs, called organelles (Figure 4.8). **Organelles** are cell structures with specialized functions that will be discussed in section 4.4.

Figure 4.8 Eukaryotic animal cell with many membrane-bound organelles visible. (credit: Betts et al. / Anatomy and Physiology OpenStax)

Unlike prokaryotic cells, eukaryotic cells possess a nucleus. The nucleus is a membrane-bound organelle that houses the DNA. The nucleus, because it contains the DNA, ultimately controls all activities of the cell and also serves an essential role in reproduction and heredity. Eukaryotic cells typically have their DNA organized into multiple linear chromosomes. The DNA within the nucleus is highly organized and condensed to fit inside the nucleus.

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 4.9). The small size of prokaryotes allows ions and organic molecules to enter and spread to other parts of the cell quickly. Similarly, any wastes produced within a prokaryotic cell can quickly move out.

Larger eukaryotic cells have evolved different structural adaptations to enhance cellular transport. The large size of these cells would not be possible without these adaptations. Cell size is limited because volume increases quicker than cell surface area. As a cell becomes larger, it becomes more and more difficult for the cell to acquire sufficient materials to support the metabolic processes occurring inside the cell. This can be explained by looking at a cell's surface-area-to-volume ratio.
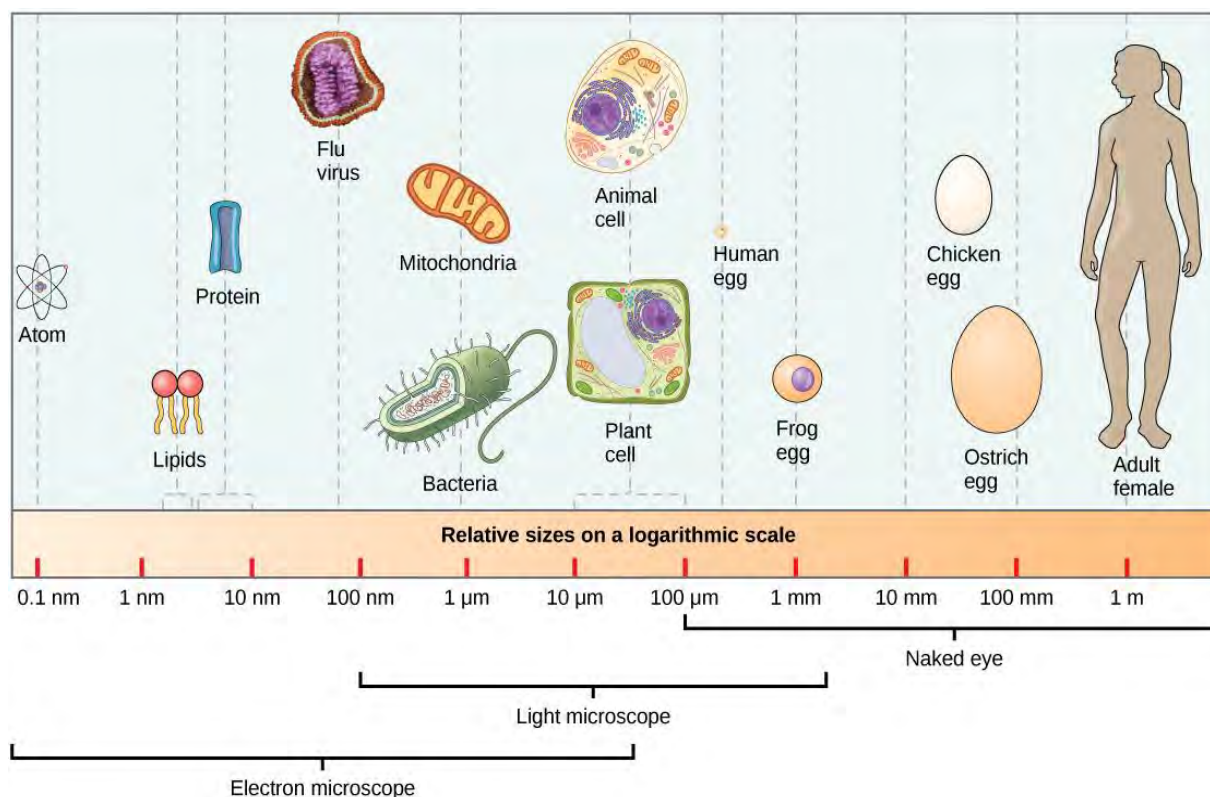
Figure 4.9 This figure shows the relative sizes of different kinds of cells and cellular components. An adult human is shown for comparison. (credit: Clark et al. / Biology 2E OpenStax)

VISUAL CONNECTION

Notice that as a cell increases in size, its surface area-to-volume ratio decreases. When there is insufficient surface area to support a cell's increasing volume, a cell will either divide or die. In Figure 4.10, the cell on the left has a volume of 1 mm^3 and a surface area of 6 mm^2. Therefore, the cell on the left has a surface area-to-volume ratio of 6 to 1. The cell on the right has a volume of 8 mm^3 and a surface area of 24 mm^2, with a surface area-to-volume ratio of 3 to 1. The cell on the right has a smaller surface-area-to-volume ratio. As a result, it would be more difficult for the cell on the right to acquire sufficient materials to support processes inside the cell compared to the cell on the left.
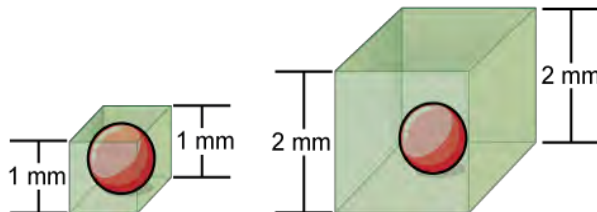
Figure 4.10 Surface area comparison of two different size cubes. (credit: Clark et al./ Biology 2E OpenStax)

CAREER CONNECTION - Microbiologist

The most effective action anyone can take to prevent the spread of contagious illnesses is to wash his or her hands. Why? Because microbes are ubiquitous. They live on doorknobs, money, your hands, and many other surfaces. If someone sneezes into his hand and touches a doorknob, and afterward you touch that same doorknob, the microbes from their mucus are now on your hands. If you touch your hands to your mouth, nose, or eyes, those microbes can enter your body and can make you sick.

However, not all microorganisms cause disease. Many microbes are beneficial. You have microbes in your gut that make vitamin K, which is required when making blood-clotting proteins. Other microorganisms are used to ferment beer and wine.

Microbiologists are scientists who study microorganisms (Figure 4.11). Microbiologists can pursue several careers. They can work in the food industry, be employed in veterinary and medical fields, and work for environmental organizations, just to mention a few.

Environmental microbiologists may look for new ways to use specially selected or genetically engineered microbes to remove pollutants from soil or groundwater. We call using these microbes bioremediation technologies. Microbiologists can also work in the bioinformatics field, providing specialized knowledge and insight for designing and developing computer models.

Figure 4.11 A microbiologist works to extract DNA to be analyzed. (credit: Sukulya/ Wikimedia)

Section Summary

All cells share four common characteristics: all cells are enclosed within a plasma membrane, contain cytoplasm, have genetic material, and have ribosomes.

Prokaryotes are predominantly single-celled organisms classified in the domains Bacteria and Archaea. All prokaryotes have plasma membranes, cytoplasm, ribosomes, a cell wall, genetic material, and lack membrane-bound organelles. 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. Eukaryotic cells are typically much larger than prokaryotic cells (10-100μm) and have a true nucleus and other membrane-bound organelles that allow for compartmentalization of functions.

Exercises

1. Which of these do all prokaryotes and eukaryotes share?
   a. nucleus
   b. cell capsule
   c. membrane-bound organelles
   d. plasma membrane

2. A typical prokaryotic cell _____ compared to a eukaryotic cell.
   a. is smaller in size
   b. is similar in size
   c. is larger in size
   d. can be smaller or larger in size

3. Describe the structures that are characteristic of a prokaryote cell.

Answers

1. (d)
2. (a)
3. Prokaryotic cells are surrounded by a plasma membrane and have DNA, cytoplasm, and ribosomes. They have cell walls and may have a cell capsule. Prokaryotes may have flagella for motility, pili for conjugation, and fimbriae for adhesion to surfaces.

Glossary

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

nucleoid: a central region in a prokaryotic cell where DNA is found

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

4.3 Eukaryotic Cell Components

Eukaryotic cells have a more complex structure than prokaryotic cells. In eukaryotic cells, membrane-bound organelles allow different functions to be compartmentalized in different areas of the cell. Before looking at cell organelles, let's first examine three essential components of the cell: the plasma membrane, cytoplasm, and the cytoskeleton.

The Plasma Membrane

Like prokaryotes, eukaryotic cells have a plasma membrane (Figure 4.12) made up of a phospholipid bilayer with embedded proteins. The plasma membrane separates the internal contents of the cell from its surrounding environment. Because of its chemical makeup, the plasma membrane allows the passage of some substances into and out of the cell while restricting the movement of others. It is important because it helps the cell maintain stable internal conditions. We will look more closely at the plasma membrane in section 5.1.
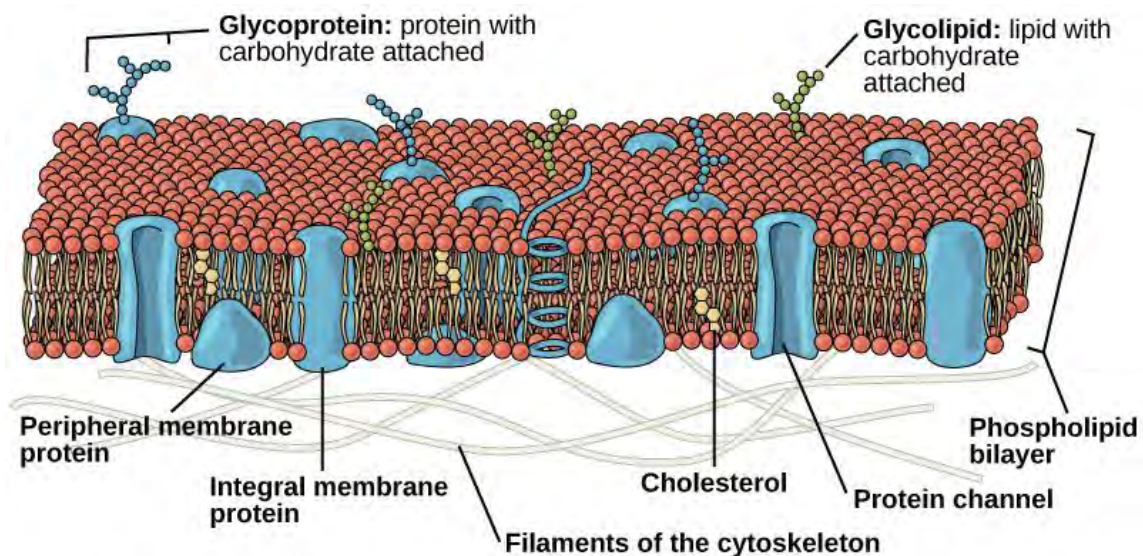
Figure 4.12 The plasma membrane is a phospholipid bilayer with embedded proteins. There are other components, such as cholesterol and carbohydrates, which can be found in the membrane in addition to phospholipids and protein. (credit: Clark et al. / Biology 2E OpenStax)

The Cytoplasm

The **cytoplasm** is made up of two parts: the cytosol and the cytoskeleton. The **cytosol** is a water-based gel-like substance that contains organelles, the cytoskeleton, and various chemicals. Glucose and other simple sugars, polysaccharides, amino acids, nucleic acids, fatty acids, and derivatives of glycerol are all found in the cytosol. Ions of sodium, potassium, calcium, and many other elements are also found here. Many metabolic reactions, including protein synthesis, take place in the cytosol.

The Cytoskeleton

Within the cytoplasm, a network of protein fibers called the **cytoskeleton** helps the cell maintain its shape, secures individual organelles in specific positions, and allows vesicles to move within the cell. Some cells, such as those that line the respiratory tract, also have cytoskeleton proteins that extend outside the cell into the external environment and can be used for motility.   The cytoskeleton also enables unicellular organisms, such as the amoeba, to move independently. There are three types of fibers within the cytoskeleton: microfilaments, intermediate filaments, and microtubules (Figure 4.13).
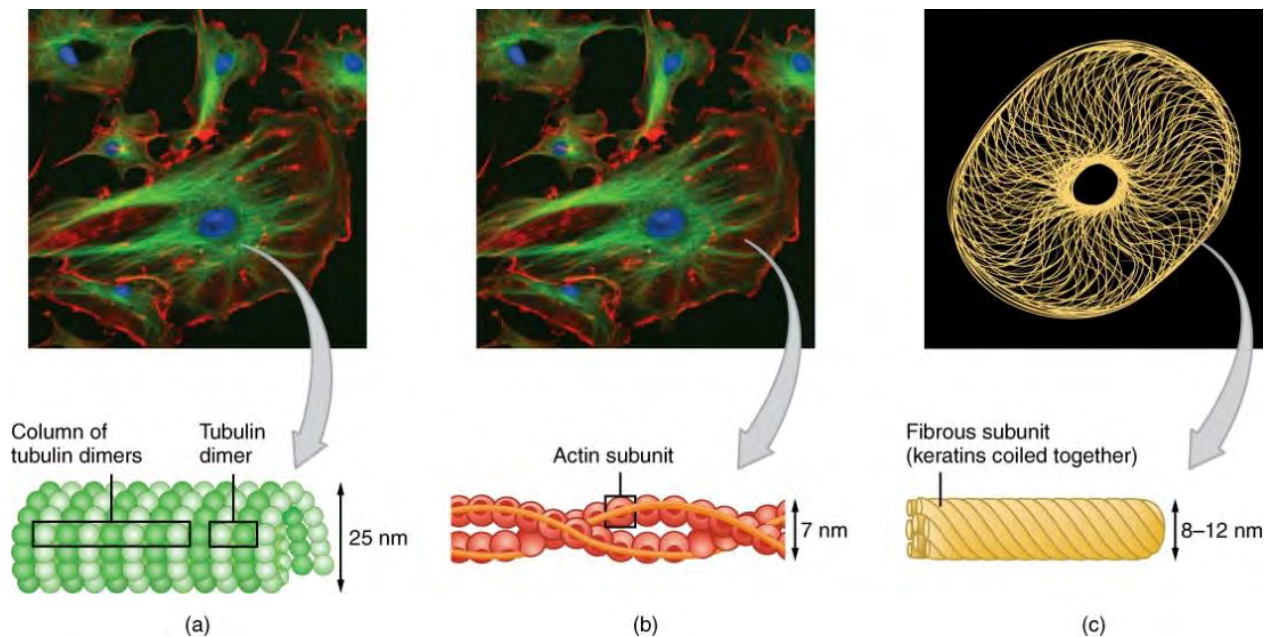
Figure 4.13 The cytoskeleton consists of (a) microtubules, (b) microfilaments, and (c) intermediate filaments. (credit: Betts et al. / Anatomy and Physiology OpenStax)

Microfilaments

Of the three types of protein fibers, **microfilaments** are the narrowest. Microfilaments are composed of two intertwined strands of actin. They function in cellular movement and have a diameter of about 7 nm. Microfilaments also provide some rigidity and help form the shape of the cell. They can disassemble and reform quickly, which enables a cell to change its shape and move (Figure 4.14). White blood cells, your body's infection-fighting cells, make good use of this ability. They can move to the site of an infection and neutralize the pathogen.
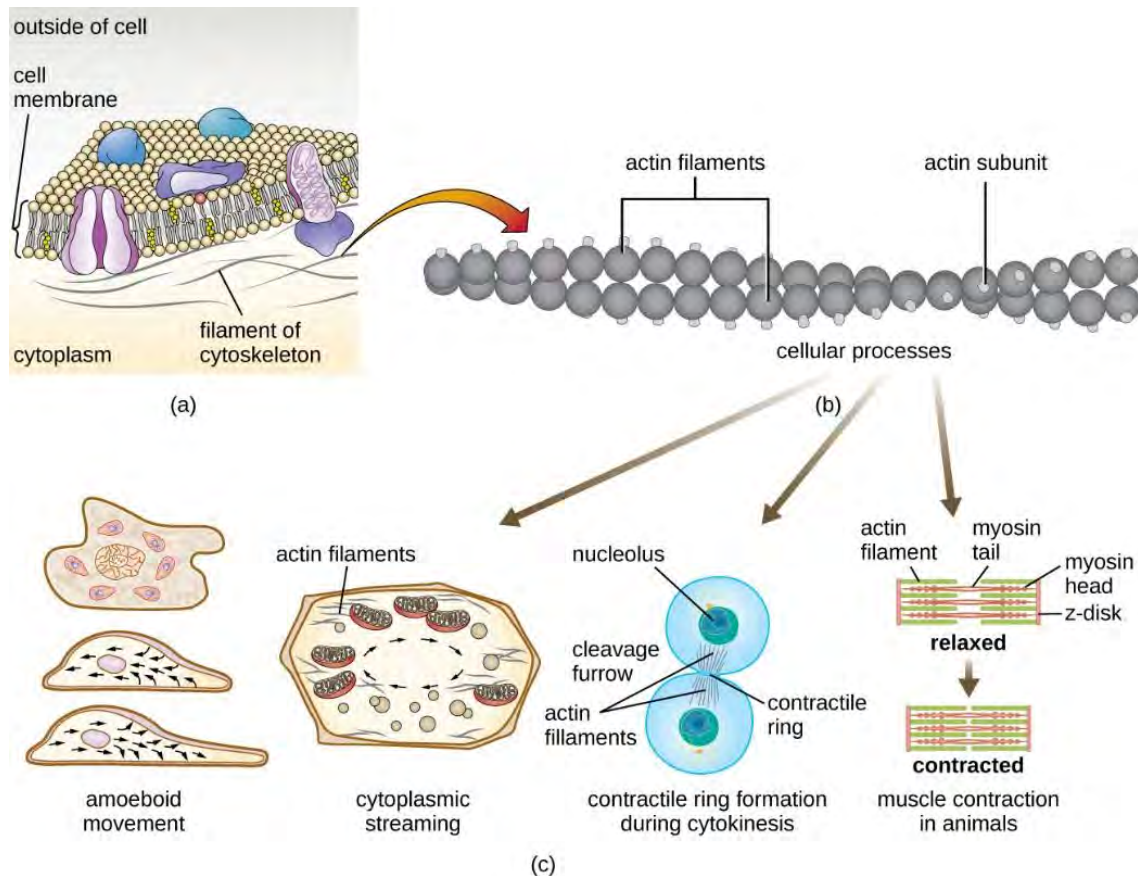
Figure 4.14 (a) A microfilament is composed of a pair of actin filaments. (b) Each actin filament is a string of polymerized actin monomers. (c) The dynamic nature of actin allows microfilaments to be involved in a variety of cellular processes (credit: Parker et al. / Microbiology OpenStax)

CONCEPTS IN ACTION - To see an example of a white blood cell in action, watch a short time-lapse video of the cell capturing two bacteria. It engulfs one and then moves on to the other bacteria.

Intermediate filaments are of intermediate diameter (between microfilaments and microtubules) and have structural functions such as maintaining the shape of the cell and anchoring organelles (Figure 4.15). Keratin, the compound that strengthens hair and nails, forms one type of intermediate filament.
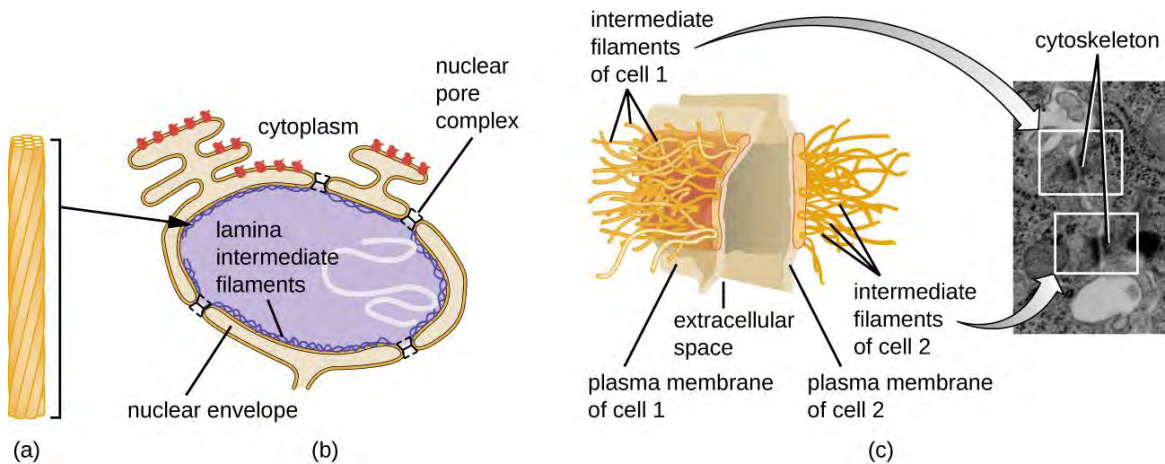
Figure 4.15 (a) Intermediate filaments are composed of multiple strands of polymerized subunits. (b) Intermediate filaments form much of the nuclear lamina. (c) Intermediate filaments form the desmosomes. (credit: c "illustration": modification of work by Mariana Ruiz Villareal / Microbiology OpenStax)

Microtubules

Microtubules are the thickest of the cytoskeletal fibers. These are hollow tubes that can dissolve and reform quickly. Microtubules work with motor proteins to move organelles and vesicles around within the cytoplasm. Also, microtubules are involved in cell division. Microtubules form the mitotic spindle that serves to separate chromosomes during mitosis and meiosis. The mitotic spindle is produced by two **centrosomes**, which are mostly microtubule-organizing centers at opposite ends of the cell. (Figure 4.16).
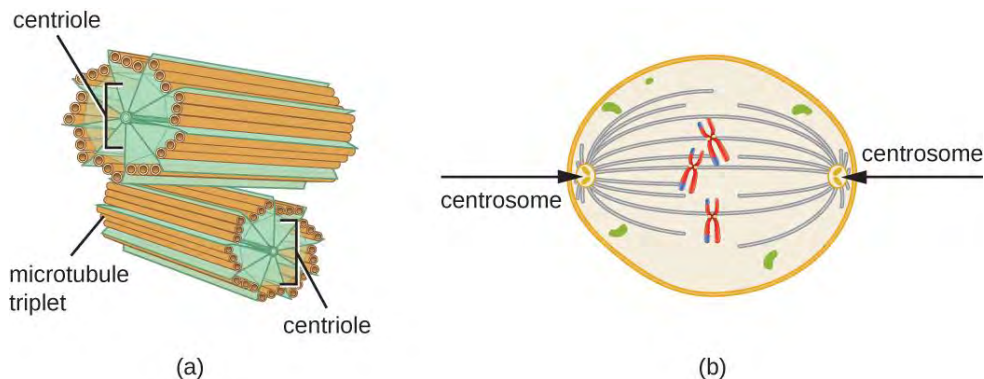
Figure 4.16 (a) A centrosome is composed of two centrioles positioned at right angles to each other. (b) In animal cells, the centrosomes (arrows) serve as microtubule-organizing centers of the mitotic spindle during mitosis. (credit: Parker et al. / Microbiology OpenStax)

Flagella and Cilia

Microtubules are also the structural components of flagella and cilia. **Flagella** (singular = flagellum) are long, hair-like structures that extend from the plasma membrane and are used to move the entire cell, for example, sperm and *Euglena*. When present, a cell may have just one flagellum or a few flagella. When **cilia** (singular = cilium) are present, they are many in number and extend along the entire surface of the plasma membrane. Cilia are short, hair-like structures that are used to move whole cells, for example the *Paramecium* in Figure 4.17 Cilia also move substances along the outer surface of the cell. For example, the cilia of cells lining the fallopian tubes move the ovum (egg) toward the uterus. Cilia lining the cells of the respiratory tract move particulate matter toward the throat where it is then trapped in mucus. These ciliated cells help prevent respiratory infections.

Figure 4.17 The ciliated protozoan *Paramecium caudatum*. (credit: Deuterostome / Wikimedia)

Section Summary

Like a prokaryotic cell, a eukaryotic cell has a plasma membrane and cytoplasm. The cytoplasm is made of two parts: the cytosol and the cytoskeleton.

The cytoskeleton has three different types of protein elements. Microfilaments provide rigidity and help shape the cell. Intermediate filaments bear tension and anchor the nucleus and other organelles in place. Microtubules help the cell resist compression and serve as tracks for motor proteins that move vesicles through the cell. They are also the structural elements of centrosomes, flagella, and cilia.

Exercises

1. Which of the following would not be considered part of the cytoskeleton?
   a. intermediate filaments
   b. flagella
   c. cytosol
   d. centrosomes

2. Which type of lipid forms the base structure of the plasma membrane?
   a. fats
   b. phospholipids
   c. oils
   d. wax

3. Describe the parts of the cytoplasm.

Answers

1. (c)
2. (b)
3. The cytoplasm is made up of two parts: the cytosol and the cytoskeleton. The cytosol contains organelles, cytoskeleton, and various chemicals. The cytoskeleton is a network of protein fibers that helps the cell maintain its shape, secures individual organelles in specific positions, and allows vesicles to move within the cell.

Glossary

centrosomes: specialized microtubules that pull chromosomes to their poles during cell division

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 maintain 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

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

intermediate filaments: fibers of the cytoskeleton that are of intermediate diameter and have structural functions, such as maintaining the shape of the cell and anchoring organelles

microfilaments: the thinnest of the cytoskeletal fibers and function in moving cellular components and maintaining cell structure

microtubules: the thickest fibers that make up the cytoskeleton and can dissolve and reform quickly.

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

4.4 Eukaryotic Cell Organelles

Learning objectives

By the end of this section, you will be able to:

- *Identify organelles that can be found in cells*
- *Know which organelles are part of the endomembrane system*
- *Summarize the functions of all major cell organelles*
- *Know which organelles are used to generate energy*
- *Identify which organelles are used during protein synthesis*
- *Be able to define and explain all bolded terms*

Unlike prokaryotic cells, eukaryotic cells have a membrane-bound nucleus and numerous membrane-bound organelles. Such organelles include the endoplasmic reticulum, Golgi apparatus, chloroplasts, mitochondria, and others (Figure 4.18). The word "organelle" means "little organ" and organelles have specialized cellular functions just as your body's organs have specialized functions.

Nucleus
Nuclear envelope: membrane enclosing the nucleus. Protein-lined pores allow material to move in and out.

Chromatin: DNA plus associated proteins.

Nucleolus: condensed region where ribosomes are formed.

Peroxisome: metabolizes waste

Endoplasmic reticulum
Rough: associated with ribosomes; makes secretory and membrane proteins.
Smooth: makes lipids.

Cytoskeleton
Microtubules: form the mitotic spindle and maintain cell shape.

Centrosome: microtubule-organizing center.

Intermediate filaments: fibrous proteins that hold organelles in place.

Microfilaments: fibrous proteins; form the cellular cortex.

Plasma membrane

Lysosome: digests food and waste materials.

Golgi apparatus: modifies proteins.

Cytoplasm

Vacuole

Mitochondria: produce energy.

Plasmodesmata channels connect two plant cells

Cell wall maintains cell shape

Plasma membrane

Cytoplasm

Central Vacuole filled with cell sap that maintains pressure against cell wall

Cytoskeleton microtubules intermediate filaments microfilaments

Endoplasmic Reticulum smooth   rough

Nucleus contains chromatin, a nuclear envelope, and a nucleolus, as in an animal cell

Ribosomes

Golgi apparatus

Mitochondria

Peroxisome

Chloroplast site of photosynthesis

Plastid store pigments

Figure 4.18 These figures show the major organelles and other cell components of (a) a typical animal cell and (b) a typical plant cell. (credit: Clark et al. / Biology 2E OpenStax)

The Endomembrane System

The **endomembrane system** (endo = "within") is a group of membranes and organelles (Figure 4.19) in eukaryotic cells that works together to modify, package, and transport lipids and proteins. It includes the nuclear envelope, lysosomes, vesicles, the endoplasmic reticulum, and the Golgi apparatus. Although not technically *within* the cell, the plasma membrane is included in the endomembrane system because it interacts with the other endomembranous organelles. The endomembrane system does not include organelles such as the mitochondria or chloroplast, which are used for energy processing.

Figure 4.19 Various organelles that are part of the endomembrane system. (credit: modification of work by Magnus Manske / Biology 2E OpenStax)
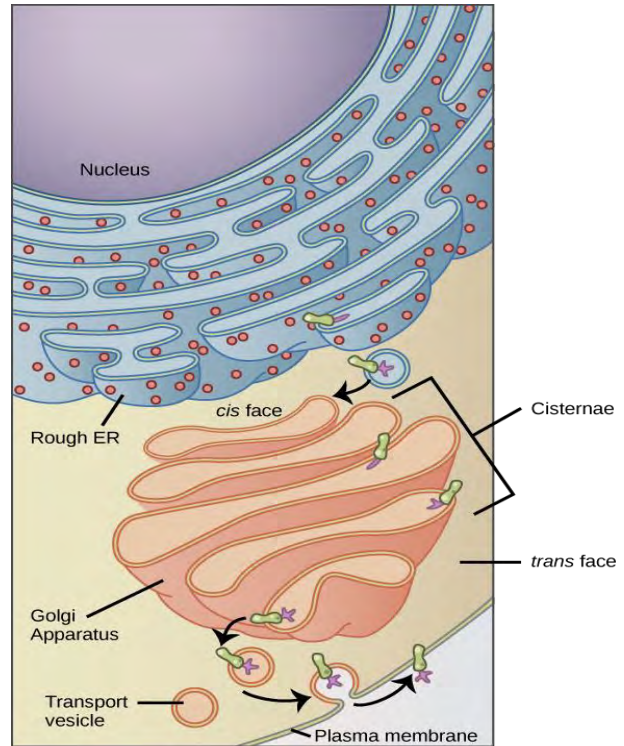
The Nucleus

Typically, the nucleus is the most prominent organelle in a cell (Figure 4.18). The **nucleus** (plural = nuclei) houses the cell's DNA in the form of chromatin and directs the synthesis of ribosomes and proteins.

The **nuclear envelope** is a double-membrane structure that constitutes the outermost portion of the nucleus. Both the inner and outer membranes of the nuclear envelope are phospholipid bilayers. The nuclear envelope is punctuated with **nuclear pores** that control the passage of ions, molecules, and RNA between the nucleus and the cytoplasm (Figure 4.20).
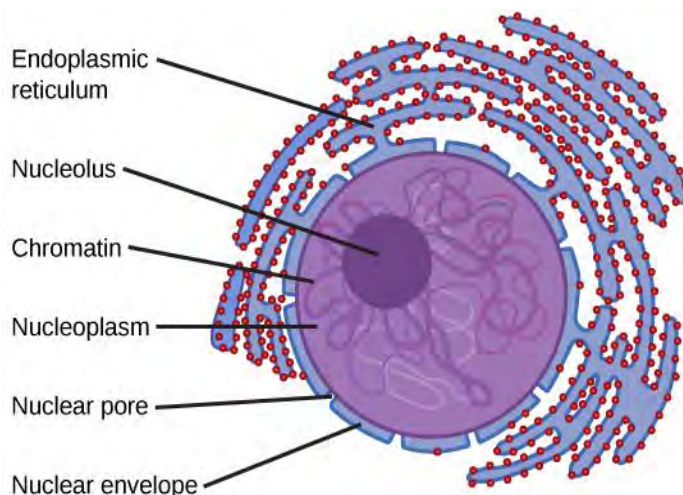
Figure 4.20 The outermost boundary of the nucleus is the nuclear envelope. (credit: modification of work by NIGMS, NIH / Concepts of Biology OpenStax)

Chromosomes, found in the nucleus, contain the cell's genetic information. They are composed of DNA wound around proteins (Figure 4.21). Together, this combination of DNA and proteins is called **chromatin** (Figure 4.21). When cells are not dividing, individual chromosomes are not visible, and the material in the nucleus is referred to as chromatin.

In eukaryotes, chromosomes are linear structures. Every species has a specific number of chromosomes in its nucleus. For example, humans should have 46 chromosomes in all their body cells except their eggs and sperm. Fruit flies, on the other hand, have a total of eight chromosomes in each of their cells.
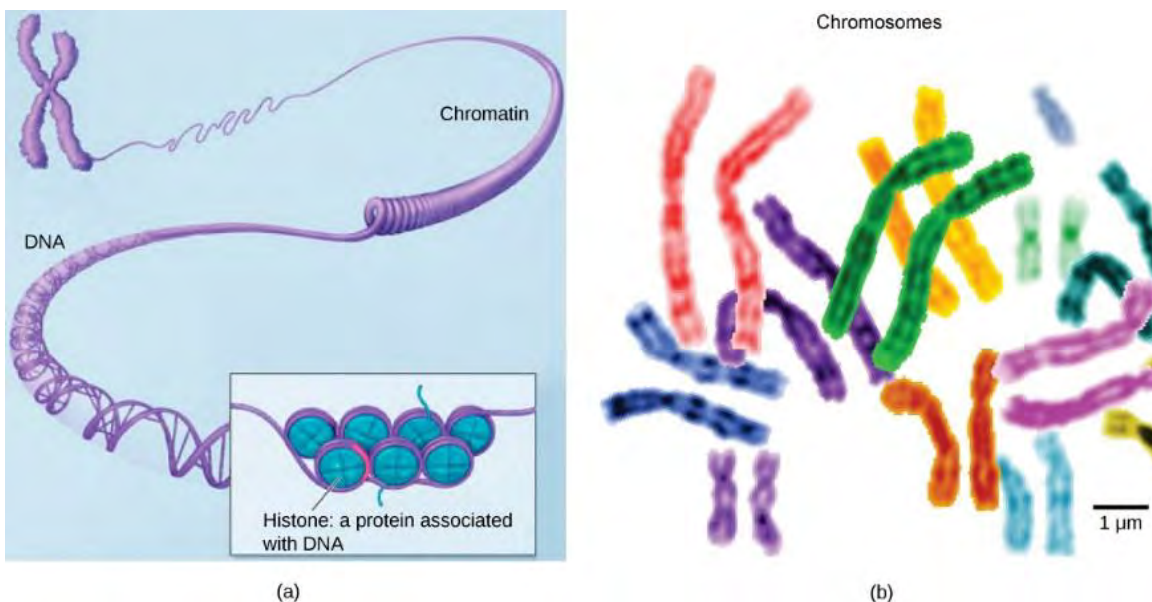
Figure 4.21 (a) This image shows various levels of chromatin's organization. (b) This image shows the paired chromosomes. (credit b: modification of work by NIH; scale-bar data from Matt Russell / Biology 2E OpenStax)

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

The DNA in 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 stained area within the nucleus, called the **nucleolus** (plural = nucleoli), indicates the location where ribosomal RNA is made and comes together with specific proteins to form the ribosomal subunits. The ribosomal subunits are then transported through the nuclear pores into the cytoplasm, where they will be used for protein synthesis.

The Endoplasmic Reticulum

The **endoplasmic reticulum** (ER) (Figure 4.22) 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: proteins are modified in the rough endoplasmic reticulum and lipids are synthesized in the smooth endoplasmic reticulum.
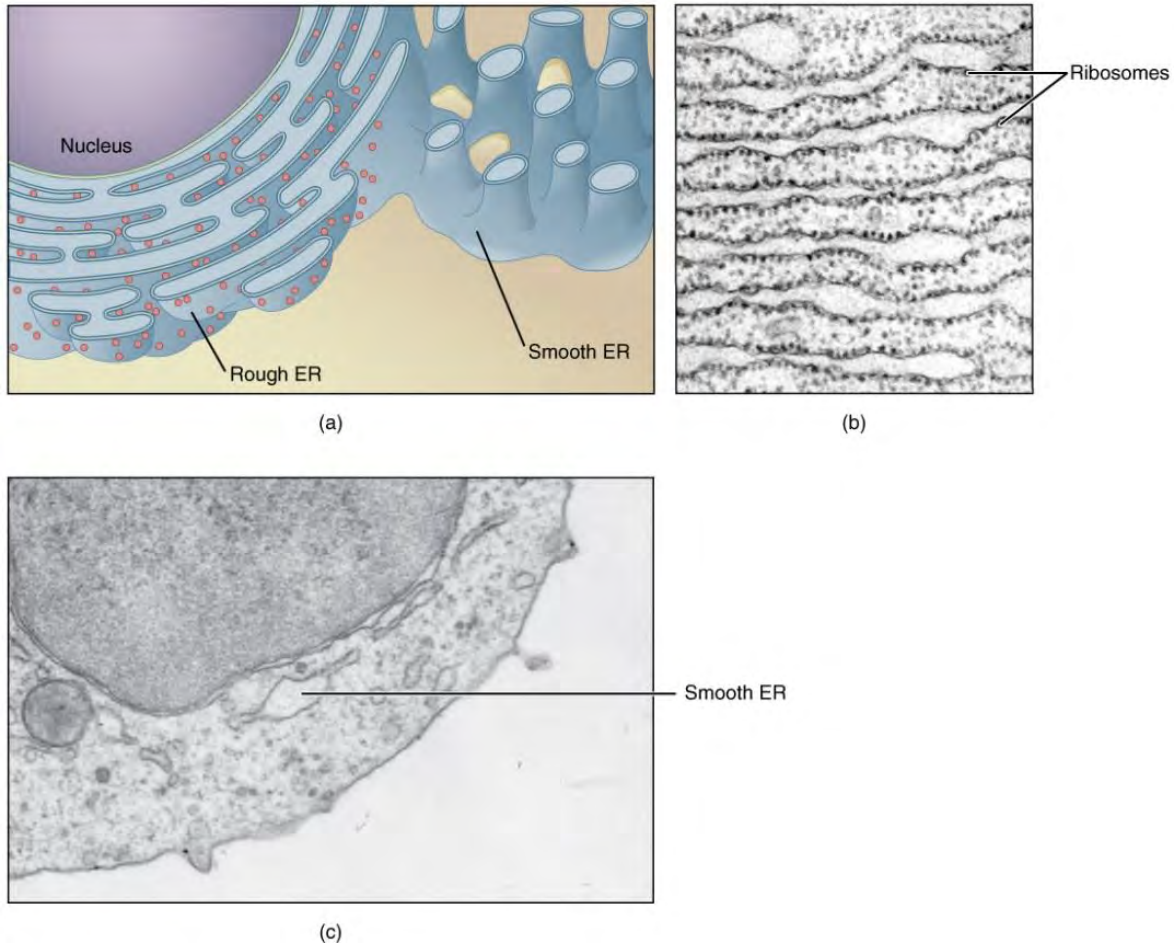
Figure 4.22 Endoplasmic Reticulum (ER) (a) The smooth and rough endoplasmic reticula are very different in appearance and function (source: mouse tissue). (b) Rough ER (source: mouse tissue). EM × 110,000. (c) Smooth ER (source: mouse tissue). EM × 110,510. (Micrographs provided by the Regents of University of Michigan Medical School © 2012 / Anatomy of Physiology OpenStax)

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 (Figure 4.22). The ribosomes synthesize proteins while attached to the ER. The newly synthesized proteins move into the lumen of the RER where they undergo modifications, such as folding or the addition of sugars. The RER also makes phospholipids for cell membranes. If the modified proteins or phospholipids are not needed in the RER, they will be packaged within vesicles and transported to the Golgi apparatus (Figure 4.23).

The **smooth endoplasmic reticulum** (SER) is continuous with the RER but has few or no ribosomes on its cytoplasmic surface (see Figure 4.22). The SER's functions include synthesis of carbohydrates, lipids (including phospholipids), and the precursors of steroid hormones, such as cholesterol. The smooth endoplasmic reticulum also plays a role in detoxification of medications and poisons, including alcohol metabolism. Finally, the SER acts as a storage space of calcium ions, which is necessary for muscle contraction, nervous system function, and cell division.

CONCEPTS IN ACTION - You can watch an excellent animation of the endomembrane system here. At the end of the animation, there is a short self-assessment.

CAREER CONNECTION - Cardiologist

Heart disease is the leading cause of death in the United States and has been linked to sedentary lifestyles and high trans-fat diets. Heart failure is just one of many disabling heart conditions. Heart failure does not mean that the heart has stopped working; rather, it means that the heart can't pump with sufficient force to transport oxygenated blood to all the vital organs. Left untreated, heart failure can lead to kidney failure and other organ failures.

Cardiac muscle tissue comprises the heart's wall. Heart failure can occur when cardiac muscle cells' endoplasmic reticula do not function properly. As a result, an insufficient number of calcium ions are available to trigger a sufficient contractile force.

Cardiologists (cardi- = "heart"; -ologist = "one who studies") are doctors who specialize in treating heart diseases. Cardiologists can diagnose heart failure via a physical examination, results from an electrocardiogram (ECG, a test that measures the heart's electrical activity), a chest X-ray to see whether the heart is enlarged, and other tests. If the cardiologist diagnoses heart failure, they may prescribe appropriate medications, recommend a reduced table salt intake, and a supervised exercise program. Depending on the severity of the diagnosis, other treatment options may need to be explored.

The Golgi Apparatus

We have already mentioned that vesicles can bud from the endoplasmic reticulum, 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 or Golgi complex), a series of flattened membranous sacs (Figure 4.23).
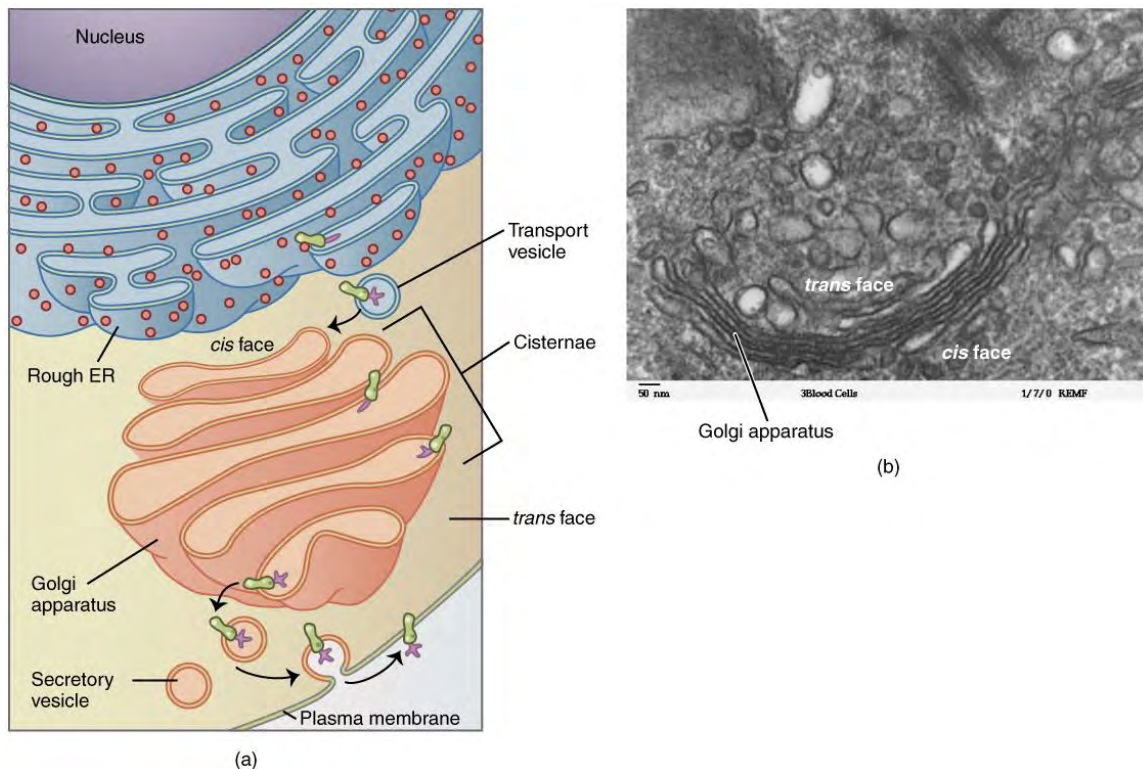
Figure 4.23 a. The Golgi apparatus b. Transmission electron micrograph of a Golgi apparatus in a white blood cell. (credit: modification of work by Louisa Howard; scale-bar data from Matt Russell / Anatomy and Physiology OpenStax)

The Golgi apparatus has a receiving face (cis) near the endoplasmic reticulum and a releasing face (trans) on the side facing away from the ER. The transport vesicles sent 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 change 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 deposit their contents into other parts of the cell, other vesicles fuse with the plasma membrane and release their contents outside the cell.

The quantity of Golgi varies in different cells. Cells that are involved in secreting large quantities of materials have higher amounts of Golgi. For example, cells that make up the salivary glands secrete digestive enzymes into the mouth, which aids in digestion. Some cells of the immune system secrete antibodies into the blood, which helps protect us from foreign invaders.

In plant cells, the Golgi has an additional role in synthesizing polysaccharides. Some of these polysaccharides are incorporated into the cell wall and while others are used in different parts of the cell.

Lysosomes

Some of the proteins packaged by the Golgi include digestive enzymes. Some of those enzymes remain inside the cell to be used for breaking down certain materials. The enzyme-containing vesicles released by the Golgi may form new lysosomes or fuse with existing lysosomes. A **lysosome** is an organelle that contains enzymes that break down and digest unneeded cellular components, such as a damaged organelle. A lysosome is like a wrecking crew that takes down old and unsound buildings in a neighborhood. Lysosomes are also important for breaking down food materials or foreign materials that may be dangerous to the cell. For example, when certain immune defense cells take up bacteria, the bacterial cell is enclosed in a vesicle (Figure 4.24) that then fuses with a lysosome. The enzymes found in the lysosome then digest the bacteria. As one might imagine, these immune defense cells contain large numbers of lysosomes.

Under certain circumstances, lysosomes perform a more grand and dire function--in the case of damaged or unhealthy cells, lysosomes can be triggered to open and release their digestive enzymes into the cytoplasm of the cell, killing the cell. This "self-destruct" mechanism is called autolysis and makes the process of cell death controlled; a mechanism called "apoptosis."

It is important to note that lysosomes are not present in plant cells. Because lysosomes are considered part of the endomembrane system, they are being discussed in this section. In plant cells, the digestive processes take place in vacuoles and not lysosomes.

Figure 4.24 A macrophage has taken up a bacterium, which then fuses with a lysosome within the cell. Other organelles are present in the cell, but for simplicity, are not shown. (credit: Modified by Elizabeth O'Grady original work by Clark et al. / Biology 2E OpenStax)
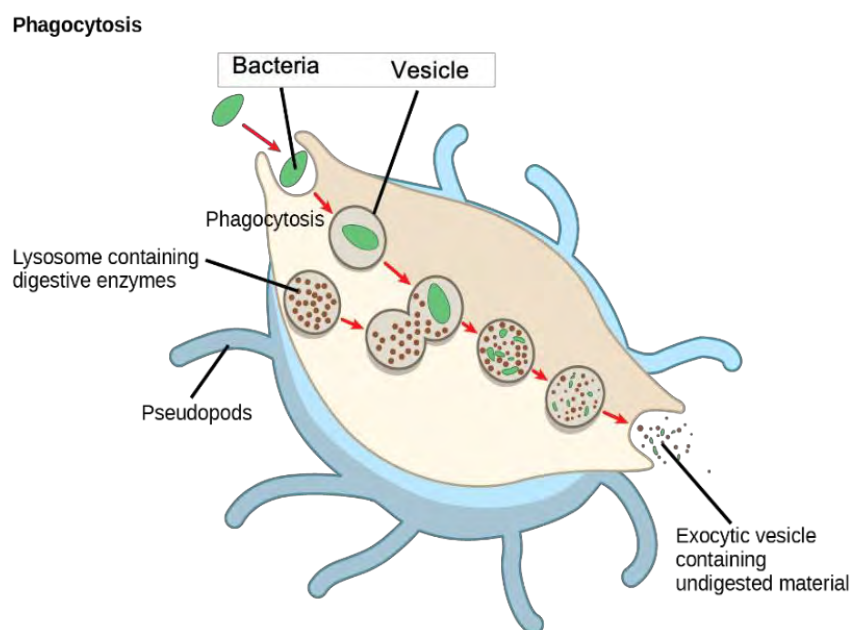
Vesicles and Vacuoles

Vesicles (Figure 4.24) and **vacuoles** (Figure 4.18) are membrane-bound sacs that function in storage and transport. Other than the fact that vacuoles are somewhat larger than vesicles, there is a very subtle distinction between them. Vesicle membranes can fuse with either the plasma membrane or other membrane systems within the cell. Additionally, some enzymes within plant vacuoles break down macromolecules (Figure 4.18).

Ribosomes

Ribosomes are the cellular structures responsible for protein synthesis and are not part of the endomembrane system. They are the only organelle not enclosed in a plasma membrane. When viewed through an electron microscope, free ribosomes appear as either clusters or single tiny dots floating freely in the cytoplasm. Ribosomes may also attach to either the plasma membrane or the rough endoplasmic reticulum (red circles in Figure 4.22). Electron microscopy has shown that ribosomes consist of large and small subunits (Figure 4.25). Ribosomes are enzyme complexes that are responsible for protein synthesis.
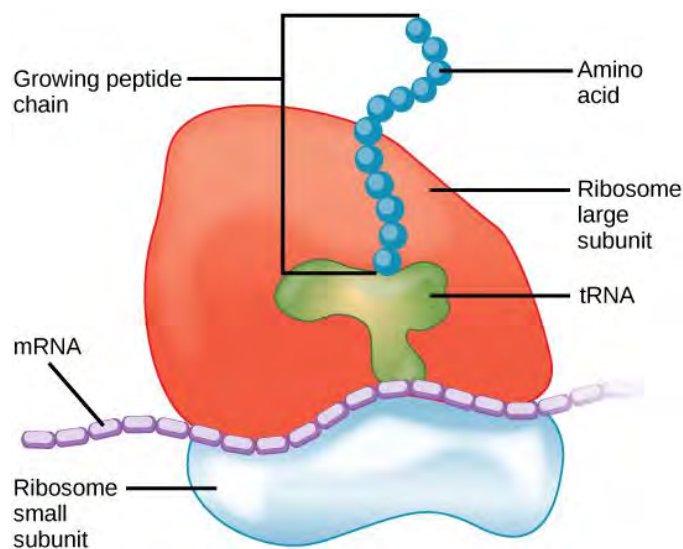
Because protein synthesis is essential for all cells, ribosomes are found in practically every cell. In prokaryotic cells, ribosomes are smaller and differ slightly in their chemical makeup when compared to ribosomes found in eukaryotic cells.

Figure 4.25 A large subunit (top) and a small subunit (bottom) comprise ribosomes. (credit: Clark et al. / Biology 2E OpenStax)

Check your knowledge

Which type of cell is most likely to have the greatest amount of smooth endoplasmic reticulum?
  a. A cell that secretes enzymes
  b. A cell that destroys pathogens
  c. A cell that makes steroids
  d. A cell that performs photosynthesis

Answer: c

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 primary energy molecule. The formation of ATP from the breakdown of glucose is known as cellular respiration. Mitochondria are oval-shaped, double-membrane organelles (Figure 4.26) 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 inner mitochondrial matrix (space). The space between the inner and outer membranes is the intermembrane space (outer mitochondrial matrix). The cristae and the matrix have different roles in cellular respiration, which will be discussed in chapter 6.
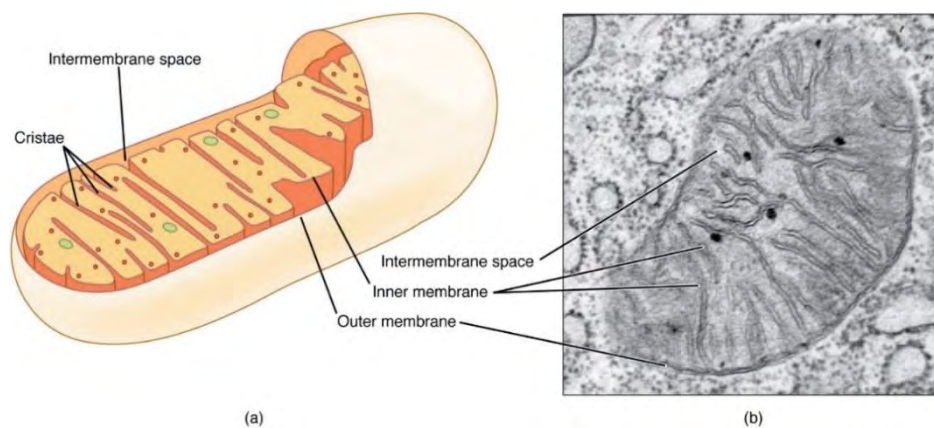
Figure 4.26 (a) A mitochondrion is composed of two separate lipid bilayer membranes. (b) An electron micrograph of mitochondria. EM × 236,000. (Micrograph provided by the Regents of University of Michigan Medical School © 2012 / Anatomy and Physiology OpenStax)

Peroxisomes

Peroxisomes are small, round organelles enclosed by single membranes (Figure 4.27). They carry out reactions that break down fatty acids and amino acids. They also detoxify many poisons that may enter the body. Peroxisomes detoxify alcohol in liver cells. A byproduct of these reactions is the highly reactive molecule hydrogen peroxide, H_2O_2. Hydrogen peroxide is contained within the peroxisomes to prevent it from causing damage to cellular components outside of the organelle. Hydrogen peroxide is safely broken down into water and oxygen with the help of the enzyme catalase. Catalase, in addition to many other enzymes, is located in the center of the peroxisome in a region called the crystalline core.
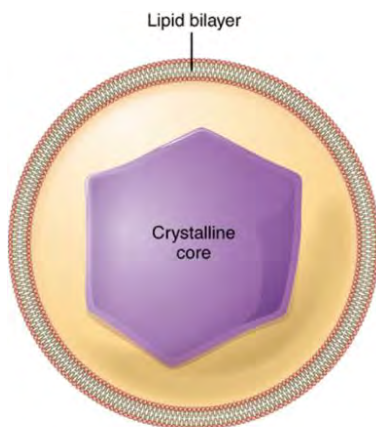
Figure 4.27 Peroxisome (credit: Betts et al. / Anatomy and Physiology OpenStax)

Section Summary

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

Eukaryotic cells have a true nucleus meaning its DNA is surrounded by a membrane. The nucleolus within the nucleus is the site for ribosome assembly. Ribosomes are found in the cytoplasm or are attached to the plasma membrane of the rough endoplasmic reticulum. Ribosomes 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.

Exercises

1. Which of the following organelles is most likely to aid in the digestion of food particles?
   a. nucleus
   b. rough endoplasmic reticulum
   c. lysosome
   d. ribosome

2. Which of the following is not a component of the endomembrane system?
   a. mitochondrion
   b. Golgi apparatus
   c. endoplasmic reticulum
   d. lysosome

3. Calcium ions are required for muscle contraction. Which organelle would you expect to find in abundance in a muscle cell that would aid in this function?
   a. mitochondrion
   b. Golgi apparatus
   c. lysosome
   d. smooth endoplasmic reticulum

4. Mitochondria contain both DNA and ribosomes.
   a. True
   b. False

5. Where in the nucleus are ribosomes formed?

6. Where are chromosomes found in a eukaryotic cell? Chromosomes are made of chromatin. What are the two materials that make up the chromatin?

7. Compare and contrast the rough endoplasmic reticulum to the smooth endoplasmic reticulum.

Answers

1. (c)
2. (a)
3. (d)
4. (a)
5. nucleolus
6. Chromosomes are found in the nucleus and are made of chromatin. Chromatin is made of DNA and protein.
7. Both types of endoplasmic reticulum are part of the endomembrane system. They are both 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.

Glossary

chromatin: substance consisting of DNA and associated proteins

chromosome: a condensed version of chromatin

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

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 primary energy-carrying molecule

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

nuclear pores: control the passage of ions, molecules, and RNA between the nucleus and the cytoplasm

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

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

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

4.5 Diversity of cell organelles within the eukaryotes

<u>**Learning objectives**</u>
By the end of this section, you will be able to:

- *Describe the differences between eukaryotic plant and animal cells*
- *Summarize the Endosymbiotic theory*
- *Understand how cells communicate with one another*
- *Know the differences between plant cell and animal cell communication*
- *Describe the cell's extracellular matrix*
- *Be able to define and explain all bolded terms*

All eukaryotic cells have a membrane-bound nucleus and numerous membrane-bound organelles. They are all enclosed within a plasma membrane, have genetic material, and use ribosomes to synthesize proteins. Despite their fundamental similarities, there are some striking differences amongst the different groups of cells that make up the eukaryotes. Those groups being Plantae, Protista, Animalia, and Fungi. We will briefly introduce the groups Protista and Fungi, before focusing our attention on the kingdoms Plantae and Animalia.

Protist

There are over 100,000 described living species of protists. Because the name "protist" serves as a catchall term for eukaryotic organisms that are not animal, plant, or fungi, it is not surprising that very few characteristics are common to all protists. Most protists are microscopic, unicellular organisms that are abundant in soil, freshwater, brackish, and marine environments. They are also common in the digestive tracts of animals and the vascular tissues of plants. Some protists have huge, macroscopic cells, such as the plasmodia of myxomycete slime molds or the marine green alga *Caulerpa*. Some protists are multicellular, such as red, green, and brown seaweeds. Because of their diversity, protists have a wide variety of different membrane-bound organelles. In the lab, you will have the opportunity to look at several protists: *Amoeba, Paramecium*, and green algae. At that time, you will observe some of the organelles found in protists.

Fungi

The kingdom Fungi includes an enormous variety of living organisms collectively referred to as Eumycota, or true Fungi. While scientists have identified about 100,000 species of fungi, this is only a fraction of the 1.5 million species of fungus likely present on Earth. Edible mushrooms, yeasts, black mold, and the producer of the antibiotic penicillin, *Penicillium notatum*, are all members of the kingdom Fungi. Because of their diversity, fungi also have a wide variety of different membrane-bound organelles. Students will not be held accountable for learning the cell organelles of fungi.

We will now focus on the groups Animalia and Plantae and discuss key differences between these two groups.

Animal vs. Plant

Despite their fundamental similarities, there are some striking differences between cells found in the groups Animalia and Plantae (see Table 4.1). Plant cells have a cell wall, chloroplasts, and a large central vacuole. Plant cells also have plastids that are used for storage. For example, cells that make up the potato have amyloplasts, a type of plastid used for storing starch. These organelles are not found in animal cells. As you learned in previous sections, animal cells have centrosomes and lysosomes. Both animal cells and plant cells have intercellular junctions for communication; however, there are distinct differences in these junctions. We will now spend some time discussing the differences in detail.

Cell Wall

In Figure 4.29b, 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. While the chief component of prokaryotic cell walls is peptidoglycan, the major organic molecule in the plant cell wall is cellulose. Cellulose is a polysaccharide made up of long, straight chains of glucose units. Some organisms have the enzyme cellulase and can digest cellulose and use it as a source of energy.

Chloroplasts

Like mitochondria, chloroplasts have their own DNA and ribosomes. **Chloroplasts** are the location of 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. One of the significant differences between plant and animal cells is that plants can make their own food and are referred to as **autotrophs.** Whereas animals, referred to as **heterotrophs,** must rely on other organisms for their organic compounds or food source.

Like mitochondria, chloroplasts have outer and inner membranes. Inside the inner membrane of the chloroplast is a fluid called stroma. In the stroma is a set of interconnected and stacked, fluid-filled membrane sacs called thylakoids (Figure 4.28). Each stack of thylakoids is called a granum (plural = grana). In chapter 7, you will learn about how different photosynthetic reactions take place in the stroma and thylakoid membranes.

Figure 4.28 This simplified diagram of a chloroplast shows the outer membrane, inner membrane, thylakoids, grana, and stroma (credit: Fowler et al. / Concepts of Biology OpenStax).
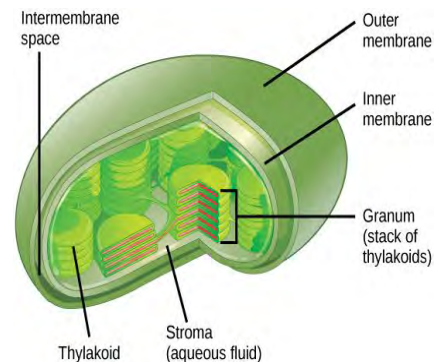
The chloroplasts contain a green pigment called chlorophyll, which captures the energy of sunlight for photosynthesis. It is this pigment that gives leaves their green appearance. Like plant cells, photosynthetic protists also have chloroplasts. Some bacteria also perform photosynthesis, but they do not have chloroplasts. Their photosynthetic pigments are located in the thylakoid membrane within the cell itself.
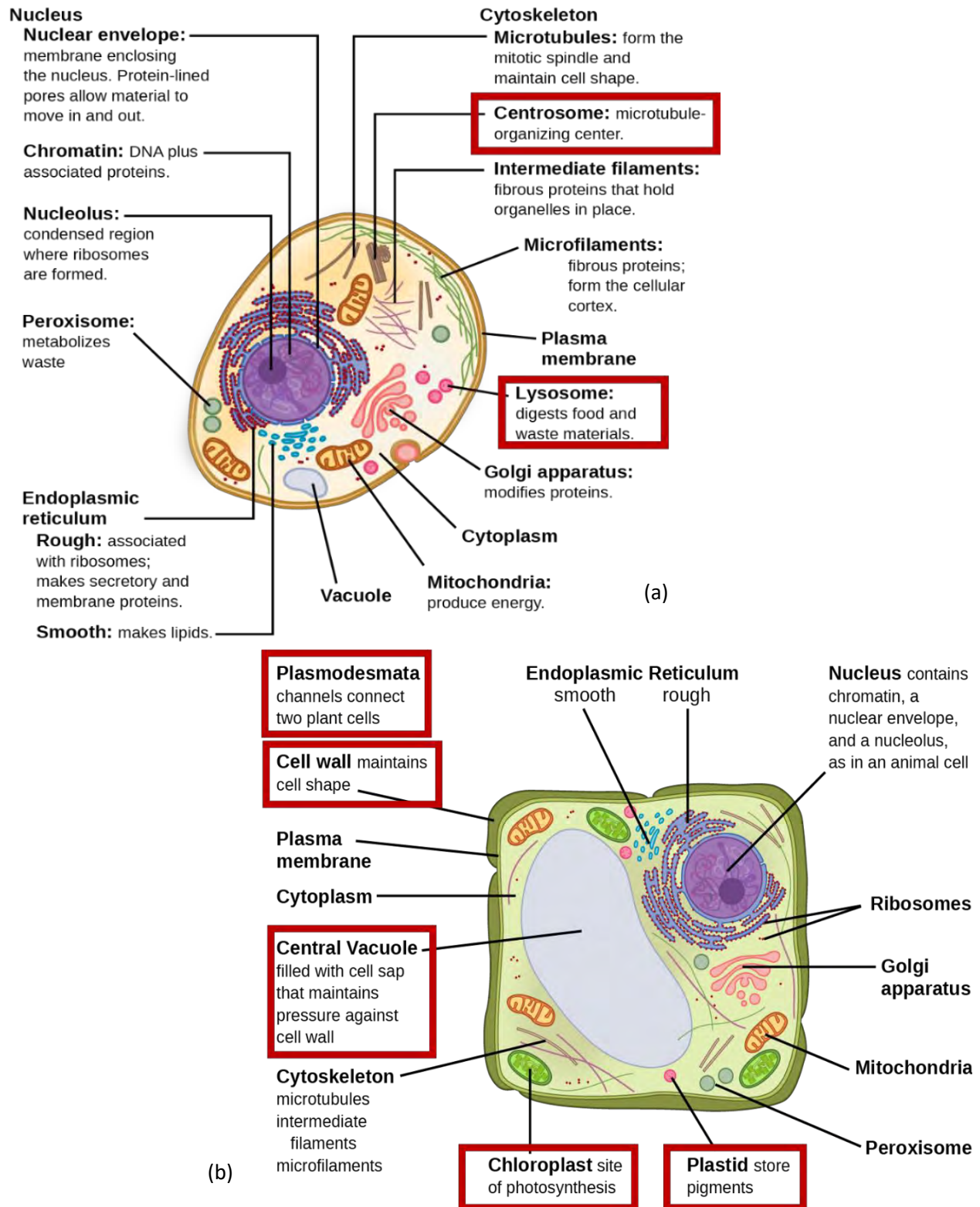
Figure 4.29 These figures show the major organelles and other cell components of (a) a typical animal cell and (b) a typical eukaryotic plant cell. (credit: Modified by Elizabeth O'Grady original work by Clark et al. / Biology 2E OpenStax)

EVOLUTION CONNECTION - Endosymbiotic Theory

We have mentioned that both mitochondria and chloroplasts have a double plasma membrane and contain their own DNA and ribosomes. Strong evidence indicates that endosymbiotic relationships between cells explains these characteristics.

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. Microbes that produce vitamin K live inside the human gut. This relationship is beneficial for us because we are unable to synthesize vitamin K and need it to produce blood-clotting proteins. It is also helpful for microbes because they are protected from other organisms and are provided a stable habitat and abundant food.

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. When the DNA found in these organelles was analyzed, it was found to resemble the DNA of current-day bacteria. Scientists hypothesize 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 selection, these ingested bacteria became more specialized in their functions, with the aerobic bacteria becoming mitochondria and the photosynthetic bacteria becoming chloroplasts (Figure 4.30). Although at one time these bacteria would have been able to live on their own, this is no longer possible because of the immense amount of specialization that has occurred.

The ENDOSYMBIOTIC THEORY

1. Infoldings in the plasma membrane of an ancestral prokaryote gave rise to endomembrane components, including a nucleus and endoplasmic reticulum.

3. In a second endosymbiotic event, the early eukaryote consumed photosynthetic bacteria that evolved into chloroplasts.

Nucleus

Endoplasmic reticulum

Proto-eukaryote

2. In a first endosymbiotic event, the ancestral eukaryote consumed aerobic bacteria that evolved into mitochondria.

Aerobic bacterium

Photosynthetic bacterium

Modern photosynthetic eukaryote

Mitochondrion

Modern heterotrophic eukaryote

Figure 4.30 The first eukaryote may have originated from an ancestral prokaryote that had undergone membrane proliferation, compartmentalization of cellular function (into a nucleus, lysosomes, and an endoplasmic reticulum), and the establishment of endosymbiotic relationships with an aerobic prokaryote. (credit: Fowler et al. / Concepts of Biology OpenStax)

Much data has been collected that supports that the mitochondria and chloroplasts originated from free-living bacteria. Scientists have drawn similar conclusions that ingested bacteria became more specialized in their functions, lost their ability to live on their own, and are now organelles that help their host cells generate energy. This concept is now known as the **endosymbiotic theory**.

Central Vacuole

If you look at Figure 4.31, you will see that plant cells each have a large, central vacuole that occupies most of the cell. The **central vacuole** plays a crucial role in regulating the cell's concentration of water in changing environmental conditions. Have you ever noticed that if you forget to water a plant for a few days, it wilts? That's because as the water concentration in the soil becomes lower than the water concentration in the plant, water moves out of the central vacuoles and cytoplasm. As the central vacuole shrinks, it leaves the cell wall unsupported and appears to wilt. The central vacuole also supports the cell's expansion. When the central vacuole holds more water, the cell becomes larger without having to invest considerable energy in synthesizing a new cytoplasm.

The central vacuole also functions to store proteins in developing seed cells, has digestive enzymes, and acts as a storage site for waste materials.
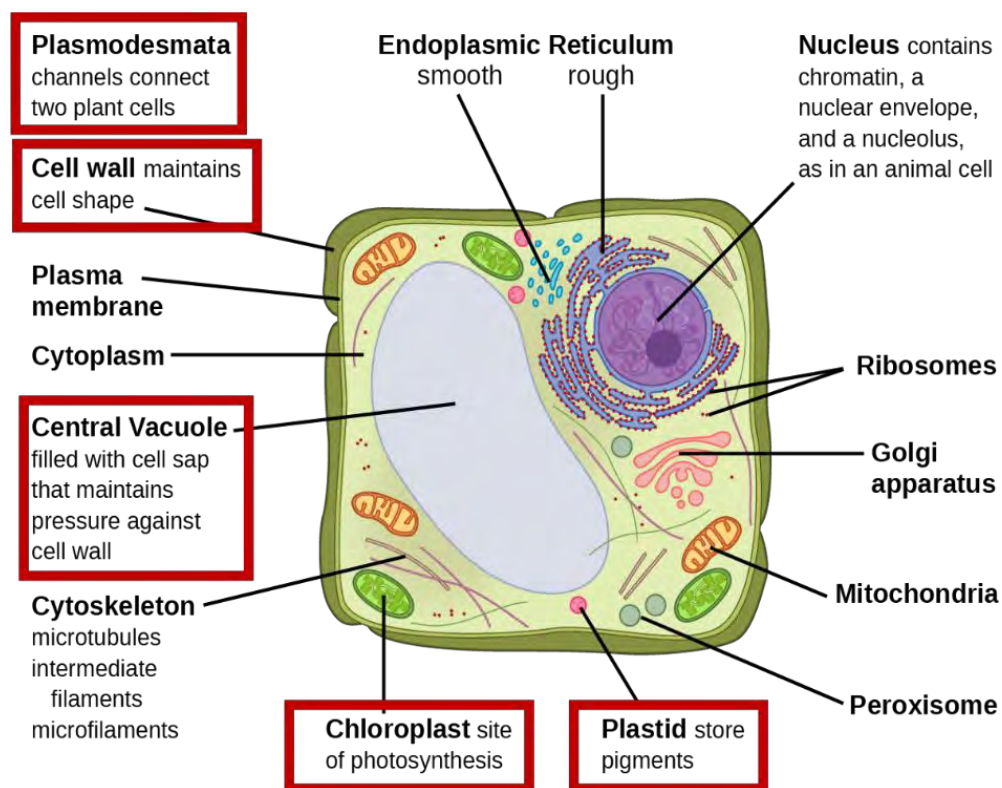
Figure 4.31 These figures show the major organelles and other cell components of a typical eukaryotic plant cell. (credit: Modified by Elizabeth O'Grady original work by Clark et al. / Biology 2E OpenStax)

Intercellular Junctions

Cells can communicate with each other by direct contact, referred to as intercellular junctions. Although both animal and plant cells communicate, there are some differences in the way that this communication is done. Plasmodesmata (singular = plasmodesma) are junctions between plant cells, whereas animal cells use tight junctions, gap junctions, and desmosomes, a type of anchoring junction (Figure 4.32).
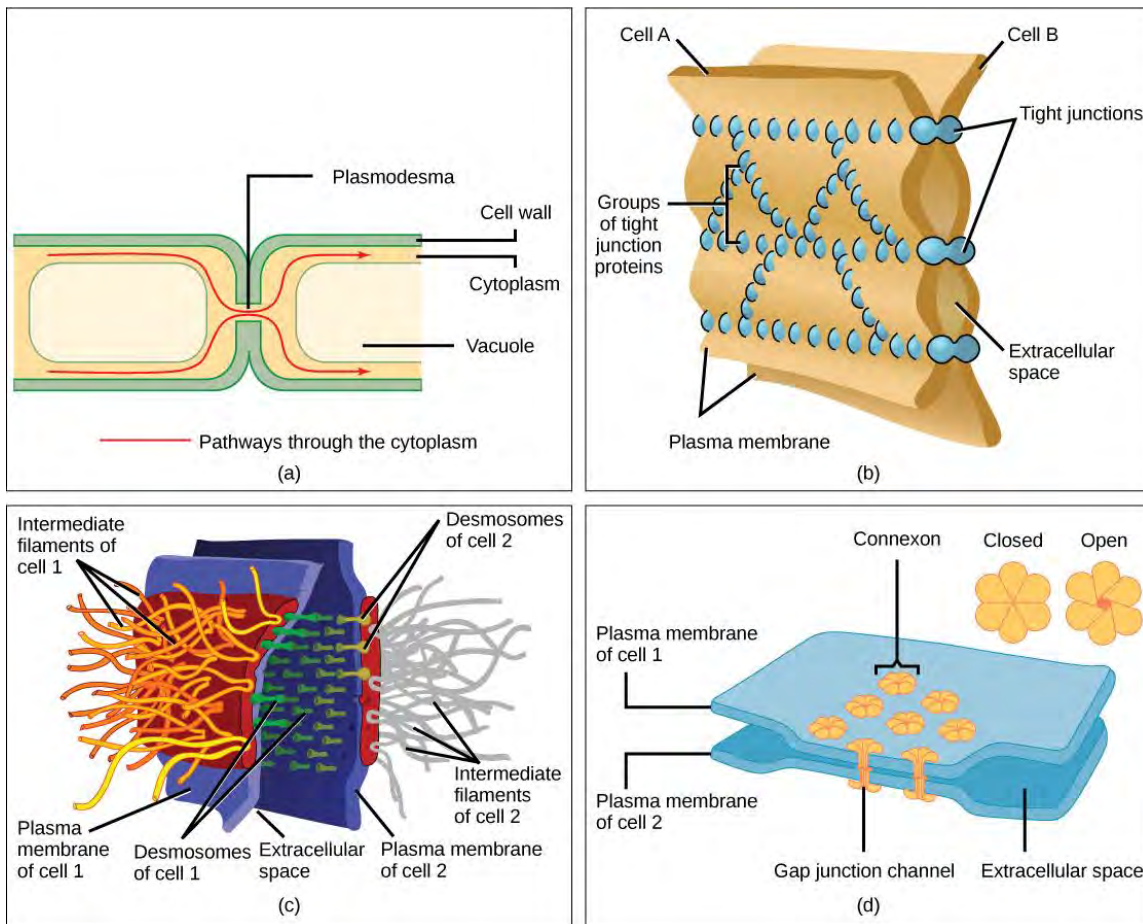
Figure 4.32 There are four kinds of connections between cells. (a) plasmodesma (b) Tight junctions (c) Desmosomes (d) Gap junctions (credit b, c, d: modification of work by Mariana Ruiz Villareal / Concepts of Biology OpenStax)

Plasmodesmata

In neighboring plant cells, the plasma membranes cannot touch one another because they are separated by the cell walls surrounding each cell. **Plasmodesmata** are channels that pass between the cell walls of adjacent cells. They connect the cytoplasm of adjacent plant cells, which enables signal molecules and nutrients to be transported from cell to cell (Figure 4.33).

These junctions between neighboring cells always remain open, and therefore, materials are continuously being shared amongst cells.

Figure 4.33 A plasmodesma is a channel between two adjacent plant cells' cell walls. (credit: Clark et al. / Biology 2E OpenStax).
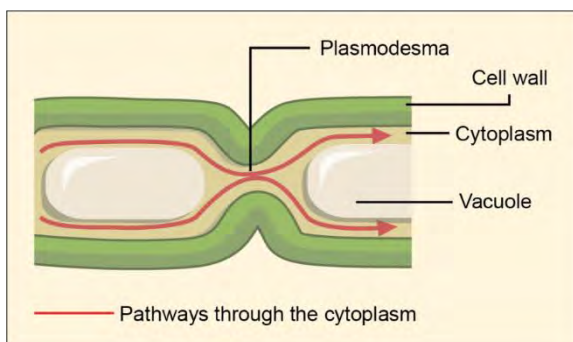
Tight junctions

A **tight junction** is a watertight seal between two adjacent animal cells (Figure 4.34). 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. For example, the tight junctions of the epithelial cells lining the urinary bladder prevent urine from leaking into the extracellular space. Tight junctions are also found between cells of the skin and play an essential role in preventing materials from the external environment from quickly moving into the body.
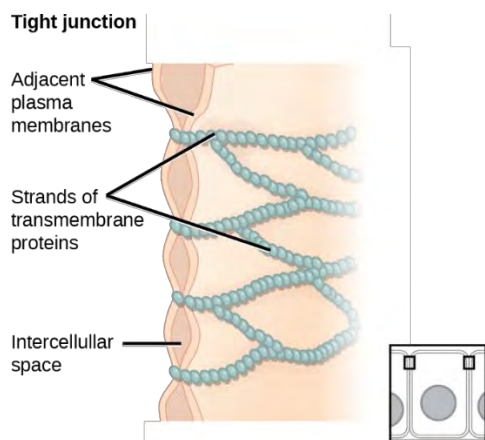
Figure 4.34 Tight junctions form watertight connections between adjacent animal cells. (credit: modification of work by Mariana Ruiz Villareal / Biology 2E OpenStax)

Demosomes

Desmosomes are another type of junction found associated with animal cells. **Desmosomes** are a type of anchoring junction, which provides strong and flexible connections (Figure 4.35). Desmosomes occur in patches on the membranes of cells. These connections are especially important in holding cells together. They keep cells together in a sheet-like formation in organs and tissues that stretch, like the skin, heart, and muscles.

Figure 4.35 A desmosome forms a very strong spot weld between cells. (credit: modification of work by Mariana Ruiz Villareal / Biology 2E OpenStax)
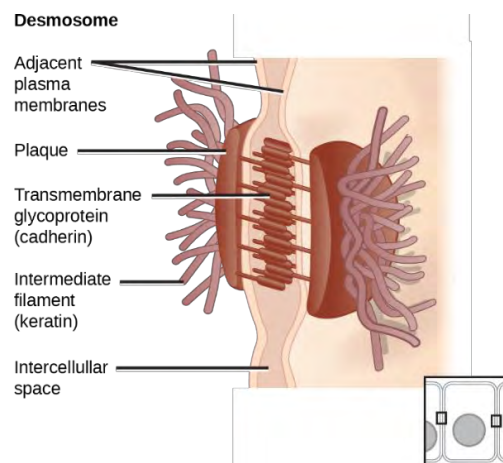
Gap junctions

Gap junctions in animal cells are like plasmodesmata in plant cells. They are channels between adjacent cells that allow for the transport of ions, nutrients, and other substances that enable cells to communicate (Figure 4.36). These junctions allow the electrical and metabolic coupling of adjacent cells. This is important because it coordinates function in large groups of cells and lets them work synchronously. Structurally, however, gap junctions and plasmodesmata differ in that gap junctions are not always "open." This allows cells to control somewhat when materials are shared amongst one another.

Figure 4.36 A gap junction allows water and small molecules to pass between adjacent animal cells. (credit: modification of work by Mariana Ruiz Villareal / Biology 2E OpenStax)
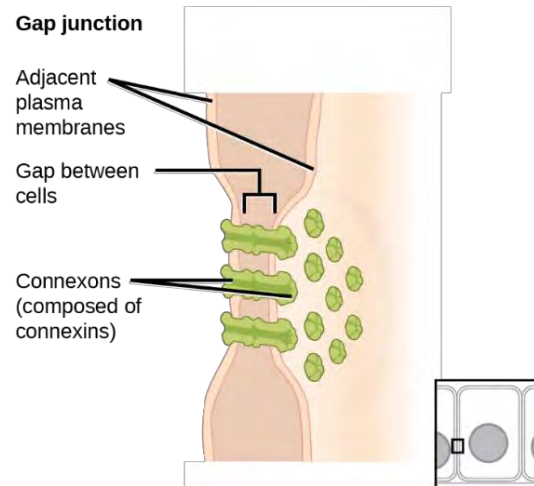
Extracellular Matrix

Most animal and plant cells release materials into the extracellular space. In animal cells, the major components released are glycoproteins and the protein collagen. In plant cells, the extracellular matrix is primarily composed of carbohydrates. Collectively, these noncellular materials are called the **extracellular matrix** (Figure 4.37). The extracellular matrix holds the cells together to form a tissue. It also allows animal cells within the tissue to communicate with each other.

Figure 4.37 Animal cell-extracellular matrix consists of a network of substances secreted by cells. (credit: Fowler et al. / Concepts of Biology OpenStax)
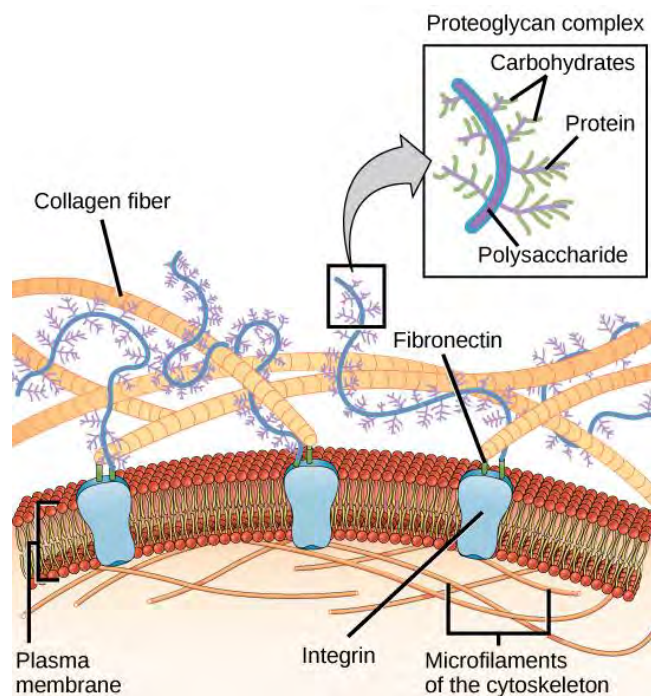
Components of Prokaryotic and Eukaryotic Cells (Animal and Plant Cells) and Their Functions

Cell Component	Function	Present in Prokaryotes?	Present in Animal Cells?	Present in Plant Cells?
Plasma membrane	Separates cell from the 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	A cell organelle that houses DNA and directs the 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

Components of Prokaryotic and Eukaryotic Cells (Animal and Plant Cells) and Their Functions

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

Table 4.1 This table provides the components of prokaryotic and eukaryotic cells and their respective functions. (credit: Fowler et al. / Concepts of Biology OpenStax)

Check your knowledge

Which of the following are only found in plant cells?
    a. chloroplasts
    b. mitochondria
    c. nucleus
    d. rough endoplasmic reticulum

Cardiac muscle that makes up the heart must contract as a unit. What type of intracellular junction is important in holding contractile muscle cells together?

Answer: (a) and desmosomes

Section Summary

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. Plant cells also have various plastids for storage.

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

Exercises

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?

2. Which two organelles are thought to have once been free-living bacteria?

3. In plant cells, the cell wall has a large abundance of what polysaccharide?
    a. chitin
    b. cellulose
    c. starch
    d. glycogen

4. Which of the following is not a junction used by animal cells?
    a. tight junction
    b. gap junction
    c. desmosomes
    d. plasmodesmata

5. Provide two pieces of evidence that support the endosymbiotic theory.

Answers

1. Plant cells have plasmodesmata, a cell wall, a large central vacuole, chloroplasts, and plastids. Animal cells have lysosomes and centrosomes.
2. Mitochondria and Chloroplast
3. (b)
4. (d)
5. They have their own DNA, ribosomes and are enclosed within two membranes.

Glossary

autotroph: an organism that can make its own food from materials in its environment

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

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

endosymbiosis: a relationship in which one organism lives inside the other

endosymbiotic theory: a theory that explains how mitochondria and chloroplasts originated

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

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

heterotroph: an organism that cannot make its own food and must consume other organisms to obtain its energy

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

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

Chapter 5: Structure and Function of the Cell Membrane and an Introduction to Energy

Figure 5.1 A hummingbird needs energy to maintain prolonged flight. (credit: modification of work by Cory Zanker / [Biology 2E OpenStax](https://openstax.org/))

Virtually every task performed by living organisms requires energy. For humans, energy is needed to exercise, to think, and even during sleep. Plants need energy to perform photosynthesis, cell division, and metabolism. Protists use energy to expel excess water and power their cilia. All living cells continuously use energy.

From where, and in what form, does this energy come? How do living cells obtain energy, and how do they use it? This chapter will discuss different forms of energy and the physical laws that govern energy transfer.

5.1 The Cell Membrane

> **Learning objectives**
> By the end of this section, you will be able to:
> - *Understand the fluid mosaic model of cell membranes*
> - *Describe the functions of phospholipids, proteins, and carbohydrates when forming the cell membrane*
> - *Be able to identify what types of molecules can pass directly through the membrane vs. those that need to use a transport protein to enter or exit the cell*
> - *Be able to define and explain all bolded terms*

Despite differences in structure and function, all living cells are surrounded by a plasma membrane. As the outer layer of your skin separates your body from its environment, the cell membrane, also known as the plasma membrane, separates the inner contents of a cell from its exterior environment. This cell membrane provides a protective barrier around the cell and regulates which materials can pass into or out of the cell.

Fluid Mosaic Model

Scientists first identified the plasma membrane in the 1890s. In 1935, Hugh Davson and James Danielli proposed the plasma membrane's structure. This was the first model that was widely accepted by the scientific community. In the 1950s, advances in microscopy allowed researchers to see that the plasma membrane's core consisted of a double, rather than a single, layer of phospholipids, now referred to as the phospholipid bilayer. In 1972, S.J. Singer and Garth L. Nicolson proposed the fluid mosaic model which provided an explanation of the different observations and explained the function of the plasma membrane.

The **fluid mosaic model** has evolved somewhat over time, but it still best accounts for plasma membrane structure and function as we currently understand them. The fluid mosaic model describes the plasma membrane as a mosaic of components, including phospholipids, cholesterol, proteins, and carbohydrates (Figure 5.2). Fluid refers to the fact that materials making up the membrane move and are not rigid. Plasma membranes range from 5 to 10 nm in thickness. For comparison, human red blood cells, are approximately 8 μm wide, or approximately 1,000 times wider than a plasma membrane.
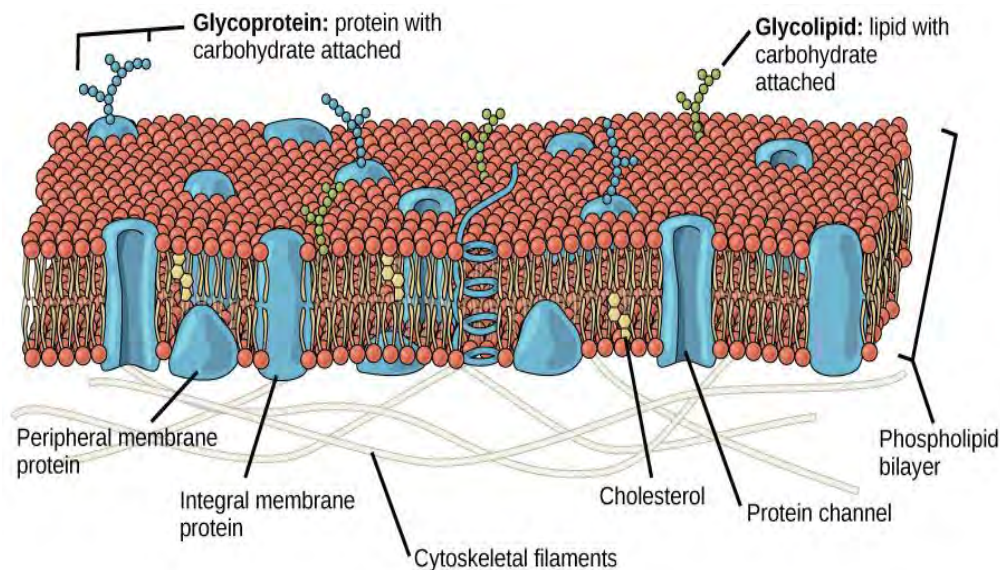
Figure 5.2 The plasma membrane fluid mosaic model describes the plasma membrane as a fluid combination of phospholipids, cholesterol, proteins, and carbohydrates. (credit: Betts et al./ Anatomy and Physiology OpenStax)

CONCEPTS IN ACTION - Visit this site to see animations of the membranes' fluidity and mosaic quality.

Structure and Composition of the Cell Membrane

The cell membrane is an extremely flexible structure. It is composed primarily of back-to-back phospholipids referred to as a phospholipid "bilayer" (Figure 5.3). Cholesterol is also present and contributes to the fluidity of the membrane. In addition, there are various proteins embedded within the membrane that have a variety of functions. We will now look separately at each component that makes up the plasma membrane.
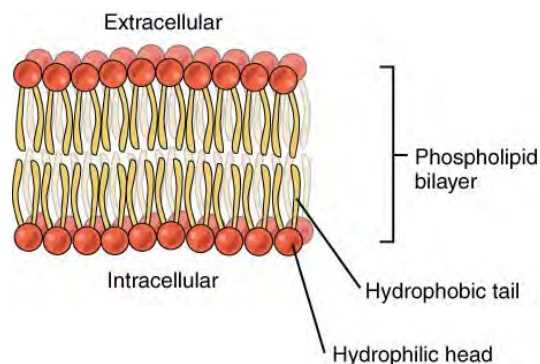
Figure 5.3 Phospholipid Bilayer (credit: Betts et al. / Anatomy and Physiology OpenStax)

Phospholipids

A single **phospholipid** molecule has a phosphate group on one end, called the "head," and two side-by-side fatty acid chains that make up the lipid "tails" (Figure 5.4). The phosphate group is negatively charged, making the head polar and hydrophilic, or "water-loving." The phosphate heads are attracted to water molecules found in both the extracellular and intracellular environments. The lipid tails are nonpolar and are hydrophobic. The hydrophobic lipid tails meet in the inner region of the membrane and exclude the watery intracellular and extracellular fluid. Most water that moves into or out of a cell does so through a transport protein called an **aquaporin**.
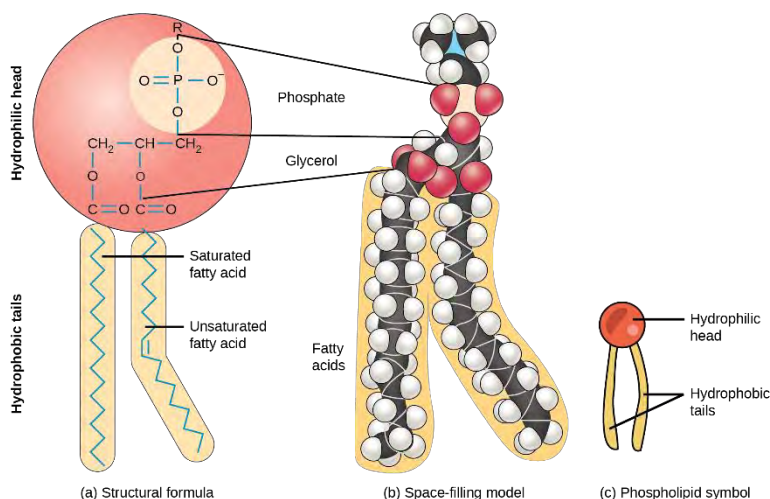
Figure 5.4 A hydrophilic head and two hydrophobic tails comprise this phospholipid molecule. (credit: Clark et al. / Biology 2E OpenStax)

Proteins

The lipid bilayer forms the basis of the cell membrane; however, there are various proteins peppered throughout. Membrane proteins are categorized as either integral proteins or peripheral proteins (Figure 5.2). As its name suggests, an **integral protein** is a protein that is embedded in the membrane. A transport protein is an example of an integral protein that selectively allows specific materials, such as ions, sugars, or molecules that are polar, to pass into or out of the cell. The aquaporin discussed above is also an example of an integral protein.

Cell recognition proteins are integral proteins that serve to mark a cell's identity so that it can be recognized by other cells. A recognition protein may also act as a receptor that can selectively bind a specific molecule outside the cell. When molecules bind to the recognition protein it causes a chemical reaction within the cell. Some integral proteins serve roles as both receptors and ion channels. The receptors on nerve cells that bind neurotransmitters, such as dopamine, are an example of integral proteins that carry out both functions. When a dopamine molecule binds to a dopamine receptor protein, a channel within the protein opens to allow specific ions to flow into the cell.

Peripheral proteins are typically found on the inner or outer surface of the lipid bilayer but can also be attached to integral proteins (Figure 5.2). These proteins perform a specific function for the cell. Peripheral proteins may serve as enzymes, as structural attachments for the cytoskeleton's fibers, or as part of the cell's recognition sites. Some peripheral proteins on the surface of intestinal cells, for example, act as digestive enzymes to break down nutrients.

Carbohydrates

Carbohydrates are the third major plasma membrane component. Carbohydrates are always on the cell exterior and are bound either to proteins, forming **glycoproteins**, or to lipids, forming **glycolipids** (Figure 5.2). The attached carbohydrate on glycoproteins aid in cell recognition. The carbohydrates that extend from membrane proteins and even from some membrane lipids collectively form the glycocalyx. The **glycocalyx** is a fuzzy-appearing coating that surrounds the cell and has various roles. For example, it may allow the cell to bind to another cell, it may contain receptors for hormones, or it might have enzymes to break down nutrients. The glycocalyces found in a person's body are a result of that person's genetic makeup. They help identify cells as belonging to the same individual. This identity is the primary way that a person's immune defense cells "know" not to attack the person's own body cells. It is also the reason organs donated by another person might be rejected.

Cholesterol

Cholesterol, which inserts within the phospholipid bilayer, is an important hydrophobic component of the membrane that helps with fluidity (Figure 5.2). It prevents phospholipids from packing too closely together, which would cause the membrane to become rigid and prevent molecules such as oxygen, carbon dioxide, and other small nonpolar molecules from moving directly through the membrane. Cholesterol also resists extreme changes in temperature. It will help keep the plasma membrane fluid even if the environment increases or decreased in temperature. The fluidity of the cell membrane is necessary for some enzymes and transport proteins to work properly within the membrane.

Plasma Membrane Components and Locations

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

Table 5.1 Plasma membrane components and the location of each component. (Modified by Elizabeth O'Grady original work of Clark et al. / Biology 2E OpenStax)

EVOLUTION CONNECTION - How Viruses Infect Specific Organs

Glycoproteins and glycolipids on the cells' surfaces give many viruses an opportunity for infection. HIV and hepatitis viruses infect only specific organs or cells in the human body. HIV can penetrate the plasma membranes of a group of cells called T-helper cells, as well as some monocytes and central nervous system cells. The hepatitis virus attacks liver cells.

These viruses are able to invade these cells because the cells have binding sites on their surfaces that the virus can recognize (Figure 5.5). Unfortunately, these recognition sites on HIV change at a rapid rate because of mutations, making it challenging to develop an effective vaccine against the virus. Viruses appear to be incredibly adaptable, and the rate at which populations are evolving is astounding. A person infected with HIV quickly develops different populations of the virus that vary in their surface markers. Although the immune system may be able to fight one population, as new populations arise it becomes more and more difficult for the immune system to keep up. In the case of HIV, the problem is compounded because the virus specifically infects and destroys cells involved in the immune response.

Figure 5.5 HIV binds to the CD4 receptor, a glycoprotein on T cell surfaces. (credit: modification of work by NIH, NIAID / Concepts of Biology OpenStax)
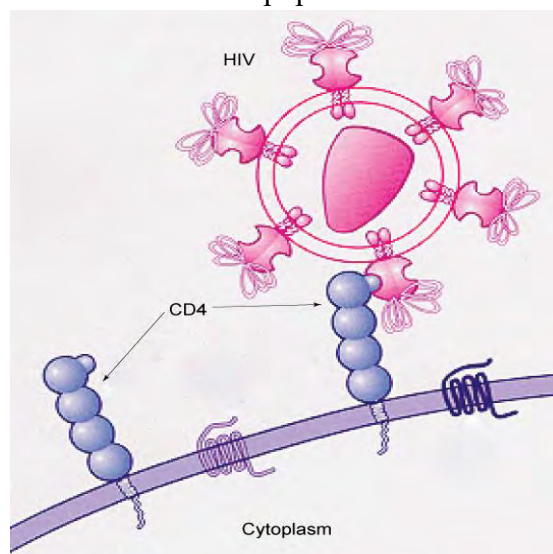
Section Summary

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. 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 can be explained by the fatty acid tails, the presence of cholesterol embedded in the membrane, and the mosaic nature of the proteins and protein-carbohydrate complexes. Plasma membranes enclose the borders of cells, but rather than being a static bag, they are dynamic and constantly in flux.

Exercises

1. 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

2. The phospholipids tails 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

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

Answers

1. (a)
2. (d)
3. The fluidity of the cell membrane is necessary for the operation of some enzymes and transport mechanisms within the membrane.

Glossary

aquaporin: channel protein that allows water through the membrane at a very high rate

cholesterol: a lipid that plays an important role in membrane fluidity

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

glycocalyx: a fuzzy-appearing coating around the cell formed from glycoproteins and other carbohydrates attached to the cell membrane.

glycolipid: a combination of carbohydrates and lipids

glycoprotein: a combination of carbohydrates and proteins

hydrophilic: a molecule with the ability to bond with water; "water-loving."

hydrophobic: a molecule that does not have the ability to bond with water; "water-fearing."

integral protein: protein integrated into the membrane structure that interacts extensively with the membrane lipids' hydrocarbon chains and often spans the membrane

peripheral protein: protein at the plasma membrane's surface either on its exterior or interior side

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

5.2 Passive Transport

One of the great wonders of the cell membrane is its ability to regulate the concentration of substances inside the cell (Figure 4.44). These substances include ions such as Ca^{+2}, Na^{+1}, K^{+1}, and Cl^{-1}; nutrients including sugars, fatty acids, and amino acids; and waste products, particularly carbon dioxide (CO_2), which must leave the cell.

The plasma membrane's lipid bilayer provides the first level of control. The phospholipids are tightly packed together, and the arrangement of the hydrophobic tails causes the membrane to be selectively permeable. A membrane that has **selective permeability** only allows substances meeting specific criteria to pass through it unaided. In the case of the cell membrane, only relatively small, nonpolar materials can move through the phospholipid bilayer. Some examples of these materials are lipids, oxygen and carbon dioxide gases, and alcohol. The chemical makeup or overall size of a molecule can prevent it from easily crossing the membrane. Water-soluble materials such as glucose, amino acids, and electrolytes cannot move directly through the membrane and need some assistance to cross. Later in this section we will discuss how these materials move into or out of the cell.

All substances that move through the membrane do so by one of two general methods, which are categorized based on whether or not energy is required. **Passive transport** is the movement of substances across the membrane without the expenditure of cellular energy. In contrast, **active transport** is the movement of materials across the membrane using energy, usually in the form of ATP.

Passive Transport

The most direct forms of membrane transport are passive. Passive transport occurs naturally and does not require the cell to expend energy to accomplish the movement. To understand *how* substances move passively across a cell membrane, it is necessary to understand concentration gradients. A **concentration gradient** is a difference in the concentration of a substance between two places. Molecules or ions will spread out or diffuse from where they are

more concentrated to where they are less concentrated until they are equally distributed in that space. When molecules move in this way, they are said to move *down* their concentration gradient.

When green food coloring is placed in a glass of water, the green food coloring molecules will spread from where they are most concentrated, the initial drop, to where they are less concentrated amongst the water molecules in the glass. The green food coloring molecules will spread out until they are evenly dispersed amongst the water molecules resulting in one homogeneous mixture (Figure 5.6).
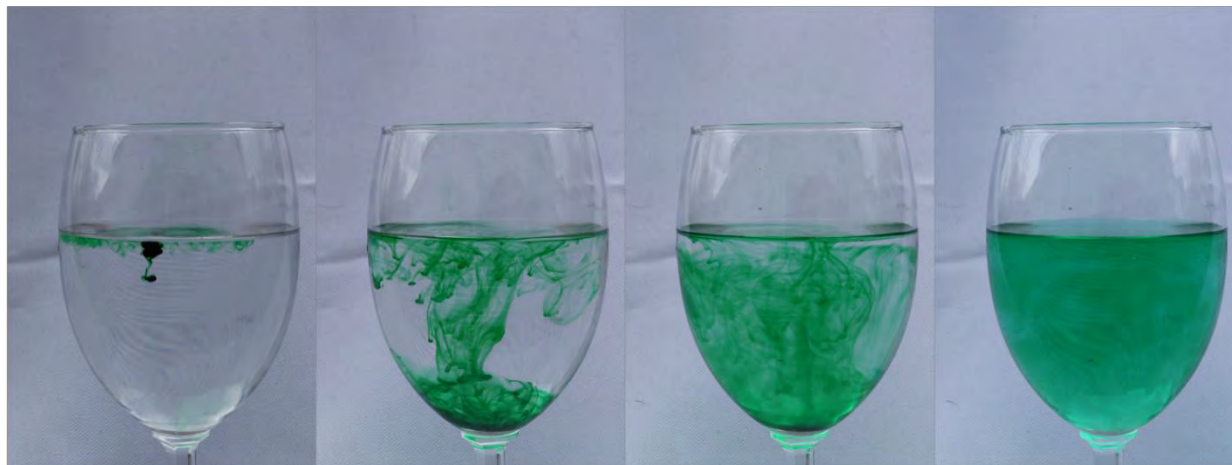
Figure 5.6 Diffusion of green food coloring in water. (credit: Robby Remedi)

Diffusion

Diffusion is a type of passive transport where substances move from an area of higher concentration to an area of lower concentration until they reach equilibrium (Figure 5.5). When something reaches equilibrium, it means the molecules are evenly spread out. You may be familiar with the 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 molecules will diffuse or spread away from the bottle, and gradually more and more people will smell the perfume.

For materials that can pass through a membrane, if there is a higher concentration on one side of the membrane that substance will move down its concentration gradient across the membrane (Figure 5.7). Consider materials that can easily diffuse through the lipid bilayer of the cell membrane, such as the gases oxygen (O_2) and CO_2. O_2 generally diffuses into cells because it is more concentrated outside of the cells. CO_2 typically diffuses out of cells because it is more concentrated inside of the cells. Energy does not need to be put in by the cells to move these gases across the membrane. When materials move directly through the lipid bilayer of the cell membrane this process is referred to as **simple diffusion** (Figure 5.7 and 5.8).

simple diffusion
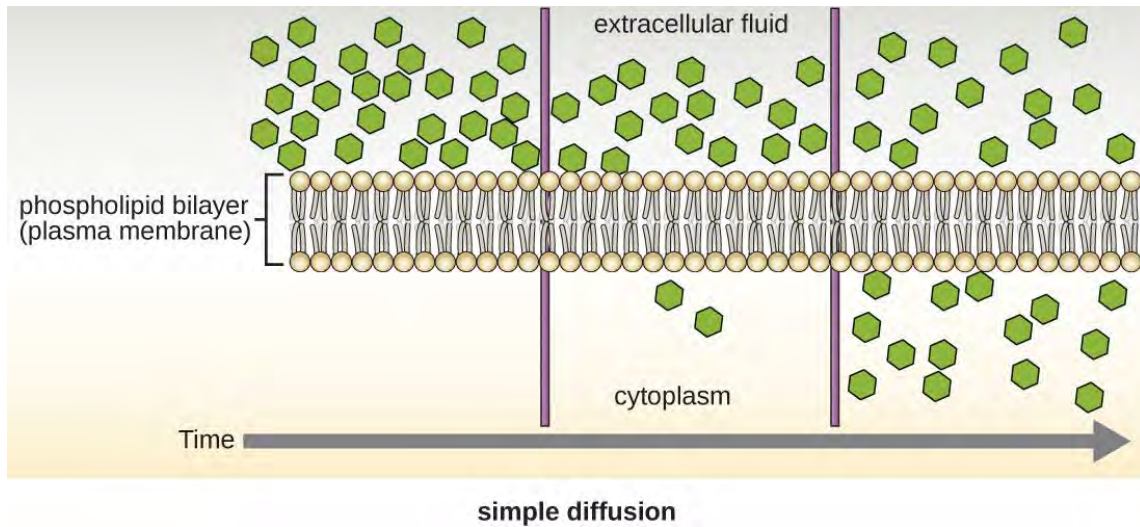
Figure 5.7 Diffusion of molecules through a permeable membrane. (credit: modification of work by Mariana Ruiz Villareal / Microbiology OpenStax)

Each separate substance in an environment has its own concentration gradient, independent of the concentration gradients of other materials in that same environment. Each material will diffuse according to its own gradient. In Figure 5.8, the molecules represented by the green circles are more concentrated within the cell, whereas the molecules represented by the blue hexagons are more concentrated outside of the cell. Each molecule will diffuse independently of one another down their respective concentration gradients until equilibrium is met. The blue hexagons will diffuse into the cell while the green circles diffuse out of the cell.
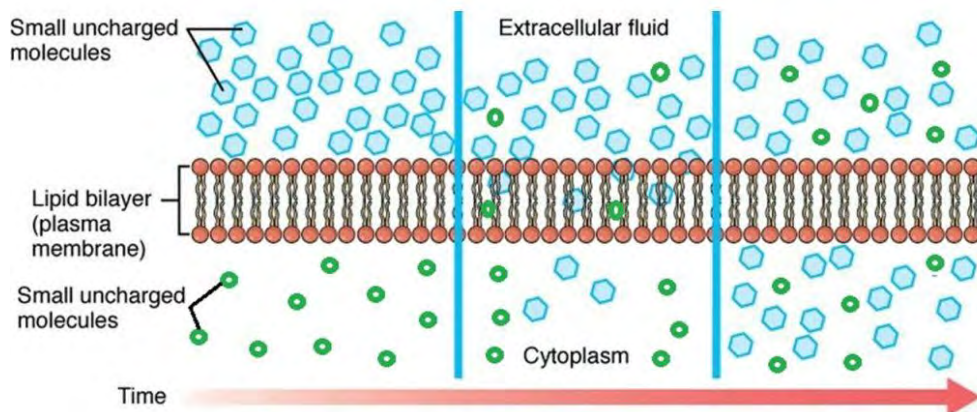
Figure 5.8 Diffusion of two different molecules through a permeable membrane in different directions. (credit: Modified by Elizabeth O'Grady original work of Mariana Ruiz Villareal / Biology 2E OpenStax)

Several factors affect the rate of diffusion.

- The extent of the concentration gradient: The more significant the difference in concentration between two points, the more quickly the substance will diffuse. The closer the substance gets to being at equilibrium, the slower the rate of diffusion.
- Mass of the molecules diffusing: Large molecules move more slowly. It is more difficult for them to move between the molecules of the substance they are diffusing through. As a result, they diffuse more slowly.
- Temperature: Higher temperatures increase the movement of the molecules, which increases 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 solvent.

CONCEPTS 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 help of transport proteins. In facilitated diffusion, materials still move down a concentration gradient from high to low concentration without investing any energy (Figure 5.9). Without the help of a transport protein however, the substances that undergo facilitated transport could not diffuse easily or quickly across the plasma membrane.

To move polar substances and other large or charged substances across the plasma membrane, there must be integral proteins that span the membrane. The material being transported is first attached to a protein or glycoprotein receptor 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 or cytoplasm. The substances are then passed to specific integral proteins that facilitate their passage. Integral proteins form channels or pores that allow certain materials to pass through the membrane. The integral proteins involved in facilitated transport are collectively referred to as transport proteins.

Figure 5.9 Facilitated diffusion of substances across the cell membrane takes place with the help of transport proteins. (credit: Parker et al./ Microbiology OpenStax)
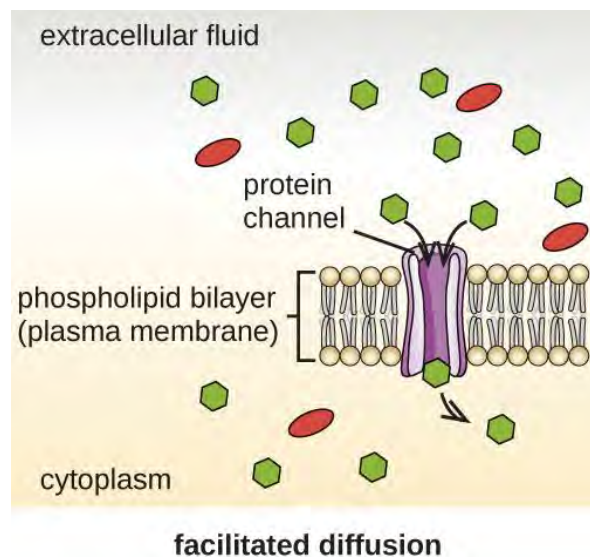
Osmosis

Osmosis is a form of passive transport that involves transporting *only* water across a membrane. **Osmosis** can be defined as the movement of water from an area of low solute concentration to high solute concentration until equilibrium is met. Water can move freely across the cell membrane of all cells, either through protein channels called aquaporins or by slipping between the lipid tails of the membrane itself. Water, like other substances, moves from an area of higher water concentration to an area of lower water concentration. Water movement is also dependent on solute concentration.

Imagine a beaker with a semipermeable membrane separating the two sides or halves (Figure 5.10). On both sides of the membrane, the amount of water molecules is the same, but there are different concentrations of a dissolved substance, or solute, on each side. For example, on one side of the beaker, there is a single teaspoon of sugar dissolved in the water; whereas, on the other side of the beaker 1/4 cup of sugar has been dissolved. The sugar cannot cross the membrane. The sugar is kept dissolved in solution due to its chemical interactions with water. The more sugar molecules that are present, the more water molecules that are needed to keep the sugar dissolved in the solution. In Figure 5.10, there is a higher concentration of sugar on the right side and, therefore, a lower concentration of free water on that side because of the chemical interactions between the sugar and the water. On the left side, there is a low concentration of sugar; therefore, a higher concentration of free water. Water will move from an area with low solute concentration, right side, to an area of high solute concentration, left side, until equilibrium is met (Figure 5.10). This can also be stated as water will move from an area of high free water concentration to an area of low free water concentration until equilibrium is met.
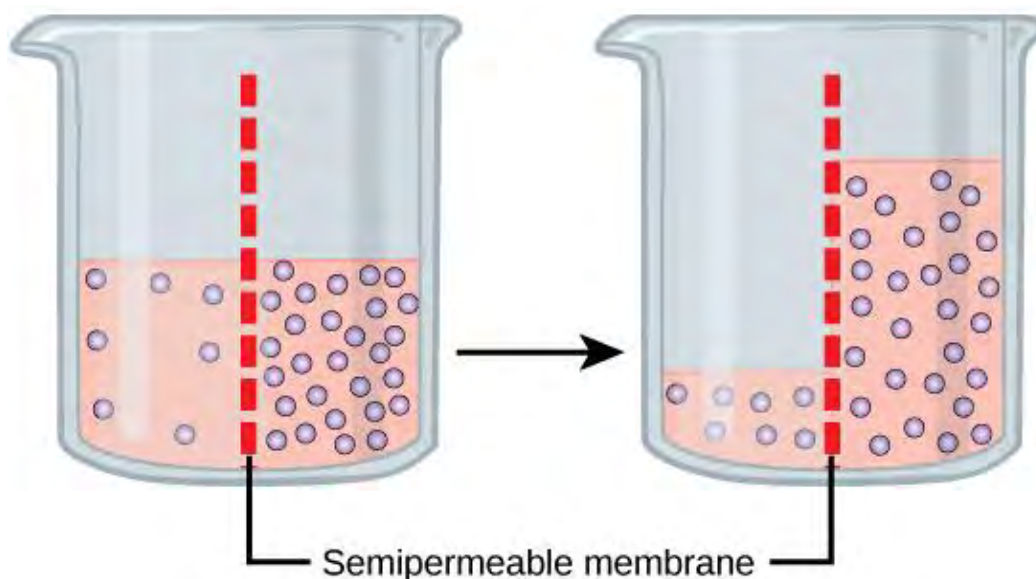
Figure 5.10 In osmosis water always moves through a semipermeable membrane from an area of low solute concentration to an area of higher solute concentration. (credit: Fowler et al. / Concepts of Biology OpenStax)

Tonicity

Tonicity describes the amount of solute in a solution. The measure of the tonicity of a 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 surrounds the cell.

In a **hypotonic solution**, such as distilled water, the extracellular fluid has a lower concentration of solutes than the fluid inside the cell. As a result, water enters the cell. In living systems, the cytoplasm is always used as the point of comparison, so the prefix *hypo*- means that the extracellular fluid has a lower concentration of solutes, or a lower osmolarity when compared to the cell cytoplasm. It also means that the extracellular fluid has a higher concentration of free water when compared to the cell's cytoplasm. In this situation, water will move down 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. Imagine putting an animal cell into a glass of seawater. Because the cell has a lower concentration of solutes when compared to the fluid surrounding the cell, water will leave 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 in a cell is approximately equal to that of the extracellular fluid, there will be no net movement of water into or out of the cell. Figure 5.11 shows what will happen if you put red blood cells in hypertonic, isotonic, and hypotonic solutions.
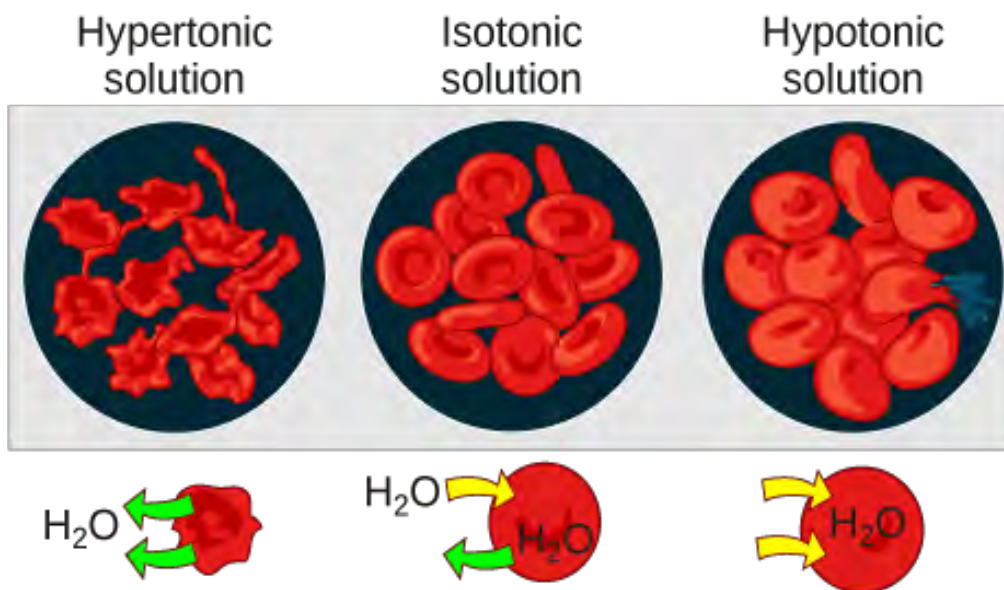
Figure 5.11 Osmotic pressure changes the shape of red blood cells in hypertonic, isotonic, and hypotonic solutions. (credit: modification of work by Mariana Ruiz Villarreal / Concepts of Biology OpenStax)

Check your knowledge

A doctor injects a patient with what the doctor thinks is an isotonic saline solution. The patient dies, and the autopsy reveals that many neurons (brain cells) have burst. Do you think the solution the doctor injected was isotonic? If not, what type of solution do you think was injected?

> No, the solution injected was most likely a hypotonic solution, such as distilled water. This resulted in the blood being hypotonic when compared to the cytoplasm of the cells. Water moved into the cells from an area of low solutes in the blood to an area of high solutes in the cytoplasm resulting in the cells bursting.

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. The cytoplasm in plants is always slightly hypertonic compared to the cellular environment. 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 5.12). In nonwoody plants, turgor pressure supports the plant. If the plant cells become hypotonic, which can occur during a drought or if a plant is not watered adequately, water will leave the cell, a process called crenation. Plants lose turgor pressure in this condition and wilt.
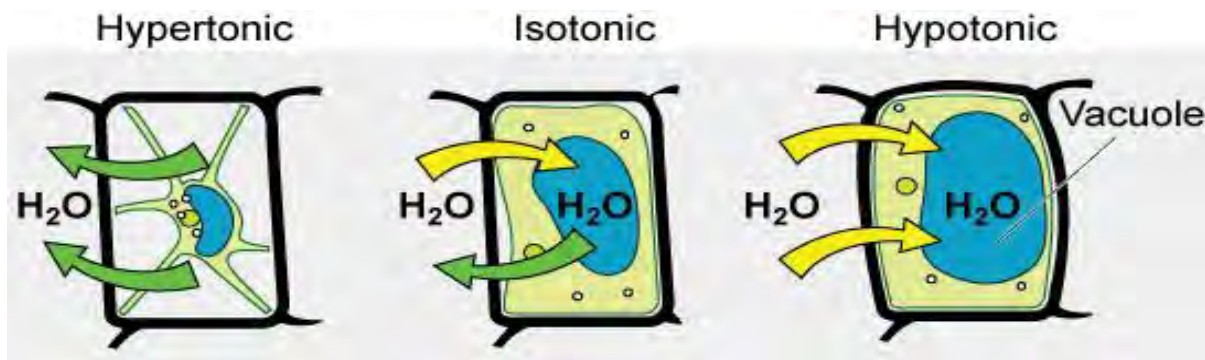
Figure 5.12 The turgor pressure within a plant cell depends on the tonicity of the solution that it is bathed in. (credit: modification of work by Mariana Ruiz Villarreal/ Concepts of Biology OpenStax)

**CONCEPTS IN ACTION** - For an animation of the diffusion process in action, view this short video on cell membrane transport. https://www.youtube.com/watch?v=JShwXBWGMyY

Section Summary

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.

Passive forms of transport, such as diffusion and osmosis, move materials without expending energy. Substances diffuse from areas of high concentration to areas of low concentration. 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.

Water also can move freely across the cell membrane of all cells, either through protein channels or by slipping between the lipid tails of the membrane itself. Osmosis is the movement of water molecules through a semipermeable membrane from an area of low solute concentration to an area of high solute concentration.

Two solutions that have the same concentration of solutes are said to be isotonic. Osmosis occurs when there is an imbalance of solutes outside of a cell versus inside the cell. A solution that has a higher concentration of solutes than another solution is said to be hypertonic, and water molecules tend to diffuse into a hypertonic solution. In contrast, a solution that has a lower concentration of solutes than another solution is said to be hypotonic, and water molecules tend to diffuse out of a hypotonic solution.

Exercises

1. A plant cell is submerged in an unknown solution. When you look at the plant cell using a microscope, the cells appear to be bulging and swelling. What type of solution do you think this plant cell was placed in: hypotonic, hypertonic or isotonic? Explain.

2. Which statement below best describes the process of diffusion?
   a. Solutes move throughout the cytoplasm from one organelle to another.
   b. Solutes move from an area with a higher solute concentration to an area of lower solute concentration.
   c. Solutes move from an area with a lower solute concentration to an area of higher solute concentration.
   d. Solutes cannot move from one area to another.

3. For molecules to move during passive transport a _____ is required.
   a. cool temperature
   b. large particle size
   c. concentration gradient
   d. transport protein

4. Why does osmosis occur in cells?

Answers

Glossary

aquaporin: channel protein that allows water through the membrane at a very high rate

active transport: the method of transporting materials into or out of a cell that requires energy

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

diffusion: a passive process of transport where solutes move from an area of high concentration to an area of low concentration until equilibrium is met

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

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

hypotonic: describes a solution in which extracellular fluid has a 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 low solute concentration to an area of high solute concentration. Water also moves from an area of high water concentration to an area of low water concentration until equilibrium is met.

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

simple diffusion: a process where solutes move directly through the membrane from an area of high concentration to an area of low concentration until equilibrium is met

solute: a substance dissolved in another to form a solution

tonicity: the amount of solute in a solution

5.3 Active Transport

All of the transport methods described in the preceding section shared one important commonality—the cell did not have to use energy, ATP, to move materials. During **active transport** energy is required to move a substance across a membrane, often with the help of integral proteins, and usually against its concentration gradient. If a material must be moved out of the cell against its concentration gradient, that means the concentration of the material outside of the cell is greater than the concentration of the material inside the cell (Figure 5.13).
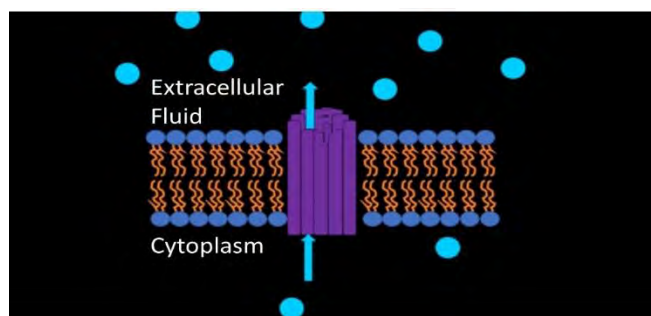
Figure 5.13 The blue circles are moving against their concentration gradient through a transport protein that requires energy. (credit: Modified by Elizabeth O'Grady original work of Emma Dittmar Wikimedia)

One of the most common types of active transport involves proteins that serve as pumps. The word "pump" probably conjures up thoughts of using energy to pump up the tire of a bicycle or a basketball. Similarly, energy from ATP is required for these membrane proteins to transport substances such as molecules or ions across the membrane.

For example, some cells have a high concentration of potassium (K^+) and a low concentration of sodium (Na^+) inside the cell when compared to that of the extracellular fluid. The sodium-potassium pump transports sodium out of a cell while moving potassium into the cell (Figure 5.14). Both ions are being pumped against their concentration gradients; therefore, energy must be used to accomplish this. The Na^+/K^+ pump is an important ion pump found in the membranes of many types of cells. These pumps are particularly abundant in nerve cells, which are continually pumping out sodium ions and pulling in potassium ions to maintain a gradient across their cell membranes.
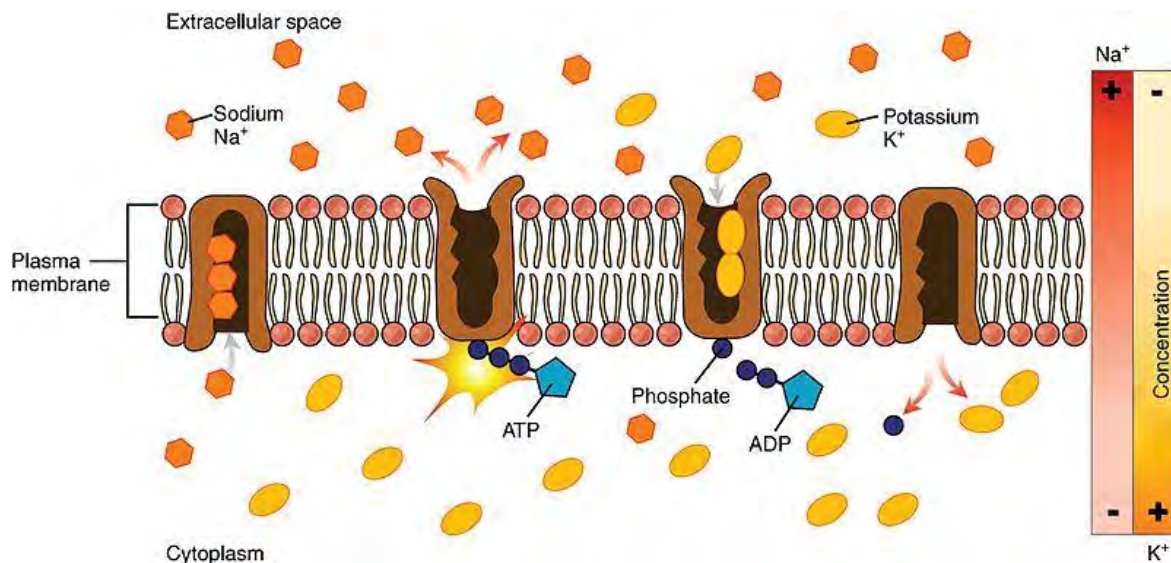
Figure 5.14 The sodium-potassium pump, which is powered by ATP, is found in the plasma membrane of many cells. (credit: Betts et al. / Anatomy and Physiology OpenStax)

Active transport can also occur when electrons are passed through a series of chemical reactions. Protein complexes can pass electrons, and as they do, small amounts of free energy are given off. This energy can then be used to transport ions or other materials across a plasma membrane. This type of active transport will be discussed in chapters six and seven when electron transport chains are used in cellular respiration and photosynthesis.

Endocytosis

Endocytosis is a type of active transport that moves large molecules into the cell. These large molecules, which can include cell parts and foreign cells, cannot be moved through integral proteins because of their large size. There are three different variations of endocytosis, however they all share a common characteristic: the plasma membrane of the cell invaginates, forming a pocket around the target substance. The pocket pinches off, resulting in the material being contained in a newly created vesicle or vacuole (Figure 5.15).
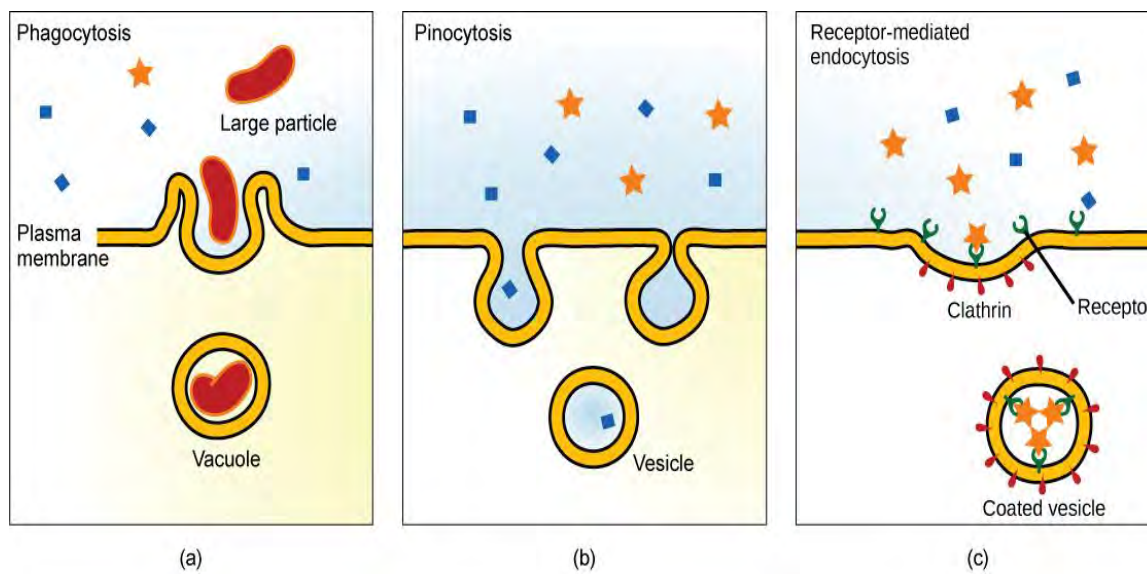
Figure 5.15 Three variations of endocytosis are shown. (a) phagocytosis (b) pinocytosis (c) receptor-mediated endocytosis (credit: modification of work by Mariana Ruiz Villarreal / Concepts of Biology OpenStax)

Phagocytosis

Phagocytosis is the process by which large particles, such as cells, are taken into the cell. For example, when microorganisms invade the human body, a type of white blood cell called a neutrophil removes the invader through this process of phagocytosis. The neutrophil surrounds and engulfs the microorganism (Figure 5.15a). The microorganism, which is now contained in a vacuole, will fuse with a lysosome and be destroyed by the digestive enzymes.

Pinocytosis

Another variation of endocytosis is called **pinocytosis**. The word pinocytosis means "cell drinking" and was named at a time when the assumption was that the cell was purposefully taking in extracellular fluid. In reality, the cell is taking in solutes that it needs from the extracellular fluid (Figure 5.15b).

Receptor-mediated endocytosis

The third variation of endocytosis, **receptor-mediated endocytosis**, involves binding specific substances to receptor proteins in the plasma membrane (Figure 5.15c). The substances bind to the receptor proteins, the plasma membrane invaginates, and both the specific material and the receptor proteins are brought into the cell. 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 because their cells cannot remove the lipid from their blood.

CONCEPTS IN ACTION - See receptor-mediated endocytosis <u>animation</u> in action.

Exocytosis

Exocytosis is a type of active transport that allows the cell to expel materials into the extracellular fluid. This process works by enclosing the materials within a vesicle, which then fuses with the interior of the plasma membrane. This fusion opens the vesicle to the exterior of the cell, and the particle is expelled into the extracellular fluid (Figure 5.16).
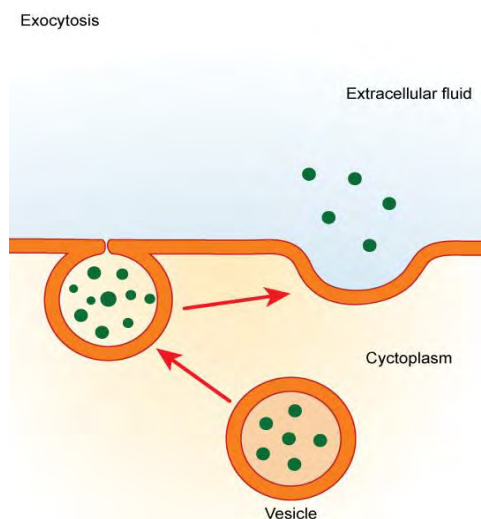
Figure 5.16 In exocytosis, a vesicle migrates to the plasma membrane, binds, and releases its contents to the outside of the cell. (credit: modification of work by Mariana Ruiz Villarreal/ <u>Concepts of Biology OpenStax</u>)

Check your knowledge

An amoeba uses pseudopods to engulf a paramecium for lunch. Will it use exocytosis or endocytosis?

Answer: endocytosis

Section Summary

Active transport uses energy stored in ATP to fuel transport. Active transport uses integral proteins to move the material either into or out of the cell against their concentration gradients. One of the most common types of active transport involves proteins that serve as pumps.

Endocytosis is a type of active transport that moves large molecules into the cell. These large molecules, which can include cell parts and foreign cells, cannot be moved in through integral proteins because of their large size. There are three different variations of endocytosis: phagocytosis, pinocytosis, and receptor-mediated endocytosis. The cell expels waste and other particles through the reverse process, exocytosis.

Exercises

1. Which statement best describes active transport.
    a. Active transport always requires the use of an integral protein.
    b. Active transport moves materials from an area of high concentration to an area of low concentration.
    c. Active transport always requires energy.
    d. Active transport is used to move water into the cell.
2. Compare and contrast the three types of endocytosis.

Answers

1. (c)
2. 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 substance. The pocket pinches off, resulting in the material being contained in a newly created vacuole. Phagocytosis is the process by which large particles, such as cells, are taken in by a cell. Pinocytosis takes in solutes that the cell needs from the extracellular fluid. Receptor-mediated endocytosis involves binding specific substances to receptor proteins in the plasma membrane.

Glossary

active transport: the method of transporting material that requires energy

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

5.4 Energy and Metabolism

All organisms require energy to maintain homeostasis. Most life forms get their energy either directly or indirectly from the sun. Producers, such as plants, can directly capture sunlight and convert it into chemical energy, such as glucose. Because producers make their own food, they are considered autotrophs. Herbivores, carnivores, and omnivores are classified as consumers because they must obtain their chemical energy by "consuming" it. They are considered heterotrophs. Consumers indirectly get their energy from the sun. Herbivores, such as cows, obtain their chemical energy by consuming producers, such as grass. In the case of carnivores, they must obtain their chemical energy by eating other consumers. Omnivores are adapted to consume both producers and other consumers. Decomposers obtain energy through the decomposition of dead and decaying materials. Figure 5.17 is a very simplified food web that shows where energy comes from and how energy flows through living systems.
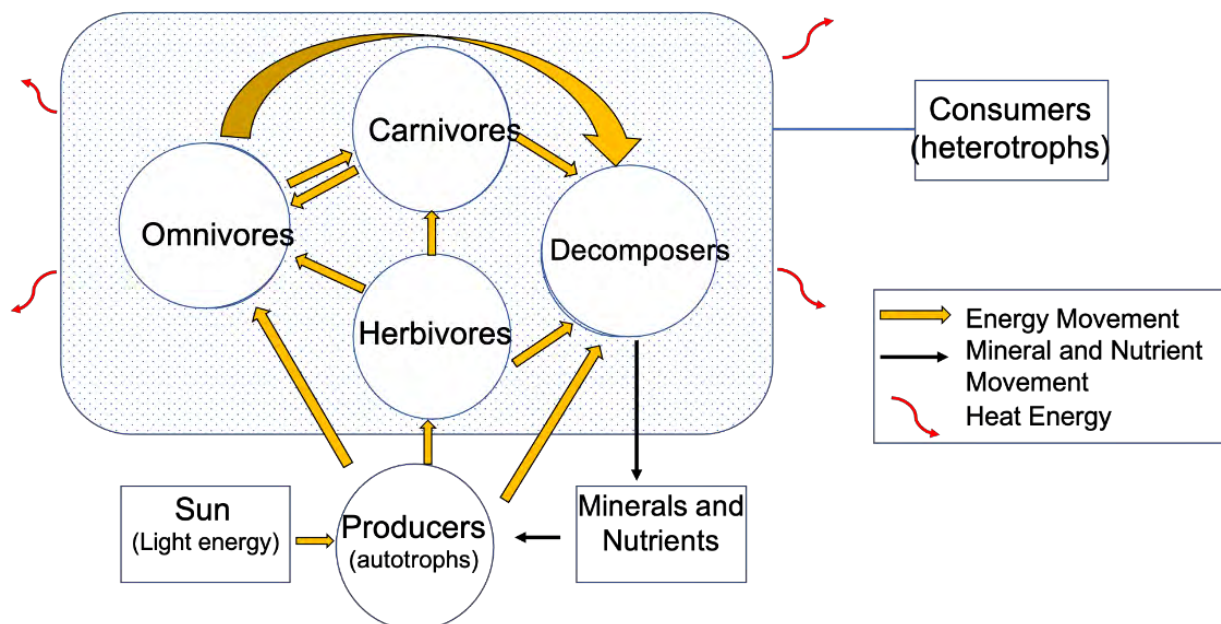
Figure 5.17 A simplified food web model of energy and mineral nutrient movement in an ecosystem. The yellow arrows indicate the flow of energy, the black arrows the movement of minerals and nutrients, and the red arrows the loss of energy in the form of heat. The circles indicate all the species that would be classified under that group. (credit: Elizabeth O'Grady)

Metabolic Pathways

How do producers such as plants capture light energy and convert it into chemical energy such as glucose (Figure 5.18)? How do all cells convert chemical energy found in glucose into ATP? To answer these questions, it is important to understand that energy conversions occur through a series of related chemical reactions called a **metabolic pathway**.

Figure 5.18a Producers capture light energy from the sun and convert it into chemical energy. (credit: At09kg/ Wikimedia) b. Herbivores, like the giraffe, consume the producer and make their own form of chemical energy. (credit: Modified by Elizabeth O'Grady original work of OpenStax; Wikimedia)
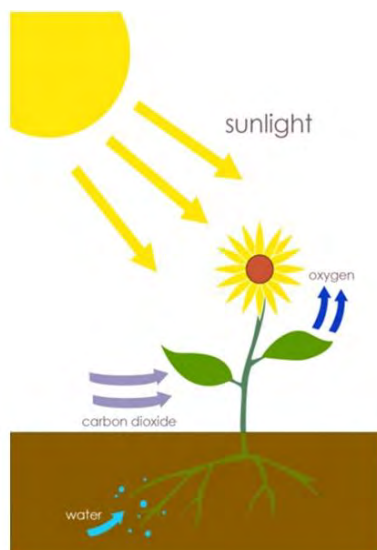
Consider the metabolic pathway of photosynthesis. During photosynthesis, plants use energy from sunlight to convert carbon dioxide gas (CO_2) and water (H_2O) into sugar molecules like glucose ($C_6H_{12}O_6$) and oxygen (Figure 5.18). This metabolic pathway is quite extensive and will be covered in chapter 7. For now, we will summarize this metabolic pathway in the following reaction:

$$6CO_2 + 6H_2O + \text{light energy} \longrightarrow C_6H_{12}O_6 + 6O_2$$

The glucose produced through photosynthesis can then be used to form adenosine triphosphate (ATP) through a process called cellular respiration. **Adenosine triphosphate (ATP)** is the primary energy currency of all living cells. Cellular respiration is a metabolic pathway that is basically the reverse reaction of photosynthesis. The reaction is summarized as:

$$C_6H_{12}O_6 + 6O_2 \longrightarrow 6CO_2 + 6H_2O + \text{energy (ATP)}$$

Both photosynthesis and cellular respiration are different metabolic pathways involved in energy transfer for living cells. However, not all cells perform both pathways. For example, animal cells can perform cellular respiration but not photosynthesis. Plant cells, on the other hand, can do both photosynthesis and cellular respiration. Figure 5.19 shows how these two metabolic pathways are connected.
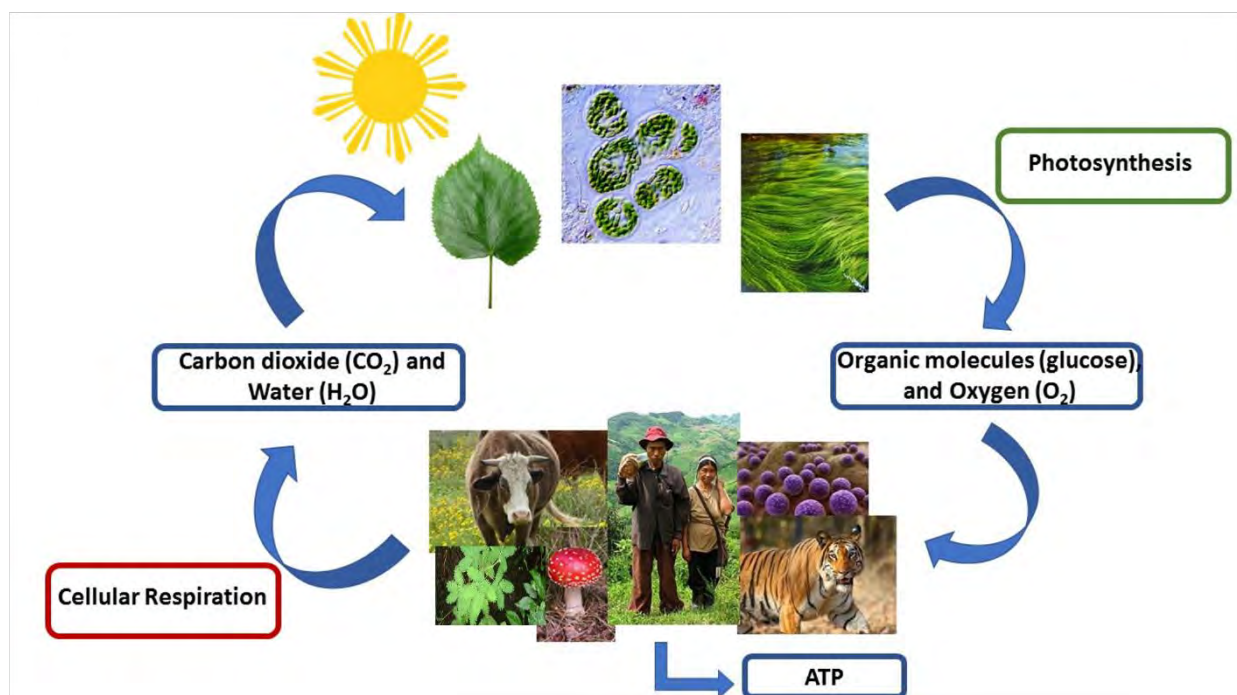
Figure 5.19 Autotrophs use carbon dioxide, water, and light energy to make organic matter and oxygen. Organisms use organic matter and oxygen to generate ATP and produce the waste products of carbon dioxide and water. (credit: Modified by Elizabeth O'Grady original work of / sun- Hariboneagle927 ; leaf-Krzysztof P. Jasiutowicz; cyanobacteria-NASA, algae-Mykola Swarnyk, cow-Chenspec , mushroom-MichaelMaggs plant- Alex Lomas/Concepts of Biology OpenStax humans-Weltenbummler84, Staphylococcus - scientificanimations, tiger-Vijaymp)

Energy converting chemical reactions are classified as either being anabolic or catabolic (Figure 5.20). In **anabolic** reactions, smaller, simpler molecules are combined into larger, more complex substances. Anabolic reactions, such as photosynthesis, require an input of energy. In **catabolic** reactions, such as cellular respiration, larger, more complex substances are broken down into smaller, simpler molecules. Catabolic reactions release energy. Figure 5.5 shows the differences between these two types of chemical reactions.
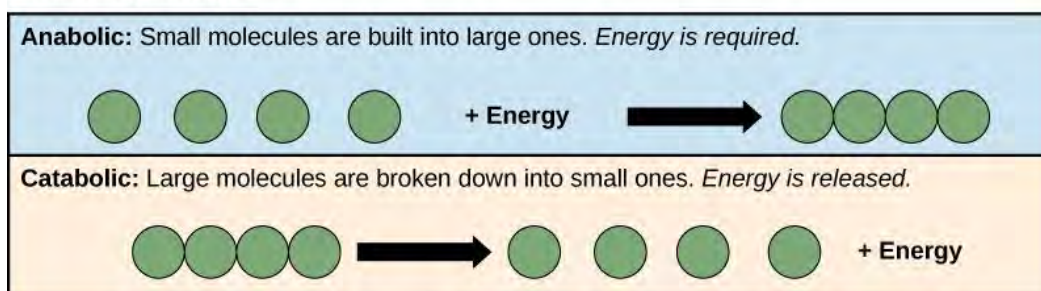
Figure 5.20 Catabolic pathways are those that generate energy by breaking down larger molecules. Anabolic pathways are those that require energy to synthesize larger molecules. (credit: Fowler et al. / Concepts of Biology OpenStax).

Taken together, these processes are called metabolism. **Metabolism** is the sum of all anabolic and catabolic reactions that take place in a cell (Figure 5.21). Both anabolism and catabolism occur simultaneously and continuously within cells. These metabolic reactions allow cells to maintain homeostasis.
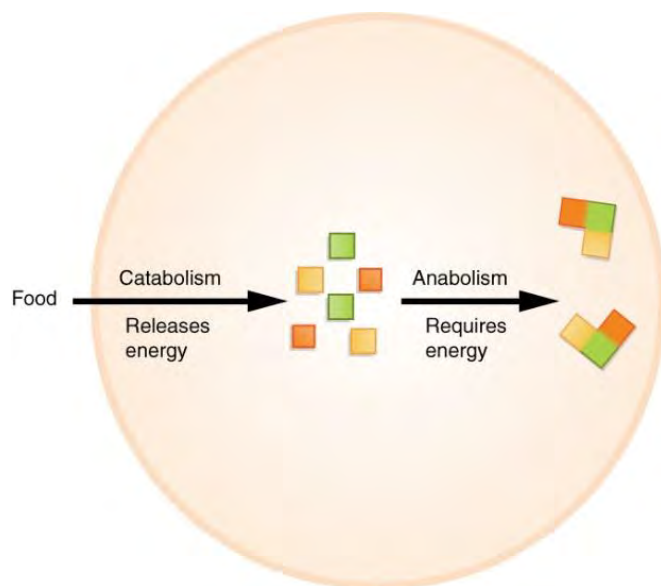
The chemical reactions that make up metabolic pathways do not take place on their own. Each reaction is facilitated, or catalyzed, by a protein called an enzyme. Enzymes are important for both anabolic and catabolic reactions and will be discussed in section 5.7.

Figure 5.21 Metabolism includes both anabolic and catabolic reactions. (credit: Betts et al. / Anatomy and Physiology OpenStax)

CONCEPTS IN ACTION - View this animation to learn more about metabolic processes. Which organs of the body likely carry out anabolic processes? What about catabolic processes?

Check your knowledge

Categorize the following events as catabolic or anabolic reactions:
• Digesting a potato chip.
• Our muscle cells making an enzyme.
• A smooth endoplasmic reticulum removing a toxin.
• A plant producing cellulose for the cell wall.

Answers: catabolic, anabolic, catabolic, anabolic

Section Summary

Cells perform life functions through various chemical reactions. A cell's metabolism refers to all the chemical reactions that take place within it. Catabolic reactions involve breaking down complex chemicals into simpler ones and are considered energy-releasing reactions. Anabolism refers to metabolic processes that build complex molecules out of simpler ones and are processes that require energy.

Exercises

1. Most organisms get their energy either directly or indirectly from the sun. Provide an example of an organism that gets its energy directly from the sun and one example that gets its energy indirectly from the sun.
2. Which of the following is not an example of an energy transformation?
   a. plants using the sun to make sugar
   b. animals eating plants
   c. animals eating animals
   d. all of the above are energy transformations
3. The energy currency used by cells is _____.
   a. ADP
   b. ATP
   c. AMP
   d. Adenosine
4. Is photosynthesis an anabolic or catabolic reaction? Explain your answer.

Answers

1. Producers, such as plants, can directly capture sunlight and convert it into chemical energy. Consumers such as such as cows, obtain their chemical energy by consuming producers, such as grass. Cows indirectly get their energy from the sun.
2. (d)
3. (b)
4. Photosynthesis is an example of an anabolic reaction. In anabolic reactions, smaller, simpler molecules such as carbon dioxide and water are combined into larger, more complex substances like glucose. Anabolic reactions, such as photosynthesis, require an input of energy.

Glossary

adenosine triphosphate (ATP): is the primary energy currency of all living cells

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

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

metabolic pathway: a series of related chemical reactions is referred to as a

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

5.5 Law of Thermodynamics

Learning objectives

By the end of this section, you will be able to:

- *Explain how thermodynamics and energy are related*
- *State the first and second laws of thermodynamics*
- *Understand what entropy is and how that relates to energy*
- *Be able to define and explain all bolded terms*

Thermodynamics refers to the study of energy and energy conversions. **Energy** can be defined as the ability to do work or to create some kind of change in matter. To appreciate what energy is and how it can be converted from one form to another, it is important to understand two laws that govern energy.

Laws of 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, the same amount of energy in the universe. Energy exists in many different forms. According to the first law of thermodynamics, energy may be transformed from one form to another, and it may be transferred from one system to another, but it cannot be created or destroyed.

Energy transfers and transformations take place around us all the time. Light bulbs transform electrical energy into light and heat energy. Plants perform one of the most biologically useful energy transformations on earth; they convert the energy of sunlight to chemical energy stored in organic molecules such as glucose (Figure 5.22).

All living organisms must obtain enough energy from their surroundings to support their metabolism. Living cells have evolved to meet this challenge. Chemical energy stored in organic molecules such as sugars can be transformed through chemical reactions into molecules of ATP. The energy in ATP molecules can then be used by cells to do work. Examples of work include building complex molecules, transporting materials, powering the motion of cilia, and contracting muscle fibers to create movement. Some examples of energy transformations are shown in Figure 5.23.
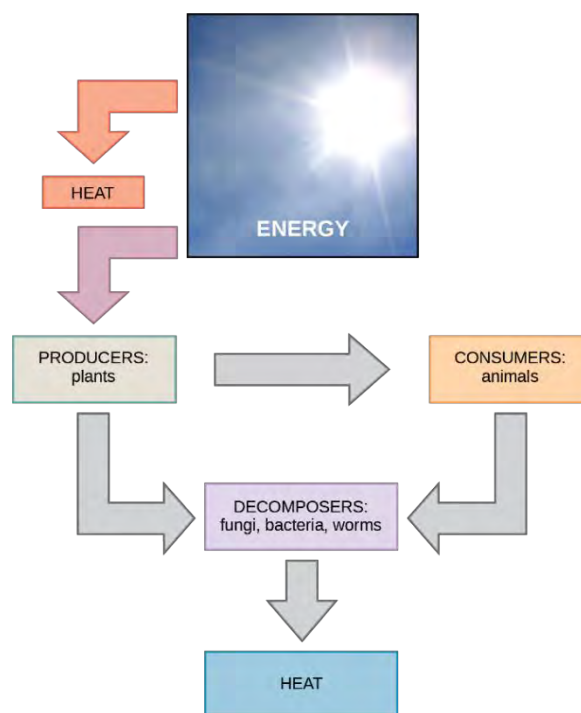
Figure 5.22 Most life forms on earth obtain their energy from the sun. (credit: Clark et al. / Biology 2E OpenStax)
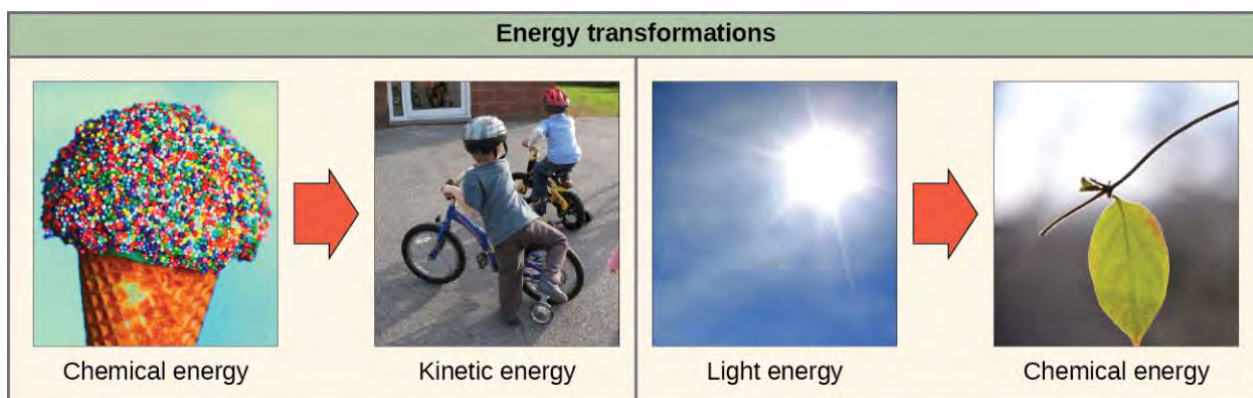
Figure 5.23 Here are two examples of energy transferring from one system to another and transformed from one form to another. (credit: "ice cream": modification of work by D. Sharon Pruitt; credit "kids on bikes": modification of work by Michelle Riggen-Ransom; credit "leaf": modification of work by Cory Zanker / Biology 2E OpenStax)

It may seem easy for living cells to obtain, transform, and use energy to do work; however, this is not the case. Energy transfers and transformations are never completely efficient. In every energy transfer, some amount of energy is lost in an unusable form. In most cases, energy is lost in the form of heat.

Heat energy is defined as the energy transferred from one object to another that is not being used for 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, when an airplane flies, it loses some of its energy as heat due to friction with the surrounding air. During metabolic reactions, such as cellular respiration, some energy is also lost in the form of heat energy. Heat energy is good for warm-blooded organisms like us because it helps us maintain our body temperature.

The more energy that is lost, the less ordered and more random the system is. Scientists refer to the measure of randomness or disorder as **entropy**. The **second law of thermodynamics** states that every energy transfer or transformation increases the universe's entropy.

High entropy means high disorder and low energy (Figure 5.24). To better understand entropy, think of a student's bedroom. If no energy or work were put into it, the room would quickly become messy. It would exist in a very disordered state, one of high entropy. Energy must be put into the system, in the form of the student doing work, to bring the room back to a state of cleanliness and order. This state of cleanliness and order is one of low entropy.
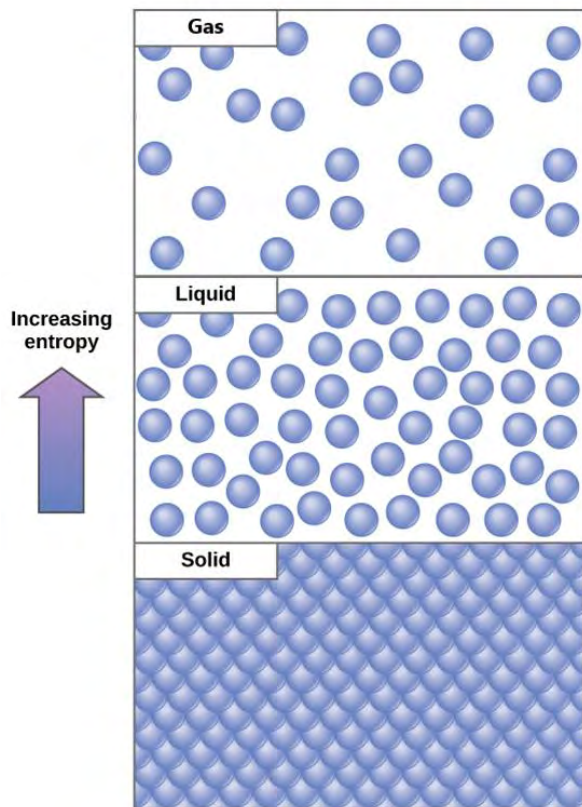
Figure 5.24 Entropy is a measure of randomness or disorder in a system. Gases have higher entropy than liquids, and liquids have higher entropy than solids. (credit: Modified by Jason Cashmore original work by Clark et al. / [Biology 2E OpenStax](https://openstax.org/))

Molecules also have varying amounts of entropy. For example, when molecules diffuse from an area of high concentration to an area of low concentration, entropy increases. A concentrated drop of food coloring has low entropy. As the food coloring molecules begin to slowly diffuse in a glass of water, the entropy increases (Figure 5.25).

Figure 5.25 Entropy increases as molecules diffuse. (credit: Modified by Elizabeth O'Grady original work of Robby Remedi)
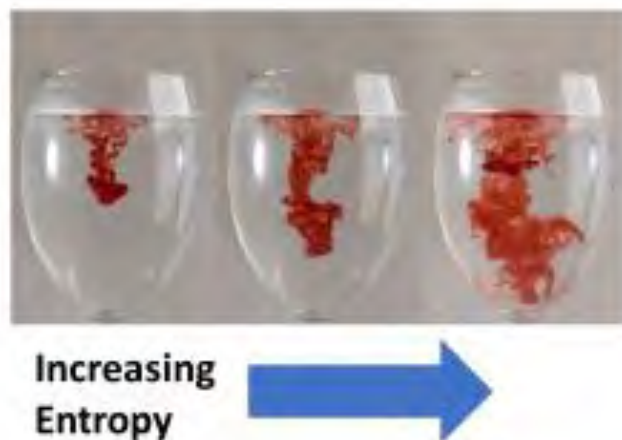
Living organisms are highly ordered. Organisms require a constant input of energy to maintain this state of low entropy. As living organisms take in energy and transform it through chemical reactions, some amount of usable energy is lost in the process. No chemical reaction is entirely efficient.

Section Summary

The laws of thermodynamics are a series of laws that describe the properties and processes of energy transfer. The first law states that the total amount of energy in the universe is constant. This means that energy cannot be created or destroyed, only transferred or transformed. The second law of thermodynamics states that every energy transfer involves some loss of energy in an unusable form, such as heat energy. This results in a more disordered system. No energy transfer is completely efficient, and all transfers trend toward disorder.

Exercises

1. High entropy means:
   a. high disorder and low energy
   b. high disorder and high energy
   c. low disorder and low energy
   d. low disorder and high energy
2. Thermodynamics refers to the study of:
   a. light
   b. sound
   c. energy
   d. equilibrium
3. Explain the second law of thermodynamics.

Answers

1. (a)
2. (c)
3. All energy transfers and transformations are never completely efficient. In every energy transfer, some amount of energy is lost in an unusable form.

Glossary

energy: the ability to do work or to create a change in matter

entropy: the measure of randomness or disorder within a system

first law of thermodynamics: states that the total amount of energy in the universe is constant and conserved

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

second law of thermodynamics: states that every energy transfer or transformation increases the universe's entropy

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

5.6 Types of Energy

Energy exists in different forms. You may be familiar with some types of energy, such as light and heat; however, there are other types of energy that are much less tangible. An object held above the ground has energy, as does a ball moving through the air. To understand how energy flows through biological systems, it's important to look more closely at the different types of energy that exist in the world.

Kinetic and Potential 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. The energy associated with objects in motion is called **kinetic energy**. A speeding bullet, a person walking, and flowing water all have kinetic energy (Figure 5.26).

Figure 5.26 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 / Concepts of Biology OpenStax)

What if that same motionless wrecking ball is lifted two stories above the 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 because of its position and the force of gravity acting on it. This type of energy is called **potential energy**. If the ball were to fall, the potential energy would be transformed into kinetic energy until the ball rested on the ground. Wrecking balls swing like a pendulum. As a pendulum swings, there is a constant change of potential energy to kinetic energy (Figure 5.27).
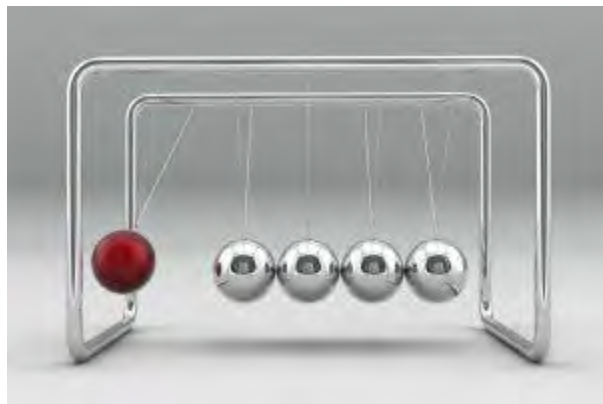
Potential energy is highest when the pendulum is at the top of the swing. As the pendulum swings, potential energy is converted into kinetic energy. Other examples of potential energy include the energy of water held behind a dam (Figure 5.26) or a person about to skydive out of an airplane.

Figure 5.27 This image shows a pendulum with one spherical ball at the top of its swing. (credit: Chris Potter ccPixs.com / Flickr)

Potential energy is not only associated with the location of matter, but also with the structure of matter. A spring on the ground, if it is compressed, or a rubber band that is pulled taut both have potential energy. On a molecular level, chemical bonds that hold a molecule together also have potential energy. Remember that anabolic reactions require energy to form complex molecules. A catabolic reaction releases energy when complex molecules are broken down. The release of energy by the breakdown of individual chemical bonds implies that those bonds have stored potential energy.

All food molecules we eat have potential energy stored within their bonds. The potential energy is released when the bonds are broken. The type of potential energy that exists within chemical bonds is called **chemical energy**.

CONCEPTS 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

According to the second law of thermodynamics, all energy transfers involve the loss of some 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 occur. In other words, **free energy** is usable energy or energy that is available to do work.

If energy is released during a chemical reaction, it means that the products of the reaction have less free energy than the reactants. This is because the reactants released some free energy during the reaction. Chemical reactions that release free energy are called **exergonic reactions** (Figure 5.28). Think: *ex*ergonic means energy is *ex*iting the system.

Exergonic reaction – Energy Released

Endergonic reaction – Energy Input
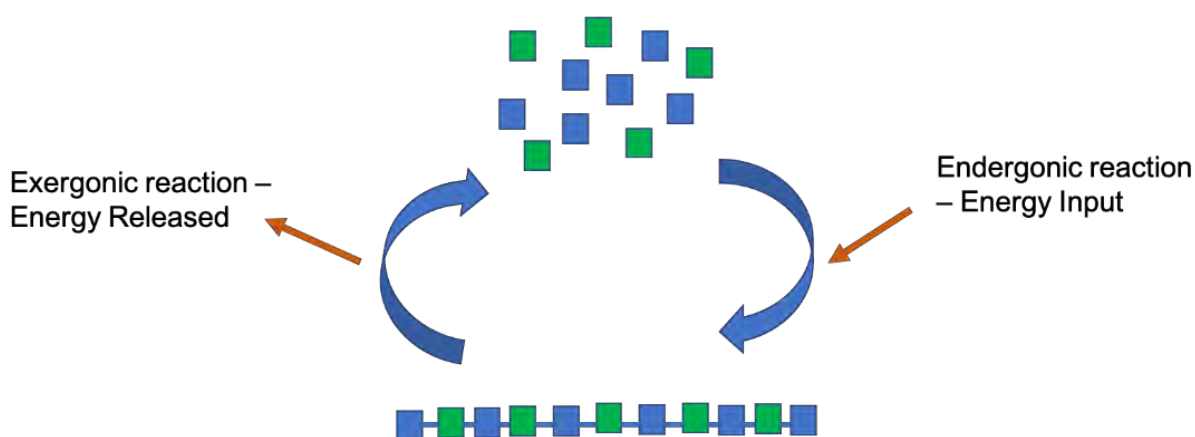
Figure 5.28 This figure shows the energy input of an endergonic reaction and the energy output of an exergonic reaction. (credit: Elizabeth O'Grady)

If a chemical reaction absorbs (requires) energy rather than releases energy, 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 (Figure 5.28). An endergonic reaction will not take place on its own without the addition or input of free energy.

Look at each of the processes shown and decide if it is endergonic or exergonic (Figure 5.29)

Figure 5.29 This figure shows some examples of endergonic processes and exergonic processes. These include (a) a compost pile decomposing, (b) a chick developing from a fertilized egg, (c) sand art destruction, and (d) a ball rolling down a hill. (credit a: modification of work by Natalie Maynor; credit b: modification of work by USDA; credit c: modification of work by "Athlex"/Flickr; credit d: modification of work by Harry Malsch / Biology 2E OpenStax)

Answers: A compost pile decomposing is an exergonic process. A baby developing from a fertilized egg is an endergonic process. Sand art destruction is an exergonic process. A ball rolling downhill is an exergonic process.

ATP in Living Systems

Within the cell, where does energy to power chemical reactions come from? The answer lies with an energy-supplying molecule called ATP (adenosine triphosphate). ATP is a simple, relatively small molecule; however, its bonds contain significant amounts of potential energy (Figure 5.30).
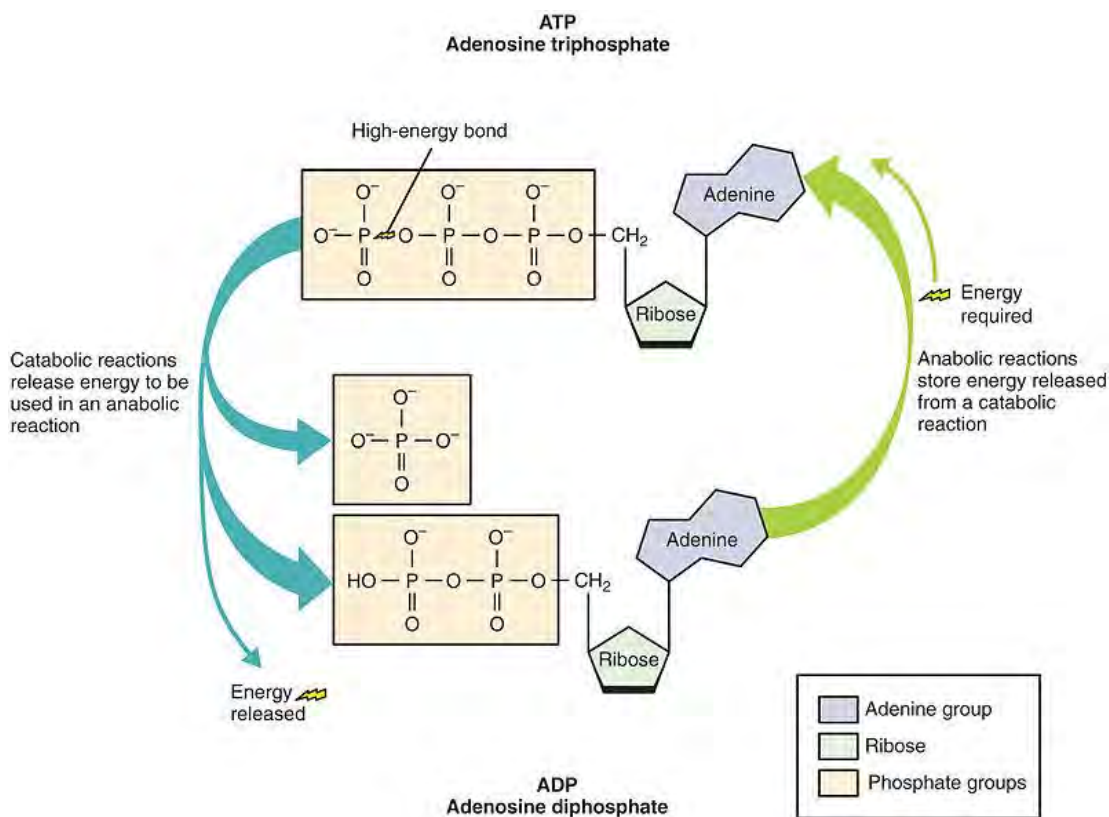
Figure 5.30 Structure of adenosine triphosphate (ATP). ATP is the energy molecule of the cell. (credit: Betts et al. / Anatomy and Physiology OpenStax)

When the bonds of ATP are broken, a quick burst of energy is released. That energy can be harnessed to perform cellular work. ATP can be thought of as the primary energy currency of living cells. ATP provides the energy used to power the majority of cellular chemical reactions and processes that occur in the cell. The energy from ATP drives all bodily functions, such as contracting muscles, maintaining the electrical potential of nerve cells, and absorbing food in the gastrointestinal tract. The metabolic reactions that produce ATP come from various sources (Figure 5.31)
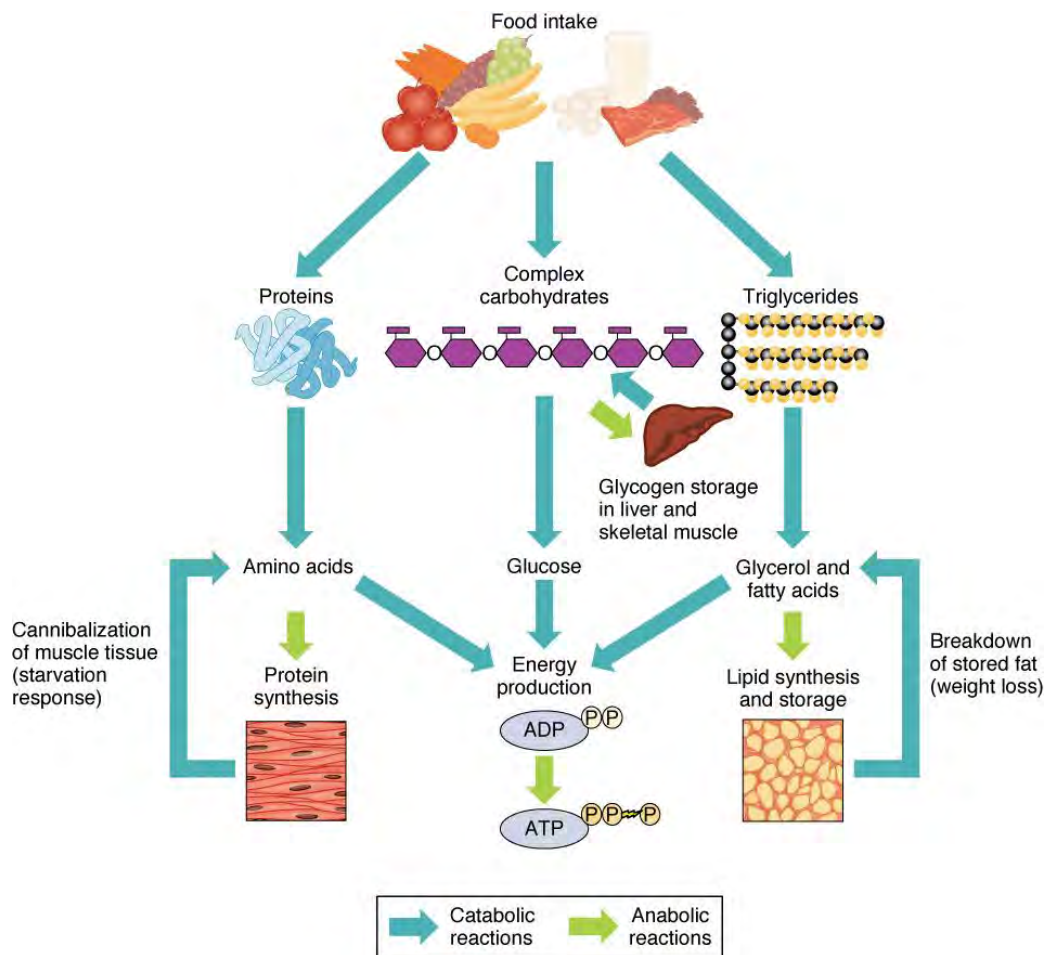
Figure 5.31 During catabolic reactions, proteins are broken down into amino acids, lipids are broken down into fatty acids, and polysaccharides are broken down into monosaccharides. These building blocks are then used for the synthesis of molecules in anabolic reactions. (credit: Betts et al. / Anatomy and Physiology OpenStax)

ATP Structure and Function

At the heart of ATP is a molecule of AMP, adenosine monophosphate. AMP is composed of an adenine molecule bonded to both a ribose 5-carbon sugar and a single inorganic phosphate group. AMP is a nucleotide, a monomer of nucleic acids. The addition of a second inorganic phosphate group results in adenosine diphosphate, ADP; the addition of a third inorganic phosphate group forms adenosine triphosphate, ATP (Figure 5.30). Phosphate groups are most often attached with the help of enzymes through a process called phosphorylation (Figure 5.32).

Figure 5.32 The enzyme ATP synthase forms a phosphate - phosphate bond. (credit: Modified by Elizabeth O'Grady original work of Klaus Hoffmeier)
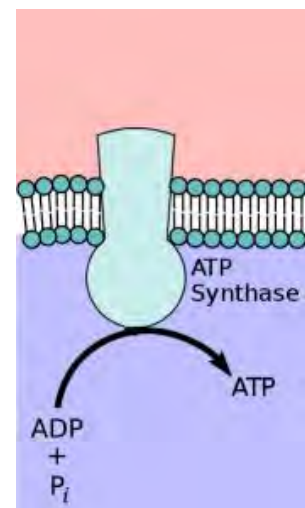
Phosphorylation, the addition of a phosphate to a molecule, requires a large amount of energy and results in a high-energy bond. Phosphate groups are negatively charged and therefore repel one another when they are arranged in series, as is the case with ADP and ATP. This repulsion makes the ADP and ATP molecules inherently unstable. Energy is released when ATP is hydrolyzed. The release of energy can be used to power active transport and other cellular processes (Figure 5.33).

Figure 5.33 The energy derived from exergonic ATP hydrolysis pumps sodium and potassium ions across the cell membrane. (credit: Clark et al. / Biology 2E OpenStax)
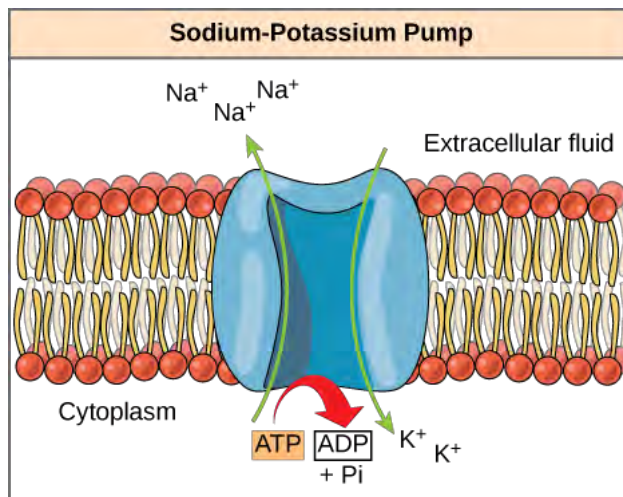
How exactly does the energy released by ATP perform work inside the cell? This depends on a strategy referred to as **energy coupling**. Cells couple exergonic processes that release energy with those endergonic processes that require energy. In Figure 5.34, this sodium-potassium pump drives sodium out of the cell and potassium into the cell against its concentration gradient. For the pump to work, it requires energy in the form of ATP. When ATP hydrolyzes, its phosphate does not simply float away but is transferred onto the pump protein. When a phosphate group is attached, the Na^+/K^+ pump has more free energy and undergoes a conformational change. This change allows it to release Na^+ outside the cell. The pump then binds extracellular K^+, which, through another conformational change, causes the phosphate to detach from the pump. The detachment of the phosphate group triggers the K^+ to be released into the cell. Essentially, the energy released from ATP is coupled with the energy required to power the pump. ATP performs cellular work using energy coupling through phosphorylation.
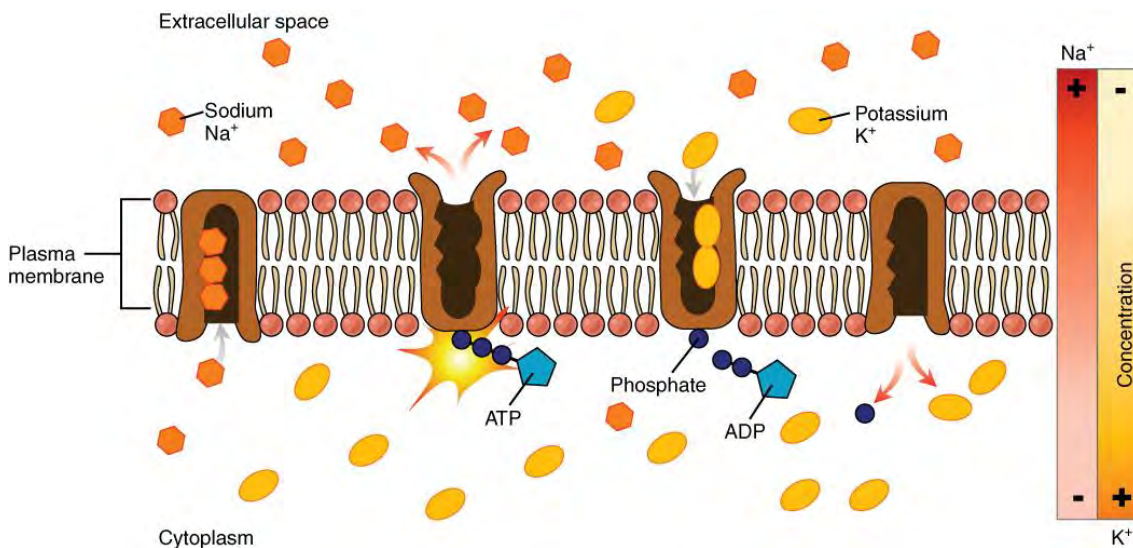
Figure 5.34 The sodium-potassium pump, which is powered by ATP, is found in many cell (plasma) membranes. (credit: Betts et al. / Anatomy and Physiology OpenStax)

Section Summary

Energy comes in many different forms. Kinetic energy is the energy of objects in motion. Objects that are not in motion may have the potential to do work, and thus, have potential energy. Molecules have potential energy because breaking molecular bonds has the potential to release energy. Living cells depend on harvesting potential energy from molecular bonds to perform work. Free energy is a measure of energy that is available to do work.

A reaction that releases energy is called an exergonic reaction. One that requires an input of energy is an endergonic reaction. Endergonic reactions' products have a higher energy state than the reactants.

ATP is the primary energy-supplying molecule for living cells. The bonds that connect the phosphates have high-energy content. The energy released from ATP hydrolysis into $ADP + P_i$ performs cellular work.

Exercises

1. Your cells are producing proteins during translation. Is this an exergonic or endergonic reaction?
2. Which of the following is not an example of an energy transformation?
   a. Heating dinner in a microwave
   b. Solar panels at work
   c. Turning on a light switch
   d. All the above are examples of energy transformations
3. Which of the following is not true about ATP?
   a. It is the primary energy currency of all living cells.
   b. The phosphate-phosphate bonds represent large amounts of kinetic energy
   c. Phosphate-phosphate bonds repel one another and make the molecule unstable
   d. ATP has three phosphate groups
4. Think about a pendulum swinging. Which type of energy (kinetic or potential) is associated with the pendulum in the following instances:
   a. the pendulum is in motion between its highest and lowest positions
   b. the moment that the pendulum is in its most elevated position but is not moving

Answers

1. Endergonic
2. (d)
3. (b)
4. a. kinetic b. potential

Glossary

ATP: adenosine triphosphate; the cell's energy currency

chemical energy: type of potential energy that exists within chemical bonds

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

energy: the ability to do work

energy coupling: energy released from exergonic processes is used to support or transferred to endergonic processes

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

free energy: usable energy or energy that is available to do work

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

phosphorylation: the addition of a phosphate to a molecule

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

5.7 Enzymes

Learning objectives

By the end of this section, you will be able to:

- *Understand what enzymes are and why they are important*
- *Discuss enzyme function*
- *Know the role enzymes play on the activation energy*
- *Explain what a metabolic pathway is and how enzymes are involved in these pathways*
- *Be able to define and explain all bolded terms*

All chemical reactions require some input of energy. For example, exergonic reactions that have a net release of energy still require some energy in order to begin. This amount of energy necessary to begin a chemical reaction is called the **activation energy**.

Enzymes

A substance that helps a chemical reaction to occur is called a **catalyst**. Molecules that catalyze chemical reactions in cells are called **enzymes**. Most enzymes are proteins that *lower the activation energy needed* for the chemical reaction to occur. To maintain homeostasis, chemical reactions must occur in a timely fashion. On their own, most of the chemical reactions in a cell happen too slowly for life to be maintained. Enzymes are used to speed up chemical reactions, allowing life to exist (Figure 5.35).
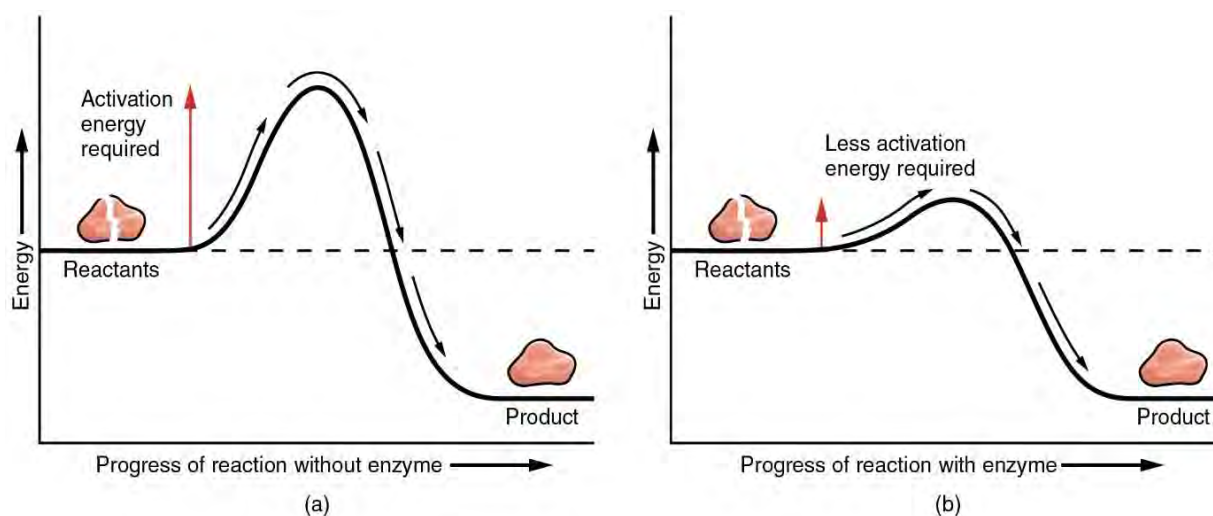
Figure 5.35 Enzymes decrease the activation energy required for a given chemical reaction to occur. (a) Without an enzyme, the energy input needed for a reaction to begin is high. (b) With the help of an enzyme, less energy is needed for a reaction to begin. (credit: Betts et al. / Anatomy and Physiology OpenStax)

Enzymes speed up the rate of chemical reactions by binding to the reactant molecules and
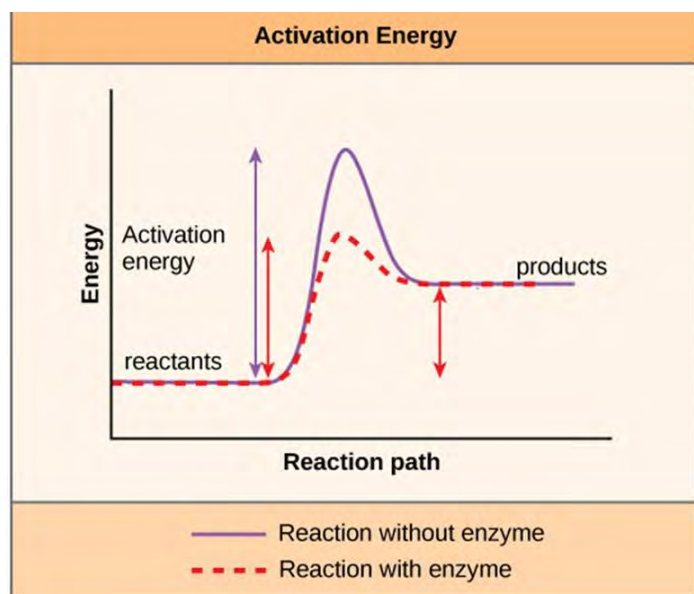
holding them in such a way that it makes the chemical bond-breaking and -forming processes take place more quickly. Enzymes do this by reducing the activation energy required for the reaction to happen (Figure 5.36). An enzyme itself is unchanged by the reaction it catalyzes. Once one reaction has been catalyzed, the enzyme can catalyze the reaction again.

Figure 5.36 Enzymes lower the activation energy of the reaction but do not change the free energy of the reaction. (credit: Modified by Elizabeth O'Grady original work of Concepts of Biology OpenStax)

During a chemical reaction, the enzyme binds to the reactants, which are called the enzyme's **substrates**. There may be one or more substrates, depending on the chemical reaction. In some reactions, two substrates may come together to create one larger molecule (Figure 5.37). In others, a single substrate is broken down into multiple products (Figure 5.38). The location within the enzyme where the substrate binds is called the enzyme's **active site**. The active site is where the "action" happens.
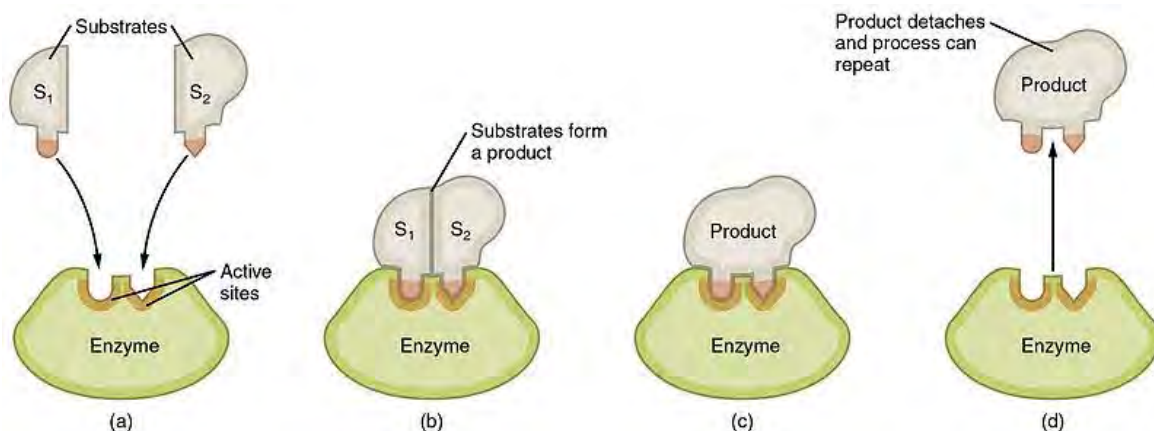
Figure 5.37 (a) Substrates approach active sites on an enzyme. (b) Substrates bind to active sites, producing an enzyme-substrate complex. (c) Changes internal to the enzyme-substrate complex facilitate the interaction of the substrates. (d) Products are released, and the enzyme returns to its original form, ready to facilitate another enzymatic reaction. (credit: Betts et al. / Anatomy and Physiology OpenStax)

Enzymes are not the only catalyst that can affect a chemical reaction. Increasing environmental temperature also generally increases chemical reaction rates. However, temperatures outside of an optimal range reduce an enzyme's ability to function. If the temperature is too hot, the enzymes will eventually **denature**. When an enzyme is denatured, it loses its three-dimensional shape and is no longer able to function properly. Enzymes are suited to work best under certain optimal conditions. Changes in pH and salt concentration range, as with temperature, can cause enzymes to denature.
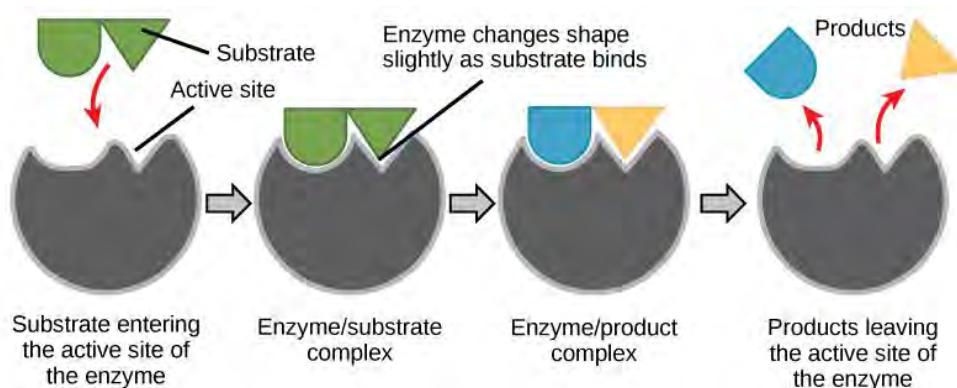
Figure 5.38 The induced-fit model explains how enzymes and substrates undergo dynamic modifications during the transition state to increase the affinity of the substrate for the active site. (credit: Fowler et al. / Concepts of Biology OpenStax)

For many years, scientists thought that enzyme-substrate binding took place in a simple "lock and key" fashion. This model stated that the enzyme and substrate fit together perfectly in one instantaneous step. However, current research supports a model called induced fit (Figure 5.38). 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. The mild shift in structure forms an ideal binding arrangement between enzyme and substrate.

CONCEPTS 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 allows the chemical reaction to happen quickly. It is important to remember that the enzyme will always return to its original state by the end of the chemical 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.

It would seem ideal if an organism's enzymes always existed in large quantities and functioned under all conditions. However, a variety of mechanisms ensures that this does not happen. Cellular needs and requirements continuously vary from cell to cell. The required enzymes of stomach cells differ from those of fat storage cells, skin cells, blood cells, and nerve cells. As cellular demands and conditions vary, so must the amounts and functionality of different enzymes.

Competitive inhibition

Enzyme activity can be regulated in several different ways. Environmental factors such as pH or temperature, as well as regulatory molecules, can either promote or reduce an enzyme's activity. Many kinds of regulatory molecules inhibit or promote enzyme function. In some cases of enzyme inhibition, an inhibitor molecule is similar enough to the substrate that it can bind to the active site and block the substrate from binding. When this happens, the enzyme is inhibited

through **competitive inhibition.** Figure 5.39 shows how the rate of a chemical reaction decreases during competitive inhibition when compared to normal enzyme activity.
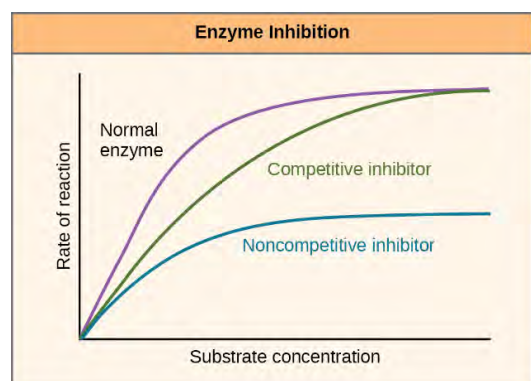
Figure 5.39 This plot shows the rate of reaction versus substrate concentration for an enzyme in the absence of the inhibitor and the enzyme in the presence of competitive and non-competitive inhibitors. (credit: Clark et al. / Biology 2E OpenStax)

Non-competitive inhibition

In **non-competitive inhibition**, an inhibitor molecule binds to the enzyme in a location other than the active site, often called an allosteric site. The inhibitor still prevents the substrate from binding to the active site; however, it does so by causing a conformational change that reduces the affinity or binding ability of the enzyme for its substrate. This type of inhibition is called **allosteric inhibition** (Figure 5.40). There are also **allosteric activators**. When an allosteric activator binds to the allosteric site in the enzyme, it induces a conformational change that increases the affinity of the enzyme's active site(s) for its substrate(s) (Figure 5.40).

Figure 5.40 Allosteric inhibition works by indirectly inducing a conformational change to the active site. In contrast, in allosteric activation, the activator molecule modifies the shape of the active site to allow a better fit of the substrate. (credit: Fowler et al. / Concepts of Biology OpenStax)
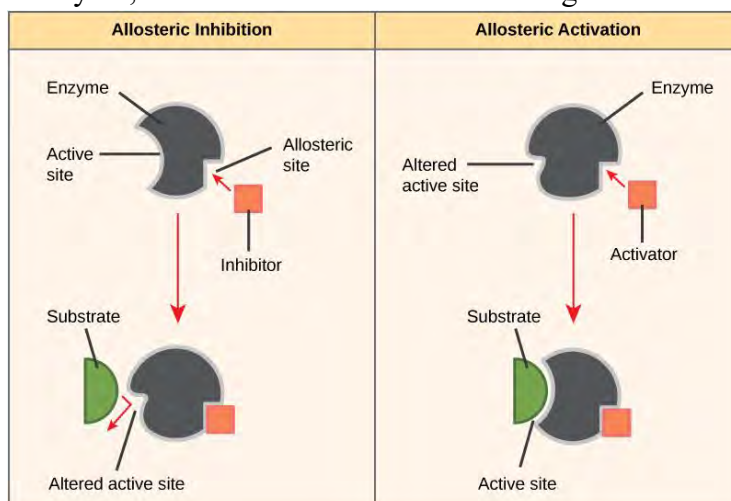
- **Pharmaceutical Drug Developer**

Understanding how enzymes work and how they can be regulated are key principles behind the development of many pharmaceutical drugs on the market today. Biologists working in this field collaborate with other scientists to design pharmaceutical drugs (Figure 5.41).

Figure 5.41 Pharmaceutical drugs can act on enzymes. (credit: Deborah Austin / Concepts of Biology OpenStax)

For example, consider statins, a class of pharmaceutical 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 also be reduced.

Cofactors and Coenzymes

Many enzymes do not work optimally, or 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 the optimal shape and function of their respective enzymes. Two examples of helper molecules are cofactors and coenzymes. **Cofactors** are inorganic ions such as iron and magnesium, whereas **coenzymes** are organic helper molecules. Like enzymes, these molecules participate in reactions without being altered and can be reused. Vitamins are a source of coenzymes (Figure 5.42). Vitamin C is a coenzyme for enzymes used to synthesize the important protein, collagen. 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.

Figure 5.42 Shown are the molecular structures for Vitamin A, folic acid, Vitamin B1, Vitamin C, Vitamin B2, Vitamin D2, Vitamin B6, and Vitamin E. Vitamins are important coenzymes or precursors of coenzymes. (credit: Clark et al. / Biology 2E OpenStax)

Feedback Inhibition in Metabolic Pathways

As mentioned in section 5.4, the chemical reactions of metabolic pathways do not take place on their own. Each reaction step is facilitated or catalyzed by an enzyme. Without the enzymes, the metabolic pathway would not occur promptly. Enzymes involved with metabolic pathways are regulated in various ways. Perhaps the most relevant source of regulation is the products of the chemical reactions themselves. Cells have evolved in such a way that they can use the products of their chemical reactions for feedback inhibition of enzyme activity. **Feedback inhibition** occurs when an end product from the reaction is used to inhibit the starting reactants or enzymes involved in the chemical reaction (Figure 5.43). This inhibition will slow down or stop the production of the final product.
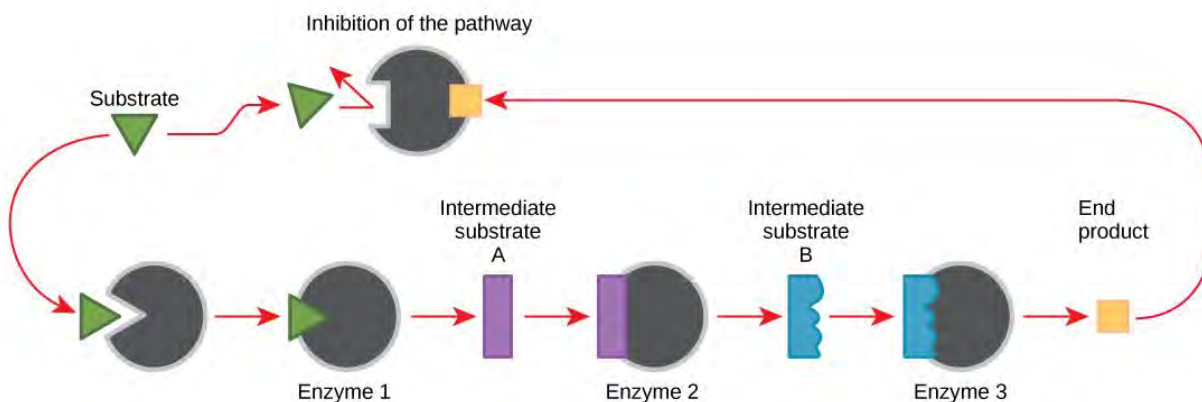
Figure 5.43 shows a metabolic pathway with feedback inhibition. (credit: Clark et al. / Biology 2E OpenStax)

Section Summary

Enzymes are chemical catalysts that speed up chemical reactions by lowering their activation energy. Enzymes have an active site 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.

Exercises

1. Which of the following analogies best describes the induced-fit model of enzyme-substrate binding?
   a. a hug between two people
   b. a key fitting into a lock
   c. a square peg fitting through the square hole and a round peg fitting through the round hole of a children's toy
   d. the fitting together of two jigsaw puzzle pieces
2. An allosteric inhibitor:
   a. Binds to the enzyme in a location other than the active site, increasing its affinity for substrate binding.
   b. Binds to the active site and blocks it from binding substrate.
   c. Binds to the enzyme in a location other than the active site, decreasing its affinity for the substrate.
   d. Binds directly to the active site and mimics the substrate.
3. 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.
4. Concerning enzymes, why are vitamins and minerals necessary for good health? Give examples.

Answers

1. (a)
2. (c)
3. (a)
4. Most vitamins and minerals act as cofactors and coenzymes for enzyme action. Many enzymes require the binding of specific cofactors or coenzymes to be able to catalyze their reactions. Since enzymes catalyze many vital 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.

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 activation: the mechanism for activating 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, allowing binding with the substrate

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

catalyst: substances that speed up the rate of chemical reactions

coenzyme: small organic molecules, such as a vitamin or its derivative, which is required to enhance an enzyme's activity

cofactor: inorganic ion, such as iron and magnesium ions, required for optimal enzyme activity regulation

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

denature: loss of shape in a protein that may be a result of changes in temperature, pH, or chemical exposure

enzyme: a molecule that catalyzes a biochemical reaction

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

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

substrate: a molecule on which the enzyme acts

Chapter 6: Introduction to Cellular Respiration

Figure 6.1 This geothermal energy plant transforms thermal energy from deep in the ground into electrical energy. (credit: modification of work by the U.S. Department of Defense / Biology 2E OpenStax)

The electrical energy plant in Figure 6.1 converts energy from one form to another. This type of electrical plant starts with underground thermal energy (heat) and transforms it into electrical energy that will be used in homes and factories. Like an electrical plant, plants and animals also must take in energy from the environment and convert it into a form that their cells can use. During photosynthesis, plants and other photosynthetic producers take in light energy and convert it into chemical energy in the form of glucose. Glucose is essential because it stores potential energy in its chemical bonds. In cellular respiration, a series of metabolic chemical reactions, energy is extracted from the bonds of glucose and used to make ATP. In this chapter, we will take a closer look at the metabolic pathway of cellular respiration.

6.1 Energy in Living Systems

Learning objectives

By the end of this section, you will be able to:

- *Explain what a redox (reduction/oxidation) reaction is*
- *Know the overall equation for aerobic cellular respiration and be able to explain which molecules are reduced or oxidized into which molecules*
- *Identify ATP and describe how it is involved in energy transfer within cells*
- *Be able to define and explain all bolded terms*

All living organisms perform cellular respiration. Cellular respiration is the process of using potential chemical energy, stored in the bonds of organic nutrients, to generate ATP (adenosine triphosphate). If oxygen is required when performing cellular respiration, the process is called **aerobic cellular respiration**. When oxygen is not required, the process is called **anaerobic cellular respiration**.

Humans, plants, some bacteria, and many other living organisms use aerobic cellular respiration to generate ATP. During aerobic cellular respiration, potential energy from glucose is used to drive the synthesis of ATP with the help of oxygen. During the process, both carbon dioxide and water are released as waste products. In addition, like all energy transformations, some energy is lost in the form of heat. Aerobic cellular respiration can be summarized by the equation below:

$$\text{glucose} \qquad \qquad \qquad \qquad \qquad \qquad \qquad \qquad \text{heat} \uparrow$$
$$C_6H_{12}O_6 + 6O_2 + 32ADP + 32P_i \rightarrow\rightarrow\rightarrow 6CO_2 + 6H_2O + 32ATP$$

Figure 6.2 shows the reaction for aerobic cellular respiration. Note that this process consists of several chemical reactions, as indicated by the multiple arrows. (credit: Jason Cashmore)

Breaking down sugar molecules occurs through a series of chemical reactions. As you can see from Figure 6.2, these reactions begin with one molecule of energy-rich glucose. Glucose is modified through a series of metabolic pathways and eventually leads to the synthesis of large quantities of ATP. Most of these pathways are combinations of oxidation and reduction reactions. Oxidation and reduction reactions occur in tandem. An **oxidation reaction** strips an electron from an atom in a molecule making that atom more positive. That electron is then gained by a different atom in a **reduction reaction**. The atom that receives or gains the electron now has more electrons than protons and therefore becomes more negative (its charge is reduced, hence the name reduction reaction). Because reduction and oxidation usually occur together, these pairs of reactions are called reduction-oxidation reactions or **redox reactions**. Figure 6.3 shows a redox reaction; sodium is oxidized when it loses an electron, and chlorine is reduced when it accepts an electron.

$$\text{Reduction}$$
$$Na + Cl \longrightarrow Na^+ + Cl^-$$
$$\text{Oxidation}$$
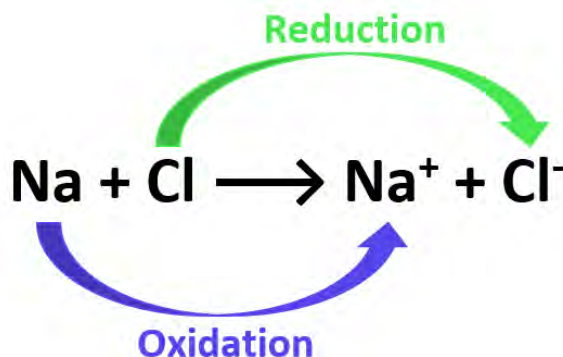
Figure 6.3 shows a redox reaction. Sodium loses an electron, so it is oxidized into a positive sodium ion. Chlorine gains an electron, so it is reduced into a negative chloride ion. (credit: Elizabeth O'Grady)

Electrons and Energy

The removal of an electron from a molecule, oxidizing it, results in a decrease in potential energy in the oxidized molecule. The electron, which is often donated from hydrogen, does not remain unbonded. Rather, the electron is shifted to a second molecule. The molecule that accepts the electron is said to be reduced. During aerobic cellular respiration hydrogen atoms from glucose are oxidized, resulting in carbon dioxide (CO_2). Oxygen molecules are reduced, resulting in water molecules (H_2O). When glucose is oxidized, it removes some potential energy from the molecule which is then used to synthesize ATP (Figure 6.4).

<div align="center">

Reduction

$C_6H_{12}O_6 + 6O_2 + 32ADP + 32P_i \rightarrow\rightarrow\rightarrow 6CO_2 + 6H_2O + 32ATP + heat$

Oxidation

</div>
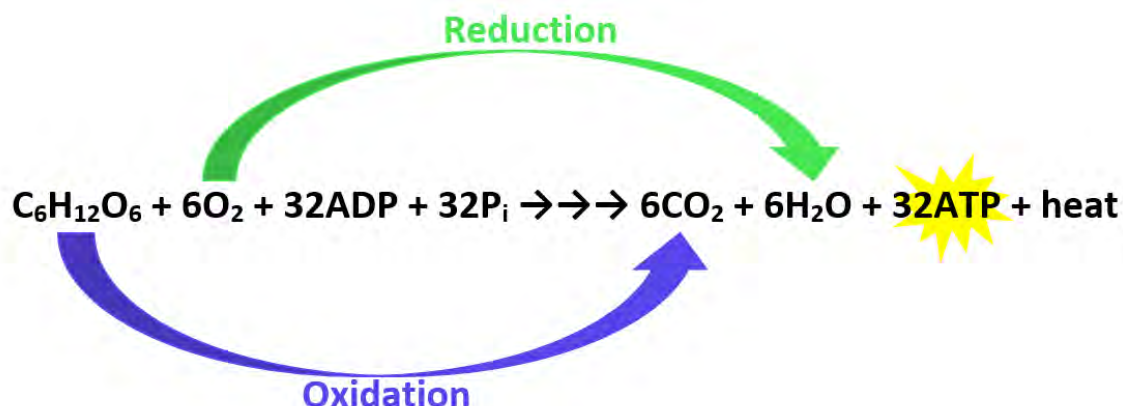
Figure 6.4 shows aerobic cellular respiration as redox reactions. (credit: Jason Cashmore)

Most of an atom's potential energy is found in the form of its high-energy electrons. The transfer of electrons between atoms allows the cell to transfer and use energy in small increments rather than a single, destructive burst. Section 6.2 will focus on how energy is extracted from glucose in small increments to generate ATP. You will see that as you track the path of the energy transfers, you are tracking the path of electrons moving through metabolic pathways. To follow electrons through metabolic pathways it is necessary to learn about electron carriers, special molecules that shuttle electrons throughout the cell.

Check your knowledge

Which of the following is true of redox reactions?
  a. Oxidation results in atoms becoming more negative.
  b. Reduction results in atoms gaining electrons.
  c. Atoms that are oxidized release oxygen.
  d. Reduced atoms become more positive.

Answer: b

Electron Carriers

In redox reactions in living systems some molecules function as electron shuttles, binding and carrying high-energy electrons between molecules in different metabolic pathways. Nicotinamide adenine dinucleotide (NAD) is a major electron carrier derived from vitamin B3 (Figure 6.5). NAD^+ is the oxidized form of the molecule. When NAD^+ accepts two electrons and a proton (hydrogen ion) it is reduced to NADH.
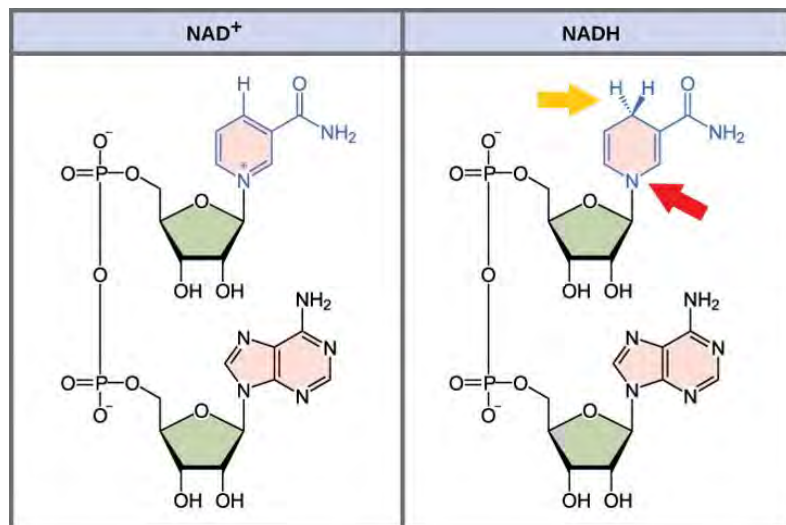
Figure 6.5 The oxidized form of the electron carrier (NAD+) is shown on the left, and the reduced form (NADH) is shown on the right. The red arrow points to where an electron is being carried and the orange arrowpoints to where an electron and a proton are being carried. (credit: Modified by Jason Cashmore original work by Clark et al. / Biology 2E OpenStax)

In Figure 6.6 below, the organic substrate, CH_2O, is being oxidized. An enzyme helps to remove the two hydrogen atoms from the organic substrate. The two hydrogen atoms transfer their two electrons along with one hydrogen ion to the electron carrier, NAD^+. When NAD^+ accepts the electrons and hydrogen ion, it is reduced to NADH. In eukaryotic cells, the NADH can now shuttle the electrons to the inner membrane of the mitochondria, where they will be used to synthesize large quantities of ATP.
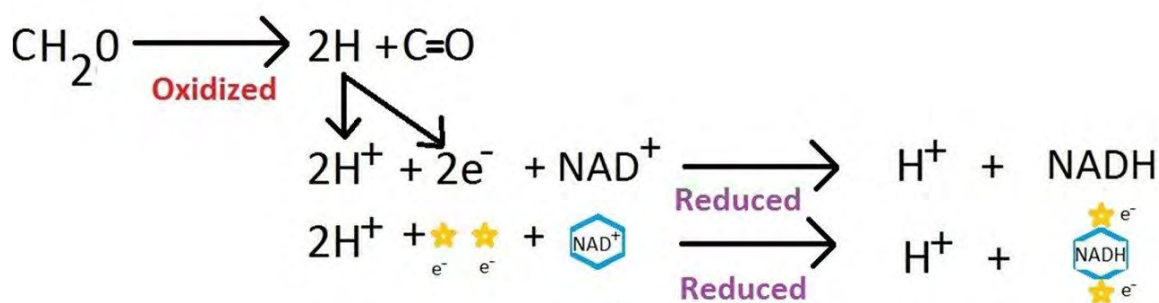
Figure 6.6 shows a redox reaction where an organic molecule is oxidized NAD^+ is reduced. (credit: Elizabeth O'Grady)

Similarly, flavin adenine dinucleotide (FAD), derived from vitamin B_2, also functions as an electron carrier. Its reduced form is $FADH_2$. Both NAD^+ and FAD are extensively used to shuttle electrons into the mitochondria and will be discussed throughout the next several sections.

ATP in Living Systems

ATP is often called the "energy currency" of a cell because it provides much of the energy needed to carry out cellular processes. ATP is classified as a high energy molecule because the covalent bonds that link the phosphate groups contain large quantities of potential energy (Figure 6.7). Phosphate groups are negatively charged and as a result, repel one another. To bring them together and form the covalent bonds large amounts of energy are necessary. Therefore, when the bonds are broken, the stored potential energy is released and can be used to power any number of different cell activities.
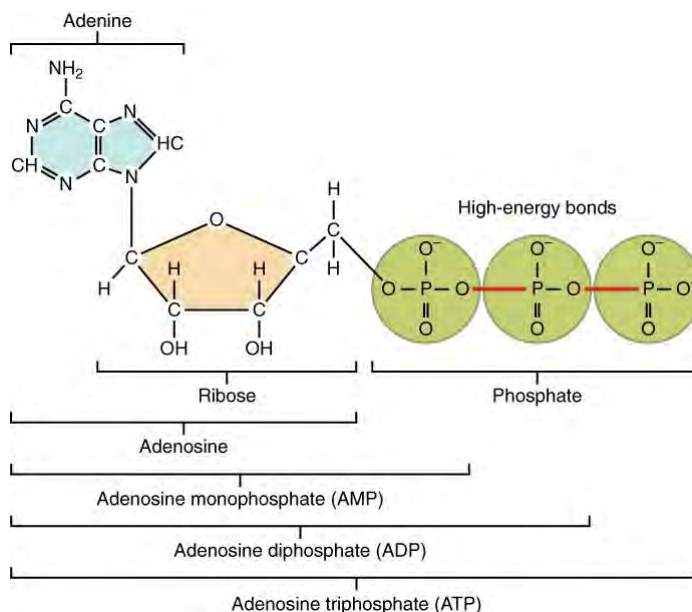
Figure 6.7 Structure of Adenosine Triphosphate (ATP) (credit: Betts et al. / [Anatomy and Physiology OpenStax](#))

Phosphorylation

ATP can be regenerated when an inorganic phosphate (P_i) is covalently bound to ADP (adenosine diphosphate) through the process of **phosphorylation**. Phosphorylation requires energy and can be done using three separate mechanisms. Where does this energy for phosphorylation come from? In almost all living organisms, the energy comes from the metabolism of simple sugars such as glucose, fructose, or galactose. Let's now take a closer look at the different types of phosphorylation.

Substrate Phosphorylation

In substrate phosphorylation, a few ATP molecules are generated when a phosphate group is removed from an intermediate reactant in the cellular respiration pathway. The free energy of the reaction is used to add the removed phosphate directly to ADP producing ATP (Figure 6.8). This direct method of phosphorylation is called **substrate-level phosphorylation** and does not require oxygen.
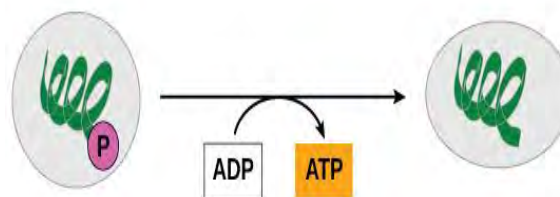
Figure 6.8 shows substrate-level phosphorylation reactions, where a phosphate is removed from a substrate and attached to ADP to make ATP. (credit: Clark et al. / [Biology 2E OpenStax](#))

Oxidative Phosphorylation

Most of the ATP generated during glucose catabolism is synthesized during oxidative phosphorylation, a complex process that takes place in the mitochondria (Figure 6.9) of eukaryotic cells or the plasma membrane of some prokaryotic cells. **Oxidative phosphorylation** is made up of two steps: the electron transfer chain and chemiosmosis. Chemiosmosis is used to generate 90 percent of the ATP made during glucose catabolism. It is also used in photosynthesis to convert light energy from the sun to chemical energy found in the bonds of ATP. Chemiosmosis yields ATP as long as oxygen is present. The details of oxidative phosphorylation will be discussed in section 6.4.
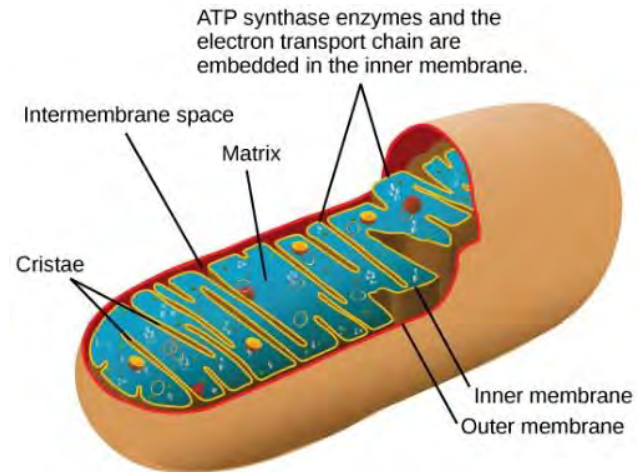
Figure 6.9 In eukaryotes, oxidative phosphorylation takes place in mitochondria. (credit: modification of work by Mariana Ruiz Villareal / Biology 2E OpenStax)

Check your knowledge

How many electrons will NAD+ carry?

When NAD+ picks up those electrons, is it oxidized or reduced?

Answers: NAD+ will pick up 2 electrons (and one hydrogen ion).

It will be reduced.

Section Summary

All cells use cellular respiration to generate ATP. The energy stored in the bonds of organic molecules such as glucose is used to drive the synthesis of ATP. The breakdown occurs through a series of chemical reactions called redox reactions. NAD^+ and FAD function as electron shuttles to the site ATP synthesis. There are two processes of ATP synthesis during cellular respiration: substrate-level phosphorylation and oxidative phosphorylation through the process of chemiosmosis.

Exercises

1. During _____ reactions electrons are donated, whereas in _____ reactions electrons are accepted.
   a. ATP; glucose
   b. reduction; oxidation
   c. glucose; ATP
   d. oxidation; reduction
2. The energy currency used by cells is _____.
   a. ATP
   b. water
   c. AMP
   d. oxygen
3. When NAD^+ accepts an electron, it is _____ to NADH.
   a. lowered
   b. oxidized
   c. reduced
   d. none of the above
4. Compare and contrast substrate level phosphorylation and chemiosmosis of oxidative phosphorylation.

Answers

1. (d)
2. (a)
3. (c)
4. In both processes, ATP is synthesized from ADP and inorganic phosphate. Substrate level does not require oxygen, whereas oxidative phosphorylation does.

Glossary

aerobic cellular respiration: the use of oxygen as an electron acceptor to complete metabolism

anaerobic cellular respiration: the use of an electron acceptor other than oxygen to complete metabolism

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

oxidation reaction: a chemical reaction that consists of an electron being donated by an atom

oxidative phosphorylation: production of ATP using the process of chemiosmosis in the presence of oxygen

phosphorylation: addition of a high-energy phosphate to a compound, usually a metabolic intermediate, a protein, or ADP

redox reaction: a chemical reaction that consists of the coupling of an oxidation reaction and a reduction reaction

reduction reaction: a chemical reaction that consists of an electron being gained by an atom

substrate-level phosphorylation: production of ATP from ADP using the excess energy from a chemical reaction and a phosphate group from a reactant

6.2 Glycolysis

Learning objectives

By the end of this section, you will be able to:

- *Describe the basic steps of glycolysis*
- *Know the starting reactants and final products of glycolysis*
- *Know which organisms are capable of glycolysis and where they carry these reactions out within the cell*
- *Be able to define and explain all bolded terms*

The carbohydrate, glucose, supplies much of the energy used by living cells. Glucose is catabolized in a series of chemical reactions called cellular respiration (Figure 6.10). This section will focus on glycolysis, the process where glucose is oxidized to produce small amounts of ATP.
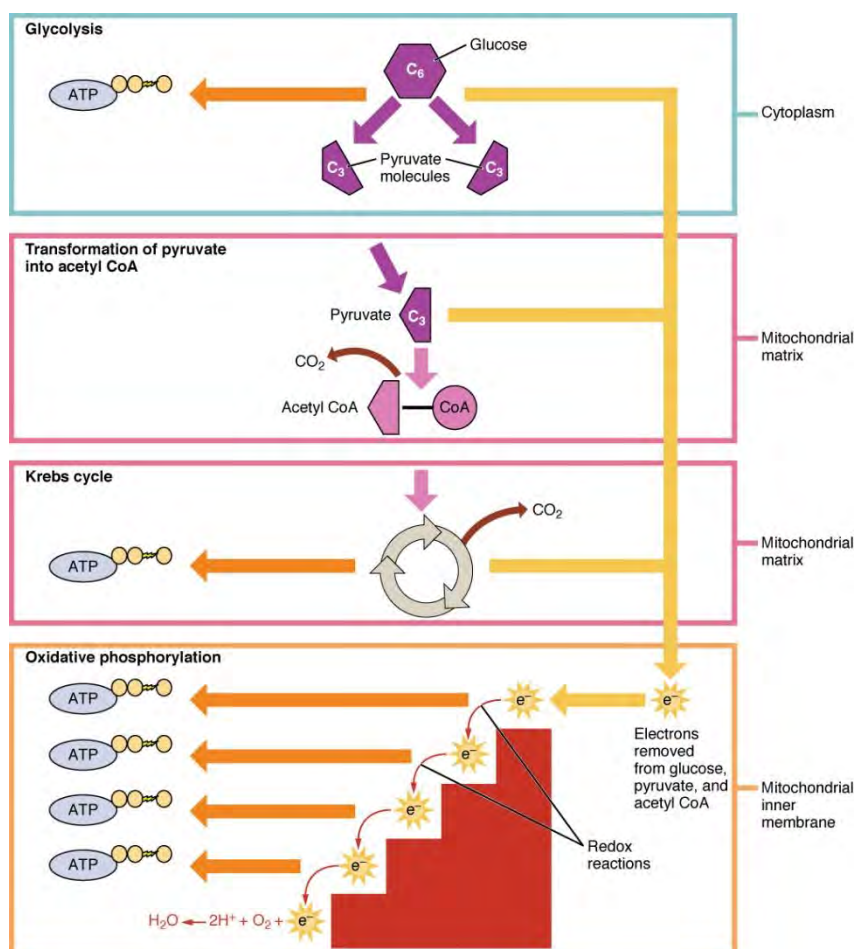
Figure 6.10 Cellular respiration oxidizes glucose molecules through glycolysis, Krebs cycle (citric acid cycle), and oxidative phosphorylation to produce ATP. (credit: Betts et al. / Anatomy and Physiology OpenStax)

Glycolysis

Glycolysis is the first metabolic pathway used to catabolize glucose. Glycolysis is thought to be the oldest energy-harvesting pathway since nearly all living organisms carry out this process. Scientific evidence suggests that atmospheric oxygen levels were very low, if not nonexistent, when life first evolved on the planet. The earliest living cells would have needed to be able to generate energy in the absence of oxygen. Glycolysis is **anaerobic,** meaning it does not require oxygen. As a result, glycolysis could have been used by the first living cells to produce energy. Also, glycolysis takes place in the cytoplasm of both prokaryotic and eukaryotic cells. Membrane-bound organelles are not necessary to carry out this metabolic pathway. Glycolysis consists of distinct phases. In the first phase, the energy-consuming phase, two ATP molecules are used to alter one six-carbon glucose molecule. In the next phase, the six-carbon sugar is split evenly into two three-carbon sugar molecules which are then oxidized. Two molecules of NAD$^+$ accept the electrons and are reduced to NADH. In the last phase, four ATP and two three-carbon sugars, called pyruvate or pyruvic acid, are produced (Figure 6.11). Note, some biochemists use the words pyruvate and pyruvic acid interchangeably. Recall that two ATP molecules were invested in the first phase of glycolysis, therefore one glucose molecule results in a *net production* of two ATP molecules.

Figure 6.11 shows an overview of glycolysis. (credit: Betts et al. / Anatomy and Physiology OpenStax)
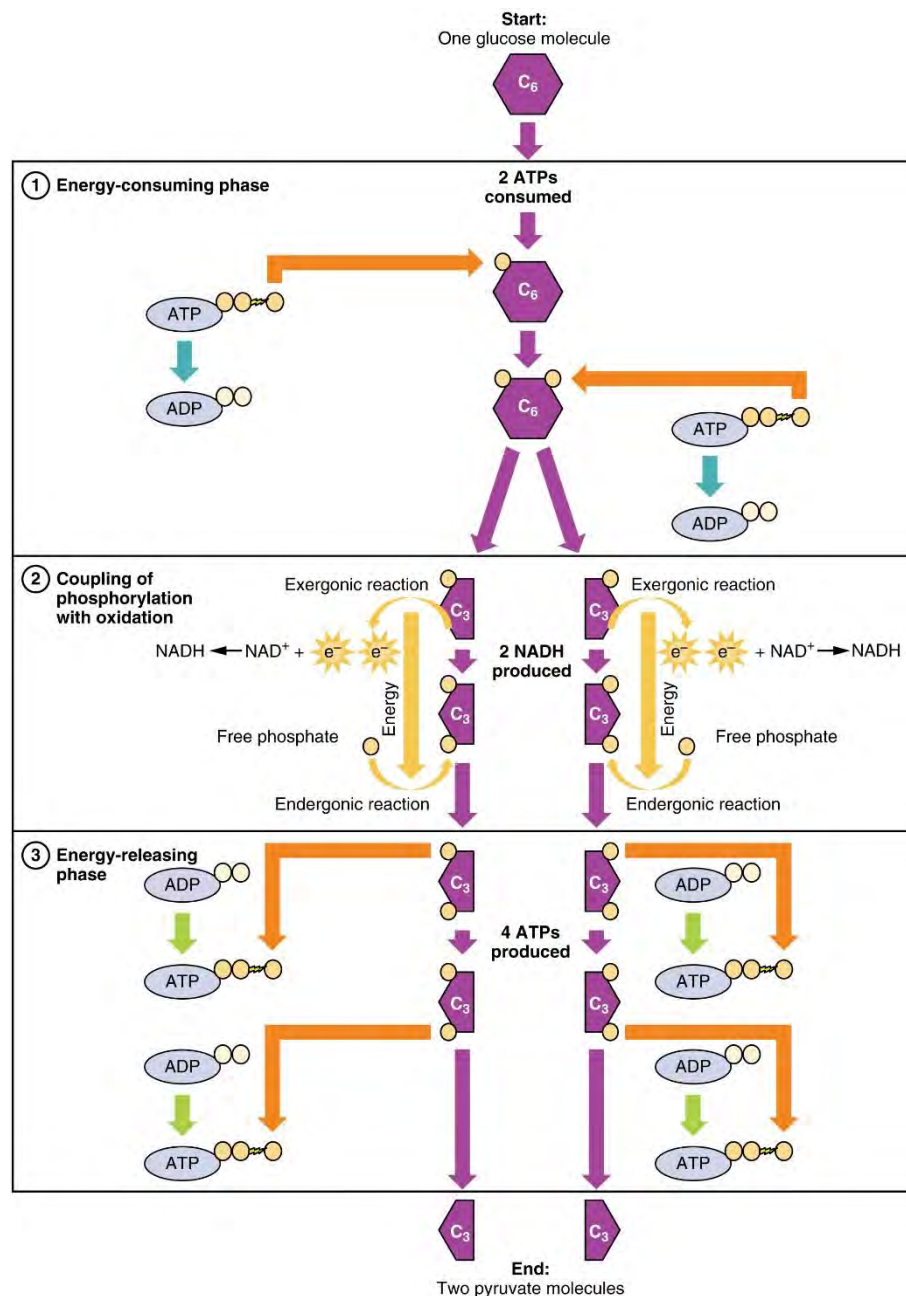
Glycolysis is a much more extensive metabolic pathway than that which is shown in Figure 6.11. Figure 6.12 provides a more accurate picture of glycolysis. Students are not responsible for learning the intermediates or the enzymes used to catalyze each reaction.
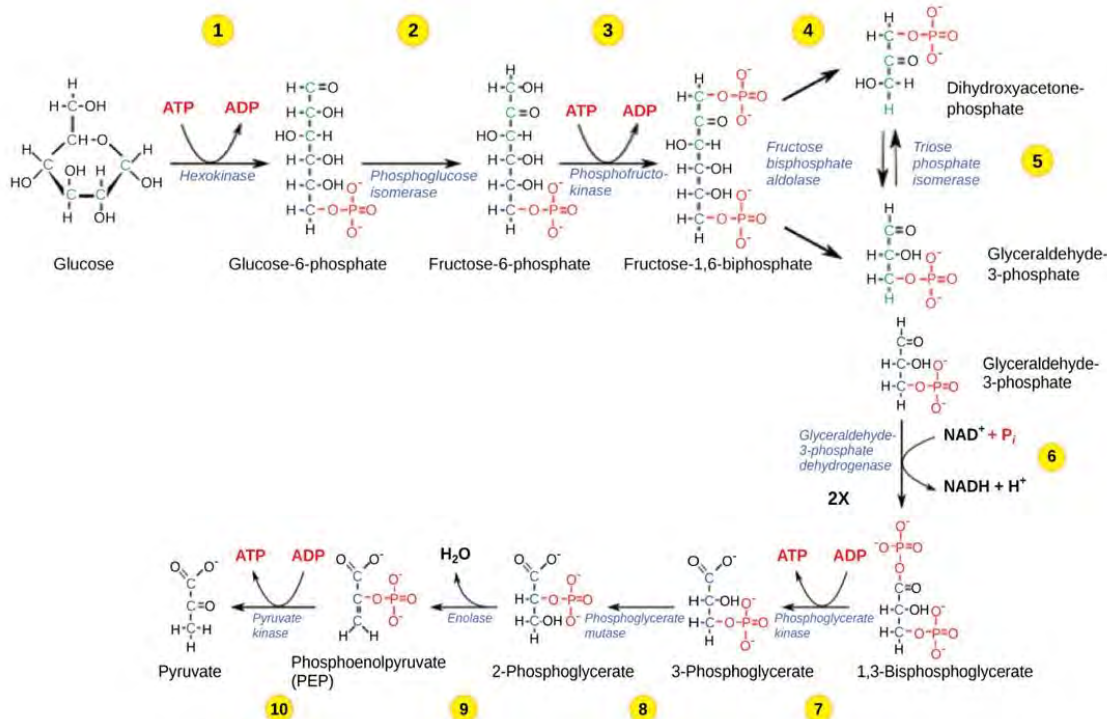
Figure 6.12 shows the glycolysis pathway in detail. (credit: Clark et al./ Biology 2E OpenStax)

The two ATP molecules that are netted during the process of glycolysis are made through **substrate-level phosphorylation**. Remember that during substrate phosphorylation, a phosphate group is removed from an intermediate substrate and attached directly to ADP producing ATP (Figure 6.13). This process does not require oxygen.
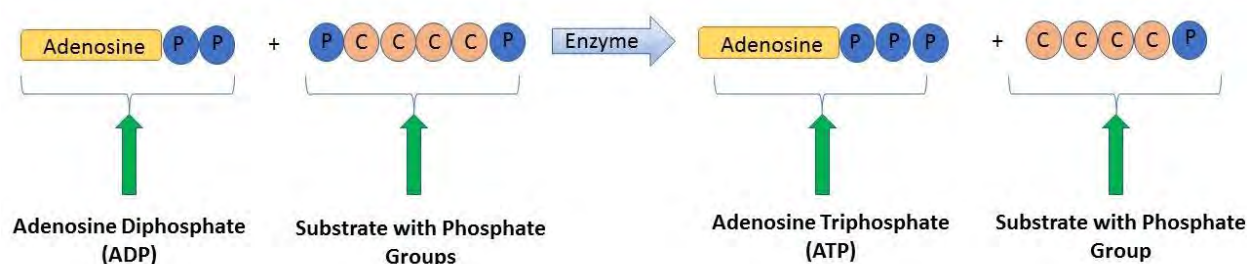
Figure 6.13 In substrate-level phosphorylation, an intermediate organic substrate provides the third phosphate of ATP with the help of an enzyme. (credit: Elizabeth O'Grady)

If oxygen is present, pyruvate will enter the mitochondria, where it will be oxidized and a large amount of ATP will be produced. If the cell cannot oxidize the pyruvate, it will only be able to generate two molecules of ATP from one molecule of glucose. For example, mature mammalian red blood cells are only capable of glycolysis. Glycolysis is their sole source of ATP, and if this pathway is interrupted, these cells will die.

CONCEPTS IN ACTION - Gain a better understanding of the breakdown of glucose by glycolysis by visiting this site to see the process in action Also view the video - *Glycolysis: An Overview*

Outcomes of Glycolysis

Glycolysis begins with one molecule of glucose, two molecules of ATP, and two molecules of NAD^+. The outputs of glycolysis are two molecules of pyruvate, four molecules of ATP, and two molecules of NADH (Figure 6.14). Note: because four new ATP molecules are generated during glycolysis but two molecules of ATP are used in the first half of the pathway, the cell has a *net gain of two ATP molecules*.

Inputs   **Outputs**

1 Glucose ⟶ 2 Pyruvate

$4e^- + 2H^+$

2 ATP ⟶ 2 ADP + P_i

2 NAD^+ ⟶ 2 NADH

4 ADP + P_i ⟶ 4 ATP
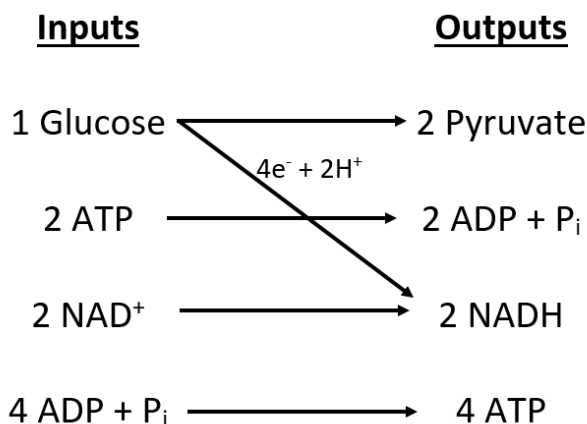
Figure 6.14 shows the inputs and outputs of glycolysis. (credit: Jason Cashmore)

Check your knowledge

If a bacteria has 4 glucose molecules, how many net ATP can it produce during glycolysis?

Answer: 8

Section Summary

Glycolysis is the first pathway used in the breakdown of glucose. Because nearly all organisms on earth use it, glycolysis is thought to have evolved early in the history of life. Glycolysis consists of different phases: The first and second phases prepare the six-carbon glucose for separation into two three-carbon sugars. Energy from ATP is invested in the molecule during this step to energize the separation. The last phase of glycolysis extracts ATP and high-energy electrons 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.

Exercises

1. During glycolysis for one molecule of glucose, a total of _____ ATP are made but of that, the cell nets _____ ATP molecules.
    a. 2; 4
    b. 6; 4
    c. 4; 2
    d. 8; 6
2. The ATP made in glycolysis is made through _____.
    a. chemiosmosis
    b. substrate-level phosphorylation
    c. oxidative phosphorylation
    d. ATP synthase
3. The glucose that enters the glycolysis pathway is split into two molecules of _____.
    a. ATP
    b. phosphate
    c. NADH
    d. pyruvate
4. 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?

Answers
1. (c)
2. (b)
3. (d)
4. If glycolysis evolved relatively late, it likely would not be as universal in organisms as it is. It probably evolved in very primitive organisms that did not require oxygen and did not need to occur in a membrane-bound organelle.

Glossary

anaerobic: process in which organisms do not require oxygen

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

substrate-level phosphorylation: production of ATP from ADP using the excess energy from a chemical reaction and a phosphate group from a reactant

6.3 Citric Acid Cycle

In eukaryotic cells, the pyruvate molecules produced at the end of glycolysis are transported into mitochondria. If oxygen is available, aerobic cellular respiration will go forward.

Pyruvate Oxidation

In the mitochondria, pyruvate will be oxidized into a two-carbon acetyl group. This process is done by removing a molecule of carbon dioxide and transferring electrons to NAD^+, reducing it to NADH. The acetyl group will then be picked up by a carrier molecule called coenzyme A (CoA). The resulting molecule is called **acetyl CoA**. (Figure 6.15).
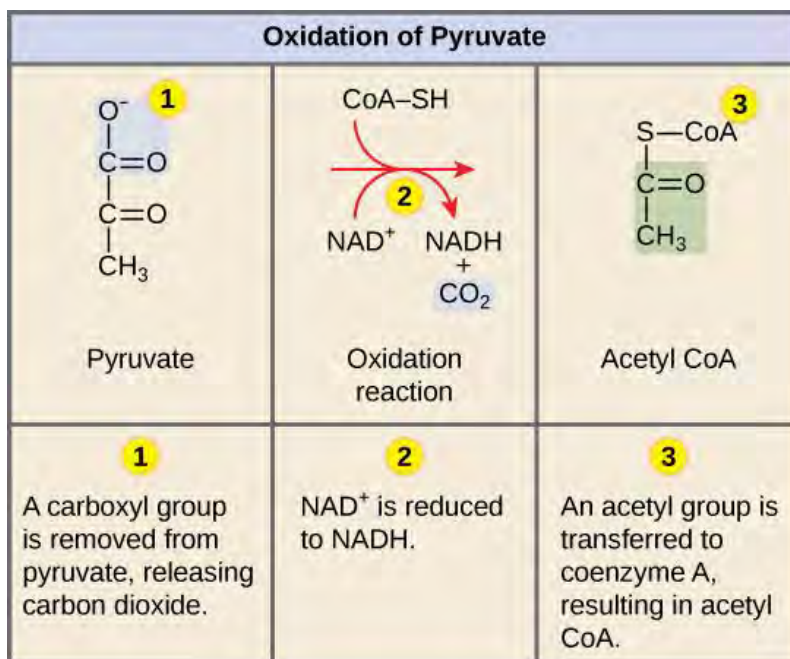
Figure 6.15 Upon entering the mitochondria, pyruvate is converted into acetyl CoA. (credit: Clark et al. / Biology 2E OpenStax)

Acetyl CoA can be used in a variety of ways by the cell. Its primary function is to deliver the acetyl group derived from pyruvate to the next pathway in glucose catabolism, the citric acid cycle (Figure 6.16). Since two pyruvate molecules exit glycolysis, pyruvate oxidation will occur twice producing a total of two Acetyl CoA, two molecules of carbon dioxide, and two molecules of NADH.
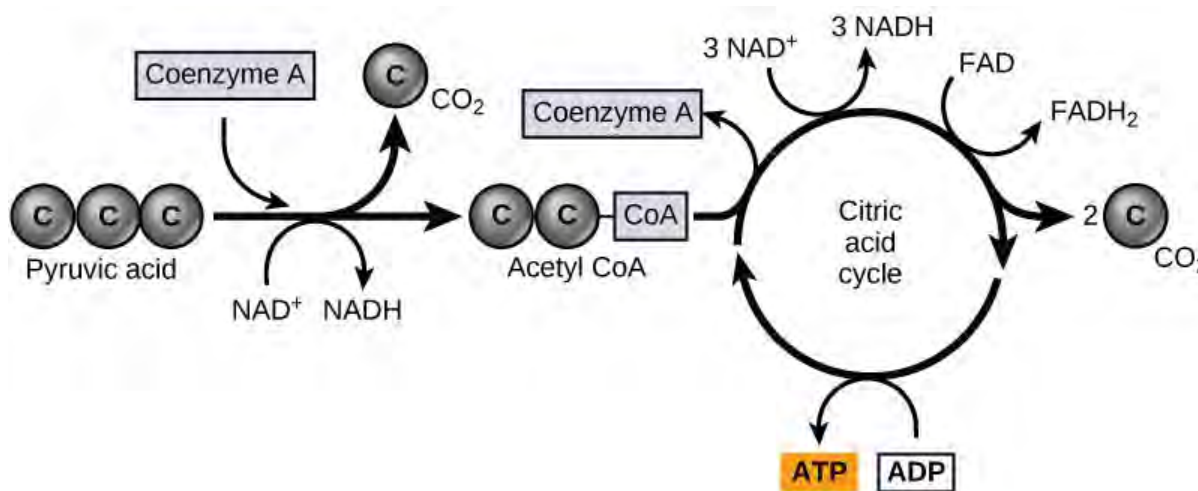
Figure 6.16 Pyruvic acid (pyruvate) is converted into acetyl-CoA before entering the citric acid cycle. (credit: Fowler et al. / Concepts of Biology OpenStax)

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 (Figure 6.9). Unlike glycolysis, the **citric acid cycle** is a closed loop. The last part of the pathway regenerates the molecule used in the very first step, oxaloacetate (Figure 6.16). The citric acid cycle is also commonly referred to as the Krebs cycle after Hans Krebs, a German-born British biochemist who discovered the metabolic pathway.

For each molecule of acetyl CoA that enters the citric acid cycle, two carbon dioxide molecules, one ATP molecule (or an equivalent), 3 NADH molecules, and 1 FADH$_2$ molecule is formed (Figure 6.17). Remember, for every one molecule of glucose that entered into glycolysis, two molecules of acetyl CoA can be formed. As a result, the citric acid cycle can make two turns for every one molecule of glucose, forming a total of four carbon dioxide, two ATP (or an equivalent), six NADH, and two FADH$_2$ molecules.

The six NADH and two FADH$_2$ are electron carriers that will transport electrons to the final stage of aerobic cellular respiration, oxidative phosphorylation. Most ATP molecules will be produced during the final stage.
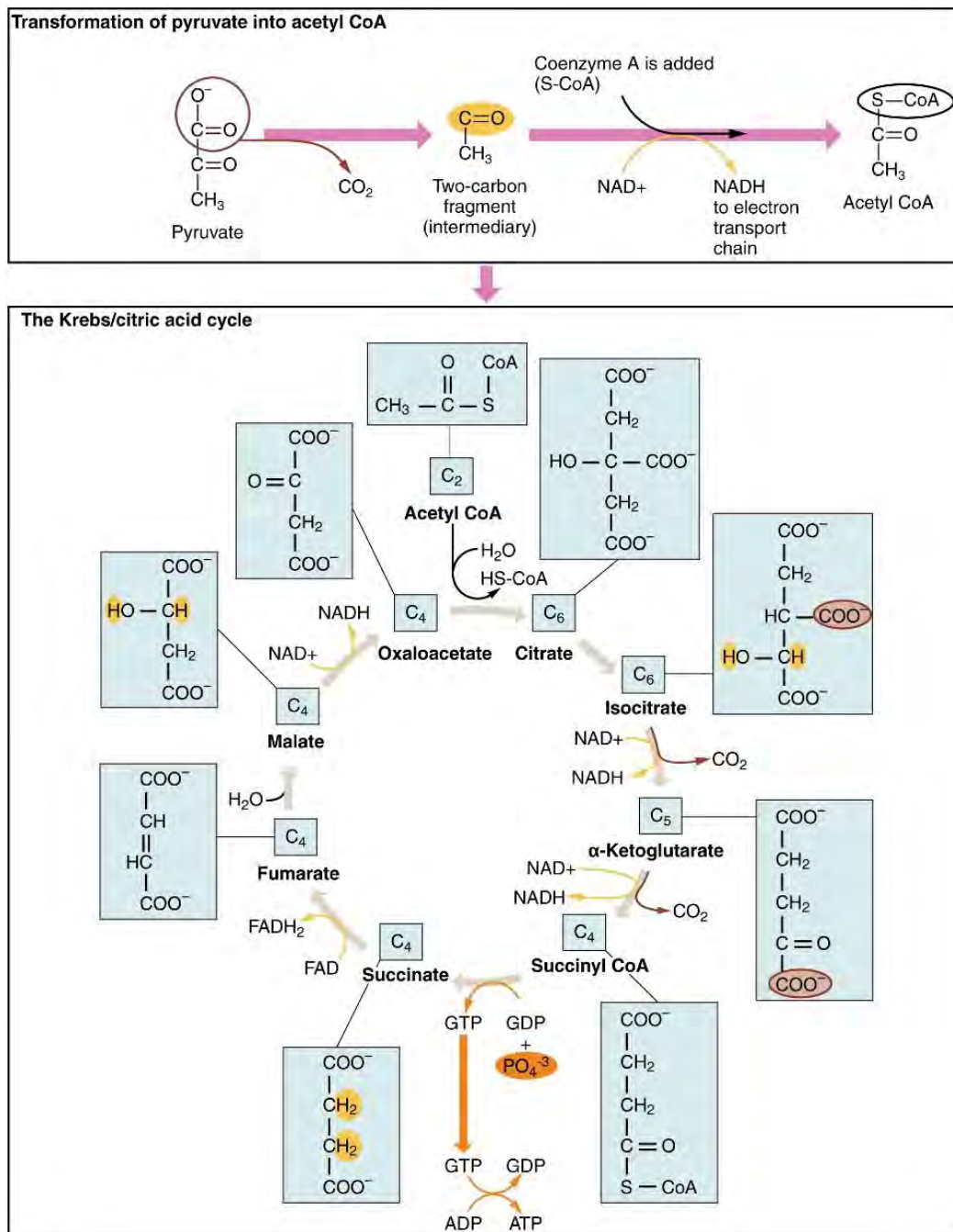
Figure 6.17 Each pyruvate (pyruvic acid) that is generated by glycolysis is converted into a two-carbon acetyl CoA molecule. In the citric acid cycle, the acetyl CoA is systematically processed through the cycle and produces carbon dioxide and high-energy NADH, FADH$_2$, and ATP molecules. (credit: Betts et al. / Anatomy and Physiology OpenStax)

The citric acid cycle is considered an aerobic pathway because it requires oxygen. The NADH and FADH$_2$ produced during the citric acid cycle must transfer their electrons to the electron transport chain, which is part of the next stage of aerobic respiration--oxidative phosphorylation. If oxygen is not present, NADH and FADH$_2$ cannot be oxidized, and the citric acid cycle cannot occur.

Section Summary

In the presence of oxygen, pyruvate is transformed into an acetyl group attached to a carrier molecule of coenzyme A. The acetyl group is delivered to the citric acid cycle for further catabolism. During the conversion of the two pyruvate molecules into the two acetyl groups, two molecules of carbon dioxide and two molecules of NADH are produced.

The citric acid cycle is a series of redox reactions. This cycle starts with acetyl CoA and oxaloacetate, which combine and form citric acid. For everyone molecule of glucose that enters glycolysis, two molecules of acetyl CoA can be formed. Therefore, the citric acid cycle can make two turns forming: 4 carbon dioxide molecules, 2 ATP molecule (or an equivalent), 6 NADH molecules, and 2 $FADH_2$ molecules.

Exercises

1. What do the electrons added to NAD^+ do?
    a. They become part of glycolysis
    b. They go on to the electron transport chain.
    c. They energize the entry of the acetyl group into the citric acid cycle.
    d. They are converted into NADP.
2. In eukaryotic cells, where does pyruvate oxidation occur?
    a. mitochondria
    b. cytoplasm
    c. nucleus
    d. plasma membrane
3. If a cell has access to three molecules of glucose, how many molecules of NADH could be made during the citric acid cycle?
    a. 3
    b. 6
    c. 12
    d. 18
4. Explain why the citric acid cycle is considered an aerobic pathway.

Answers
    1. (b)
    2. (a)
    3. (d)
    4. It is an aerobic pathway 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.

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)

citric acid cycle: a series of enzyme-catalyzed chemical reactions of central importance in all living cells that harvest 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

6.4 Oxidative phosphorylation

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Learning objectives

By the end of this section, you will be able to:

- *Describe the location of oxidative phosphorylation in the cell*
- *Describe the overall outcome of oxidative phosphorylation in terms of the products of each*
- *Describe the relationships of glycolysis, the citric acid cycle, and oxidative phosphorylation in terms of their ATP outputs.*
- *Describe the relationships of glycolysis, the citric acid cycle, and oxidative phosphorylation in terms of electron carriers.*
- *Be able to define and explain all bolded terms*

</div>

You have just read about two pathways in glucose catabolism, glycolysis and the citric acid cycle. Both pathways generate only small amounts of ATP. Most of the ATP is made during the final stage of aerobic cellular respiration, oxidative phosphorylation. **Oxidative phosphorylation** consists of two parts, the electron transport chain and chemiosmosis. Both processes of oxidative phosphorylation take place on the inner membrane of the mitochondria of eukaryotic organisms and on the inner part of the cell membrane of prokaryotic organisms. Let us take a closer look at the processes that make up oxidative phosphorylation.

Electron Transport Chain

The **electron transport chain** is the only part of glucose catabolism that uses oxygen directly. Electron transport is a series of chemical redox reactions that resemble a bucket brigade or a ball rolling down a staircase (Figure 6.18).

Figure 6.18 The electron transport chain resembles a staircase. As the electron moves down each stair energy are given off, which can be used to generate ATP. (credit: Modified by Elizabeth O'Grady original work of Betts et al. / Anatomy and Physiology OpenStax)
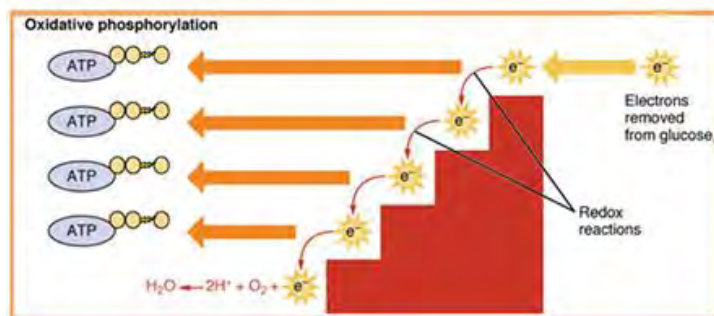
As electrons are passed rapidly from one protein to the next in a series of redox reactions, some energy is released. At the end of the protein chain, oxygen acts as the final electron acceptor. Each oxygen atom accepts two electrons and two hydrogen ions and is reduced to water. See the below equation. Note the equation begins with one oxygen molecule, which is two atoms of oxygen covalently bound together.

$$O_2 + 4H^+ + 4e^- \longrightarrow 4H_2O$$
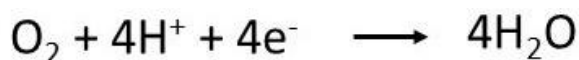
NADH and FADH$_2$ from glycolysis and citric acid cycle arrive at the electron transport chain, where they are both oxidized. Electrons from NADH and FADH$_2$ are passed to protein complexes located in the inner membrane of the mitochondria. The electron transport chain consists of four protein complexes labeled I through IV and several mobile electron carriers, labeled Q and Cyt c (Figure 6.19).
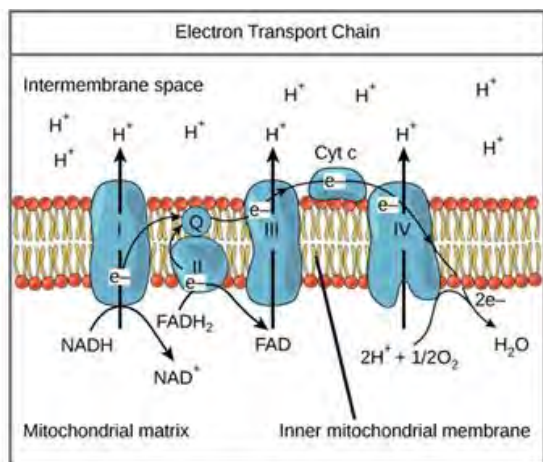
Figure 6.19 The electron transport chain is a series of electron transporting proteins embedded in the inner mitochondrial membrane that shuttles electrons from NADH and FADH$_2$ to molecular oxygen. (credit: Modified by Elizabeth O'Grady original work of Clark et al. / Biology 2E OpenStax)

As each electron is transferred through the electron transport chain, some of the electron's energy is transferred to the protein complexes. The potential energy can be used by the protein complexes to pump hydrogen ions across the inner mitochondrial membrane against their concentration gradient using active transport (Figure 6.18). The ions are pumped into the intermembrane space, which creates a hydrogen ion gradient that will be used in chemiosmosis.

In the fourth protein complex, the electrons are accepted by oxygen, the terminal acceptor. It takes four electrons to split one molecule of oxygen. Each oxygen atom then accepts two electrons and two hydrogen ions from the electron transport chain and is reduced to water (Figure 6.18). If no oxygen was present in the mitochondrion, the electrons could not be removed from the system, and the entire electron transport chain would back up and stop. Without the electron transport chain, new ATP would not be synthesized during oxidative phosphorylation, and the cell would ultimately die from a lack of energy. This is the reason we must inhale oxygen.

CONCEPTS IN ACTION - Watch this video to learn about the electron transport chain.

Chemiosmosis

As electrons are passed through the electron transport chain, the energy released is used to establish a hydrogen ion concentration gradient. Because of their charge, hydrogen ions can only diffuse across the inner membrane of the mitochondria through integral transport proteins. **ATP synthase**, an integral protein and an enzyme, acts as a tiny generator which allows hydrogen ions to easily diffuse across the inner membrane (Figure 6.20). The movement of hydrogen ions through ATP synthase regenerates ATP from ADP plus inorganic phosphate. The flow of hydrogen ions across the membrane through ATP synthase is called **chemiosmosis**.

Figure 6.20 ATP synthase is a complex, molecular machine that uses a proton (H_+) gradient to form ATP from ADP and inorganic phosphate (P_i). (Credit: modification of work by Klaus Hoffmeier / Biology 2E OpenStax)
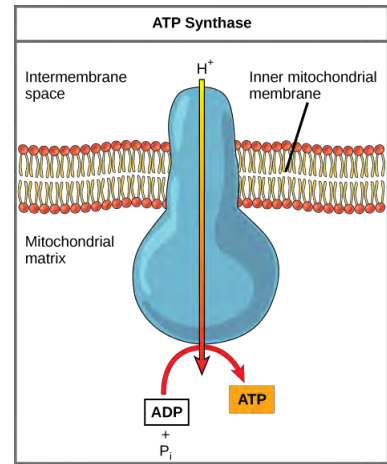
The energy generated from the electron transport chain and chemiosmosis (Figure 6.21) generates 90 percent of the ATP made during aerobic glucose catabolism. Chemiosmosis and the electron transport chain are also used during the light reactions of photosynthesis. Both these processes will be discussed again when we get to chapter 7.
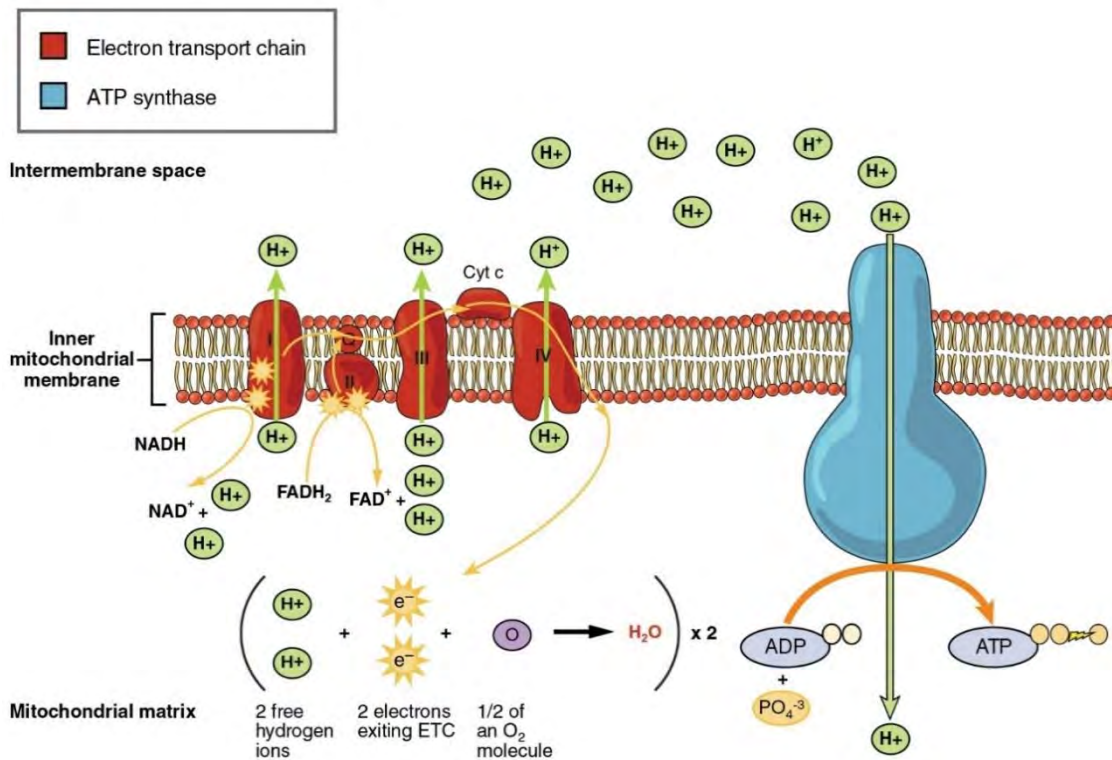
Figure 6.21 Shows the electron transport chain and chemiosmosis (credit: Betts et al. / Anatomy and Physiology OpenStax)

ATP Yield

The number of ATP molecules generated from glucose catabolism varies. For example, different species vary in the number of hydrogen ions that the electron transport chain can pump through the membrane. This variation impacts the hydrogen ion concentration gradient and, therefore, the rate of ATP synthesis. Another difference stems from the electron carriers' ability to cross the mitochondrial membrane. The NADH generated from glycolysis cannot easily enter the mitochondria. As a result, electrons from NADH produced during glycolysis 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. It is estimated that for every NADH molecule that arrives at the electron transport chain, approximately two to three molecules of ATP can be synthesized. For everyone molecule of $FADH_2$ oxidized at the electron transport chain, the cell can synthesize one to two molecules of ATP. NADH results in more ATP because it delivers its electrons to protein complex I and they travel through the entire electron transport chain. $FADH_2$, in contrast, delivers its electrons to protein complex II and they only travel through part of the transport chain.

When accounting for the total number of ATP produced per glucose molecule, it is important to remember the following points:

- A net of two ATP is produced through glycolysis (four produced, but two are consumed during the energy-consuming stage).
- A net of two ATP is produced through the citric acid cycle.
- A net of 28 molecules of ATP is produced during oxidative phosphorylation. Approximately 25 ATP molecules from the oxidation of NADH and three molecules of ATP from the oxidation of $FADH_2$ (see Figure 6.22).

Check your knowledge

Are the following options active or passive transport?
- Chemiosmosis
- Proteins moving H+ into the intermembrane space (outer matrix)
- Sodium/Potassium pump
- Sugar dissolving in a glass of water.

Answers: passive, active, active, passive

Glycolysis

4 ATP
− 2 ATP used
2 ATP

Glucose

C_6

2 NADH

C_3 — Pyruvate molecules — C_3

Transformation of pyruvate to acetyl CoA

Pyruvate C_3

1 NADH
x 2 pyruvates
2 NADH

CO_2

Acetyl CoA — CoA

Krebs cycle / Citric acid cycle

CO_2

3 NADH
x 2 pyruvates
6 NADH

1 ATP
x 2 pyruvates
2 ATP

1 $FADH_2$
x 2 pyruvates
2 $FADH_2$

Electron transport chain

e^-

Electron carrier total per glucose:
• 10 NADH
• 2 $FADH_2$

2.5 ATP x 10 NADH = 25 ATP
+1.5 ATP x 2 $FADH_2$ = 3 ATP
28 ATP

Redox reactions

$H_2O \leftarrow 2H^+ + O_2 + e^-$

Total ATP produced:
Glycolysis = 2 ATP
Pyruvate into acetyl CoA = 0 ATP
Krebs cycle = 2 ATP
+ ETC = 28 ATP
Approximately 32 ATP per glucose

Figure 6.22 Shows the ATP yield for one molecule, one glucose catabolism. (credit: Modified by Elizabeth O'Grady original work of Betts et al. / Anatomy and Physiology OpenStax)

Mitochondrial Disease

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 people affected by these types of diseases 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 four-year college education degree, 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 diseases.

Section Summary

Oxidative phosphorylation begins with the electron transport chain, where electrons are passed through a series of redox reactions to a final electron acceptor, oxygen. Oxygen accepts two electrons and two hydrogen ions, forming water. The energy released as the electrons are passed through the electron transport chain is used to generate a hydrogen ion gradient across the inner mitochondrial membrane. The potential energy of the gradient is used to generate ATP with the help of the enzyme ATP synthase through the process of chemiosmosis.

Exercises

1. Name the enzyme involved in chemiosmosis that helps the cell make ATP.
2. What happens to NADH when it arrives at the electron transport chain?
    a. It is reduced to NAD^+
    b. It is oxidized to NAD^+
    c. It is reduced to FAD
    d. It is oxidized to FAD
3. Chemiosmosis in eukaryotic cells involves:
    a. the movement of electrons across the cell membrane
    b. the movement of hydrogen atoms across the outer cell membrane
    c. the movement of hydrogen ions across the mitochondrial membrane
    d. the movement of glucose through the cell membrane
4. We inhale oxygen and exhale carbon dioxide. What is the oxygen used for, and where does the carbon dioxide come from?

Answers

1. ATP synthase
2. (b)
3. (c)
4. The oxygen we inhale is the final electron acceptor in the electron transport chain and allows aerobic respiration to proceed. The carbon dioxide we breathe out is formed during pyruvate oxidation and the citric acid cycle when the bonds in carbon compounds are broken.

Glossary

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

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

6.5 Fermentation

For aerobic cellular respiration to occur, oxygen must be present to accept electrons from NADH and $FADH_2$ produced during glycolysis, pyruvate oxidation, and citric acid cycle. What happens when oxygen levels are low or absent? Can cells still produce ATP?

Remember that glycolysis is an anaerobic pathway that allows cells to generate small amounts of ATP through substrate-level phosphorylation in the absence of oxygen. Glycolysis is a type of anerobic cellular respiration. **Anaerobic cellular respiration** enables organisms to generate ATP in the absence of oxygen. However, cells still need a way to oxidize the NADH produced during this pathway. Some living organisms are able to use an organic molecule as the final electron acceptor in times when oxygen levels are low or absent. Processes that use an organic molecule to regenerate NAD^+ from NADH are collectively referred to as **fermentation**. In contrast, some living systems use an inorganic molecule as a final electron acceptor.

Lactic Acid Fermentation

Lactic acid fermentation is a method of fermentation used by animals and some bacteria like those in yogurt (Figure 6.23). This occurs routinely in mammalian red blood cells and in skeletal muscle that has insufficient oxygen supply. When oxygen is in low supply, cells can continue to carry out glycolysis to produce small quantities of ATP. However, because oxygen cannot be used to accept electrons from NADH, an organic molecule must be used in its place. In **lactic acid fermentation**, electrons from NADH are transferred to pyruvate, forming lactic acid (also called lactate). When NADH is oxidized NAD^+ is regenerated, and glycolysis can continue.

In mammals, lactic acid fermentation allows muscle cells to generate small amounts of ATP for short periods of time. Lactic acid build-up causes muscle stiffness and fatigue. Once the lactic acid has been removed from the muscle it is circulated to the liver, where it can be converted back to pyruvate and further catabolized for energy.

Figure 6.23 Lactic acid fermentation is common in muscles that have become exhausted by use. (credit: Jason Cashmore)
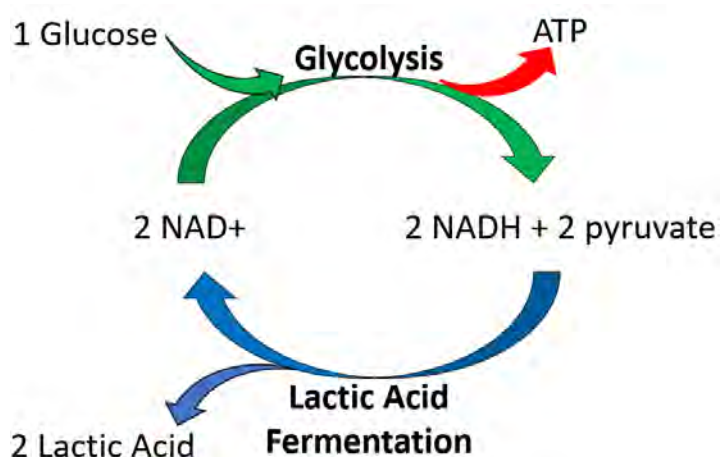
Alcohol Fermentation

Another familiar fermentation process is **alcohol fermentation**. During alcohol fermentation ethanol, a type of alcohol, is produced. In the first reaction, a carboxyl group is removed from pyruvate, releasing carbon dioxide as a gas (Figure 6.24).

Figure 6.24 shows alcohol fermentation (credit: Jason Cashmore)
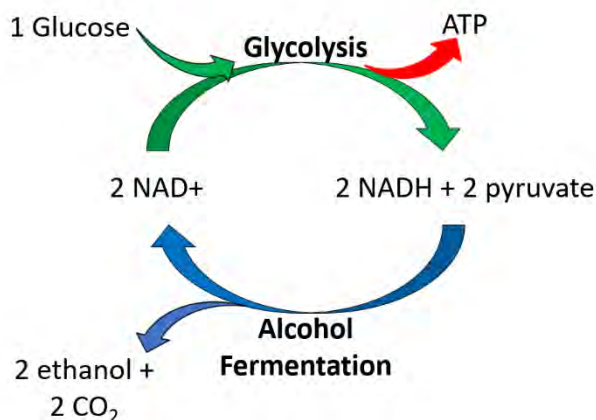
The loss of carbon dioxide reduces the molecule by one carbon atom, making acetaldehyde. The second reaction removes an electron from NADH, oxidizing it to NAD^+. When acetaldehyde is reduced, ethanol is formed (Figure 6.25).
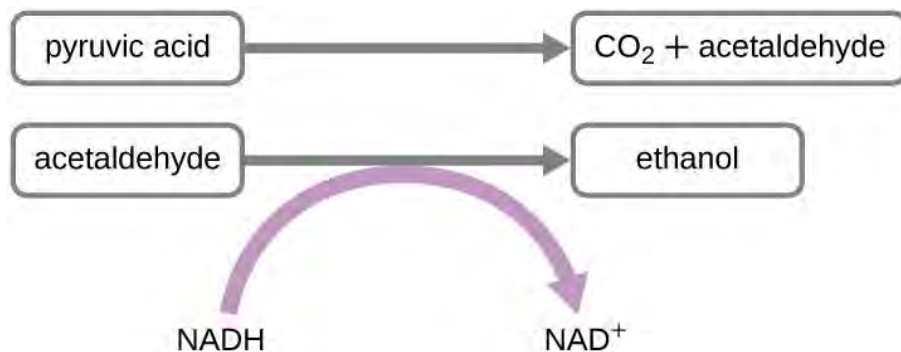
Figure 6.25 The chemical reactions of alcohol fermentation are shown here. (credit: Parker et al. / Microbiology OpenStax)

The fermentation of pyruvate by yeast produces the ethanol found in alcoholic beverages (Figure 6.26). 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 6.26 The fermentation of grape juice to make wine produces CO2 as a byproduct. Fermentation tanks have valves so that pressure inside the tanks can be released. (credit: Clark et al. / Biology 2E OpenStax)

Anaerobic Cellular Respiration

Certain prokaryotes, including some species of bacteria and Archaea, solely use anaerobic respiration. To oxidize its NADH, a group of Archaea called methanogens reduces carbon dioxide to methane. These microorganisms are found in soil and in the digestive tracts of animals, such as cows and sheep. Similarly, sulfate-reducing bacteria and Archaea, most of which are anaerobic (Figure 6.27), reduce sulfate to hydrogen sulfide to regenerate NAD^+ from NADH.
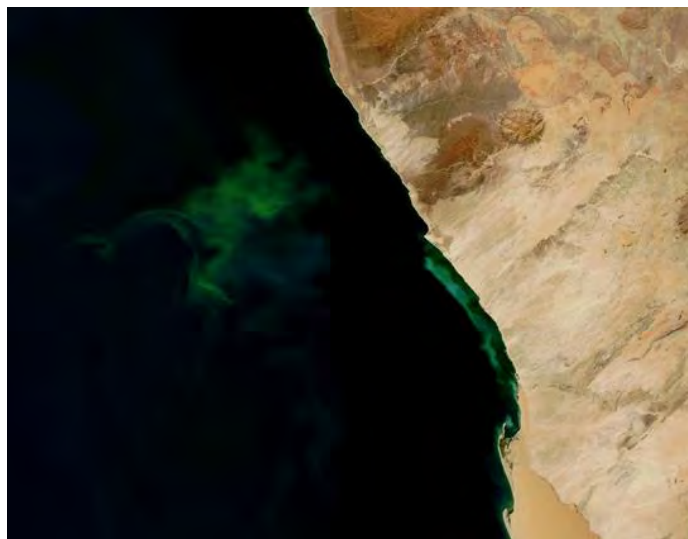
Figure 6.27 The green color seen in these coastal waters is from an eruption of hydrogen sulfide. Anaerobic, sulfate-reducing bacteria release hydrogen sulfide gas as they decompose algae in the water. (credit: NASA image courtesy Jeff Schmaltz, MODIS Land Rapid Response Team at NASA GSFC / Biology 2E OpenStax)

CONCEPTS IN ACTION- Visit this site to see anaerobic cellular respiration in action.

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 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. In a laboratory, some bacteria can be identified based on their gas production.

Section Summary

If NADH cannot be oxidized through aerobic cellular respiration, another electron acceptor must be used. Most organisms will use some form of fermentation to accomplish the regeneration of NAD^+, ensuring that glycolysis continues. The regeneration of NAD^+ in fermentation does not directly generate ATP. However, once NAD^+ is regenerated, it can again be used in glycolysis where small amounts of ATP can be made through substrate-level phosphorylation.

Exercises

1. True or False: Lactic acid can be converted back to pyruvate.
2. 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
3. When muscle cells run out of oxygen, what happens to the potential for energy extraction from sugars, and what pathways do the cell use?

Answers

1. True
2. (a)
3. 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.

Glossary

alcohol fermentation: the steps that follow the partial oxidation of glucose via glycolysis to regenerate NAD^+ and produces the products ethanol and carbon dioxide

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

lactic acid fermentation: the steps that follow the partial oxidation of glucose via glycolysis to regenerate NAD^+ and produces the products lactic acid

6.6 Connections to Other Metabolic Pathways

You have learned about the catabolism of glucose, which provides energy to living cells. However, 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 the catabolic pathways for carbohydrates, proteins, and lipids eventually feed into glycolysis, pyruvate oxidation, and the citric acid cycle pathways (Figure 6.28).
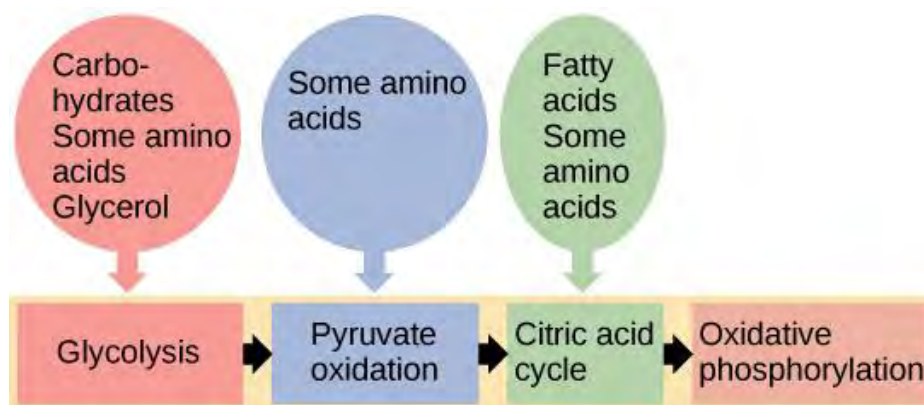
Figure 6.28 Different organic food molecules can feed into the catabolic pathways for carbohydrates. (credit: Fowler et al. / Concepts of Biology OpenStax)

Connections of Other Sugars to Glucose Metabolism

Sucrose and lactose are both disaccharides that can be used during aerobic cellular respiration. Both sugars must be hydrolyzed before they can be utilized. Sucrose, commonly referred to as table sugar, is broken down into glucose and fructose with the help of the enzyme sucrase. Lactose, a sugar found in milk, is hydrolyzed into glucose and galactose with the help of the enzyme lactase. Both fructose and galactose can be used during glycolysis; however, they cannot begin the process as glucose does. Both sugars can enter glycolysis as intermediates and produce the same amount of ATP molecules as glucose.

Connections of Proteins to Glucose Metabolism

In cells, proteins are broken down by a variety of enzymes called proteases. Most of the time, amino acids are recycled into new proteins. If there are excess amino acids or if the body is in a state of starvation, some amino acids will be shunted into the citric acid cycle to generate ATP. Other amino acids are used to create intermediates of glycolysis or generate acetyl CoA (Figure 6.29). Each amino acid must have its amino group removed before entering into these metabolic pathways. The amino group is converted into ammonia and along with carbon dioxide forms urea, the main waste product found in mammalian urine.
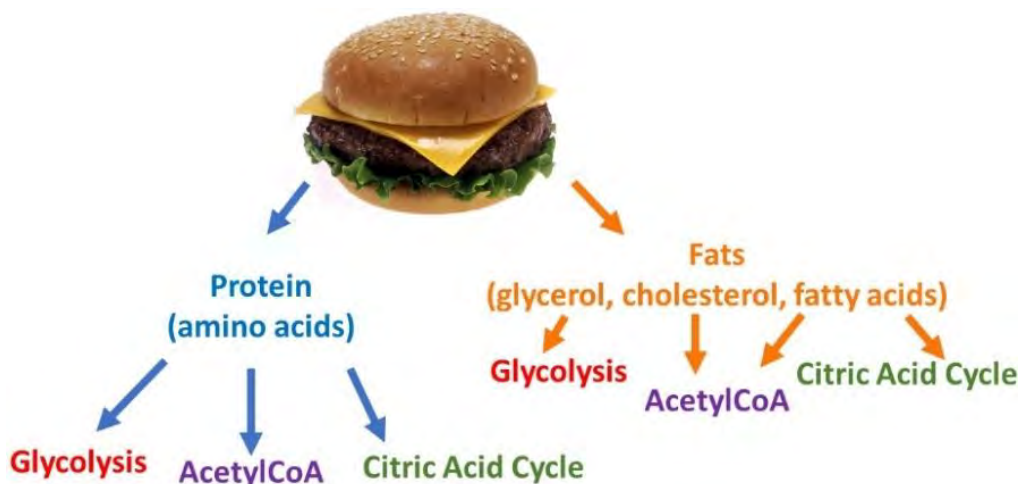
Figure 6.29 shows a cheeseburger that contains carbohydrates, lipids, and protein. (credit: Elizabeth O'Grady / cheeseburger image original work by National Cancer Institute [Wikimedia commons](#))

Connections of Lipids to Glucose Metabolism

Cholesterol and triglycerides are the most common lipids used to generate ATP. Cholesterol is a lipid that contributes to the flexibility of the cell membrane and is a precursor of steroid hormones. The synthesis of cholesterol starts with acetyl CoA (Figure 6.28). Remember that acetyl CoA is a necessary reactant in the citric acid cycle. The citric acid cycle can be used to generate ATP, NADH, and $FADH_2$.

Triglycerides are used long-term to store energy in animals. Triglycerides store about twice as much energy as carbohydrates and are made of glycerol and three fatty acids. Glycerol can be phosphorylated and enter as an intermediate of glycolysis. Fatty acids are broken into two-carbon units that enter the citric acid cycle as acetyl CoA.

Section Summary

The breakdown and synthesis of carbohydrates, proteins, and lipids can be used to generate ATP. Galactose and fructose are additional carbohydrates that can feed into glycolysis. The amino acids from proteins can be used to generate pyruvate, acetyl CoA, and components of the citric acid cycle. Cholesterol, glycerol, and fatty acids can be used in the citric acid cycle.

Exercises

1. Which of the following is generated during cholesterol synthesis?
    a. glucose
    b. acetyl CoA
    c. pyruvate
    d. carbon dioxide
2. Which of the following cannot be used to generate ATP in eukaryotic animal cells?
    a. lipids
    b. carbohydrates
    c. proteins
    d. water
    e. all of the above are used in the catabolism of energy
3. True or False Galactose can start the process of glycolysis

Answers

1. (b)
2. (d)
3. False

Chapter 7: Photosynthesis
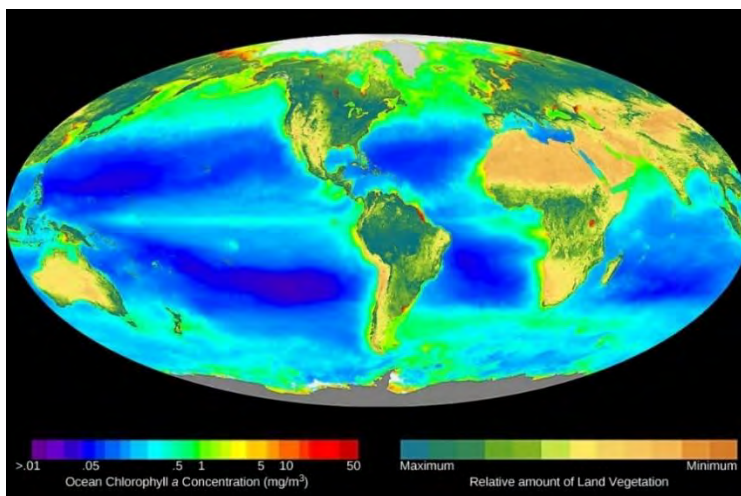
Figure 7.1 This world map shows Earth's distribution of photosynthetic activity determined by chlorophyll a concentration. On land, chlorophyll is evident from terrestrial plants, and within oceanic zones, from chlorophyll of phytoplankton. (credit: modification of work by SeaWiFS Project, NASA/Goddard Space Flight Center and ORBIMAGE / Biology 2E OpenStax)

All organisms from bacteria to humans require energy to carry out their metabolic processes. Many organisms obtain energy by eating; that is, by ingesting other organisms. But where does the stored energy in food come from? The vast majority of this energy can be traced back to photosynthesis. In this chapter, students will learn how the process of photosynthesis works.

7.1: Overview of Photosynthesis

Learning objectives

By the end of this section, you will be able to:

- *Summarize the process of photosynthesis*
- *Explain the relevance of photosynthesis to other living things*
- *Identify the reactants and products of photosynthesis*
- *Describe the main structures involved in photosynthesis*
- *Be able to define and explain all bolded terms*

Photosynthesis is essential to all life on earth. It is the only biological process that can capture light energy from the sun and convert it into chemical energy found in the covalent bonds of sugar. Plants, algae, and a group of bacteria called cyanobacteria are the only organisms capable of performing photosynthesis (Figure 7.2). These organisms are called **photoautotrophs,** literally "self-feeders using light," because they use light to generate their own food. Other organisms, such as animals, fungi, and most other bacteria, are called **heterotrophs** because they must rely on photosynthetic organisms for their energy needs. A third group of bacteria synthesizes sugars, but not by using light energy. These organisms extract energy from inorganic chemical compounds and are referred to as **chemoautotrophs**.
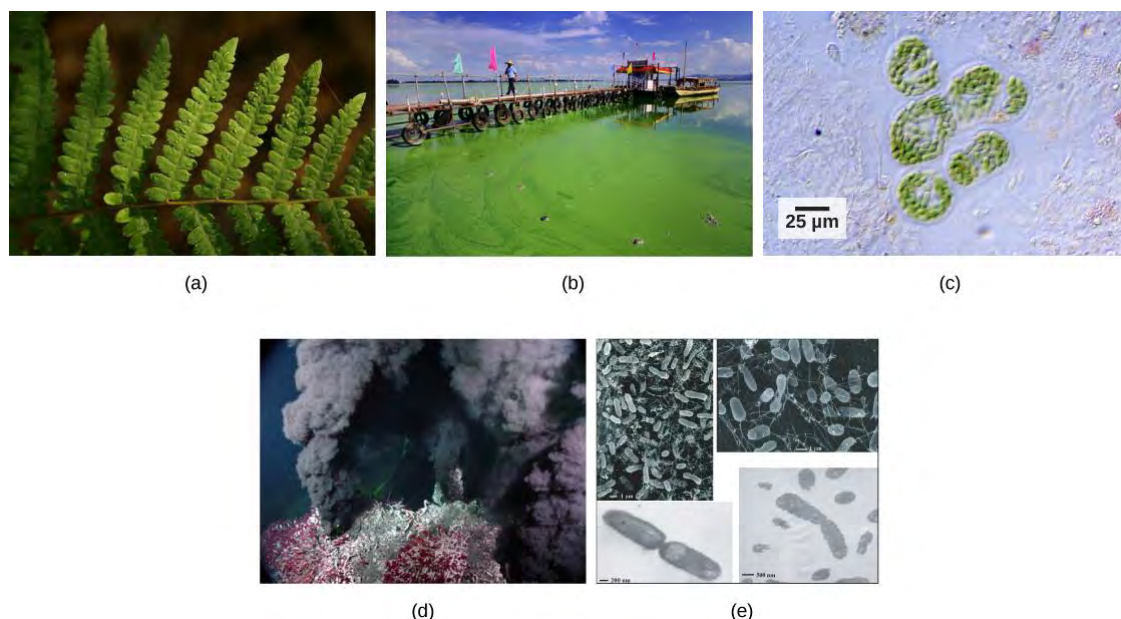
Figure 7.2 Photoautotrophs including (a) plants, (b) algae, and (c) cyanobacteria synthesize their organic compounds via photosynthesis. In a (d) deep-sea vent, chemoautotrophs, such as these (e) thermophilic bacteria, capture energy from inorganic compounds to produce organic compounds. (credit a: modification of work by Steve Hillebrand, U.S. Fish and Wildlife Service; credit b: modification of work by "eutrophication&hypoxia"/Flickr; credit c: modification of work by NASA; credit d: University of Washington, NOAA; credit e: modification of work by Mark Amend, West Coast and Polar Regions Undersea Research Center, UAF, NOAA / Biology 2E OpenStax)

Solar Dependence and Food Production

Photosynthesis is a chemical process by which certain cells convert kinetic light energy to potential chemical energy stored in carbohydrates made from carbon dioxide and water. Autotrophs use these carbohydrates to generate ATP through cellular respiration. Excess carbohydrates are stored in their tissues, and certain heterotrophs consume them to generate their own ATP through cellular respiration. The waste products of aerobic cellular respiration, carbon dioxide and water, can then be used as the starting reactants for photosynthesis. In this way, photosynthesis and aerobic cellular respiration are interrelated metabolic pathways (Figure 7.3).
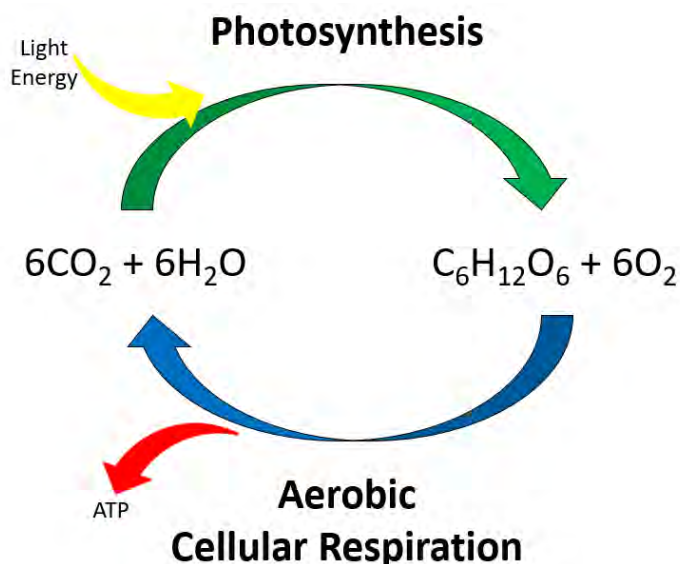
Figure 7.3 Photosynthesis and aerobic cellular respiration are interrelated metabolic pathways. (credit: Jason Cashmore)

Photosynthesis powers 99 percent of Earth's ecosystems. When a top predator, such as a wolf preys on a deer (Figure 7.4), the wolf is at the end of an energy pathway. The pathway begins with light energy from the sun. Light energy is captured by photoautotrophs that carry out photosynthesis to produce carbohydrates. Heterotrophs such as the deer consume the carbohydrates in the vegetation. When a wolf eats a deer, it obtains energy that was initially produced by plants.
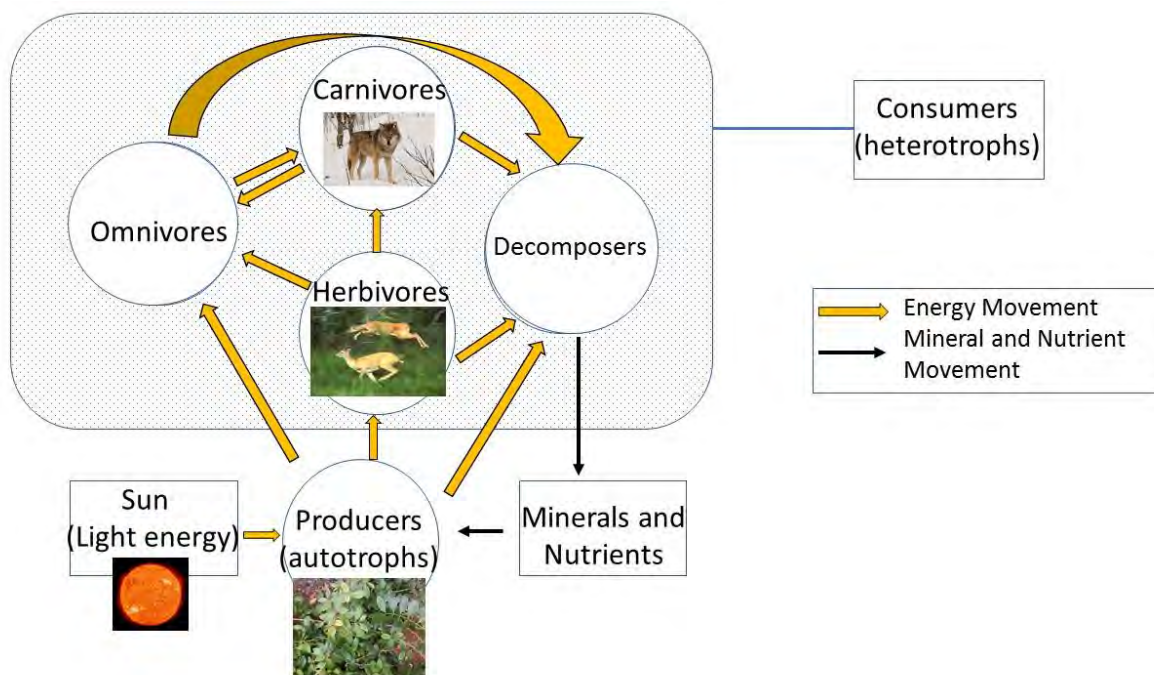
Figure 7.4 The predator that eats these deer receives a portion of the energy that originated in the photosynthetic vegetation. (credit: Elizabeth O'Grady original pictures by: wolf - Mas3cf / deer - modification of work by Steve VanRiper / plant - Katpatuka /sun - NASA/SDO)

CONCEPTS IN ACTION- Click the following link to learn more about photosynthesis.

Main Structures and Summary of Photosynthesis

Photosynthesis is a multi-step process that requires specific wavelengths of visible sunlight, carbon dioxide, and water (Figure 7.5). After the process is complete, producers release oxygen and produce glyceraldehyde-3-phosphate (G3P). G3P is a simple carbohydrate molecule that can be converted into glucose, sucrose, or dozens of other sugar molecules.
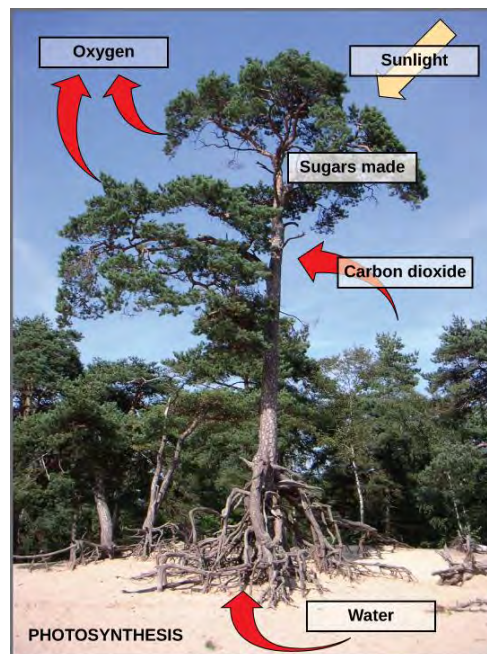
Figure 7.5 Photosynthesis uses solar energy, carbon dioxide, and water to release oxygen to produce energy-storing sugar molecules. (credit: Fowler et al. Concepts of Biology / OpenStax)

The complex reactions of photosynthesis can be summarized by the chemical equation shown in Figure 7.6. Although the equation looks simple, many steps must take place, and photosynthesis is quite complex. To better understand photosynthesis, students will first become familiar with leaf anatomy.

Light energy

$$6CO_2 + 6H_2O \rightarrow \rightarrow \rightarrow C_6H_{12}O_6 + 6O_2$$
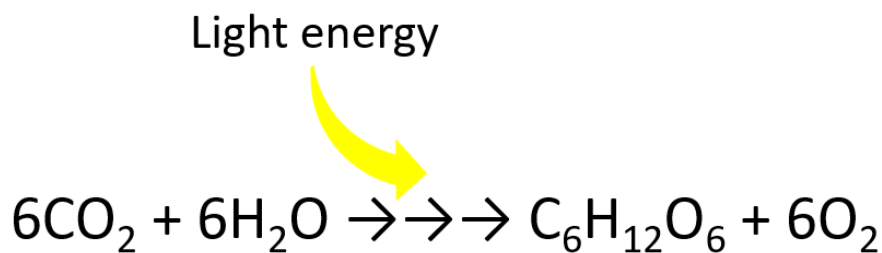
Figure 7.6 The process of photosynthesis can be represented by an equation. Inorganic carbon dioxide and water are combined with light energy to form glucose and oxygen. As with cellular respiration in chapter 6, the multiple arrows in this equation indicates that multiple chemical reactions are involved. (credit: Jason Cashmore).

Basic Photosynthetic Structures

In plants photosynthesis generally takes place in the leaves, which consist of several layers of cells. The process of photosynthesis occurs in a middle layer called the **mesophyll** (Figure 7.7). There are two layers that make up the mesophyll, the palisade mesophyll and the spongy mesophyll. The palisade mesophyll is made up of elongated cells that contain a large quantity of chloroplasts. The palisade mesophyll is the major site of photosynthesis. Spongy mesophyll cells also contain chloroplasts, but fewer than the palisade mesophyll. These cells are irregularly shaped with spaces between them. The spaces allow gases such as oxygen and carbon dioxide to pass through to and from the palisade mesophyll.
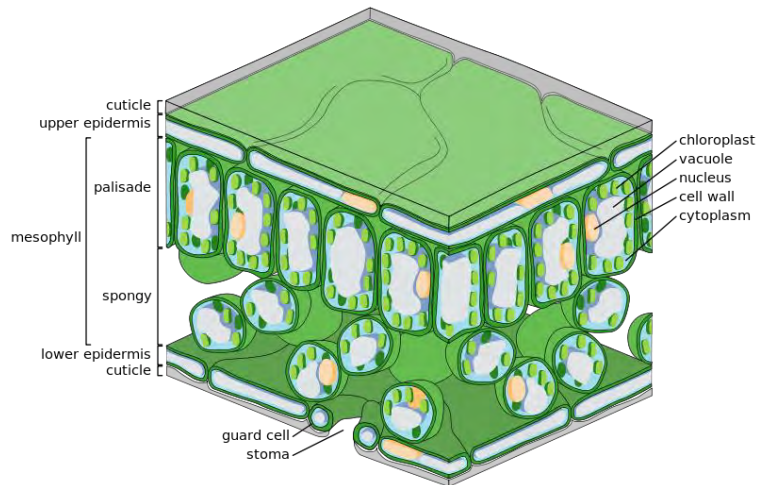
Figure 7.7 Cross section of a plant leaf. (credit: Zephris / Wikimedia commons)

During photosynthesis, plants take in carbon dioxide and release oxygen. Gas exchange into and out of the leaf occurs through small openings called **stomata** (singular: stoma). Stomata play roles in both the regulation of gas exchange and water balance. The stomata are typically located on the underside of the leaf, which helps to minimize water loss due to higher temperatures on the upper surface of the leaf. Each stoma is flanked by **guard cells** that regulate and control the opening and closing of the stomata. Guard cells close the stomata when too much water is evaporating from the leaf. In many plants the stomata are located in the **epidermis**, a protective outer cell layer covering leaves, stems, and roots. The epidermis can be found on both the upper and lower surfaces of leaves and secretes a waxy substance called the cuticle. The **cuticle** is an important adaptation that helps plants conserve water and acts as a protective barrier limiting water intake.

In all autotrophic eukaryotes, photosynthesis takes place inside an organelle called a **chloroplast**. Chloroplasts have a double membrane envelope composed of an outer and an inner plasma membrane. The inner membrane is ancestrally derived from ancient free-living cyanobacteria. **Thylakoids** are stacked, disc-shaped structures found within the chloroplasts. Thylakoids are made up of membranes embedded with proteins and chlorophyll. **Chlorophyll** is a pigment molecule necessary to absorb light. The thylakoid membrane encloses an internal space called the thylakoid lumen. As shown in Figure 7.8, a stack of thylakoids is called a **granum**, and the liquid-filled space surrounding the granum is called **stroma.** Do not confuse the stroma with the stoma, an opening on the leaf epidermis used for gas exchange.
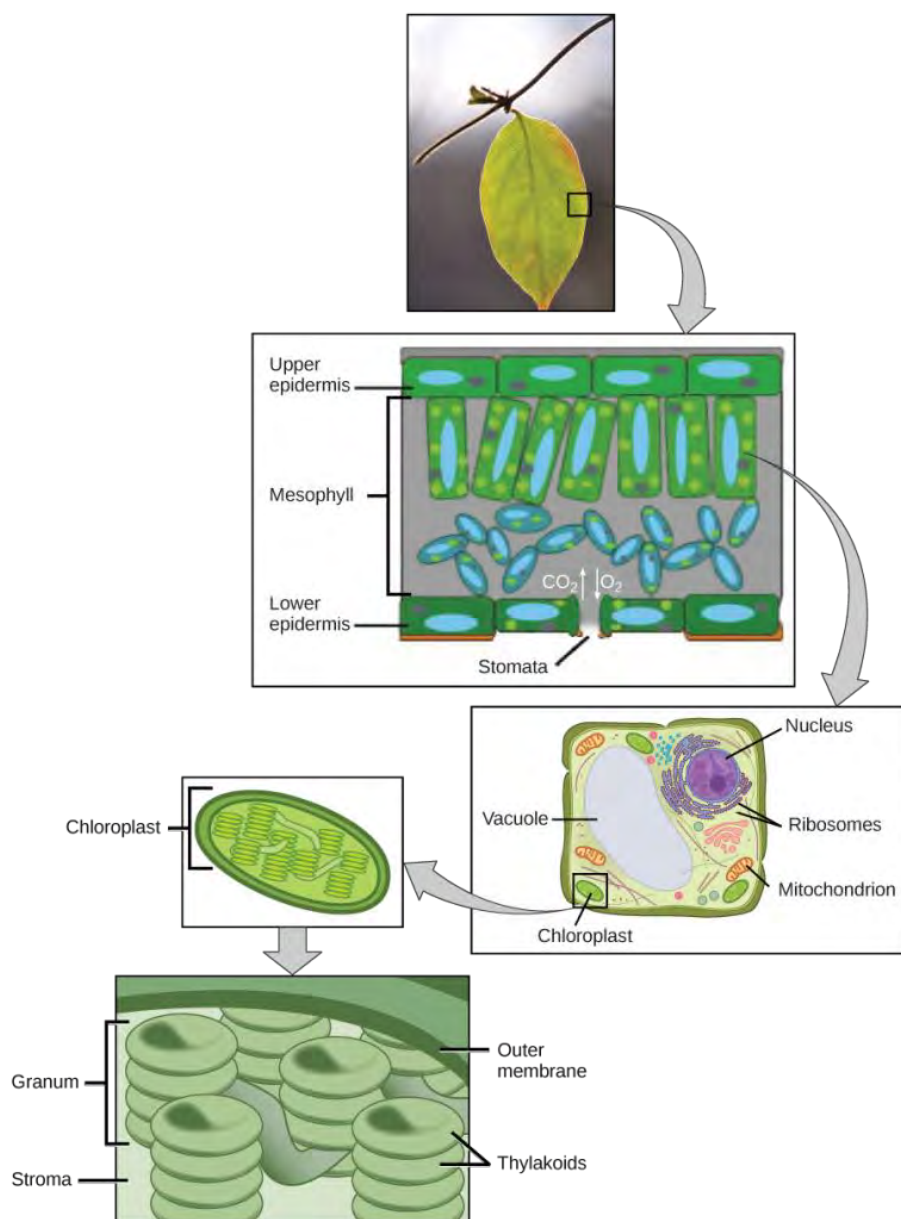
Figure 7.8 Cells within the middle layer of a leaf have chloroplasts, which contain the photosynthetic apparatus. (credit: modification of work by Cory Zanker / Concepts of Biology OpenStax)

Check your knowledge

On hot, dry days, plants close their stomata to conserve water. What impact will this have on photosynthesis?

Answer: With the stomata closed, plants cannot exchange gases. If plants cannot take in carbon dioxide, they cannot carry out the process of photosynthesis.

A Summary of the Two Parts of Photosynthesis

Photosynthesis takes place in two stages: the light-dependent reactions and the Calvin cycle (Figure 7.9). The **light-dependent reactions** take place in the thylakoid membrane, where chlorophyll absorbs light energy and then converts it into chemical energy with the help of water. In the light-dependent reactions water is broken down, and oxygen is released as a byproduct. The Calvin cycle takes place in the stroma. During the **Calvin cycle**, the chemical energy produced in the light-dependent reactions drives the synthesis of sugar molecules from carbon dioxide. The two reactions use carrier molecules to transport the energy from one stage to another. The carriers, NADPH and ATP, move energy from the light-dependent reactions to the Calvin cycle. $NADP^+$ is an electron carrier similar to $NAD^{+,}$ which is used in aerobic cellular respiration.

NADPH and ATP can be thought of as being "full" because they bring energy produced in the light-dependent reactions to the Calvin cycle. After the energy is released, the "empty" energy carriers, $NADP^+$ and $ADP + P_i$, return to the light-dependent reactions to obtain more energy (Figure 7.9).
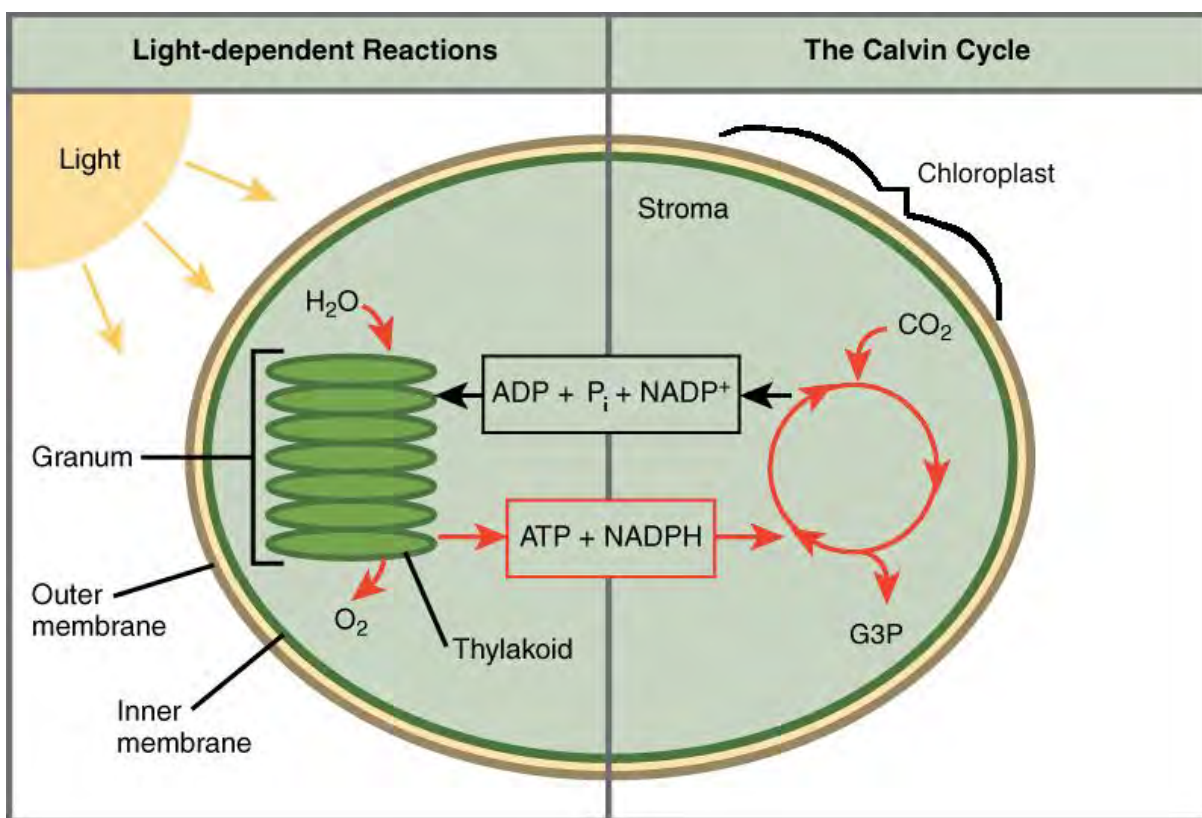
Figure 7.9 Photosynthesis takes place in two stages: light-dependent reactions and the Calvin cycle. (credit: Kahn Academy / original work by Clark et al. / Biology 2E OpenStax)

CONCEPTS IN ACTION - Click the link to learn more about photosynthesis.

Section Summary

The process of photosynthesis transformed life on earth. By harnessing energy from the sun, photosynthesis allows living things to access enormous amounts of energy. Only autotrophs can perform photosynthesis. These organisms require pigments, such as chlorophyll, to absorb light and convert it into chemical energy. Photosynthesis uses light energy, carbon dioxide, and water to synthesize carbohydrates, such as glucose, and releases oxygen. Eukaryotic autotrophs, such as plants and algae, have organelles called chloroplasts in which photosynthesis takes place.

Exercises

1. On a hot, dry day, plants close their stomata to conserve water. What impact will this have on photosynthesis?
2. What two products result from photosynthesis?
    a. water and carbon dioxide
    b. water and oxygen
    c. glucose and oxygen
    d. glucose and carbon dioxide
3. Which statement about thylakoids in eukaryotes is *not* correct?
    a. Thylakoids are assembled into stacks.
    b. Thylakoids lack membranes.
    c. The space surrounding thylakoids is called stroma.
    d. Thylakoids contain pigments such as chlorophyll.
4. Heterotrophs directly obtain their energy from:
    a. the sun
    b. the sun and eating other organisms
    c. eating other organisms
    d. consuming water
5. Why are carnivores, such as lions, dependent on photosynthesis to survive?
6. Label the following diagram.
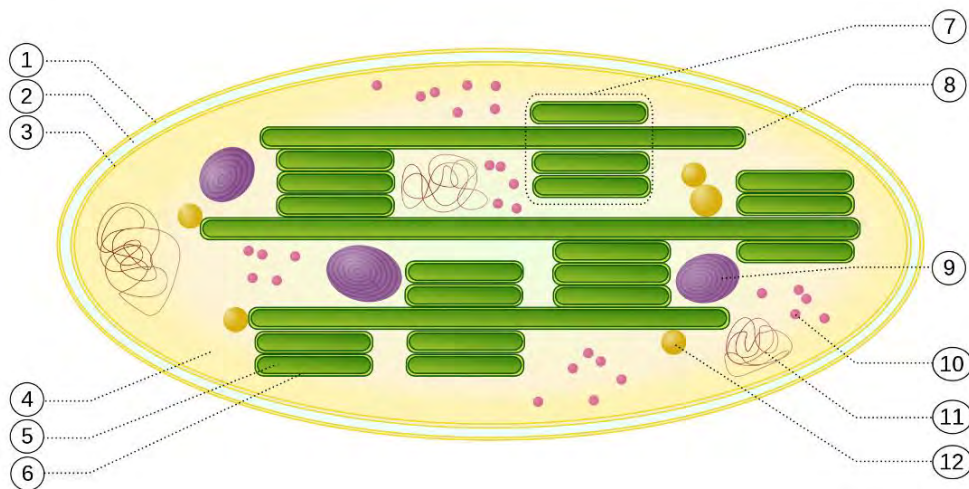
Credit: SuperManu / CC BY SA 3.0

Glossary

Calvin cycle: the second stage of photosynthesis where chemical energy produced in the light-dependent reactions drives the synthesis of sugar molecules

chemoautotrophs: an organism capable of producing its own food by extracting energy from inorganic chemical compounds

chlorophyll: the green pigment that captures the light energy that drives the reactions of photosynthesis

chloroplast: the organelle where photosynthesis takes place

granum: a stack of thylakoids located inside a chloroplast

guard cells: specialized plant cells that control the opening and closing of the stomata

heterotroph: an organism that consumes other organisms for food

light-dependent reaction: the first stage of photosynthesis where visible light is absorbed to form two energy-carrying molecules (ATP and NADPH)

mesophyll: the middle layer of cells in a leaf

photoautotroph: an organism capable of synthesizing its own food molecules (storing energy), using the energy of light

photosynthesis: a multi-step chemical reaction that requires light energy, carbon dioxide, and water and produces sugar and oxygen

pigment: a molecule that is capable of absorbing light energy

stoma: the opening that regulates gas exchange and water regulation between leaves and the environment; plural: stomata

stroma: the fluid-filled space surrounding the grana inside a chloroplast where the Calvin cycle reactions of photosynthesis take place

thylakoid: a disc-shaped membranous structure inside a chloroplast where the light-dependent reactions of photosynthesis take place using chlorophyll embedded in the membranes

7.2: The Light-Dependent Reactions of Photosynthesis

How can light be used to make food? It is easy to think of light as just something that allows living organisms to see, but light is a form of energy. Like all energy, light can travel, change forms, and be harnessed to do work. In the case of photosynthesis, some autotrophs can take light energy and transform it into chemical energy to build carbohydrates (Figure 7.10).
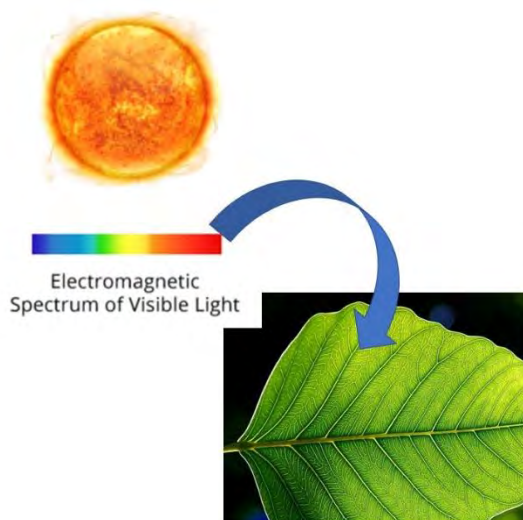
Figure 7.10 Plants can use light from the sun to photosynthesize. (credit: Elizabeth O'Grady original work of Geson Perry Wikimedia commons (sun and electromagnetic spectrum) /original work of Jon Sullivan Wikimedia commons (leaf))

What Is Light Energy?

The sun emits an enormous amount of electromagnetic radiation, more commonly referred to as solar or light energy. Light energy travels as waves. Scientists can determine the amount of energy a wave has by measuring its wavelength. **Wavelength** is the distance between two consecutive, similar points in a series of waves. For example, the wavelength can be measured by taking the distance from crest to crest or trough to trough in Figure 7.11.
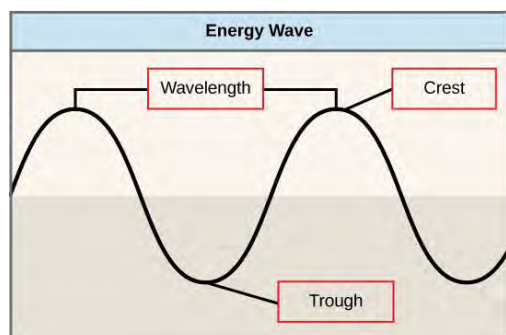
Figure 7.11 The wavelength of a single wave is the distance between two consecutive points along with the wave (credit: Clark et al. / Biology 2E OpenStax).

The sun emits a broad range of electromagnetic radiation (energy) including visible light, X-rays, and ultraviolet (UV) rays (Figure 7.12). The electromagnetic spectrum is the range of all possible wavelengths of energy.

Each wavelength corresponds to different amounts of energy. The longer the wavelength or the more stretched out it appears, the less energy it contains. Short, tight waves provide the most energy. For example, Figure 7.12 shows the wavelengths that correspond to the visible light spectrum. Visible light, which can be seen by humans and is used for photosynthesis, has wavelengths ranging from about 380 nanometers up to 750 nanometers. Note that Figure 7.12 shows that the red waves are considerably longer than the blue wavelengths and therefore have significantly less energy associated with them.

Keep in mind that living organisms cannot utilize all parts of the electromagnetic spectrum. For example, high-energy waves are dangerous to living organisms. Exposure to large quantities of X-rays and UV rays can be harmful to humans and have been identified as causes of cancer.
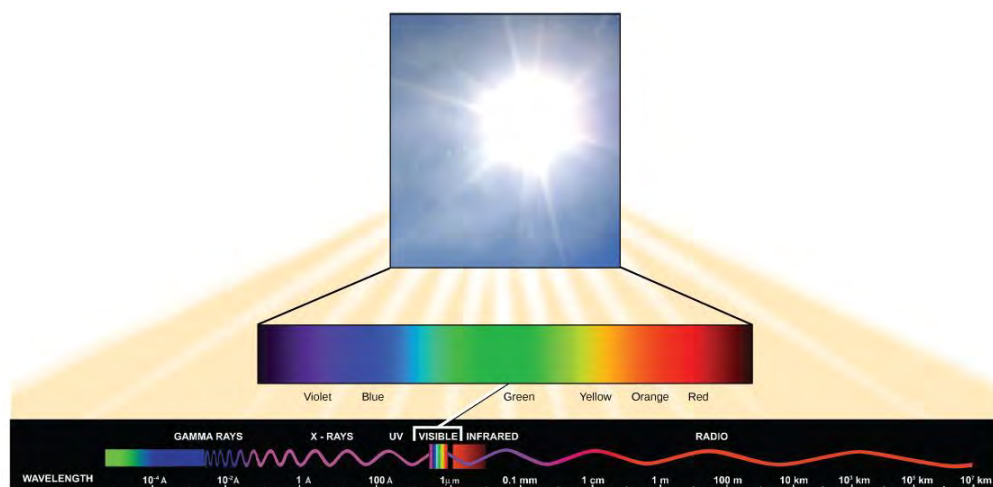
Figure 7.12 The sun emits energy in the form of electromagnetic radiation. (credit: Clark et al. / Biology 2E OpenStax)

Absorption of Light

During photosynthesis, plants use pigments to absorb parts of the visible light spectrum. The human eye perceives the visible light portion of the electromagnetic spectrum as a rainbow of colors (Figure 7.13). Certain objects, such as a prism or a drop of water, can disperse white light to reveal these colors.

Figure 7.13 The illustration shows the colors of visible light. In order of decreasing wavelength, these are red, orange, yellow, green, blue, indigo, and violet. (credit: modification of work by NASA / Biology 2E OpenStax)
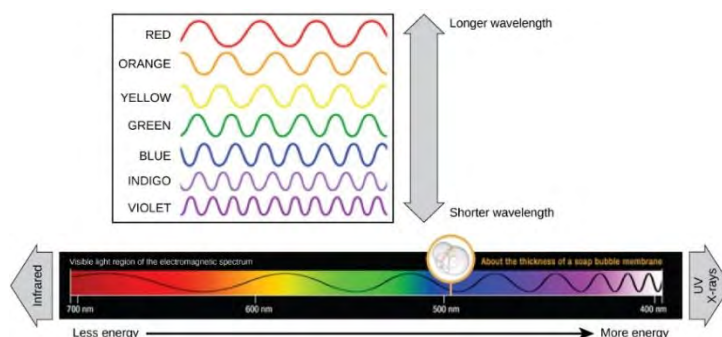
Understanding Pigments

Photosynthetic organisms use pigments to absorb light energy from the visible spectrum. **Pigments** are molecules which absorb certain wavelengths of light and reflect or transmit the other wavelengths. All photosynthetic organisms contain a pigment called **chlorophyll *a*.** Chlorophyll *a* absorbs wavelengths of light from either end of the visible spectrum: violet, indigo, blue, and red light. Chlorophyll *a* reflects the colors in the middle of the visible spectrum: green and yellow light. This explains why most plants appear to be green in color.

Plants use accessory pigments to absorb additional parts of the visible light spectrum. Other pigment types include chlorophyll *b,* xanthophyll, and beta-carotene. Chlorophyll *b* absorbs blue, red, and orange light whereas xanthophyll and beta-carotene absorb blue and violet light. The specific pattern of wavelengths can identify each type of pigment.

Not all photosynthetic organisms have full access to sunlight. Some organisms grow underwater, where the light intensity decreases with depth, and the water absorbs certain wavelengths. Other organisms grow in places where they must compete for light. For example, plants on the rainforest floor must be able to absorb any bit of light that comes through because taller trees block most of the sunlight (Figure 7.14). Keep in mind, if plants cannot absorb enough light to carry out photosynthesis, they will die.

Figure 7.14 Plants that commonly grow in the shade benefit from having a variety of light-absorbing pigments. (credit: Jason Hollinger / Concepts of Biology OpenStax)

How Light-Dependent Reactions Work

The overall purpose of the **light-dependent reactions** is to convert light energy into chemical energy in the form of ATP and NADPH. $NADP^+$ is an electron carrier, much like NAD^+ which is used during aerobic cellular respiration. When $NADP^+$ is reduced to NADPH, it shuttles high energy electrons from the light-dependent reactions to the Calvin cycle. Both ATP and NADPH will be used in the Calvin cycle to drive the synthesis of sugar molecules.

The light-dependent reactions begin in a complex called a **photosystem** (Figure 7.15). Photosystems are located in the thylakoid membrane and are made up of both pigments and proteins. Pigments in the photosystem absorb photons of light. A **photon** is a discrete quantity or "packet" of light energy.

Figure 7.15 shows a photosystem with chlorophyll molecules that absorb light energy. (credit: Fowler et al. / Concepts of Biology OpenStax)
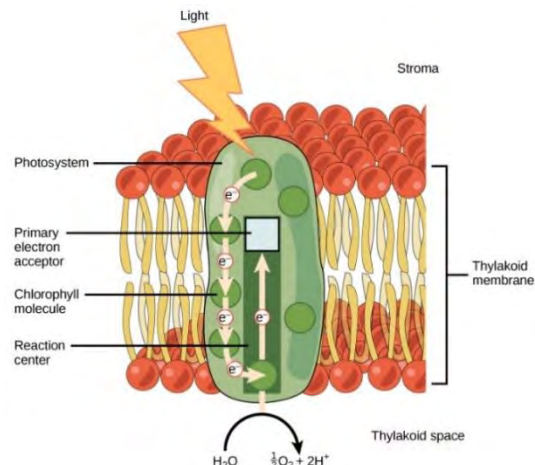
In eukaryotes and some prokaryotes, two photosystems exist. The first photosystem used in the light-dependent reactions is called photosystem II. Photosystem II was named for the order of its discovery rather than for the order in which it functions (Figure 7.16).
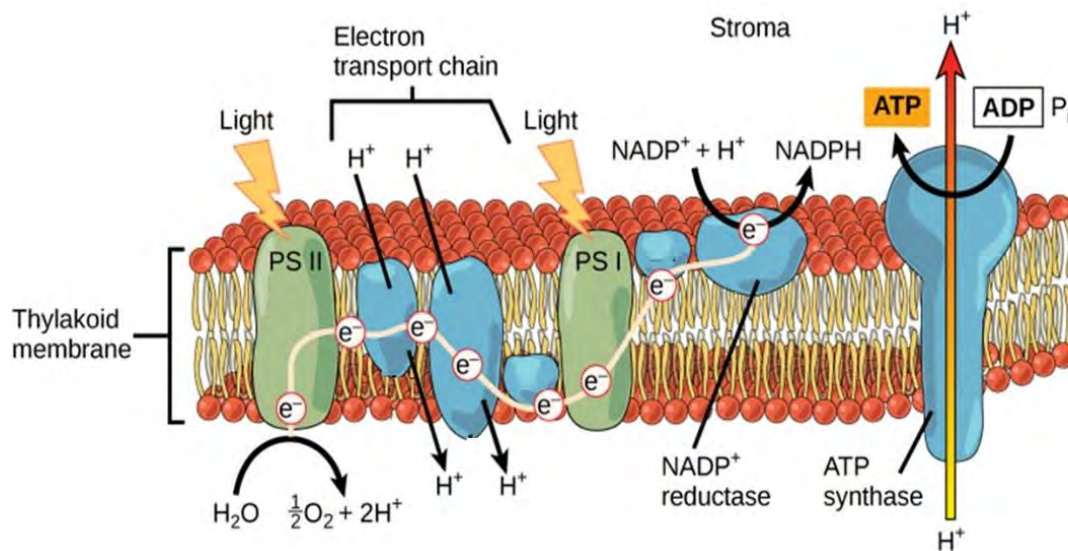
Figure 7.16 From photosystem II, the electron travels along the electron transport system, and energy from the electron is used to pump hydrogen ions into the interior of the thylakoid. (credit: Modified by Elizabeth O'Grady original work of Fowler et al. / Concepts of Biology OpenStax)

As pigments in photosystem II absorb light energy, it is passed to a special pair of chlorophyll *a* molecules located in the reaction center of the photosystem (Figure 7.17). The reaction center is located in the middle of the photosystem and contains both the special chlorophyll *a* molecules and a primary electron acceptor molecule.
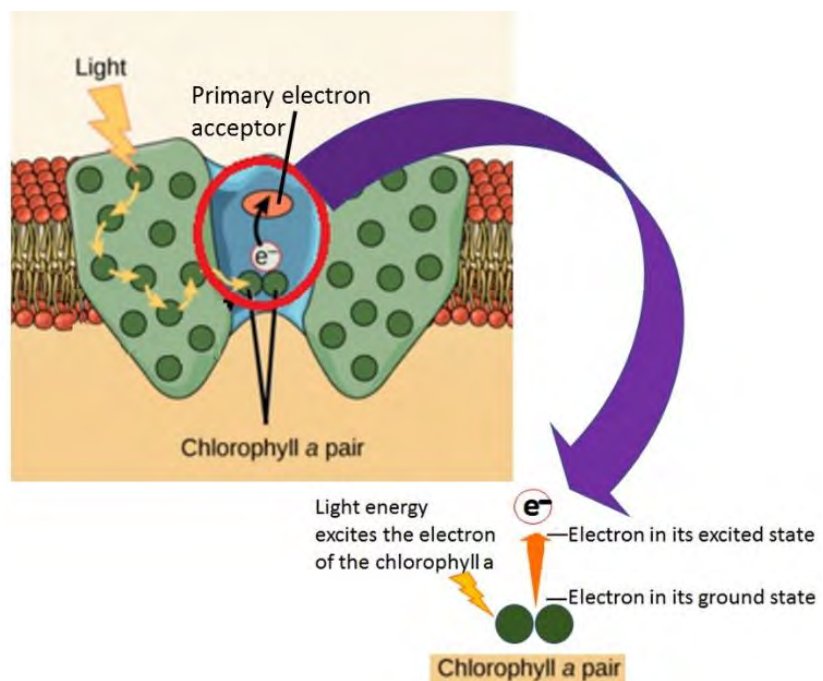
Figure 7.17 Light energy is absorbed by pigments and passed to the special pair of chlorophyll *a* molecules where the electron is excited from its ground state to its excited state. (credit: Modified by Elizabeth O'Grady original work of Clark et al. / Biology 2E OpenStax)

Light energy causes an electron in the reaction center chlorophyll *a* molecules to become "excited" (Figure 7.17). As the electron is excited, the energy associated with the electron increases. In the excited state, the electron is donated by the chlorophyll *a* molecules and passed to the primary electron acceptor, also located in the reaction center (Figure 7.17).

High-energy electrons in photosystem II are passed through a series of proteins in the thylakoid membrane called the electron transport chain (Figure 7.18). As the electrons are passed along, energy from the electrons is transferred to membrane proteins that function as pumps. Using active transport, protein pumps use the energy to move hydrogen ions against their concentration gradient from the stroma into the thylakoid space. Because of their charge, hydrogen ions can only diffuse across the thylakoid membrane through integral proteins. ATP synthase allows hydrogen ions to diffuse across the thylakoid membrane generating ATP.

The process of using light energy to synthesize ATP from ADP plus inorganic phosphate is called **photophosphorylation** (Figure 7.18). Using photophosphorylation, a plant cell must generate 18 ATP molecules to synthesize one molecule of glucose in the Calvin cycle.
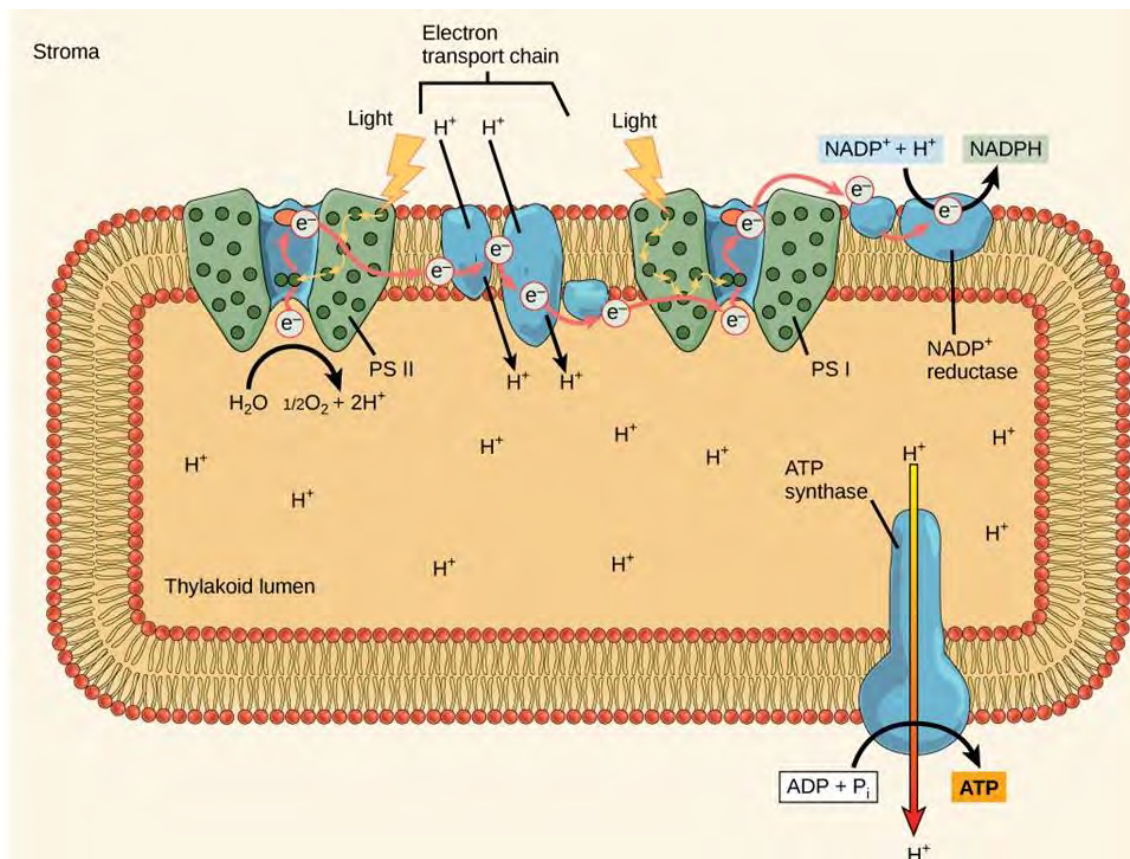
Figure 7.18 shows the light-dependent reactions in the thylakoid. (credit: Clark et al. / <u>Biology 2E OpenStax</u>)

Once the electron returns to its ground state, it is accepted by a pigment molecule in the reaction center of the next photosystem. This photosystem is called photosystem I (Figure 7.18). At photosystem I, the electron is re-energized with more light energy. The excited electron is oxidized from photosystem I and passed to $NADP^+$. When $NADP^+$ accepts two high energy electron and a hydrogen ion (H^+), it is reduced to NADPH. The NADPH will now carry the high energy electrons to the stroma where they will be used in the Calvin cycle.

To synthesize one molecule of glucose, the plant cell must generate 12 NADPH molecules in the light-dependent reactions. For this to be done, the electrons from the reaction center chlorophyll *a* molecules in photosystem II must be replaced. To replace the electrons, water is oxidized (Figure 7.17). When water is split, oxygen (O_2) and hydrogen ions (H^+) are formed and accumulate in the thylakoid space. The oxygen molecules are released to the surrounding environment, and the hydrogen ions become part of the hydrogen ion gradient, which is used to generate ATP.

The light-dependent reactions are necessary because they provide energy in the form of ATP and NADPH to generate sugar. ATP and NADPH carry energy from the thylakoid membrane to the stroma where the second stage of photosynthesis, the Calvin cycle, will now take place.

Check your knowledge

What part of the electromagnetic spectrum is used by plants?

You know plants need water. Now explain what they use water for?

Answers: Plants use the visible light spectrum. Violet, blue and a small bit of red are used most heavily. Plants use water as a source of electrons as part of the electron transport chain during the light-dependent reactions. Those electrons will be used to power carbon fixation in the Calvin cycle.

Section Summary

In the first part of photosynthesis, the light-dependent reaction, pigment molecules absorb energy from the sunlight. The most common and abundant pigment is chlorophyll *a*. Light energy strikes photosystem II to initiate photosynthesis. Energy travels through the electron transport chain, which pumps hydrogen ions into the thylakoid space. This forms a concentration gradient. The ions flow through ATP synthase from the thylakoid space into the stroma in a process called chemiosmosis to form molecules of ATP. ATP is used for the formation of sugar molecules in the second stage of photosynthesis, the Calvin cycle. Photosystem I absorbs a second photon, which results in the formation of an NADPH molecule. NADPH is an energy carrier that transports high energy electrons to the Calvin cycle. A total of 6 water molecules will be oxidized during the light dependent reactions, which releasees electrons to the photosystem, and 6 O_2 molecule as waste products. 12 NADPH and 18 ATP are generated during the light-dependent reactions and will then be used in the Calvin cycle.

Exercises

1. What is light energy used for in the light-dependent reactions?
   a. split a water molecule
   b. energize an electron
   c. produce proteins
   d. synthesize glucose
2. Which molecule absorbs light energy?
   a. ATP
   b. glucose
   c. chlorophyll
   d. water
3. Plants produce oxygen when they photosynthesize. Where does the oxygen come from?
   a. splitting water molecules
   b. ATP synthesis
   c. the electron transport chain
   d. chlorophyll
4. Which color(s) of light does chlorophyll *a* reflect?
   a. red and blue
   b. green
   c. red
   d. blue
5. Describe the pathway of energy in light-dependent reactions.

Glossary

chlorophyll *a*: the form of chlorophyll that absorbs violet-blue and red light

chlorophyll *b*: the form of chlorophyll that absorbs blue and red-orange light

light-dependent reactions: convert light energy into chemical energy in the form of ATP and NADPH

photon: a distinct quantity or "packet" of light energy

photosystem: a group of proteins, chlorophyll, and other pigments that are used in the light-dependent reactions of photosynthesis to absorb light energy and convert it into chemical energy

wavelength: the distance between consecutive points of a wave

7.3: The Calvin Cycle

Learning objectives

By the end of this section, you will be able to:

- *Describe the Calvin cycle*
- *Define carbon fixation*
- *Explain what photorespiration is*
- *Explain how photorespiration has led to the evolution of C4 and CAM plants*
- *Be able to define and explain all bolded terms*

After energy from the sun is converted and packaged into ATP and NADPH, the cell has the chemical energy needed to build carbohydrates. However, chemical energy alone is not enough; the cell also must have a carbon source. Where does the carbon come from? The carbon atoms used to build carbohydrates come from carbon dioxide. The **Calvin cycle** is a set of chemical reactions that uses the ATP and NADPH generated in the light-dependent reactions to form glucose and other carbohydrates (Figure 7.19).
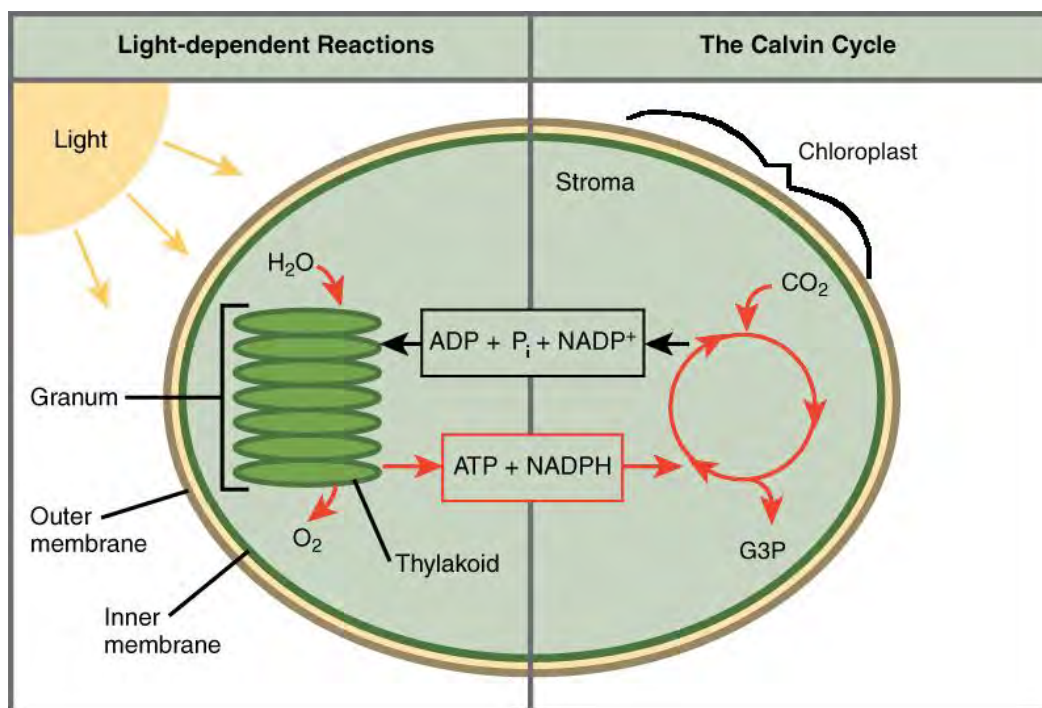
Figure 7.19 Photosynthesis takes place in two stages: light-dependent reactions and the Calvin cycle. (credit: Kahn Academy / original work by Clark et al. / Biology 2E OpenStax)

The Interworking's of the Calvin Cycle

In plants, carbon dioxide (CO_2) enters the plant through the stomata. The carbon dioxide then diffuses into the stroma of the chloroplast where the Calvin cycle reactions take place (Figure 7.20). The reactions are named after Nobel Prize-winning American scientist Melvin Calvin, who discovered them.

Figure 7.20 Light-dependent reactions harness energy from the sun to produce ATP and NADPH. These energy-carrying molecules travel into the stroma where the Calvin cycle reactions take place. (credit: Fowler et al. / Concepts of Biology OpenStax)
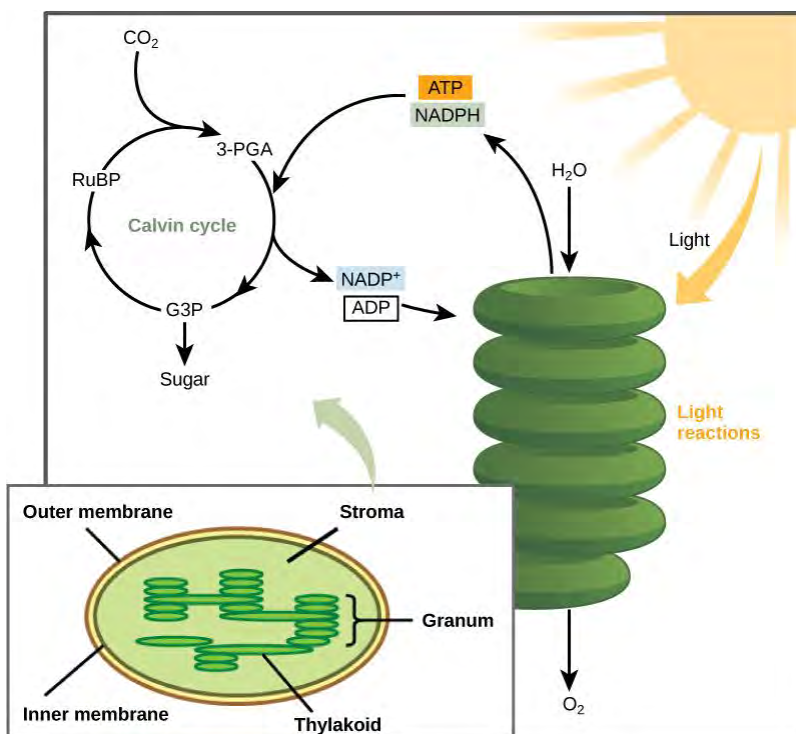
The Calvin cycle reactions (Figure 7.21) can be organized into three basic stages: carbon fixation, reduction, and regeneration. In addition to CO_2, two other molecules are needed to start the Calvin cycle: Rubisco (an enzyme), and the molecule ribulose bisphosphate (RuBP). RuBP is a five-carbon molecule with a phosphate group at the end of the molecule.
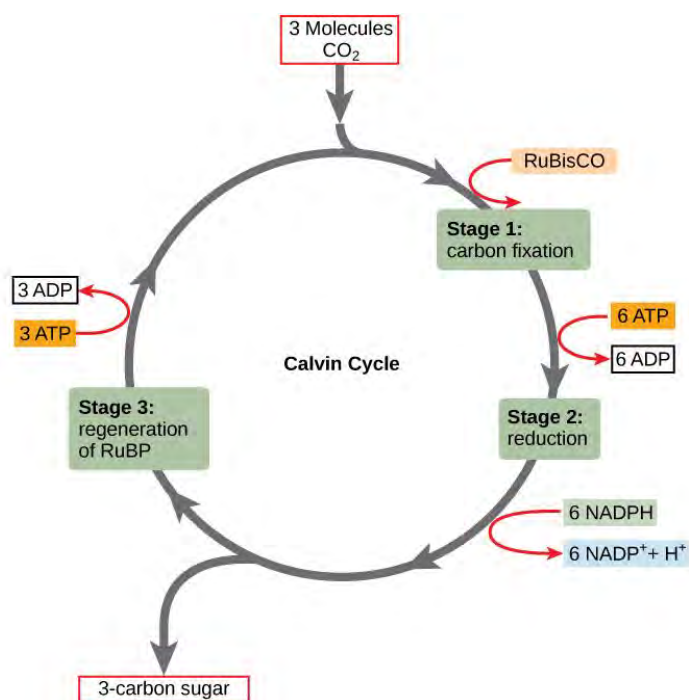
Figure 7.21 The Calvin cycle has three stages. (credit: Fowler et al. / Concepts of Biology OpenStax)

Rubisco catalyzes a reaction between 3 molecules of CO_2 and three molecules of RuBP. This reaction results in the formation of three six-carbon compounds. These three six-carbon molecules immediately split into six three-carbon compounds called 3-PGA (Figure 7.22). This process is called carbon fixation because CO_2 is "fixed" from its inorganic form into the organic form of 3-PGA.

ATP and NADPH use their stored energy to convert the six 3-PGA, into another three-carbon compound called G3P (Glyceraldehyde 3-phosphate) (Figure 7.22). This type of reaction is called a reduction reaction because it involves the gain of electrons. The molecules of ADP and $NADP^+$ resulting from the reduction reaction return to the light-dependent reactions to be re-energized.

One of the G3P molecules leaves the Calvin cycle and can be used to form carbohydrates. To form a glucose molecule, a six-carbon sugar, it takes two molecules of G3P. The Calvin cycle needs to make two turns before it can yield one glucose molecule. The remaining G3P molecules regenerate RuBP, which enables the system to prepare for another round of carbon-fixation (Figure 7.22). ATP is also used in the regeneration of RuBP.
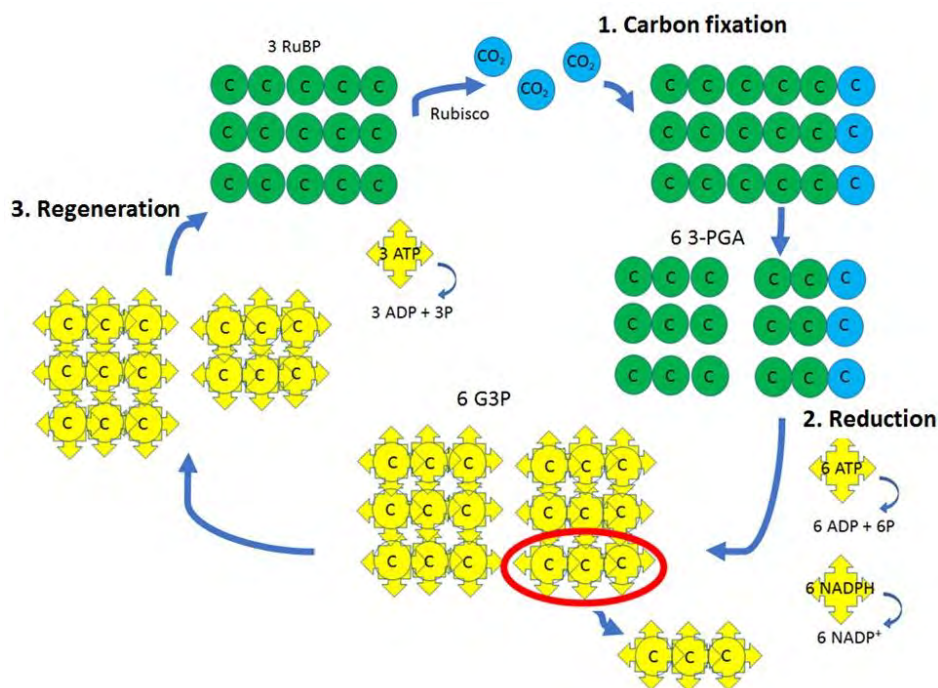
Figure 7.22 The Calvin cycle has three stages. (credit: Elizabeth O'Grady)

In summary, nine ATP, six NADPH, and three molecules of carbon dioxide are needed to start each round of the Calvin cycle. Both the ATP and NADPH are generated in the thylakoid membrane through the light-dependent reactions (Figure 7.23). The Calvin cycle occurs in the stroma and begins when carbon dioxide is fixed to RuBP with the help of the enzyme rubisco. For one turn of the Calvin cycle, the plant cell gets to use one G3P to synthesize carbohydrates (Figure 7.23). Simple carbohydrates, such as glucose, can then be used by the plant to perform aerobic cellular respiration.
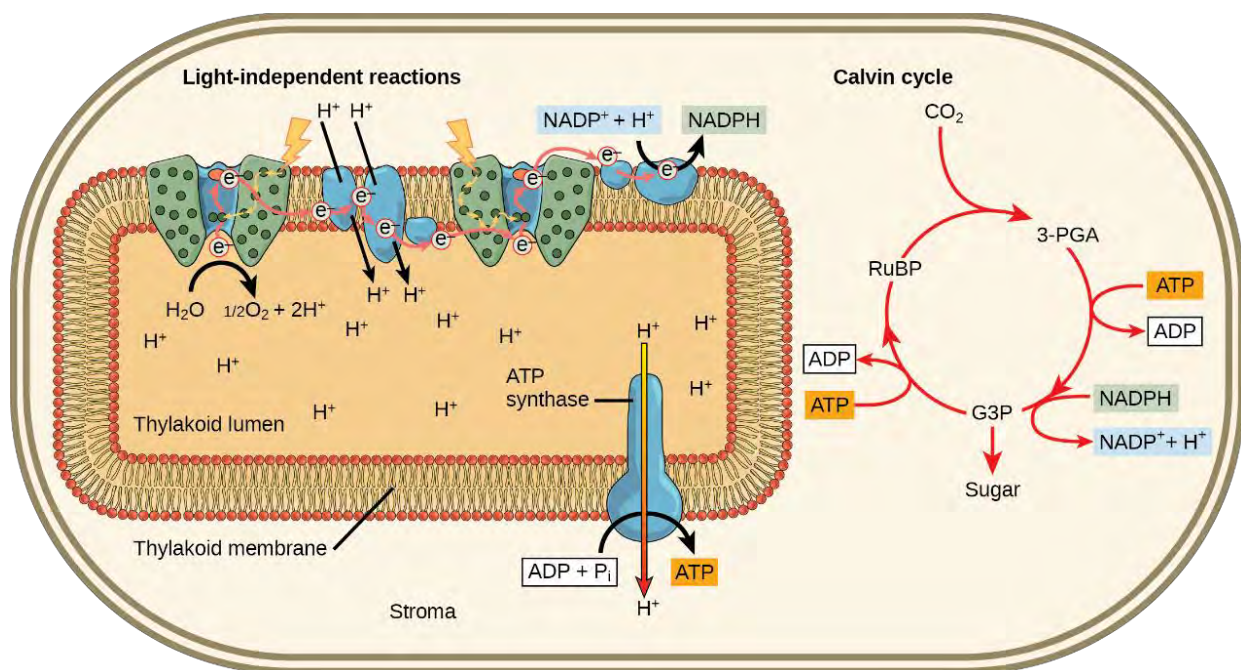
Figure 7.23 Light reactions harness energy from the sun to produce chemical bonds, ATP, and NADPH. These energy-carrying molecules are made in the stroma where carbon fixation takes place. (credit: Clark et al. / Biology 2E OpenStax)

CONCEPTS IN ACTION- The following is a link to an animation of the Calvin cycle. Click Stage 1, Stage 2, and then Stage 3 to see G3P and ATP regenerate to form RuBP.

Photorespiration

The basic process of photosynthesis has changed very little over time. The light-dependent reactions work to absorb light and produce short-term energy carriers. The energy is then used in the Calvin cycle reactions to make sugar. As with all biochemical pathways, a variety of conditions has led to different adaptations.

When plants are forced to close their stomata for prolonged periods of time, gas exchange cannot occur or is extremely limited. Because plants can continue to do the light-dependent reactions, oxygen builds up in the cells. Recall, in the light-dependent reactions, water is split to replace the electron on the special chlorophyll *a* molecule. This reaction generates oxygen as a by-product. Rubisco, the enzyme used for carbon fixation in the Calvin cycle, can bind to carbon dioxide *or oxygen* and fix it to RuBP. In times when oxygen is in a higher concentration than carbon

dioxide, for example when the stomata are closed on hot days, rubisco will fix oxygen to RuBP, a process called **photorespiration** (Figure 7.24). The process of photorespiration wastes the energy carriers that were produced in the light-dependent reaction and does not lead to the production of glucose. When photorespiration happens, the plant cannot generate sugar, which it must have to carry out aerobic cellular respiration.
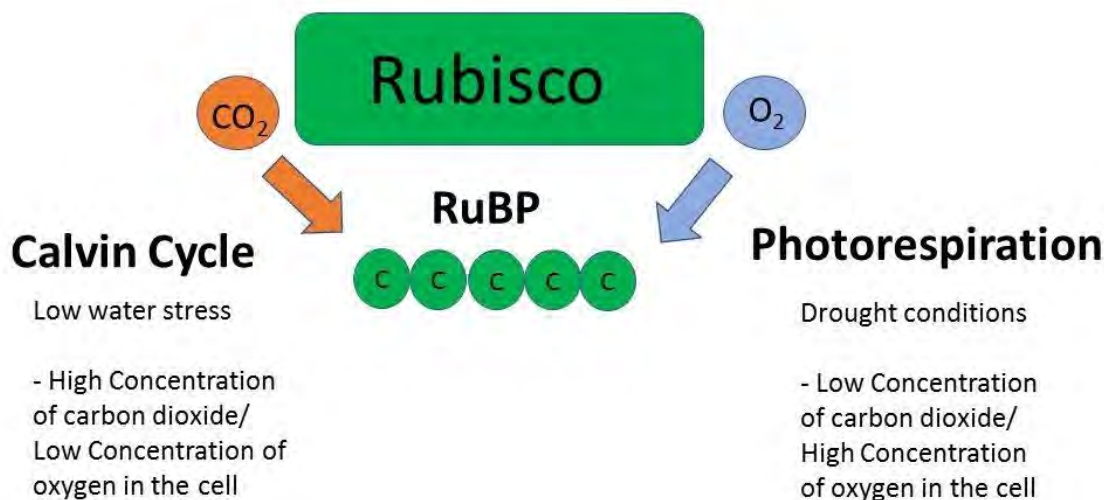
Figure 7.24 shows the difference between rubisco in the Calvin cycle and photorespiration. (credit: Elizabeth O'Grady)

Drought-adapted plants have evolved in such a way that they are able to reduce the impact of photorespiration. C4 plants, such as corn and sugar cane, can photosynthesize even when CO_2 is in short supply. When it is extremely hot and dry, plants are forced to close most or all of their stomata to prevent water loss. With their stomata closed, gas exchange is extremely limited and O_2 builds up. By using special enzymes and carrying out the Calvin cycle reactions in mesophyll cells called bundle sheath cells, photosynthesis can continue. They are called C4 plants because carbon dioxide must first be fixed into a four-carbon molecule, oxaloacetate, before it can be used to produce glucose.

CAM (Crassulacean Acid Metabolism) plants such as cacti (Figure 7.25), pineapple, and Spanish moss, open their stomata at night to exchange gas. By doing so, the plant can preserve water. Carbon dioxide can be stored in the central vacuoles until the daytime when the light dependent reactions can occur and produce the energy carriers needed to fix carbon dioxide during the Calvin cycle.

Both C4 and CAM plants have different adaptations that allow them to avoid photorespiration and carry out photosynthesis under water stress.

Figure 7.25 Cactus is an example of a CAM plant. (credit: Piotr Wojtkowski / Concepts of Biology OpenStax)

Photosynthesis in Prokaryotes

The two parts of photosynthesis, the light-dependent reactions and the Calvin cycle, have been described as they take place in chloroplasts. However, prokaryotes, such as cyanobacteria, lack membrane-bound organelles. Prokaryotic photosynthetic autotrophic organisms have infoldings of the plasma membrane for chlorophyll attachment and photosynthesis (Figure 7.26). It is here that prokaryotes, like cyanobacteria, can carry out photosynthesis.

Figure 7.26 A photosynthetic prokaryote has folded regions of the plasma membrane that function like thylakoids. (credit: scale-bar data from Matt Russell / Concepts of Biology OpenStax)
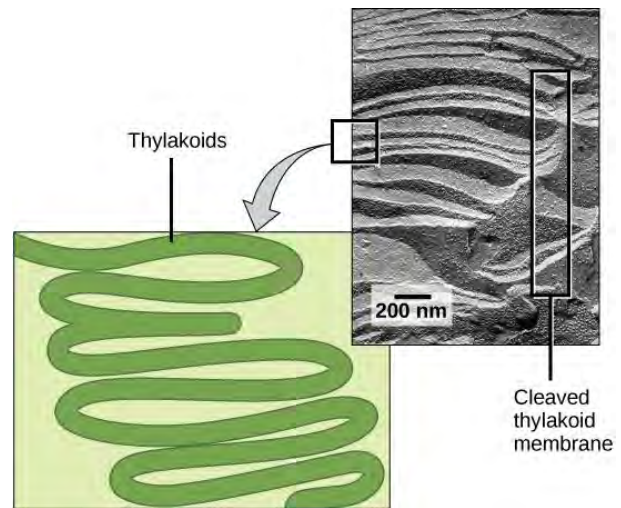
Check your knowledge

Name the location of the light-dependent reactions in prokaryotes. Where is it in eukaryotes?

What are the inputs of the Calvin cycle?

Answer: In prokaryotes, the light-dependent reaction components are found in folds along the plasma membrane. In eukaryotes, they are on the thylakoid membranes in the chloroplast.
The Calvin cycle needs 18 ATP and the electrons carried by 12 NADPH from the light dependent reactions to fix the 6 CO2 into 2 G3P.

Section Summary

Using the energy carriers formed in the first stage of photosynthesis, the Calvin cycle reactions fix CO_2 from the environment to build carbohydrates. An enzyme, rubisco, catalyzes the carbon fixation reaction, by combining CO_2 with RuBP. The resulting six-carbon compound is broken down into two three-carbon compounds, and the energy in ATP and NADPH is used to convert these molecules into G3P. One of the three-carbon molecules of G3P leaves the cycle to become a part of a carbohydrate molecule. The remaining G3P molecules stay in the cycle to regenerate the RuBP, which is ready to react with more CO_2. Three carbon dioxide molecules are required to make each G3P. Two G3P molecules can be combined to form one glucose molecule. C4 and CAM plants have evolved variations of photosynthesis that allow them to survive in dry, hot climates, which reduces photorespiration.

Exercises

1. Where in plant cells does the Calvin cycle take place?
    a. thylakoid membrane
    b. thylakoid space
    c. stroma
    d. granum
2. Which statement correctly describes carbon fixation?
    a. the conversion of inorganic CO_2 to an organic compound
    b. the use of RUBISCO to form 3-PGA
    c. the production of carbohydrate molecules from G3P
    d. the formation of RuBP from G3P molecules
    e. the use of ATP and NADPH to reduce CO_2
3. What is the molecule that leaves the Calvin cycle to be converted into glucose?
    a. ADP
    b. G3P
    c. RuBP
    d. 3-PGA
4. Which part of the Calvin cycle would be affected if a cell could not produce the enzyme rubisco?

Answers
1. (c)
2. (a)
3. (b)
4. None of the cycle could take place because rubisco is essential in fixing carbon dioxide. Specifically, rubisco catalyzes the reaction between carbon dioxide and RuBP at the start of the cycle.

Glossary

Calvin cycle: the reactions of photosynthesis that use the energy stored by the light-dependent reactions to form glucose and other carbohydrate molecules

photorespiration: when oxygen is in a higher concentration than carbon dioxide, rubisco will fix oxygen to RuBP

Chapter 8: Introduction to Reproduction at the Cellular Level
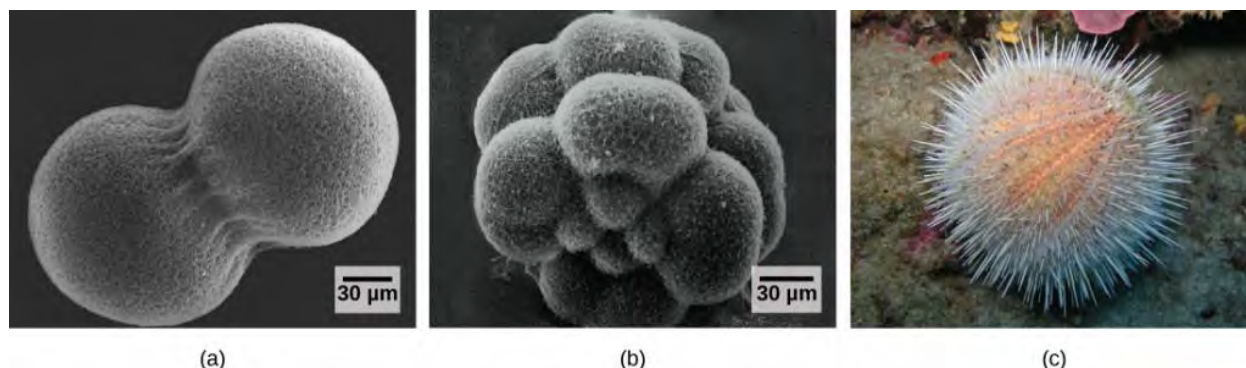
Figure 8.1 A sea urchin begins life as a single cell that (a) divides to form two cells, visible by scanning electron microscopy. After four rounds of cell division, (b) there are 16 cells, as seen in this SEM image. After many rounds of cell division, a (c) mature sea urchin is formed. (credit a: modification of work by Evelyn Spiegel, Louisa Howard; credit b: modification of work by Evelyn Spiegel, Louisa Howard; credit c: modification of work by Marco Busdraghi; scale-bar data from Matt Russell / Biology 2E OpenStax)

One of the seven properties of life is that all organisms must reproduce. Reproduction can be done both on a cellular and an organismal level. Many multicellular organisms, including humans, reproduce sexually by first making specialized reproductive cells. Life begins when these reproductive cells come together to form a fertilized egg. The single fertilized cell then begins to divide through a process that generates trillions of genetically identical cells. All multicellular organisms use cell division for growth, maintenance, and cell repair.

Single-celled organisms, such as bacteria or yeast, must also reproduce; however, they do so on their own, asexually. At the end of asexual reproduction, the new daughter cells should be identical to the parent cell.

In this chapter, students will learn about different forms of cell division. Students will become familiar with the steps that must occur for cell division to take place and the consequences of what happens if cell division does not occur in a precise, controlled manner.

8.1 The Genome

Learning objectives

By the end of this section, you will be able to:

- *Describe the DNA of prokaryotic and eukaryotic genomes*
- *Explain why DNA must be condensed in the cell*
- *Describe how DNA is condensed to fit in the cell*
- *Be able to define and explain all bolded terms*

Collectively, all the DNA found within the cell is called its **genome**. An organism's genome determines its overall characteristics. Prokaryotic and eukaryotic cells differ in both the quantity and organization of their genomes; therefore, they differ in their characteristics. Before learning how cells replicate, students will first take a closer look at both prokaryotic and eukaryotic genomes.

Genomic DNA

In prokaryotes, the genome is typically composed of a single chromosome. The chromosome is made of a double-stranded DNA molecule organized in a loop or a circle. The circular chromosome is found in a region called the nucleoid (Figure 8.2). Some prokaryotes also have smaller loops of DNA called plasmids. Plasmids are not essential for normal growth, but often contain unique genes that confer beneficial properties, such as antibiotic resistance. These plasmids can be exchanged between different bacteria, and therefore, the beneficial properties can propagate.
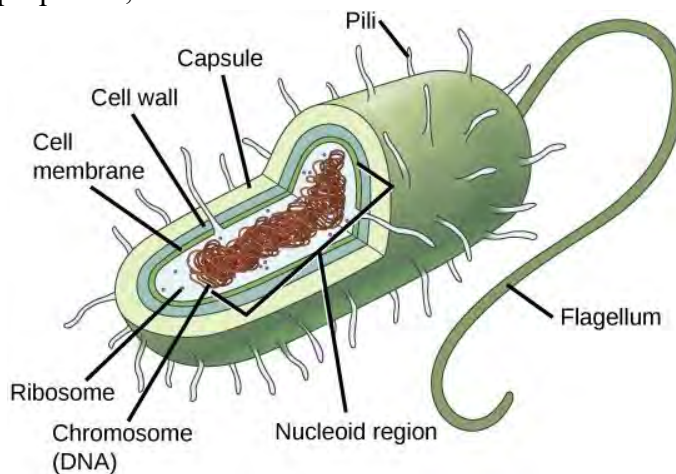
Figure 8.2 Prokaryotes, including both Bacteria and Archaea, have a single, circular chromosome located in a central region called the nucleoid. (credit: Clark et al. / Biology 2E OpenStax)

In eukaryotes, the genome is made up of several linear chromosomes (Figure 8.3). **Chromosomes** consist of double-stranded DNA molecules wrapped around proteins. Each eukaryotic species has a characteristic number of chromosomes in its nuclei. In humans, all cells (with the exception of our eggs and sperm) contain 46 chromosomes, or 23 pairs of chromosomes (Figure 8.3)**.**
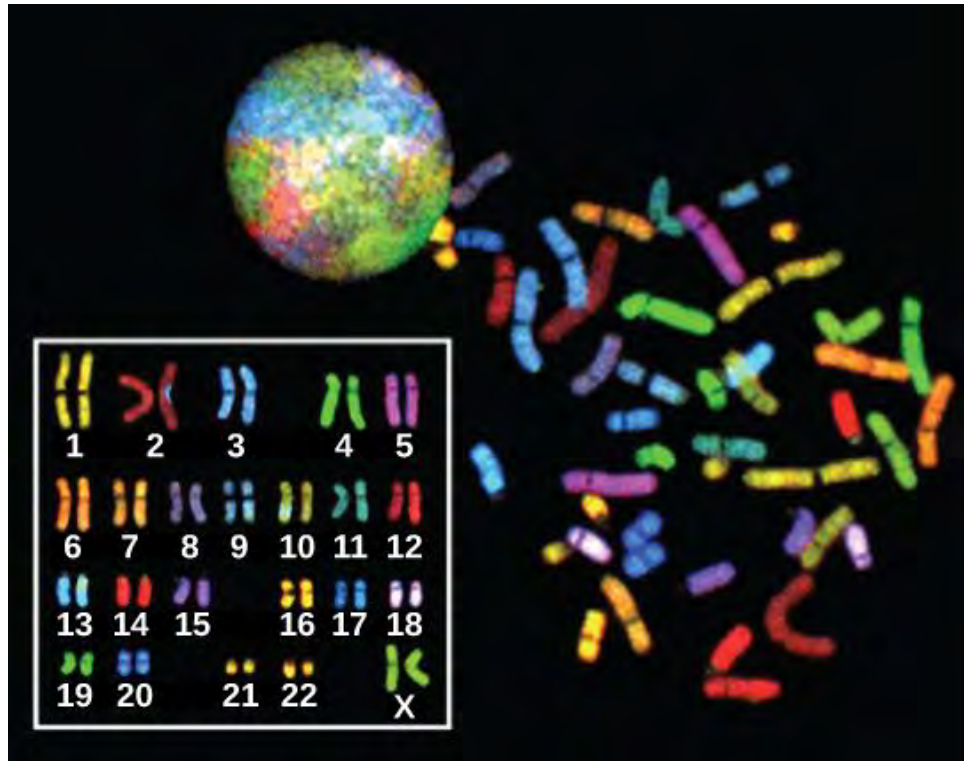
Figure 8.3 There are 23 pairs of chromosomes in a female human cell. In this image, the chromosomes were exposed to fluorescent stains to distinguish them. (credit: "718 Bot"/Wikimedia Commons, National Human Genome Research / Biology 2E OpenStax)

Eukaryotic Chromosomal Structure and Packaging

If the DNA from all 46 chromosomes in a human cell were laid out end-to-end, it would measure approximately two meters! The average size of a human cell is about 10 µm; this means that the DNA must be *packaged* or *condensed* to fit into the cell's nucleus. At the same time, it must also be readily accessible so that it can be used to make proteins. For this reason, the long strands of DNA are either loosely or tightly condensed with the help of different proteins.

To begin, DNA is loosely condensed by winding it around special proteins called histone proteins. As the DNA is wound around the protein, it forms a long fiber-like strand called **chromatin**. Within the chromatin fibers, stretches of DNA wind around several histone proteins simultaneously forming beadlike complexes called nucleosomes. The nucleosomes can coil, which *condenses* the DNA even more (Figure 8.4).

When a cell divides, the DNA will be condensed even more and individual chromosomes will become visible. Chromosomes are always present in the form of chromatin; however, they cannot be easily seen until the cell is preparing to divide.
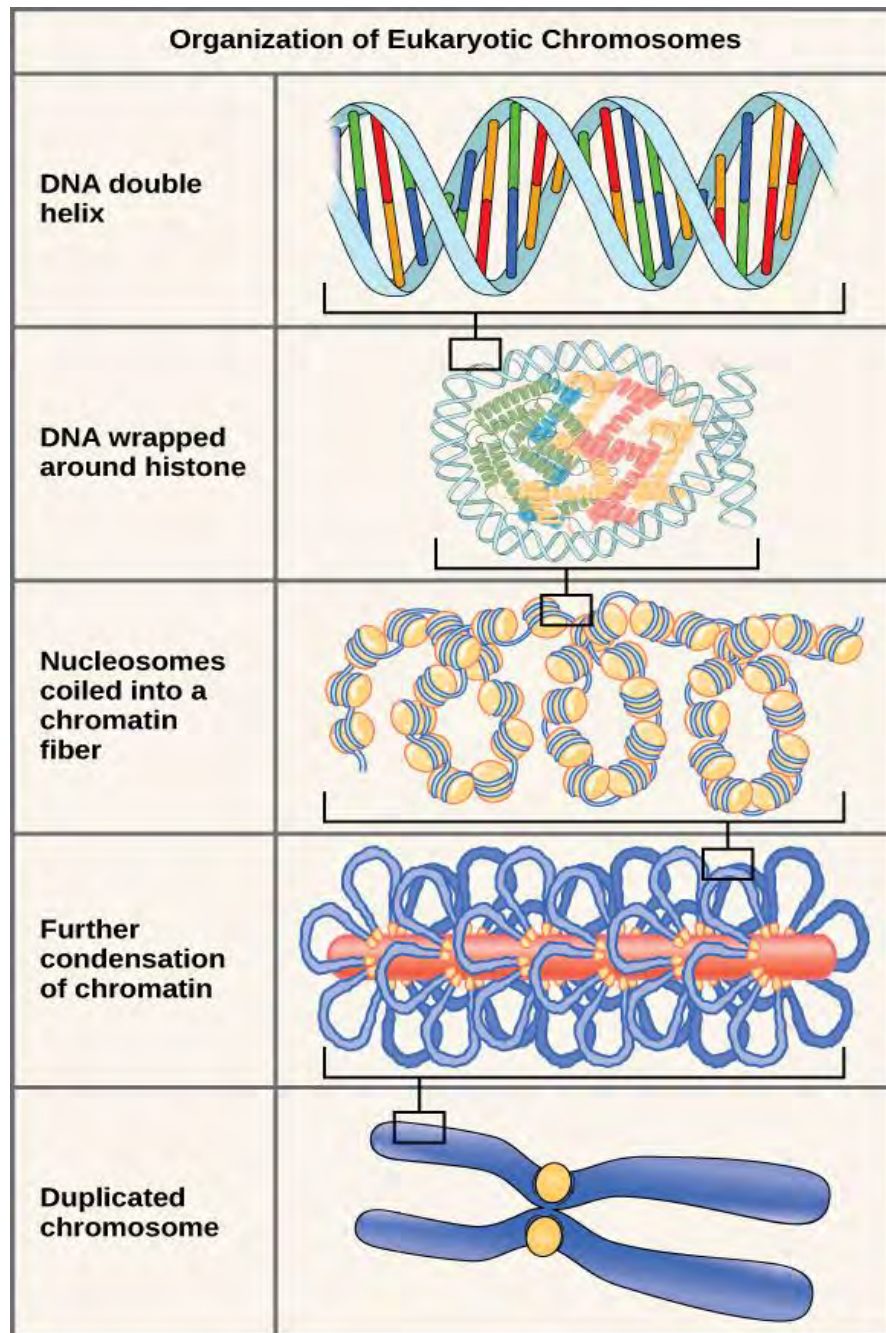
Figure 8.4 From top to bottom: The top panel shows a DNA double helix. The second panel shows the double helix wrapped around histone proteins, which makes a nucleosome. The middle panel shows multiple nucleosomes. The fourth panel shows that the chromatin fiber further condenses into the chromosome shown in the bottom panel. (credit: Clark et al. / Biology 2E OpenStax)

CONCEPTS IN ACTION - This animation illustrates the different levels of chromosome packing.

Section Summary

All the DNA found within the cell is called its genome. Prokaryotic and eukaryotic cells differ in both the quantity and organization of their genomes. Prokaryotes have a single loop chromosome, whereas eukaryotes have multiple linear chromosomes. Human cells, except for eggs and sperm, have 46 chromosomes.

Exercises

1. Chromatin is made of:
    a. DNA only
    b. DNA and protein
    c. DNA and carbohydrate
    d. DNA and lipid
2. A prokaryotic cell _____.
    a. has one circular chromosome
    b. has several linear chromosomes
    c. does not have chromosomes
    d. has homologous pairs of chromosomes
3. Contrast a prokaryotic chromosome and eukaryotic chromosomes.

Answers

1. (b)
2. (a)
3. In prokaryotes, the genome is typically composed of a single chromosome. The chromosome is made of a double-stranded DNA molecule organized in a loop or a circle. The circular chromosome is found in a region called the nucleoid. In eukaryotes, the genome is made up of several linear chromosomes. Chromosomes consist of double-stranded DNA molecules wrapped around proteins. Each eukaryotic species has a characteristic number of chromosomes in its nuclei.

Glossary

chromatin: DNA wound around proteins forming long fiber-like strands

chromosome: structures made of chromatin that are visible when the cell is dividing

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

8.2 The Cell Cycle and Mitosis

The **cell cycle** is a series of events involving both cell growth and division. The cell cycle begins when a cell is first formed and continues until it divides and produces two new daughter cells. When a cell is dividing, it proceeds through a series of carefully timed and regulated stages of growth, DNA replication, and division.

Many multicellular organisms, including humans, reproduce sexually by the completing the process of meiosis. Meiosis is a process that produces specialized reproductive cells called eggs and sperm (Figure 8.5). **Sexual reproduction** requires the egg and sperm to come together to form a fertilized egg, also called a zygote. In humans, gametes are produced in the testes of males and the ovaries of females. The process of sexual reproduction and meiosis will be discussed in detail in section 8.5.
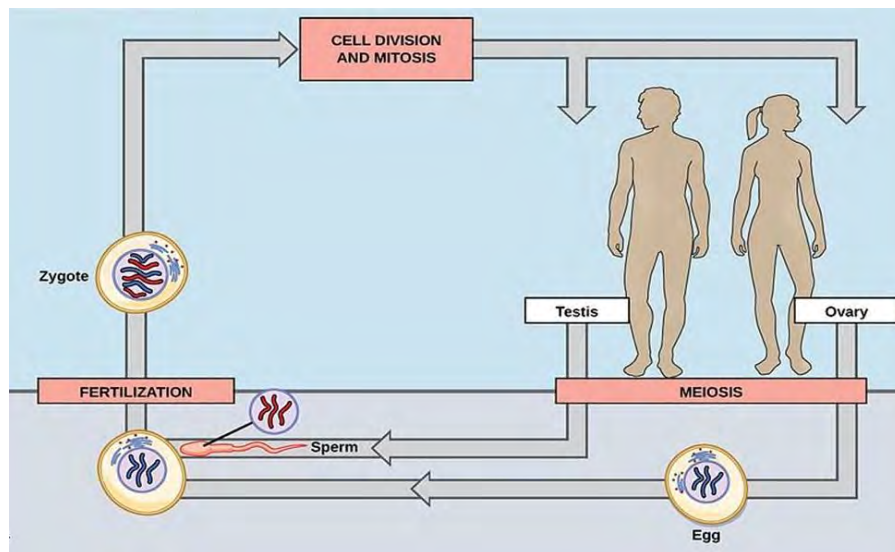
Figure 8.5 The human cell cycle includes two types of cell division: mitosis and meiosis. (credit: Biology OpenStax / Wikimedia Commons)

Interphase and the Mitotic phase

Once the zygote is formed, it will begin to reproduce or divide through a process called mitosis (Figure 8.5). Mitosis must occur billions of times to produce the billions of genetically identical cells that make up one multicellular human. All multicellular organisms use mitosis for growth, maintenance, and cell repair.

The cell cycle has two major phases: interphase and the mitotic phase (Figure 8.6). During **interphase**, the cell grows, and DNA is replicated. The mitotic phase consists of two subphases: mitosis and cytokinesis. In **mitosis**, the nucleus breaks down and the genetic material is equally divided. Once the DNA is divided, two new identical nuclei are formed. **Cytokinesis** then divides the cytoplasm into two new distinct cells.
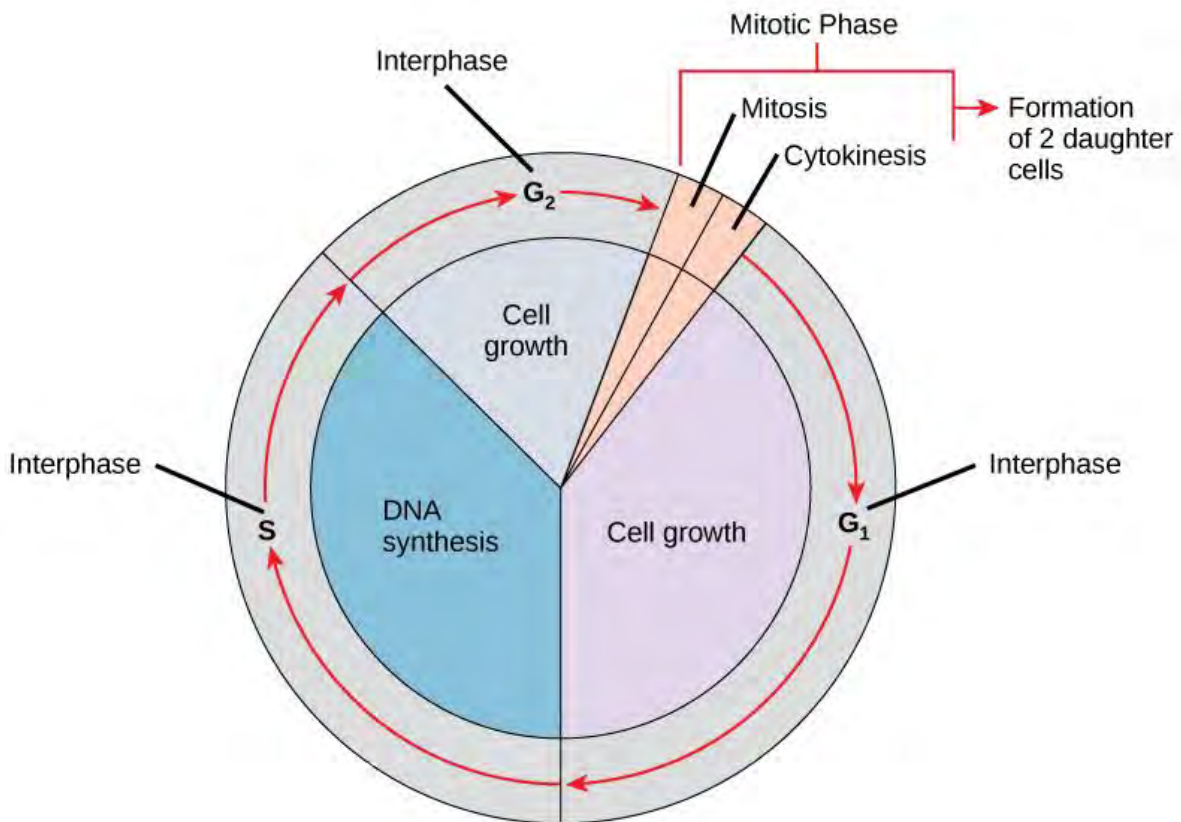
Figure 8.6 A cell moves through a series of phases called the cell cycle. (credit: Clark et al. / Biology 2E OpenStax)

Interphase

Most cells spend the majority of their time in interphase. During interphase, the cell undergoes normal processes while also preparing for cell division. The three stages of interphase are called G_1 (gap 1), S (synthesis), and G_2 (gap 2).

G₁ Phase

The first stage of interphase is called the **G₁ phase**, or gap 1. Although it may not seem like much happens in gap one, especially given its name, the cell is actually very active at the biochemical level. During the G₁ phase, the cell is accumulating the materials it will need to replicate its chromosomes. The cell must also generate enough energy to perform the processes of DNA replication and cell division. The cell also continues to carry out its normal cell function.

S Phase

Throughout interphase, chromosomes are in a semi-condensed state, meaning chromatin is visible; however, individual chromosomes are not. In the **S phase** or synthesis phase, DNA replication occurs. DNA replication involves making an identical copy of each chromosome. It is helpful to refer to chromosomes as being in either the unduplicated state or the duplicated state (Figure 8.7).

Chromosome in the unduplicated state

Chromosome in the duplicated state

Sister chromatids
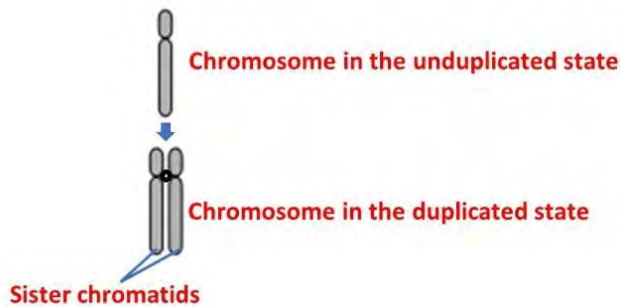
Figure 8.7 Chromosome in the unduplicated state versus a chromosome in the duplicated state. (credit: Elizabeth O'Grady)

For example, in G₁ all chromosomes exist in the unduplicated state. After S phase chromosomes exist in the duplicated state. Chromosomes in the duplicated state each consist of two identical sister chromatids. **Sister chromatids** are firmly attached to one another at a location called the centromere region (Figure 8.8).

chromosome in the duplicated state after synthesis of Interphase

nucleus

cell

centromere

sister chromatids

nucleosomes

bases pair

histones

DNA of double helix
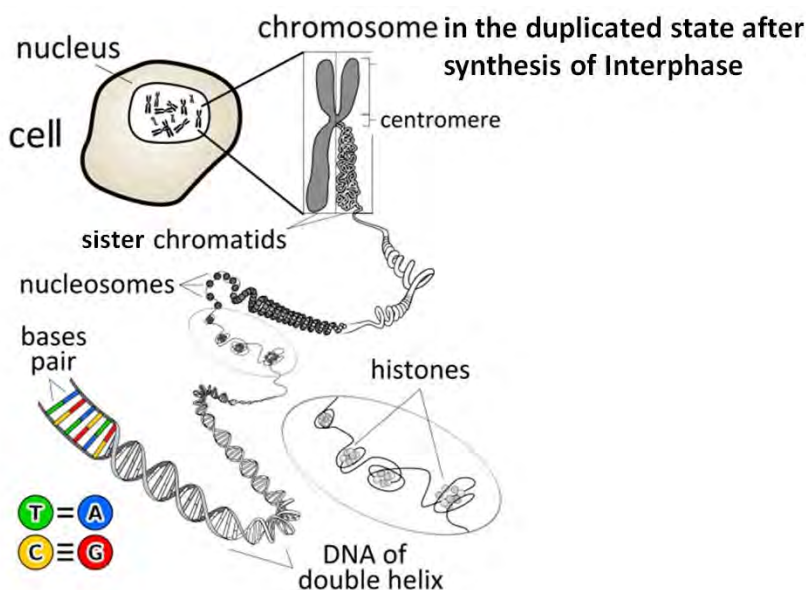
Figure 8.8 shows a chromosome in the duplicated state consisting of two identical sister chromatids. (credit: Modified by Elizabeth O'Grady original work of KES47 Wikimedia commons)

Centrosomes are also duplicated during the S phase. Recall from chapter 4 that **centrosomes** are mostly microtubule-organizing centers (Figure 8.9). The two centrosomes give rise to the **mitotic spindle,** a microtubule network used to physically move the chromosomes during mitosis. The centrosomes consist of a pair of rod-like centrioles at right angles to each other (Figure 8.9). Centrioles help organize cell division in human cells and different types of animal cells. Neurons found in the brain and spinal cord lack centrioles and are therefore amitotic, meaning they do not divide. Plants and most fungi also do not use centrioles for cell division.

(a)   (b)
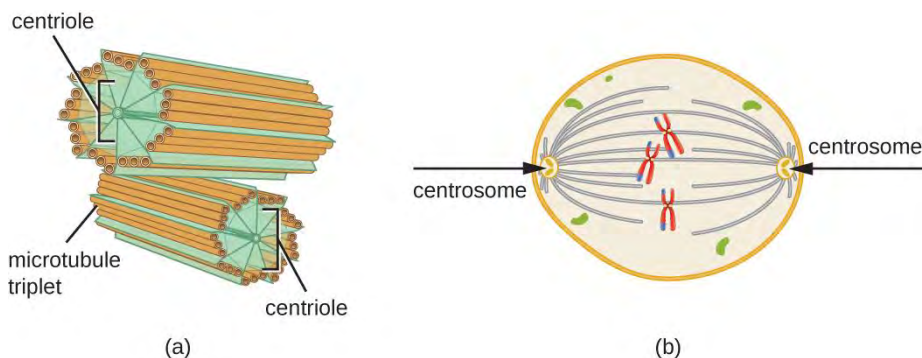
Figure 8.9 (a) A centrosome is composed of two centrioles positioned at right angles to each other. (b) In animal cells, the centrosomes (arrows) serve as microtubule-organizing centers of the mitotic spindle during mitosis. (credit: Parker et al. / Microbiology OpenStax)

G₂ Phase

In the **G₂ phase**, or gap 2, the cell replenishes its stored energy and synthesizes the proteins necessary for separating the chromosomes. 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 can enter the first stage of mitosis.

G₀ Phase

Some cells can also enter a resting phase called the G_0 phase (Figure 8.10). Cells, such as muscle cells and hair follicle cells, can temporarily stop dividing and will not enter the S phase. At that time, these cells are said to be in the **G₀ phase**. When cued, the cells can enter back into gap one of interphase. Some cells, such as nerve cells or mature cardiac muscle, have permanently stopped dividing and are also said to be in the G_0 phase.
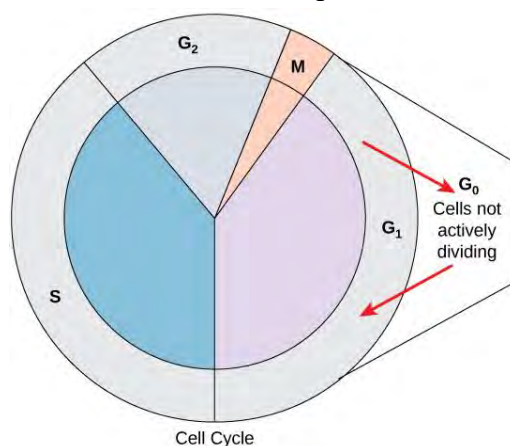
Figure 8.10 Cells that are not actively preparing to divide enter an alternate phase called G0. (credit: Fowler et al. / Concepts of Biology OpenStax)

The Mitotic Phase

The mitotic phase is a multistep process where chromosomes in the duplicated state are aligned, separated, and moved to opposite poles of the cell. The cell is then divided into two new *identical* daughter cells. The first portion of the mitotic phase, **mitosis**, is composed of five stages. Each stage has key events which allow for the chromosomes to be equally divided amongst the two daughter cells. The second portion of the mitotic phase, called **cytokinesis**, is the physical separation of the cytoplasmic components into two new daughter cells.

Mitosis

Mitosis is divided into five phases: prophase, prometaphase, metaphase, anaphase, and telophase. Each of these phases includes important events that allow for equal division of the chromosomes into two new daughter cells (Figure 8.11).

Figure 8.11 Animal cell mitosis is divided into five stages—prophase, prometaphase, metaphase, anaphase, and telophase—visualized here by light microscopy with fluorescence. (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/ Concepts of Biology OpenStax)

Prophase

During **prophase**, the first phase of mitosis, several events occur which will allow chromosomes in the duplicated state to be divide. During this phase, the nuclear envelope starts to breakdown into small vesicles. The Golgi apparatus and endoplasmic reticulum fragment and disperse to the outer edges of the cell, and the nucleolus disappears. The centrosomes begin to move to opposite poles of the cell with the help of microtubules. As the microtubules begin to form the mitotic spindle, they extend between the centrosomes, pushing the centrosomes farther and farther apart. The sister chromatids begin to coil tightly and become visible when using a light microscope.

Prometaphase

During **prometaphase**, many of the processes that began in prophase continue. The remaining nuclear envelope completely disappears. The mitotic spindle continues to develop as more microtubules are formed and then stretched across the entire length of the cell. Chromosomes become more condensed, and individual chromosomes become more visible. A protein complex called the **kinetochore** attaches each sister chromatid to microtubules at the centromere region.
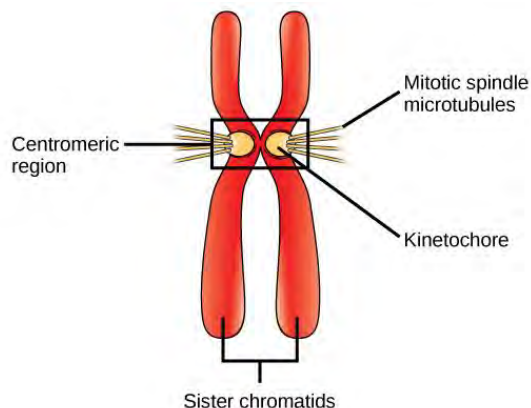
Figure 8.12 During prometaphase, mitotic spindle microtubules from opposite poles attach to each sister chromatid at the kinetochore. (credit: Clark et al. / Biology 2E OpenStax)

Metaphase

During **metaphase**, all the chromosomes align in a region called the metaphase plate with the help of the mitotic spindle. The **metaphase plate** is a region midway between the two poles of the cell. The sister chromatids are tightly attached to one another. At this time, the chromosomes are in their most condensed form.

Anaphase

During **anaphase**, the sister chromatids are split apart with the help of both the kinetochore proteins and the spindle fibers. Each chromatid is now referred to as a chromosome in the unduplicated state. Each chromosome is rapidly pulled toward the centrosome to which its microtubule is attached. The cell becomes visibly elongated as the microtubules slide against each other at the metaphase plate.

Telophase

During **telophase**, as the chromosomes reach the opposite poles, they begin to decondense or unravel. The mitotic spindles are broken down into amino acid monomers that will be used to assemble the cytoskeleton for each daughter cell. Two nuclear envelopes begin to form around each separated group of chromosomes.

Cytokinesis

Cytokinesis is the second part of the mitotic phase. During **cytokinesis**, cell division is completed when the cytoplasmic components are physically separated into two identical daughter cells. Although the stages of mitosis are similar for most eukaryotes, the process of cytokinesis is very different for eukaryotes that have cell walls, such as plant cells.

In cells that lack cell walls, such as animal cells, cytokinesis begins during anaphase. A contractile ring composed of actin protein filaments forms just inside the plasma membrane at the center of the cell. The microfilaments pull the equator of the cell inward, forming a fissure called the **cleavage furrow**. The cleavage furrow deepens as the actin ring contracts, and eventually, the membrane and cell are cleaved into two separate identical daughter cells (Figure 8.12).

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 two daughter cells. During interphase, the Golgi apparatus accumulates enzymes, structural proteins, and glucose molecules, which will later be used to build the new cell wall. Once these materials are collected, the Golgi apparatus breaks into vesicles that disperse throughout the dividing cell. During telophase, microtubules move these Golgi vesicles to the metaphase plate. Once there, the vesicles begin to fuse, forming a structure called the **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 help build a new cell wall of cellulose. (Figure 8.13).

Figure 8.13 In part (a) a cleavage furrow forms at the former metaphase plate in the animal cell. In part (b) The cell plate grows from the center toward the cell walls. (credit: Clark et al. / Biology 2E OpenStax)

CONCEPTS 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.

Length and Control of the Cell Cycle

The length of the cell cycle varies greatly depending on the organism. Even within a multicellular organism, not all cells will divide at the same rate. In humans, the frequency of cell division ranges from embryonic cells that divide in just a few hours to cells like the neurons of the brain that never divide. 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. 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

Daughter cells must be exact copies of the parent cell. Mistakes in the duplication or distribution of the chromosomes lead to mutations that will then be passed on to every new cell produced. To prevent a compromised cell from continuing to divide, there are internal control mechanisms or **cell cycle checkpoints** at which the cell cycle can be stopped until conditions are favorable. There are three checkpoints where cell division can be stopped; they occur near the end of G_1, at the G_2–M transition, and during metaphase (Figure 8.14).
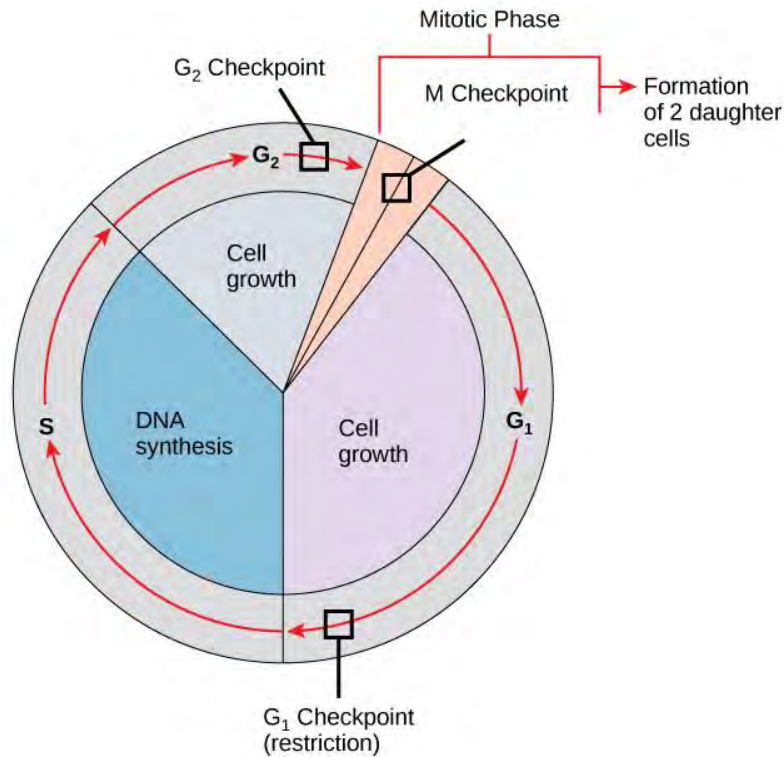
Figure 8.14 The cell cycle is controlled at three checkpoints. (credit: Fowler et al. / <u>Concepts of Biology OpenStax</u>)

The G₁ 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 protein 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 enter the S phase.

The G₂ Checkpoint

The G_2 checkpoint prevents the cell from entering 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 crucial role of the G_2 checkpoint is to ensure that all the chromosomes have been replicated and that the replicated DNA is not damaged.

The M Checkpoint

The M checkpoint occurs near the end of metaphase 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 microtubules that make up the mitotic spindle. Because the separation of the sister chromatids during anaphase is an irreversible step, the cycle will not proceed until each pair of sister chromatids is firmly anchored to spindle fibers arising from opposite poles of the cell.

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

CANCER CONNECTION: *The Implication of an Out of Control Cell Cycle*

Cancer is a collective name used to describe many different diseases caused by uncontrolled cell division. Despite the redundancy of the cell cycle, errors can occur. Proper replication of DNA during the S phase is monitored closely during the cell cycle checkpoints. However, even with the checkpoints, a small percentage of replication errors, called mutations, can occur and be passed on to the daughter cells. If one of these mutations occurs within a gene, a gene mutation occurs.

All cancers begin when a gene mutation gives rise to a faulty protein that is used during cell division. Even minor mistakes allow subsequent mistakes to occur more readily. Over and over, small, uncorrected errors are passed from parent cell to daughter cells. 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.

Inherited genetic abnormalities may cause loss of cell cycle control. Environmental factors, such as UV light or smoking, can also damage DNA and impact control of the cell cycle. Often, a combination of both genetic predisposition and environmental factors lead to cancer.

The process of a cell escaping its normal control system and becoming cancerous may happen throughout the body quite frequently. Fortunately, specific cells of the immune system are capable of recognizing cancerous cells and destroying them. However, in some instances, the cancerous cells remain undetected and continue to proliferate.

If the resulting tumor does not pose a threat to surrounding tissues, it is said to be benign and can usually be easily removed. A tumor becomes malignant, or cancerous, when it spreads beyond the tissue it originates in. The specific names of cancers reflect the tissues they arise in. For example, when the cancerous cells originate in white blood cells, important immune defense cells, the cancer is called leukemia.

Depending on the type and stage of cancer a person has, treatments vary. Traditional approaches, including surgery, radiation, chemotherapy, and hormonal therapy, aim to remove or kill rapidly dividing cancer cells, but these strategies have their limitations. Depending on a tumor's location surgeons may be unable to remove it. Radiation and chemotherapy are difficult, and it is often impossible to target only the cancer cells. The treatments inevitably destroy healthy tissue, as well. To address this, researchers are working on pharmaceuticals that can target specific proteins produced only in cancer-associated cells.

Section 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 a cleavage furrow, 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. Cancer is the result of unchecked cell division caused by a breakdown of the mechanisms regulating the cell cycle.

Exercises

1. Which phase will come between prophase and metaphase?
    a. Telophase
    b. S phase
    c. Anaphase
    d. Prometaphase
2. Chromosomes are duplicated during what portion of the cell cycle?
    a. G_1 phase
    b. S phase
    c. prophase
    d. prometaphase
3. Separation of the sister chromatids is a characteristic of which stage of mitosis?
    a. prometaphase
    b. metaphase
    c. anaphase
    d. telophase
4. Cancers can begin when a mutation occurs in the DNA
    a. TRUE
    b. FALSE
5. What is necessary for a cell to pass the G_2 checkpoint?
    a. the 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
6. Describe the similarities and differences between the cytokinesis mechanisms found in animal cells versus those in plant cells.

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 the formation of a cell wall to separate the two daughter cells

centrosomes: microtubule-organizing centers that give rise to the mitotic spindle

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 called gap 1) a cell-cycle phase; the first phase of interphase centered on cell growth during mitosis

G_2 phase: (also called gap 2) 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

sexual reproduction: requires the egg and sperm to come together to form a zygote

sister chromatids: two identical chromosomes attached to one another at a location called the centromere region

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

8.3 Prokaryotic Cell Division

<table>
<tr><td>

Learning objectives

By the end of this section, you will be able to:

- *Describe the process of binary fission in prokaryotes*
- *Be able to define and explain all bolded terms*

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For unicellular organisms, cell division is the only method to produce new individual cells. In both prokaryotic and eukaryotic cells, cell reproduction should produce two daughter cells that are genetically identical to the parent cell.

To produce identical daughter cells, the following steps are essential. First, the genomic DNA must be replicated and then divided into each of the new daughter cells. Next, the cytoplasmic materials must be divided equally to give both new cells the machinery necessary to sustain life. These steps are required for both eukaryotic and prokaryotic cells.

Prokaryotic Cell Division

Prokaryotic cells have genomes that consist of a single, circular DNA chromosome located in a region called the nucleoid. The process of cell division, called **binary fission**, is simplified. First, DNA can be replicated at a faster rate given bacteria only have one chromosome to replicate. Second, the steps of mitosis are unnecessary because there is no nucleus that needs to be broken down nor multiple chromosomes that need to be divided.

Binary Fission

Before dividing, a prokaryotic cell must first grow and increase the number of its cellular components (Figure 8.15). Next, DNA replication starts at a location on the circular chromosome called the origin of replication. The chromosome is attached to the cell membrane, and replication continues in opposite directions along the chromosome. Next, the cell elongates, and the duplicated chromosomes separate and move to opposite poles of the cell.

Finally, the cell begins cytokinesis. Cytokinesis is directed by proteins that result in the formation of a **septum.** The septum consists of the bacterial cell wall and outer cell membranes. Once the septum is complete, the cell pinches apart, forming two new independent cells.

Binary Fission in Prokaryotes

1. Replication of the circular prokaryotic chromosome begins at the origin of replication and continues in both directions at once.

Origin of replication

Prokaryotes have a single, circular chromosome

FtsZ protein

2. The cell begins to elongate. FtsZ proteins migrate toward the midpoint of the cell.

3. The duplicated chromosomes separate and continue to move away from each other toward opposite ends of the cell. FtsZ proteins form a ring around the periphery of the midpoint between the chromosomes.

Cleavage furrow

FtsZ ring

4. The FtsZ ring directs the formation of a septum that divides the cell. Plasma membrane and cell wall materials accumulate.

Septum

Septum

5. After the septum is complete, the cell pinches in two, forming two daughter cells. FtsZ is dispersed throughout the cytoplasm of the new cells.

Figure 8.15 The binary fission of a bacterium is outlined in five steps. Note the image provides the name of a protein, FtsZ, which assembles into a ring structure, which directs the formation of the septum. (credit: modification of work by "Mcstrother"/Wikimedia Commons)

Binary fission is a less complicated and a much quicker process than cell division performed by eukaryotic cells. As a result, some bacteria like *E. coli* can divide in as little as twenty minutes. *Salmonella typhimurium,* one of the species of bacteria that causes food poisoning, can divide in 40 minutes allowing for their population to grow rapidly (Figure 8.16). Most people infected with *Salmonella* show signs of the illness 12-72 hours after being exposed to the bacteria.

Figure 8.16 The electron micrograph depicts two cells of *Salmonella typhimurium* after a binary fission event. (credit: Parker et al. / Microbiology OpenStax)
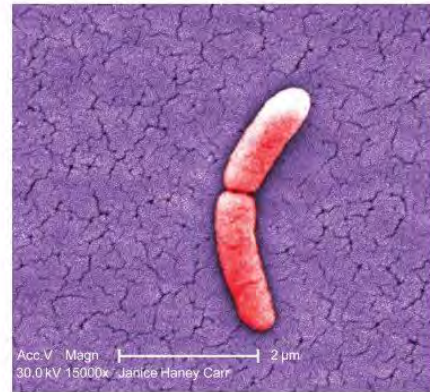
Check your knowledge

Which of the following will complete binary fission?
a. *Staphylococcus aureus* (a bacteria)
b. *Trichophyton rubrum* (a fungus)
c. *Rhytidiadelphus squarrosus* (a moss)
d. *Apis mellifera* (an insect)

Answer: a, the Staphlococcus aureus is the only prokaryote in this list.

Section 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 into 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 for bacterial cell division. Bacterial cytokinesis is directed by a ring composed of a protein called FtsZ. During cytokinesis, a septum consisting of the outer cell membrane and cell-wall forms, and eventually, the cell pinches apart, forming two new cells.

Exercises

1. Which eukaryotic cell-cycle event is missing in binary fission?
   a. cell growth
   b. DNA duplication
   c. mitosis
   d. cytokinesis
2. FtsZ proteins direct the formation of a _____ that will eventually form the new cell walls of the daughter cells.
   a. plasma membrane
   b. cell plate
   c. cytoskeleton
   d. septum
3. Name the common components of eukaryotic cell division and binary fission.

Answers

1. (c)
2. (d)
3. The common components of eukaryotic cell division and binary fission are DNA duplication, separation of the duplicated chromosomes, and the division of the cytoplasmic materials.

Glossary

binary fission: the process of prokaryotic cell division

septum: a wall formed between bacterial daughter cells as a precursor to cell separation

8.4 Sexual Reproduction

Many unicellular organisms, such as yeast, and some multicellular organisms, including strawberry plants, can produce genetically identical clones through a process called **asexual reproduction**. Other single-celled organisms and most multicellular organisms, including the Commander butterfly, reproduce sexually (Figure 8.17). Recall, **sexual reproduction** requires two different reproductive cells to fuse and form a single, genetically unique cell called a zygote.

Figure 8.17 Different life cycle stages of the Commander butterfly. (credit: Rajeeshraghav / Wikimedia Commons)

Sexual reproduction was an early evolutionary innovation. The process is thought to have started shortly after the appearance of the first eukaryotic cells. In many animals, it is the only mode of reproduction. However, scientists recognize that there are disadvantages when it comes to the process of sexual reproduction.

For example, although an individual may be successful in their given environment, it does not guarantee the offspring will be equally as successful. One or both parents may pass on non-functional or mutated genetic material to their offspring. Cystic fibrosis is one such example. With this condition, healthy parents pass on faulty DNA to their offspring. The faulty DNA leads to the production of abnormally thick mucus in the lungs, often resulting in respiratory failure. If an organism that reproduces asexually is successful in their environment, their offspring should also be equally successful because they have the same identical traits as the parent.
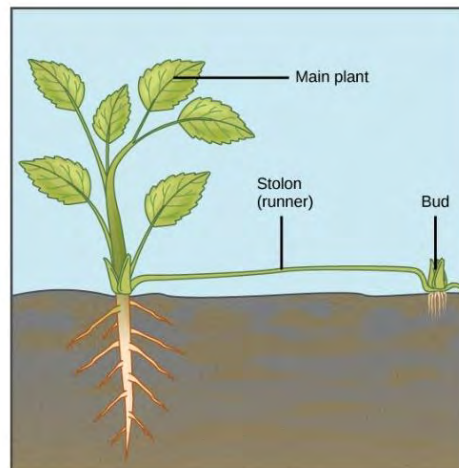
Figure 8. 18 shows a plant reproducing asexually through a process called budding. (credit: Biology OpenStax / Wikimedia Commons)

An organism that can produce offspring by asexual budding, fragmentation, or asexual eggs also has an advantage in that they do not require another organism of the opposite sex to reproduce (Figure 8.18). There is no need to expend energy finding or attracting a mate. That energy can be spent on producing more offspring. The opposite is true for organisms that reproduce through sexual reproduction.

On the surface, organisms that perform asexual reproduction may appear to be more advantageous. However, multicellular organisms that exclusively depend on asexual reproduction are exceedingly rare.

Why is sexual reproduction so common? A likely explanation is that sexual reproduction creates variation amongst individuals (Figure 8.19). Variation is very important to the survival and reproduction of the population. As the habitat or the environment around the organism changes, variation allows different individuals within the population to be successful. In asexual organisms, if the environment changes and an individual is negatively impacted, then all individuals would be negatively impacted due in part to the lack of genetic variation.

The only source of variation in asexual organisms is a mutation. This is also a source of variation

in sexual organisms; however, it is not the only source of variation. Also, different mutations are continually reshuffled from one generation to the next when different parents combine their unique reproductive cells. Other sources of genetic variation occur when reproductive cells are produced during meiosis. Meiosis will be discussed in the next section.

Figure 8.19 shows human skin color genetic diversity. (credit: truthseeker08/ Pixabay)

Section Summary

Many unicellular organisms and a few multicellular organisms can produce genetically identical clones through a process called asexual reproduction. Other single-celled organisms and most multicellular organisms reproduce sexually. 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.

Exercises

1. 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
2. Explain the advantage that populations of sexually reproducing organisms have over asexually reproducing organisms?

Answers

1. (c)
2. 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. Also, 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 outcompete them.

Glossary

asexual reproduction: produces genetically identical clones to the parent organism

sexual reproduction: requires that two different gametes come together to form a zygote

8.5 Meiosis

Sexual reproduction requires **fertilization**, a fusion between two specialized cells, called **gametes**. Each gamete is **haploid,** meaning it contains one set of chromosomes. When gametes unite, they form a **zygote**, or fertilized egg (Figure 8.20). Each zygote is **diploid,** meaning that it contains two sets of chromosomes, one from each biological parent.

Most of the cells that make up the human body are called **somatic cells.** Each somatic cell, also called a body cell, should contain 46 chromosomes. **Germline cells** lead to the production of gametes and makeup only a small percentage of our overall cells. In humans, gametes are our sex cells, and should each contain 23 chromosomes. Female gametes are called **eggs,** whereas male gametes are called **sperm.**
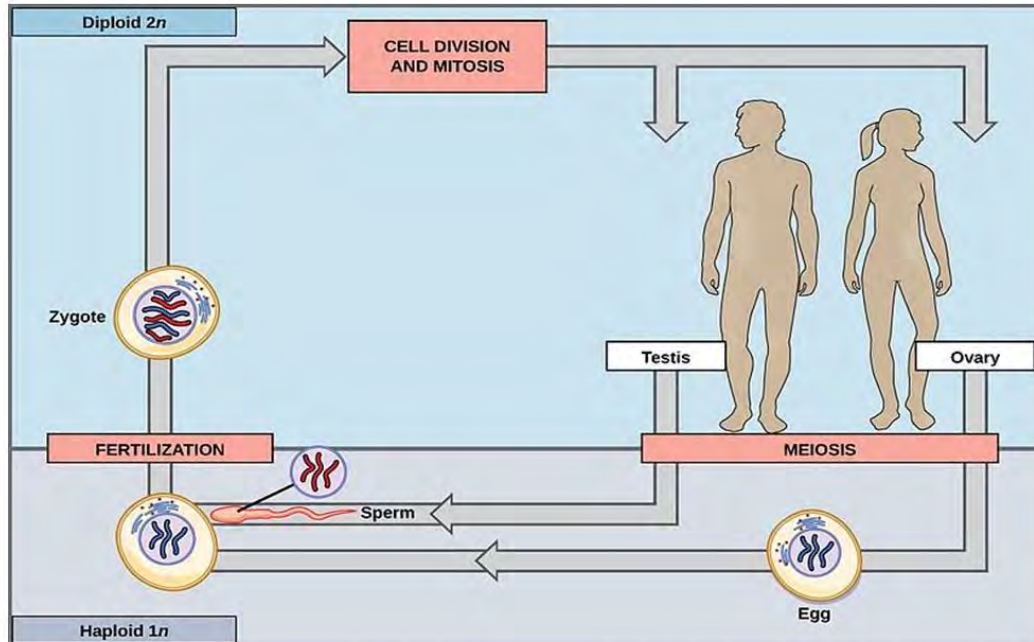
8.20 In animals, sexually reproducing adults form haploid gametes from diploid germ cells. (credit: Biology OpenStax / Wikimedia Commons)

A typical diploid somatic cell contains two copies of each chromosome, called **homologous chromosomes**. Homologous chromosomes are the same length and have specific nucleotide sequences called **genes** in exactly the same location, or **locus** (Figure 8.21). Genes, the functional units of chromosomes, determine an organism's specific characteristics.

Figure 8.21: Homologous chromosomes. Each chromosome is in the duplicated state. (credit: Elizabeth O'Grady)
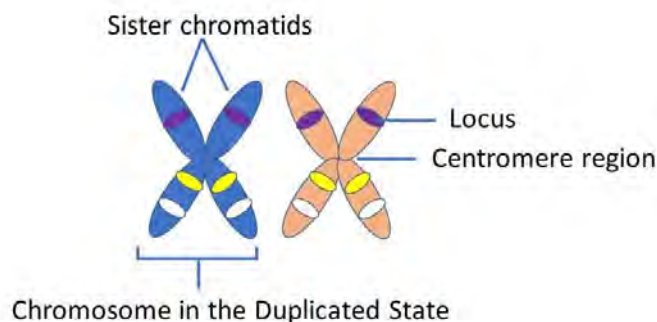
Homologous chromosomes may have different variations of the same gene at the same location. For example, on a homologous pair of chromosomes, one of the chromosomes may have a gene for attached earlobes at a specific location. On the other chromosome, at the same location, there may be a gene that causes earlobes to be unattached. In the end, it is the genes on the chromosome pairs that determine the physical characteristics of an individual.

Both human males and females have twenty-two pairs of homologous chromosomes called autosomes. **Autosomes** are chromosome pairs one through twenty-two and do not determine a person's biological sex (Figure 8.22). The twenty-third pair of chromosomes are referred to as the **allosomes** (Figure 8.22). Humans contain the allosomes X and Y. Some resources use the term "sex chromosomes" instead of allosomes. "Sex chromosome" is misleading. Many non-sex determining genes are found on the X chromosome and autosomes do contain genes involved in sex determination. In phenotypic females, the twenty-third pair of chromosomes are homologous, X and X. Phenotypic males, however, have a twenty-third pair, X and Y, that are not homologous (Figure 8.22). The genes found on the X and Y chromosomes do not code for the same characteristics. For example, on the Y chromosome, there is a set of genes called the SRY genes that allow males to develop testes. Those genes are not typically located on the X chromosome; thus, this pair is not homologous.
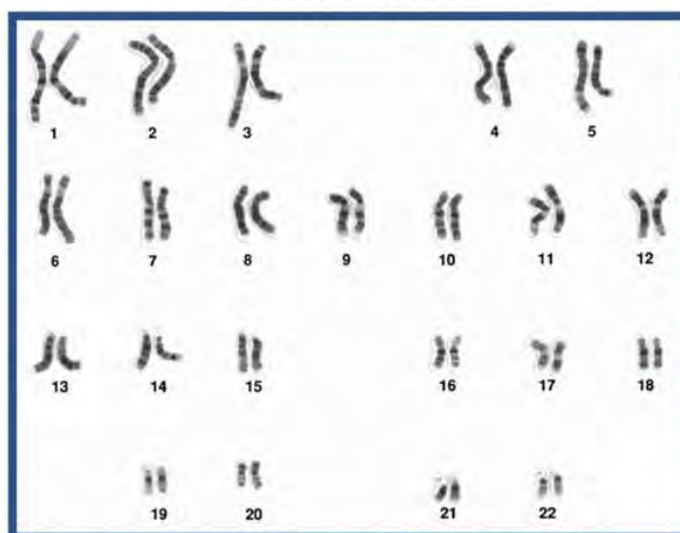
Figure 8.22 shows a human karyotype. (credit: Modified by Elizabeth O'Grady and Marsha Hay original work of National Human Genome Research Institute Public Domain)

If the reproductive cycle is going to occur, specialized diploid cells called adult stem cells must carry out a process called meiosis. In males, the adult stem cells are called spermatogonia and lead to the production of gametes called sperm. In females, these cells are called oogonia and lead to the production of female gametes called eggs or ova.

Plants do not reproduce the same way as animals; however, they still produce two separate and distinct gametes. In flowering plants, the male gametes form in the anthers and are enclosed within a pollen grain. Flowering plants make their female gametes in a structure called the ovary and the gametes are called ovules.

Meiosis is the process that produces haploid gametes by reducing the number of chromosome pairs by half. If this did not occur, the number of chromosomes would double with every future round of fertilization. Meiosis includes many of the same cellular events as mitosis. However, as you have learned, mitosis produces daughter cells who are genetically identical to one another. In mitosis, both the parent and the daughter cells should have the same genetic material and, therefore, the same chromosome number. Both the parent cell and the daughter cells are said to have the same "ploidy level." This means that a diploid parent cell will produce daughter cells that are also diploid. The process of mitosis should result in the ploidy level remaining the same.

In meiosis, the starting adult stem cell is always diploid. The daughter cells that are produced are haploid; therefore, with meiosis, the ploidy level changes. To achieve this reduction in chromosome number, meiosis consists of one round of chromosome replication followed by two rounds of chromosome division. Because the events that occur during each of the stages are similar to the events of mitosis, the same stage names are assigned. However, because there are two rounds of division, the major processes and the stages are designated with a "I" or a "II." Thus, **meiosis I** is the first round of meiotic division and consists of prophase I, prometaphase I, and so on. Likewise, **meiosis II**, during which the second round of meiotic division takes place, includes prophase II, prometaphase II, and so on. Let's take a closer look at the stages that make up meiosis (Figure 8.23).

Check your knowledge

Which chromosomes are homologous? How can you tell?
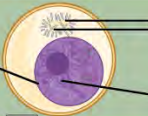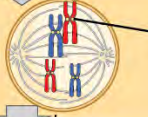
a.　　b.　　c.　　d.

Chromosome images modified by Marsha Hay from Figure 8.22

Answer: d are homologous chromosomes. They are the same size and shape so will carry similar gene sequences.

Stage		Event	Outcome
INTERPHASE	**S phase**	Nuclear envelope — Centrosomes (with centriole pairs) — Chromatin	Chromosomes are duplicated during interphase. The resulting sister chromatids are held together at the centromere. The centrosomes are also duplicated.
MEIOSIS I	**Prophase I**	Sister chromatids — Spindle — Chiasmata — Tetrad	Chromosomes condense, and the nuclear envelope fragments. Homologous chromosomes bind firmly together along their length, forming a tetrad. Chiasmata form between non sister chromatids. Crossing over occurs at the chiasmata. Spindle fibers emerge from the centrosomes.
	Prometaphase I	Centromere (with kinetochore)	Homologous chromosomes are attached to spindle microtubules at the fused kinetochore shared by the sister chromatids. Chromosomes continue to condense, and the nuclear envelope completely disappears.
	Metaphase I	Microtubule attached to kinetochore — Metaphase plate	Homologous chromosomes randomly assemble at the metaphase plate, where they have been maneuvered into place by the microtubules.
	Anaphase I	Sister chromatids remain attached. — Homologous chromosomes separate.	Spindle microtubules pull the homologous chromosomes apart. The sister chromatids are still attached at the centromere.
	Telophase I and Cytokinesis	Cleavage furrow	Sister chromatids arrive at the poles of the cell and begin to decondense. A nuclear envelope forms around each nucleus, and the cytoplasm is divided by a cleavage furrow. The result is two haploid cells. Each cell contains one duplicated copy of each homologous chromosome pair.
MEIOSIS II	**Prophase II**		Sister chromatids condense. A new spindle begins to form. The nuclear envelope starts to fragment.
	Prometaphase II		The nuclear envelope disappears, and the spindle fibers engage the individual kinetochores on the sister chromatids.
	Metaphase II		Sister chromatids line up at the metaphase plate.
	Anaphase II	Sister chromatids separate.	Sister chromatids are pulled apart by the shortening of the kinetochore microtubules. Non kinetochore microtubules lengthen the cell.
	Telophase II and Cytokinesis	Haploid daughter cells	Chromosomes arrive at the poles of the cell and decondense. Nuclear envelopes surround the four nuclei. Cleavage furrows divide the two cells into four haploid cells.

8.23 An animal cell with a diploid number of four (2n = 4) proceeds through the stages of meiosis to form four haploid daughter cells. (credit: Clark et al. / Biology 2E OpenStax)

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. Once this occurs, the chromosomes are said to be in the duplicated state. Chromosomes in the duplicated state 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 during interphase. This prepares the cell for the first meiotic phase.

Meiosis I

Prophase I

Prophase I is the first phase of meiosis. Early in prophase I, the chromosomes begin to condense, and the nuclear envelope begins to break down.
Homologous chromosomes are brought together with the help of unique proteins. Each homologous chromosome pair is held together by proteins forming a **tetrad**, a complex consisting of four sister chromatids (Figure 8.24). Recall that in mitosis, homologous chromosomes do not pair together.

Figure 8.24 Homologous chromosomes pair together during prophase I to form a tetrad. (credit: Clark et al./ Biology 2E OpenStax)
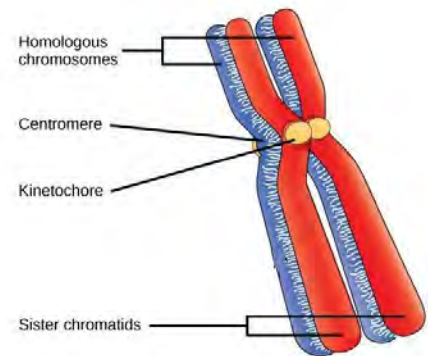
When the tetrad is formed, the genes on the non-sister chromatids of the homologous pair are precisely aligned with each other. This alignment allows for chromosome segments to be exchanged between non-sister chromatids; a process called **crossing over** or **recombination**. Crossing over occurs at precise locations called **chiasmata** (singular = *chiasma*) (Figure 8.25).
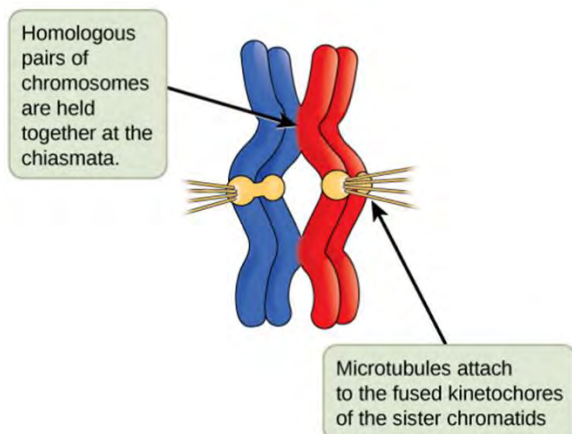
Figure 8.25 Chiasmata hold the homologous chromosomes together. (credit: Biology OpenStax / Wikimedia Commons)

Crossover events are the first source of genetic variation produced during meiosis. A single crossover event between homologous non-sister chromatids results in chromosomes that differ from the two parents. The recombinant sister chromatid has a combination of maternal and paternal genes that did not exist before the crossover (Figure 8.26). Crossover events can occur almost anywhere along the length of the chromosomes; therefore, each gamete produced will have unique combinations of both maternal and parental genes.

In humans, even though the X and Y allosomes are not considered homologous in that most of their genes differ, there is a small region of homology that allows the X and Y chromosomes to pair up during prophase I. There have also been documented cases where the SRY gene located on the Y chromosome has crossed over to the X chromosome. Recall that the SRY genes result in the development of testes. This has resulted in XX males who are phenotypically male, even though they have 2 X chromosomes.
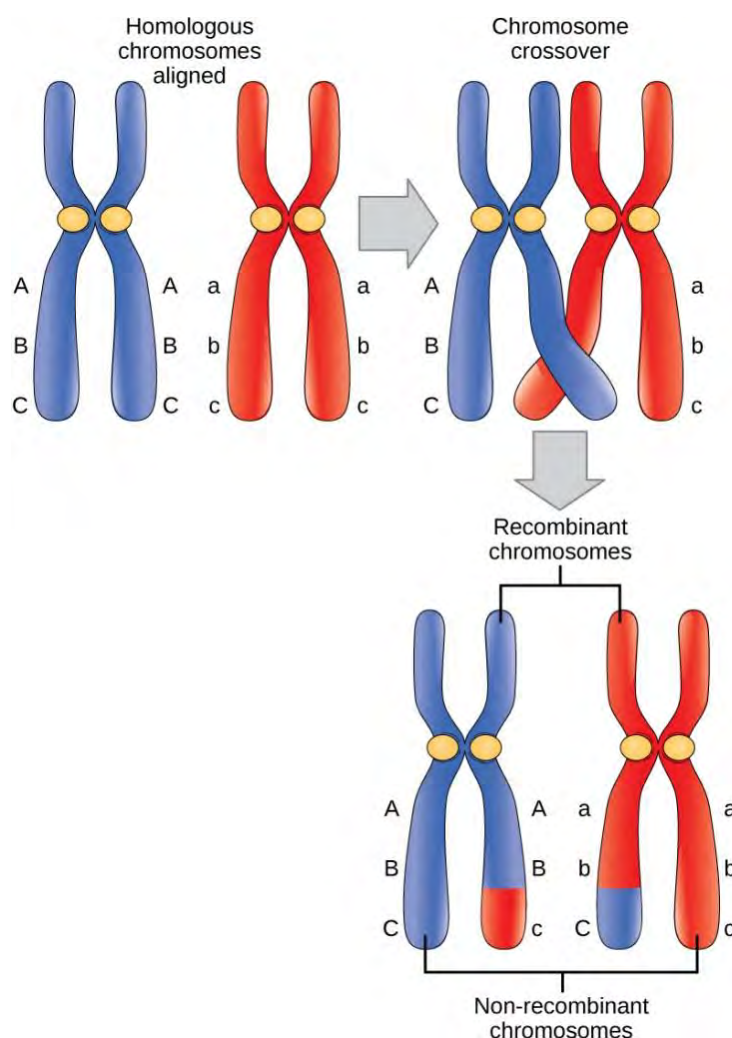
Figure 8.26 This illustration shows the effects of crossing over; the blue chromosome came from the individual's father, and the red chromosome came from the individual's mother. (credit: Clark et al./ Biology 2E OpenStax)

Prometaphase I

The key event in prometaphase I is the attachment of the microtubules to each sister chromatid's kinetochore proteins (Figure 8.25). The microtubules assemble from centrosomes at opposite poles of the cell and grow toward the middle of the cell. Homologous chromosomes are still held together at the chiasma. In addition, the nuclear membrane has broken down entirely.

Metaphase I

During metaphase I, the homologous chromosomes are arranged in the center of the cell, a region called the metaphase plate. Each tetrad is attached to microtubules from both poles. Within the tetrad, one homologous chromosome is attached at one pole, and the other homologous chromosome is attached to the opposite pole. The orientation or arrangement of each homologous pair on the metaphase plate is random.

This randomness of how the chromosomes align at the metaphase plate, called **independent assortment**, also generates genetic variation in offspring. Using humans as an example, the female provides one set of 23 maternal chromosomes via the egg or ova. The male provides the other set of 23 paternal chromosomes in the sperm which fertilizes the egg. In metaphase I, these pairs line up at the midway point between the two poles of the cell. The arrangement of the tetrads at the metaphase plate is random. This is because a microtubule is just as likely to attach to a maternal chromosome as it is to attach to a paternally inherited chromosome. Thus, any maternally inherited chromosome may face either pole. Likewise, 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. Each tetrad has two possible orientations; thus, the potential 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 crossing over. Given these two mechanisms, it is highly unlikely that any two haploid cells resulting from meiosis will have the same genetic composition (Figure 8.27).

Anaphase I

In anaphase I, the spindle fibers pull the linked homologous chromosomes apart. Once the homologous chromosomes are separated, one chromosome, in its duplicated state, is slowly pulled towards one pole while the other is pulled to the opposite pole. The sister chromatids that make up each chromosome remain tightly bound together at the centromere.

Telophase I

In telophase I, the separated chromosomes arrive at opposite poles. Other events that may occur in telophase depend on the species. In some organisms, including animal cells, the chromosomes decondense and the nuclear envelopes reform in telophase I. In other organisms, such as some protists, cytokinesis occurs without the reformation of the nuclei.
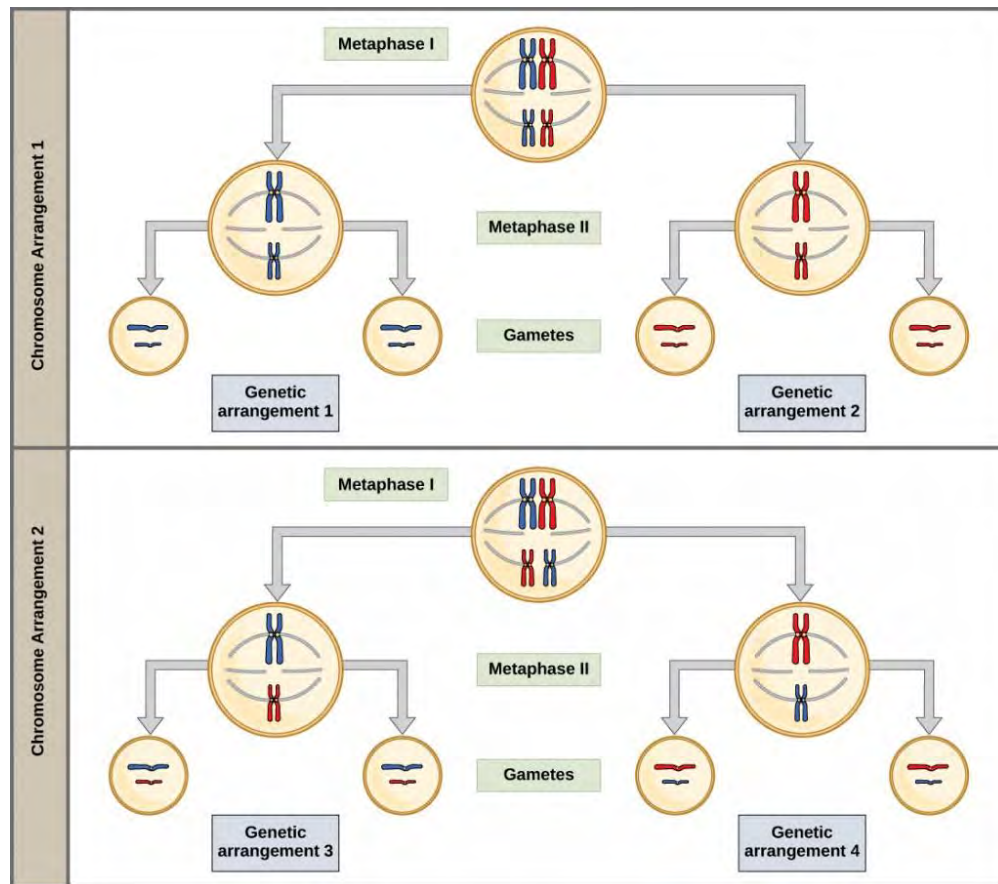
Figure 8.27 demonstrates independent assortment in metaphase I. (credit: Clark et al./ Biology 2E OpenStax)

Cytokinesis I

In nearly all species, cytokinesis I separate the cell contents by either a cleavage furrow in animals and some fungi, or a cell plate in plant cells. The cell plate will ultimately lead to the formation of a cell wall between the two new plant cells. At this point, each daughter cell is considered haploid; each cell contains only one set of chromosomes. Each of the chromosomes found in the daughter cells is in the duplicated state, meaning each chromosome consists of two sister chromatids that are still attached to each other. Although in interphase, the sister chromatids were exact copies of one another, they are no longer identical at this stage because of the process of crossing over.

In some species, cells enter a brief interphase, or **interkinesis**, before entering meiosis II. Interkinesis lacks an S phase, so chromosomes are not duplicated. The two haploid cells produced in meiosis I go through the events of meiosis II in synchrony. During meiosis II, the sister chromatids within the two daughter cells separate, forming four new haploid gametes. The mechanics of meiosis II are similar to mitosis, except that each dividing cell has only one set of homologous chromosomes, each consisting of two sister chromatids.

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

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Meiosis II

In meiosis II, the connected sister chromatids will be split and separated into four haploid cells. Let's take a closer look at the events of meiosis II, which begins with prophase II.

Prophase II – Prometaphase II

In prophase II, if the chromosomes decondensed in telophase I, they condense again. If nuclear envelopes were formed, they once again break down. The centrosomes once again 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's kinetochore attaches to microtubules from the opposite poles (Figure 8.28).

Metaphase II – Anaphase II

In metaphase II, the sister chromatids are completely condensed and align on the metaphase plate. In anaphase II, the sister chromatids are pulled apart by the spindle fibers and move toward opposite poles (Figure 8.28).

Telophase II – Cytokinesis II

In telophase II, the chromosomes, now in the unduplicated state, arrive at opposite poles and begin to decondense. Nuclear envelopes now form around the chromosomes. Cytokinesis II separates the two cells into four genetically unique haploid cells (Figure 8.27). At this point, the newly produced cells are haploid and genetically unique because of the crossing over and independent assortment.
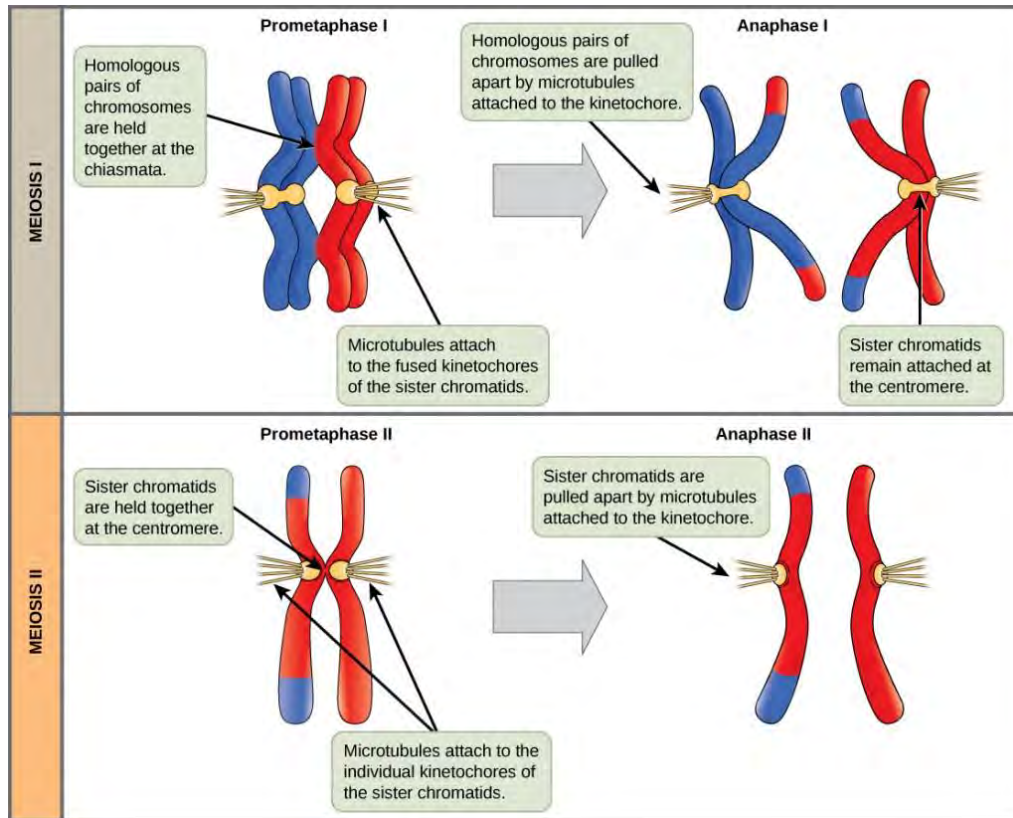
Figure 8.28 In prometaphase I, microtubules attach to the fused kinetochores of homologous chromosomes. In anaphase I, the homologous chromosomes are separated. In prometaphase II, microtubules attach to individual kinetochores of sister chromatids. In anaphase II, the sister chromatids are separated. (credit: Clark et al./ Biology 2E OpenStax)

Comparing Meiosis and Mitosis

Mitosis and meiosis are both necessary processes of the eukaryotic cell cycle. These processes share some similarities, but also exhibit several important and distinct differences that lead to very different outcomes (Figure 8.29). Mitosis is a process where one single diploid cell divides and produces two new genetically identical daughter cells.

On the other hand, meiosis is a process that begins with one diploid cell, which then goes through two rounds of chromosome divisions. The four daughter cells produced at the end of meiosis are genetically unique because of processes like crossing over and independent assortment. Each of the daughter cells produced during meiosis is haploid. Keep in mind haploid cells each contain only one chromosome set, which is half of the original chromosome number.

In humans, cells produced by mitosis will function in different parts of the body and are essential for growth and/or replacing dead or damaged cells. Cells produced by meiosis are used for organismal reproduction.

Check your knowledge

In the following list, decide if the event occurs in mitosis, meiosis, or both.
- Crossing over
- One DNA replication
- End in haploid cells
- Nucleus degrades
- Cytokinesis
- Homologous chromosomes align on the metaphase plate

Answers: Meiosis only, Both, Meiosis only, Both, Both, Meiosis only

	PROCESS					OUTCOME
	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 8.29 Meiosis and mitosis are both preceded by one round of DNA replication; however, meiosis includes two nuclear divisions. (credit: Clark et al./ Biology 2E OpenStax)

CONCEPTS 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. Meiosis is the process used to produce haploid cells. 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 genetically unique haploid daughter cells. During meiosis, variation in the daughter cells is introduced because of crossing over in prophase I and independent assortment in metaphase I.

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 chromosomes as the original cell. Meiotic divisions are two nuclear divisions that produce four haploid daughter cells that have half as many chromosomes as the original parent cell. 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.

Exercises

1. Meiosis produces _____ daughter cells.
   a. two haploid
   b. two diploid
   c. four haploid
   d. four diploid
2. At which stage of meiosis are sister chromatids separate from each other?
   a. prophase I
   b. prophase II
   c. anaphase I
   d. anaphase II
3. A part of meiosis that is similar to mitosis is _____.
   a. meiosis I
   b. anaphase I
   c. anaphase II
   d. interkinesis
4. If a somatic muscle cell of an organism contains 32 chromosomes, how many would you find in a gamete?
   a. 8
   b. 16
   c. 32
   d. 64
5. Explain how the independent assortment of homologous chromosomes during metaphase I contribute to variation in gametes produced by meiosis.
6. In what ways is meiosis II similar to and different from mitosis of a diploid cell?

Answers

1. (c)
2. (d)
3. (c)
4. (b)
5. Random alignment leads to new combinations of traits. The chromosomes that were initially 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.
6. 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). Also, each chromosome consists of two sister chromatids that will be pulled apart. The two divisions are different because in meiosis II there is 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.

Glossary

allosome: chromosomes that play a role in sex determination

autosome: any non-allosome

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

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

egg (ovum): the female gamete; a haploid cell

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

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

germline cell: specialized cell line that produces gametes, such as eggs or sperm

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

homologous chromosomes: the randomness of how the homologous chromosome pairs align at the metaphase plate during metaphase I of meiosis I

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

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

locus: the position of a gene on a chromosome

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

sperm: the male gamete; a haploid cell

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

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

zygote: a fertilized egg produced when a sperm and egg fuse

8.6 Errors in Meiosis

Inherited chromosomal disorders can occur when mistakes happen during meiosis. Chromosome disorders can be divided into two categories: abnormalities in chromosome number and chromosome structural rearrangements. Chromosomal disorders are characteristically noticeable and often fatal. We will look at how errors occur during meiosis and the impact this has on an individual's health and homeostasis.

Disorders in Chromosome Number

Chromosomal abnormalities in humans can be detected by first isolating chromosomes and then observing them using a microscope. A **karyotype** is the number and appearance of an individual's chromosomes, including their length, banding pattern, and centromere position.
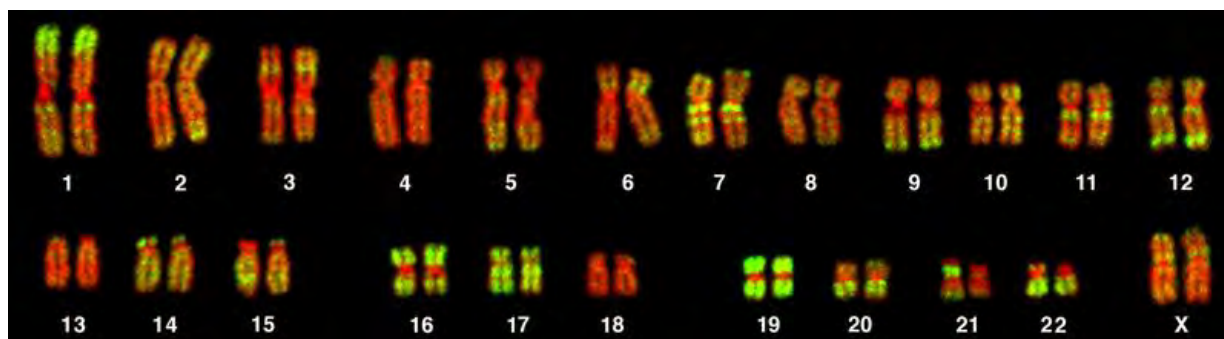
Figure 8.30 This karyogram shows the chromosomes of a female human immune cell during mitosis. (credit: Andreas Bolzer, et al / Biology 2E OpenStax)

To observe an individual's karyotype, a person's cells, such as their white blood cells, are first collected from a blood sample or other tissue sample. The isolated cells are stimulated to begin mitosis. A chemical is then applied to the cells to arrest mitosis during metaphase, and the cells are then fixed to a slide. Chromosomes are stained with one of several dyes to better visualize the distinct and reproducible banding patterns of each homologous chromosome pair. An experienced medical professional can identify each band, size, and centromere location. To generate the **karyogram**, the chart that shows an individual's karyotype, homologous pairs of chromosomes are manually aligned in numerical order from longest to shortest (Figure 8.30).

Chromosomal Number Disorders

Of all chromosomal disorders, abnormalities in chromosome number are the most obvious when looking at a karyogram. Duplicating or losing entire chromosomes can occur through a process called nondisjunction. **Nondisjunction** occurs when homologous chromosome pairs or sister chromatids fail to separate during meiosis I or meiosis II. Misaligned chromosomes, chromosome pairs not forming tetrads, or failure of the microtubules to attach and then move chromosomes to opposite poles can all cause nondisjunction to occur. The risk of nondisjunction occurring increases with the parents' age.

Nondisjunction can occur during either meiosis I or II (Figure 8.32). If homologous chromosomes fail to separate during meiosis I, 100% of the gametes will be affected. In this case, two gametes will lack a particular chromosome, and two gametes will have additional copies of that particular chromosome (Figure 8.31). If sister chromatids fail to separate during meiosis II, there is a chance that 50% of the gametes will contain the correct number of chromosomes (Figure 8.31). Regardless of whether nondisjunction happens in meiosis I or II, some gametes, if not all, will have the wrong chromosome number. If those gametes participate in fertilization, it will result in an individual that has a genetic condition.

Figure 8.31 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. (credit: Clark et al. / Biology 2E OpenStax)
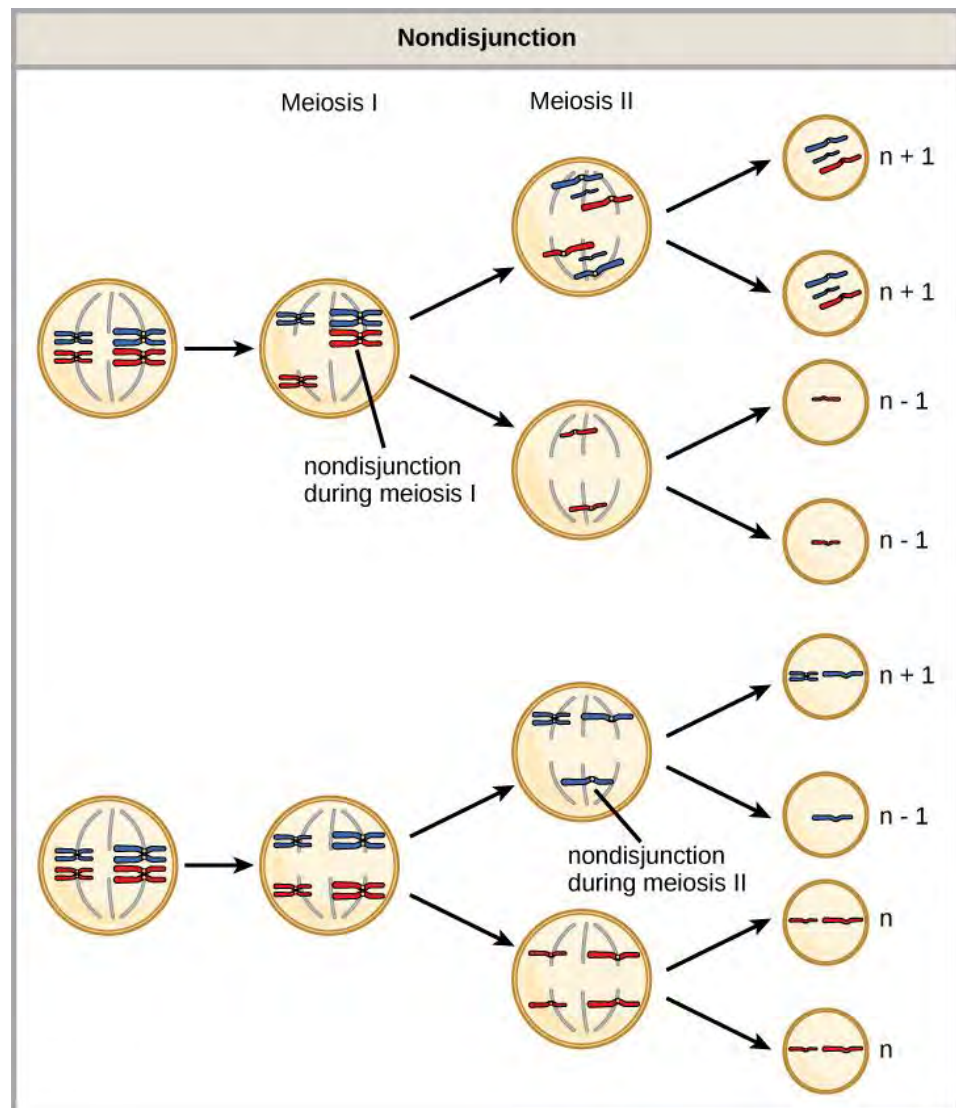
Aneuploidy

Scientists call an individual with the appropriate number of chromosomes for their species **euploid**. In humans, euploidy corresponds to 22 pairs of autosomes and one pair of allosomes. An individual with an error in chromosome number is described as **aneuploid**, a term that includes **monosomy**, losing one chromosome, or **trisomy**, gaining an extra chromosome.

Trisomy 21, or Down syndrome, is a condition that occurs when an individual has a third copy of chromosome 21. Down syndrome is characterized by short stature, stunted digits, facial distinctions that include a broad skull and large tongue, and significant developmental delays. The occurrence of Down syndrome can be correlated with parental age. Older parents are more likely to produce fetuses carrying the trisomy 21 genotype (Figure 8.32). Turner syndrome, which is characterized by the presence of only one X allosome, is an example of a monosomy condition. Females that have Turner syndrome are typically sterile and cannot reproduce.

Figure 8.32 The incidence of having a fetus with trisomy 21 increases dramatically with maternal age. (credit: Clark et al. / Biology 2E OpenStax)
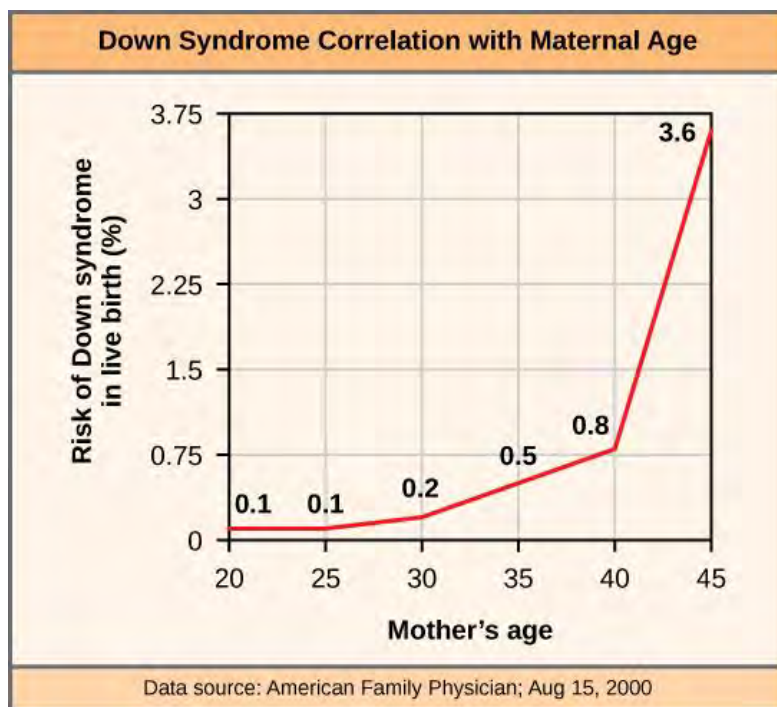
CONCEPTS IN ACTION- Visualize the addition of a chromosome that leads to Down syndrome in this video simulation.

Polyploidy

We call an individual with more than the correct number of chromosome pairs a **polyploid**. For instance, fertilizing an abnormal diploid egg with a normal haploid sperm would yield a polyploid. Polyploid animals are extremely rare, with only a few examples including some flatworms, crustaceans, amphibians, fish, and lizards. Polyploid animals are sterile because meiosis cannot occur normally. Rarely, polyploid animals can reproduce asexually when an unfertilized egg divides mitotically to produce offspring. In contrast, polyploidy is very common in plants, and polyploid plants tend to be larger and more robust than the euploids of their species (Figure 8.33).

Figure 8.33 As with many polyploid plants, this triploid orange daylily (*Hemerocallis fulva*) is particularly large and robust and grows flowers with triple the number of petals of its diploid counterparts. (credit: Steve Karg / Biology 2E OpenStax)

Chromosomal Structural Rearrangements

In addition to errors in chromosome number, numerous structural chromosomal rearrangements can occur. These include duplications, deletions, inversions, and translocations.

Duplications and Deletions

In chromosomal **duplications**, a part of a chromosome is duplicated. The duplicated DNA can then either be inserted into a different position on the same chromosome or a completely different chromosome (Figure 8.34). In chromosomal **deletions**, a part of the chromosome is lost or removed (Figure 8.34).
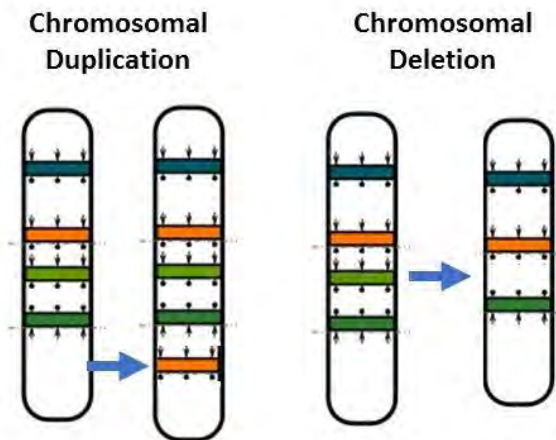
Figure 8.34 Chromosomal arrangements include both duplications and deletions. (credit: Modified by Elizabeth O'Grady original work of Guy Leonard Wikimedia Commons)

Both duplications and deletions often produce offspring that survive but exhibit physical and mental abnormalities. A deletion of a region on chromosome 11 leads to a condition called 11q terminal deletion disorder or Jacobsen syndrome. Jacobsen syndrome involves distinct changes to facial features as well as heart and bleeding defects. A gene duplication on chromosome 17 leads to a condition known as Hereditary motor and sensory neuropathy or Charcot-Marie-Tooth (CMT) disorder. CMT results in individuals that have nervous system issues involving nerves that carry and deliver information to an individual's legs, arms, hands, and feet.

Inversions

A chromosome **inversion** is a detachment, 180° rotation, and reinsertion of part of a chromosome (Figure 8.35). Inversions may occur in nature as a result of damaged or cut DNA or from transposable elements, special DNA sequences capable of rearranging chromosome segments. Unless a gene sequence is disrupted, inversions are likely to have minor effects. However, inversions that disrupt genes can result in abnormally high or low levels of specific proteins.
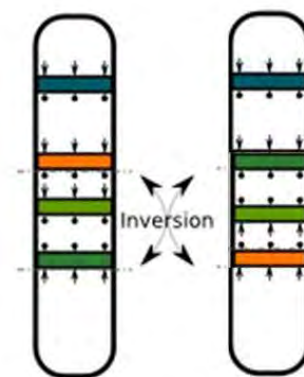
Figure 8.35 An inversion is an example of a chromosomal arrangement. (credit: Modified by Elizabeth O'Grady original work of Guy Leonard Wikimedia Commons)

Translocations

A **translocation** occurs when a segment of genetic material breaks from one chromosome and reattaches to another chromosome or a different part of the same chromosome. Translocations can either have minimal to no impact or have devastating effects depending on how the positions of genes are altered. Notably, specific translocations have occurred with several cancers and with schizophrenia. Reciprocal translocations result from exchanging chromosome segments between two nonhomologous chromosomes such that there is no genetic information gain or loss (Figure 8.36).
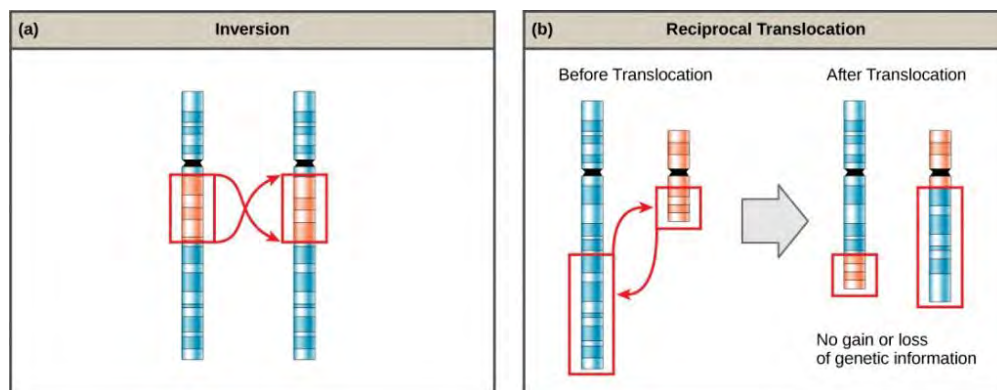
Figure 8.36 (a) chromosomal inversion   (b) reciprocal translocation (credit: modification of work by National Human Genome Research Institute / Concepts of Biology OpenStax)

Section Summary

A karyotype is the number and appearance of an individual's chromosomes, including their length, banding pattern, and centromere position. The number, size, shape, and banding pattern of chromosomes make them easily identifiable in a karyogram. A karyogram allows for the assessment of many chromosomal abnormalities. Disorders in chromosome number are typically lethal to the embryo, although a few trisomy and monosomy conditions are viable. Chromosome number abnormalities can occur because of nondisjunction, the failure of homologous chromosomes or sister chromatids to separate properly. Chromosomal structural abnormalities may also occur and include segments of the chromosome being duplicated, deleted, inverted, or translocated. All of these aberrations can result in problematic phenotypic effects.

Exercises

1. The genotype XXY would be:
    a. A monosomy condition
    b. A trisomy condition
    c. A deletion
    d. A polyploid

2. Nondisjunction is:
    a. failure of homologous chromosomes to separate properly
    b. is an example of a chromosomal rearrangement
    c. only occurs during meiosis II
    d. involves only autosomes

3. Polyploidy often happens in animal cells.
    a. True
    b. False

4. Explain what a karyotype is and why a karyogram helps identify different genetic conditions.

Answers

1. (b)
2. (a)
3. (b)
4. A karyotype is the number and appearance of an individual's chromosomes, including their length, banding pattern, and centromere position. Abnormalities in chromosome numbers are obvious when looking at a karyogram because it shows if an extra chromosome is present of whether an entire chromosome has been lost.

Glossary

aneuploid: an individual with an error in chromosome number; includes deletions and duplications of chromosome segments

deletion: a part of a chromosome is lost or removed

duplication: a part of a chromosome is duplicated and either inserted into a different position on the same chromosome or a completely different chromosome

euploid: an individual with the appropriate number of chromosomes for their species

inversion: the detachment, 180° rotation, and reinsertion of a chromosome arm

karyogram: the photographic image of a karyotype

karyotype: the number and appearance of an individual's 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

Footnotes

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.

Chapter 9: Introduction to Patterns of Inheritance

Figure 9.1 Experimenting with thousands of garden peas, Mendel uncovered the fundamentals of genetics. (credit: modification of work by Jerry Kirkhart / Biology 2E OpenStax)

Genetics is the study of heredity, the ability to pass on traits from one generation to the next. Johann Gregor Mendel set the framework for genetics long before chromosomes or genes had been identified. Mendel selected a simple biological system, the common garden pea plant, and conducted methodical, quantitative analyses using large sample sizes. Mendel's work identified the fundamental principles of heredity, and as a result, he is often referred to as the "father of genetics."

Today, the work put forth by Mendel forms the basis of classical, or Mendelian, genetics. It is important to note that not all traits are passed from parents to offspring according to Mendelian genetics. However, Mendel's experiments serve as an excellent starting point for thinking about how inheritance works.

9.1 Gregor Mendel and Genetic Crosses

Learning objectives

By the end of this section, you will be able to:

- *Explain the history of Mendel and his work*
- *Explain the difference between characteristics and traits*
- *Understand the difference between continuous and discontinuous variation*
- *Describe the expected outcomes of different Mendelian crosses*
- *Be able to define and explain all bolded terms*

Johann Gregor Mendel (1822–1884) (Figure 9.2) was a lifelong learner, teacher, scientist, and man of faith. As a young adult, he joined the Augustinian Abbey 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 started studying inheritance patterns in honeybees and plants. His research would span well over a decade, and much of what he found became a cornerstone for the field of genetics.

Figure 9.2 Johann Gregor Mendel set the framework for the study of genetics. (credit: Clark et al. / Biology 2E OpenStax)

Ultimately, Mendel settled on pea plants as his primary model system. Pea plants were an ideal model organism for several reasons. First, pea plants grow to maturity within one season, meaning that several generations could be evaluated over a relatively short time. Second, large quantities of pea plants could be cultivated simultaneously. This allowed Mendel to perform quantitative statistical tests that supported his results.

Pea plants also have seven different heritable characteristics that could be studied. A **characteristic** is a physical feature of an organism. The characteristics Mendel studied in pea plants were stem length, flower color and position, seed texture and color, and pod texture and color. Each of these characteristics has two easily identifiable traits (Figure 9.3). A **trait** is defined as variation in the physical form of a characteristic that is heritable. For example, pea plants produce either yellow or green seeds. The seeds are either wrinkled or smooth. These different variations, yellow or green, or wrinkled or smooth, are referred to as traits.

Figure 9.3 The seven characteristics Mendel studied in pea plants, and the two traits for each. (credit: Modified by Elizabeth O'Grady original work of Mariana Ruiz / Public Domain)

In 1865, Mendel presented the results of his experiments, which were based on nearly 30,000 pea plants, to the local Natural History Society. In 1866 he published his work, *Experiments in Plant Hybridization,*[1] in the proceedings of the Natural History Society of Brünn. Although he published his findings, Mendel's work went virtually unnoticed. At this time, the scientific community thought, incorrectly, that the process of inheritance involved a blending of parental traits. The **blending hypothesis of inheritance** stated that when two individuals made an offspring, their original parental traits were lost because their traits blended together when the offspring was formed. For example, if two horses with different coat colors, white and black, were mated, the coat colors would blend together, resulting in an offspring with an intermediate grey color. Once blended, the colors, black and white, would not appear again in the offspring's future generations.

We now know that this is not the case. Many people supported the blending hypothesis because of what is commonly referred to as continuous variation. **Continuous variation** is when a population displays a wide range of values for a character, such as height in humans. We now know this occurs when a character is influenced by several different genes. Continuous variation can also be observed with human characteristics such as skin, hair, and eye color. Offspring often appear to be a "blend" of their parents' traits; however, this is not completely true and will be discussed later in section 9.3.

Mendel worked with traits that show discontinuous variation. **Discontinuous variation** is when each individual exhibits one of two easily distinguishable traits, such as violet or white flowers. Mendel's decision to use traits that show discontinuous variation allowed him to see experimentally that offspring were not a result of "blending." Mendel hypothesized that each trait was kept distinct from one another and, as a result, could be passed on and reappear in future generations. 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. 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 Model System

As mentioned earlier, Mendel studied inheritance using the common garden pea plant, *Pisum sativum*. This species of plant naturally self-fertilizes itself, such that pollen encounters ova (eggs) within individual flowers. The flower petals remain sealed tightly until after pollination, preventing pollination from other plants. The result is highly inbred, or "true-breeding," pea plants. These plants always produce offspring that look like the parent plant. By experimenting with true-breeding pea plants, Mendel avoided the appearance of unexpected traits in offspring, which might occur if the plants were not true-breeding.

Mendelian Crosses

Mendel performed **hybridizations**, or **cross-fertilizations**, which involve mating two true-breeding individuals that have different traits. For example, Mendel would take pollen from a true-breeding violet-flowered plant and use it to fertilize the egg of a true-breeding white-

flowered plant. In this cross, the true-breeding violet flower plant and true-breeding white-flowered plant are called the parental generation, or **P generation** (Figure 9.4). After each cross, Mendel collected the seeds belonging to the P generation and grew them the following season.

These offspring were called the first filial generation, or the **F_1 generation**. Filial means offspring, daughter or son. Once Mendel examined the characteristics in the F_1 plants, he allowed them to self-fertilize naturally. He then collected and grew the seeds from the F1 plants to produce the second filial generation, or **F_2 generation**. Mendel's experiments extended beyond the F_2 generation to the F_3 and F_4 generations, and so on. It was the ratio of characteristics in the P, F_1, and F_2 generations that were by far the most intriguing and became the basis for Mendel's hypotheses.

Figure 9.4 Mendel's experiments involved cross-fertilizing true-breeding plants with different traits, such as purple-flowered plant and a white-flowered plant. These plants are the P generation. Their offspring, the F_1 generation, were allowed to self-fertilize, resulting in the F_2 generation. (credit: Clark et al. / Biology 2E OpenStax)

Cross between True-breeding Pea Plants

P generation

×

Violet flowers   White flowers

Hybridization of true-breeding plants

F_1 generation

All hybrid progeny have violet flowers.

Self-fertilization of hybrid plants

F_2 generation

705 Violet flowers   224 White flowers
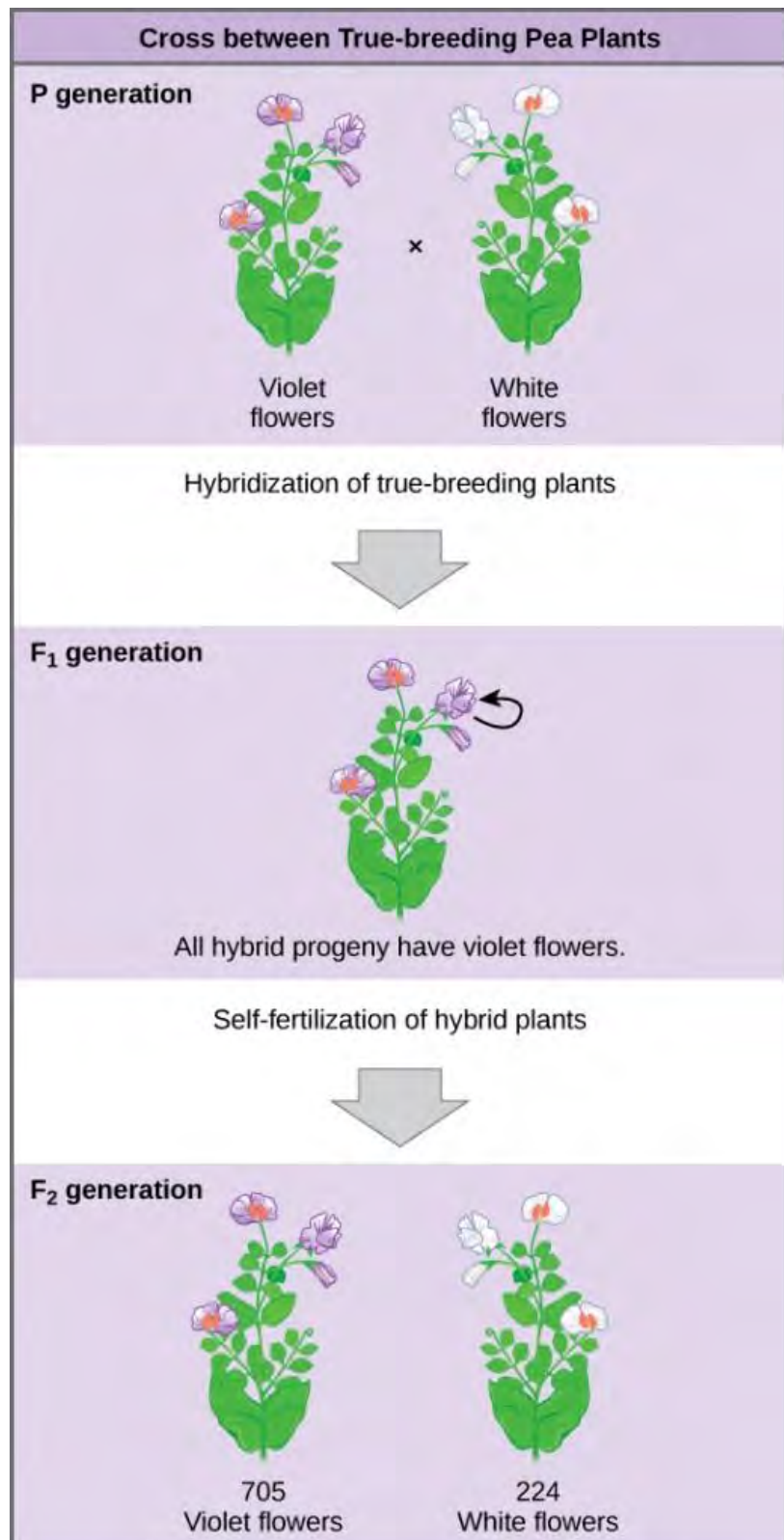
Section Summary

The blending hypothesis of inheritance stated that when two individuals made an offspring, their original parental traits were lost because their traits blended together when the offspring was formed. We now know that this is not the case. Many people supported the blending hypothesis because of what is commonly referred to as continuous variation. Continuous variation occurs when a character, such as height in humans, is influenced by several different genes. Mendel worked with traits that show discontinuous variation. Discontinuous variation is when each individual exhibits one of two easily distinguishable traits, such as violet or white flowers. Mendel's decision to use traits that show discontinuous variation allowed him to see experimentally that offspring were not a result of "blending." Mendel studied inheritance using the common garden pea plant, *Pisum sativum*. This species of plants naturally self-fertilizes itself, always producing offspring that look like the parent plant. By experimenting with true-breeding pea plants, Mendel avoided the appearance of unexpected traits in offspring. Mendel performed hybridizations, or cross-fertilizations, which involve mating two true-breeding individuals that have different traits.

Exercises

1. Height in humans is an example of:
    a. Discontinuous variation
    b. Continuous variation
    c. The blending hypothesis
    d. Both b and c
2. Describe one of the reasons that made the garden pea an excellent choice of a model system for studying inheritance.

Answers

1. (b)
2. 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.

Glossary

blending hypothesis of inheritance: states that when two individuals made an offspring, their original parental traits were lost because their traits blended together when the offspring was formed

characteristic: different heritable, physical features

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 significant differences between them

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/cross-fertilization: the process of mating two individuals that differ, to achieve a certain characteristic in their offspring

P: the parental generation in a cross

trait: a variation in an inherited characteristic

Footnotes

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 http://www.mendelweb.org/Mendel.plain.html]

9.2 Laws of Inheritance

To fully examine each characteristic, Mendel generated large numbers of F_1 and F_2 plants, reporting results from 19,959 F_2 plants alone. His findings, based on a large sample size, were both reproducible and consistent. Furthermore, Mendel used quantitative statistical analysis to verify his results, making it difficult to refute his findings. Let's take a closer look at some of Mendel's results.

Mendel's Data and Results

What were Mendel's results when he crossed plants with different flower colors? First, Mendel confirmed that he was using plants that were true-breeding for white or violet flower color. Mendel found that regardless of the number of generations he looked at, true breeding white-flowered plants that self-fertilized always produced white-flowered offspring. The same result was confirmed for true-breeding violet-flowered plants; they always produced offspring with violet flowers. Mendel also confirmed that, other than flower color, the pea plants were physically identical. This was important because it confirmed that the two varieties of pea plants only differed with respect to one trait, the flower color.

Once these results were validated, Mendel performed a cross between a plant with violet flowers and a plant with white flowers. After gathering and planting the seeds 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. In other words, the parental traits were expected to blend in the offspring. Instead, Mendel's results demonstrated that the violet flower trait was retained and the white flower trait had disappeared entirely 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 (Figure 9.4). This was a ratio of 3.15 violet flowers to one white flower, or approximately 3:1 ratio. 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.

Why did Mendel repeatedly obtain a 3:1 ratio in his crosses? To understand how Mendel deduced the basic mechanisms of inheritance that lead to such ratios, we must first review probability.

Probability Basics

Probabilities are mathematical measures of likelihood. The empirical probability of an event is calculated by dividing the number of times the event occurs by the total number of opportunities for the event to occur. It is also possible to calculate theoretical probabilities by dividing the number of times that an event is *expected* to occur by the number of times that it could occur. Empirical probabilities come from observations, like those of Mendel. Theoretical probabilities, on the other hand, come from knowing how the events are produced and assuming that the probabilities of individual outcomes are equal. A probability of one for some event indicates that it is guaranteed to occur, whereas a probability of zero indicates that it is guaranteed not to occur. An example of a genetic event is a round seed produced by a pea plant.

In one experiment, Mendel demonstrated that when one true-breeding parent has round seeds, and one true-breeding parent has wrinkled seeds, the probability of the F_1 offspring having "round seeds" was one. When the F_1 plants were subsequently self-crossed, the probability of any given F_2 offspring having round seeds was now three out of four. In other words, in a large population of F_2 offspring chosen at random, 75 percent were expected to have round seeds, whereas 25 percent were expected to have wrinkled seeds. Using large numbers of crosses, Mendel was able to calculate probabilities and use these to predict the outcomes of other crosses. The fact that Mendel confirmed his work with statistical analysis made it relatively easy for others to repeat his experiments and verify his results.

Mendel's Laws of Inheritance

Mendel simplified the results of his pea plant experiments into four hypotheses, some of which are sometimes called "laws." These hypotheses or laws describe the basis of inheritance in diploid organisms, as understood by Mendel.

Mendel first hypothesized that for each characteristic, plants have two copies of the heritable trait, one from each parent. Today, we use the word **gene** to describe the basic unit of heredity. Based on what he saw in pea plants, Mendel recognized that different versions of genes must exist for the same characteristic. These different gene versions are called **alleles**. For example, because pea plants could have either violet or white flowers, he argued that there had to be at least two different alleles for flower color. Mendel hypothesized that it was possible for a plant to either have two identical alleles or to have two different alleles for a specific gene. Individuals that have two identical alleles are said to be **homozygous**. Mendel's true-breeding violet-flowered and white-flowered pea plants are both homozygous; they have two identical alleles, both resulting in either violet or white flower color. When individuals have two different alleles

for a gene, they are said to be **heterozygous**. For example, a plant that has one allele for violet flowers and one allele for white flowers is heterozygous for the characteristic of flower color.

Mendel suspected that each parent passed on only one of its two alleles to its offspring. For example, both the male and female gamete would each only carry one copy of an allele for flower color. When fertilization occurred, the new zygote would then have two alleles for flower color, just like the parents that produced it.

Mendel found that when he crossed true-breeding violet-flowered pea plants and true-breeding white-flowered pea plants, all the offspring were violet. The violet flower color is therefore considered dominant. An allele is considered **dominant** when it is expressed in heterozygous individuals. Mendel's F_1 pea plants were heterozygous because they had one violet-flowered allele and one white-flowered allele. Violet flower color was expressed in this generation, making that the dominant allele. The white-flowered allele is therefore considered recessive. An allele is considered **recessive** if it is masked (does not appear) in the F_1 offspring. The recessive trait does, however, reappear in the F_2 generation. Mendel hypothesized that if he saw the recessive trait being expressed, it meant that the plant did not have a dominant allele, rather they must carry two recessive alleles. He also suggested that because the recessive trait reappeared in the F_2 generation, this meant that the traits remained separate and not blended in the F_1 generation plants.

Based on his observations of the F_1 and F_2 generations, Mendel proposed the **law of segregation**. This law states that paired unit factors, today called genes, must segregate equally into gametes such that offspring have an equal likelihood of inheriting either gene. Recall that in meiosis, homologous chromosomes are separated into different haploid gametes arbitrarily (Figure 9.5). An individual's characteristics are a result of the genes carried on chromosomes. When a haploid gamete from one parent fertilizes a haploid gamete from another parent, a diploid offspring is formed. The diploid offspring has two copies of each chromosome, and therefore two copies of each gene, supporting Mendel's hypothesis.
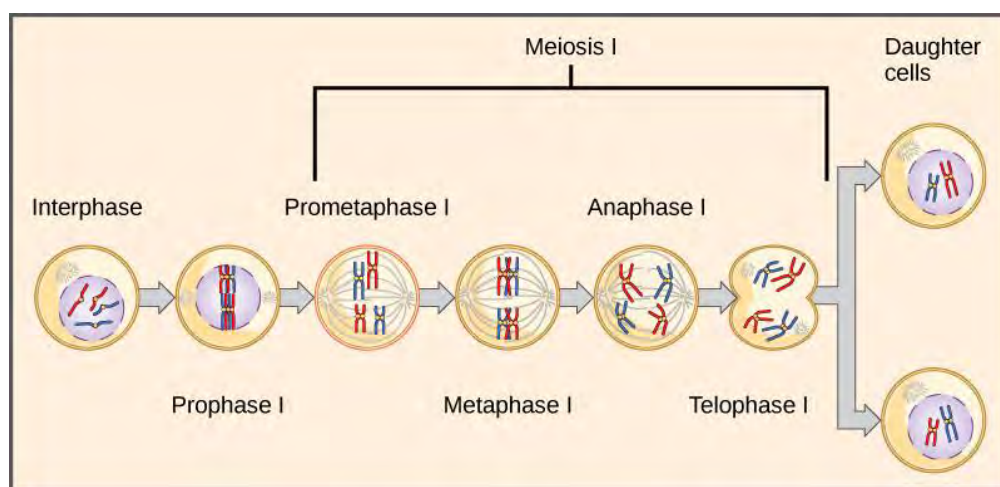
Figure 9.5 The random segregation into daughter nuclei that happens during the first division in meiosis supports Mendel's law of segregation. (credit: Fowler et al. / Concepts of Biology OpenStax)

Mendel's hypotheses were based on the physical characteristic that he could observe. An organism's observable physical traits are referred to as its **phenotype**; for example, violet or white flowers (Figure 9.6). Mendel could not examine an organism's genetic makeup. He made inferences on whether an organism was homozygous or heterozygous for a particular gene but could not provide genomic data that supported this. An organism's underlying genetic makeup is called its **genotype** (Figure 9.6). A genotype is usually denoted by using two of the same letters (Figure 9.6). The letter that is used is often the first letter of the dominant trait, but geneticists prefer to use letters that have distinct upper- and lower-case forms (P and p may be mistaken for each other, while B and b are more distinct). The genotype may be two upper case letters, two lower case letters, or an upper and a lower-case letter (BB, bb, or Bb).

9.6 Phenotype shows an organism's physical observable traits, whereas genotype is an organism's genetic makeup. (credit: Modified by Elizabeth O'Grady original work of Madeleine Price Ball)

What do the genotype letters represent? The P generation plants that Mendel used in his experiments were each homozygous for the trait he was studying, meaning that for a given gene, it had two identical alleles for that gene. Genotypes of individuals that have two identical alleles are represented by either two identical upper-case letters (BB) which represent homozygous dominant individuals, or two identical lower-case letters (bb) which represent homozygous recessive individuals. The dominant allele is capitalized, and the recessive allele is lower case. When P plants with contrasting traits, for example, violet flowers (BB) vs. white flowers (bb), were cross-fertilized, all offspring were heterozygous. Heterozygous plants have two different alleles, one violet and one white, from each corresponding parent. The heterozygous genotype is denoted by one upper-case letter and one lower-case letter (Bb). It is the phenotype that is observed in a heterozygous individual that determines which trait is dominant and which trait is recessive.

Monohybrid cross and Punnett Square

Mendel's cross-fertilization experiments demonstrate the difference between phenotype and genotype. When fertilization occurs between two true-breeding parents that differ in only one characteristic, the process is called a **monohybrid cross**.

To demonstrate a monohybrid cross, consider the case of true-breeding pea plants with yellow seeds versus green seeds. The dominant seed color is yellow; therefore, the parental genotypes were *YY* for the homozygous dominant plants with yellow seeds and *yy* for the homozygous

recessive plants with green seeds. A **Punnett square**, devised by the British geneticist Reginald Punnett, can be drawn that applies the rules of probability to predict the possible genotype outcomes of a genetic cross and their expected frequencies. To prepare a Punnett square, a table is drawn where all possible combinations of the parental alleles are listed along the top for one parent, and all possible combinations of the second parental alleles are listed on the left side of the table (Figure 9.7). This allows the alleles to be separated into separate boxes, which represent their meiotic separation into haploid gametes. The different combinations of egg and sperm are made in the boxes in the table to show which alleles are combining. Each box then represents the diploid genotype of a zygote, or fertilized egg, that could result from this fertilization event. Because each possibility is equally likely, genotypic ratios can be determined from a Punnett square. If the pattern of inheritance is known, the phenotypic ratios can be inferred as well. For a monohybrid cross of two true-breeding parents, each parent contributes one type of allele. In this case, only one genotype is possible. All F_1 offspring are heterozygous, *Yy,* and have yellow seeds because they have a dominant allele (Figure 9.7).
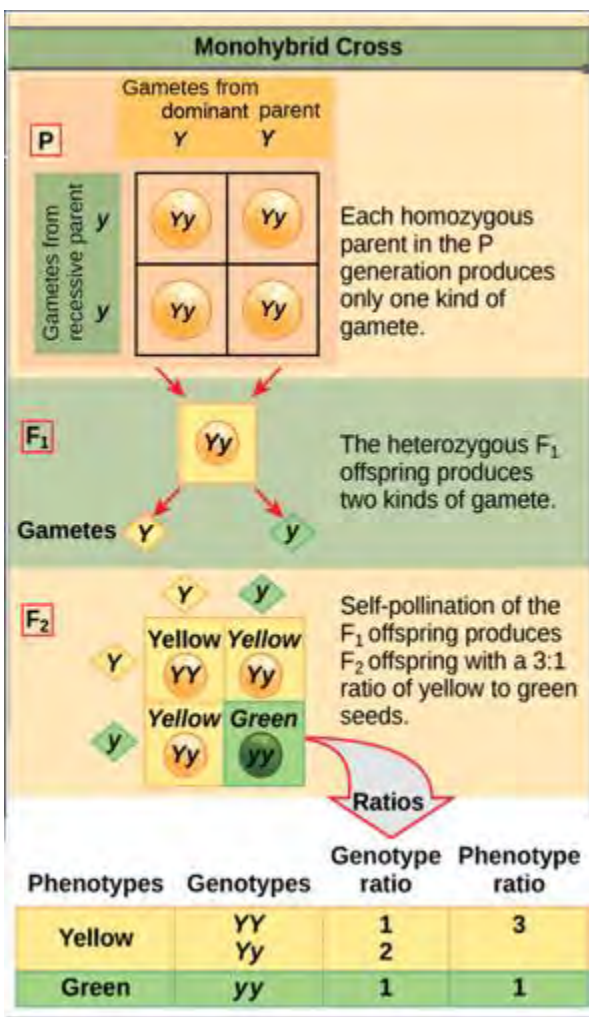
Figure 9.7 This Punnett square shows the cross between plants with yellow seeds and green seeds. The cross between the true-breeding P plants produces F_1 heterozygotes that can be self-fertilized. The self-fertilization of the F_1 generation can be analyzed with a Punnett square to predict the genotypes of the F_2 generation. Given an inheritance pattern of dominant–recessive, the genotypic and phenotypic ratios can then be determined. (credit: Modified by Elizabeth O'Grady original work of Clark et al. / Biology 2E OpenStax)

A self-cross of one of the *Yy* heterozygous F_1 offspring can also be represented in a Punnett square. Notice that there are two ways to obtain the *Yy* genotype: a *Y* from the egg and a *y* from the sperm, or a *y* from the egg and a *Y* from the sperm. Both possibilities must be counted. Because fertilization is a random event, we expect each combination to be equally likely and for the offspring to exhibit a ratio of *YY*:*Yy*:*yy* genotypes of 1:2:1 (Figure 9.7). Furthermore, the *YY* and *Yy* offspring all have yellow seeds and are phenotypically identical. Therefore, we expect the offspring to exhibit a phenotypic ratio of 3 yellow:1 green. In all the characteristics that Mendel observed, he found this ratio in every F_2 generation.

Mendel's law of independent assortment and Dihybrid cross

Mendel's **law of independent assortment** states that genes do not influence each other with regard to the sorting of alleles into gametes. It also states that every possible combination of alleles for every gene is equally likely to occur. The independent assortment of genes can be illustrated by the **dihybrid cross**, a cross between two true-breeding parents that express different traits for two characteristics. Consider the characteristics of seed color and seed texture for two pea plants. One pea plant has yellow, round seeds (*YYRR*), and is crossed with a different pea plant that has green, wrinkled seeds (*yyrr*). Because each parent is homozygous, the law of segregation indicates that the gametes for the green/wrinkled plant all are *yr*, and the gametes for the yellow/round plant are all *YR*. Therefore, the F$_1$ generation of offspring all are *YyRr* (Figure 9.8).
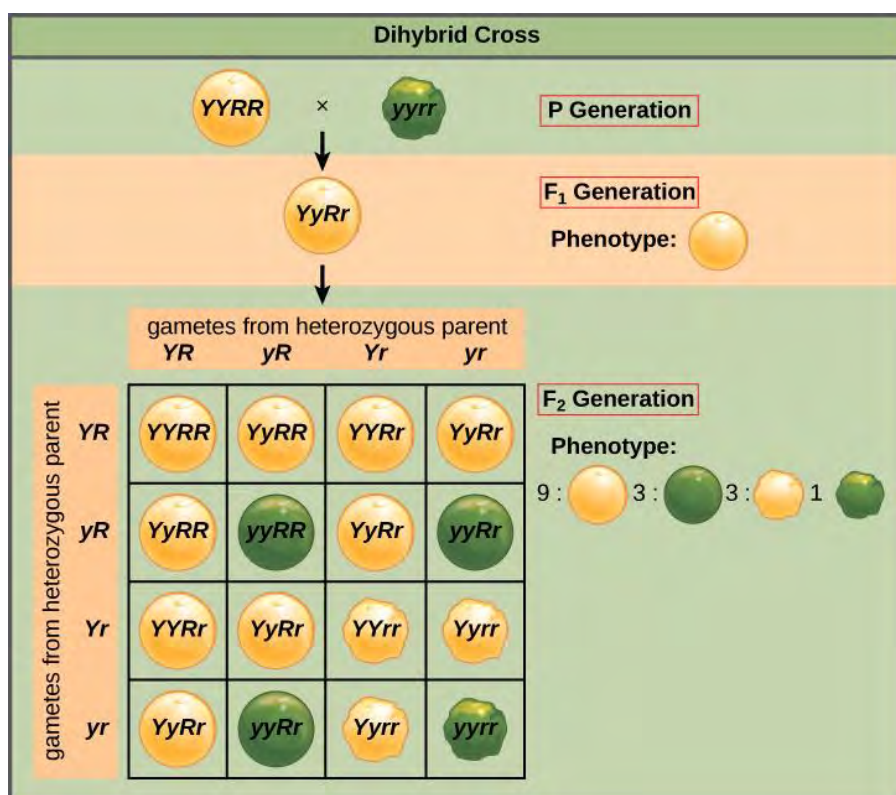
Figure 9.8 A dihybrid cross in pea plants involves the genes for seed color and texture. The P cross produces F$_1$ offspring that are all heterozygous for both characteristics. The resulting 9:3:3:1 F$_2$ phenotypic ratio is obtained using a Punnett square. (credit: Fowler et al. / Concepts of Biology OpenStax)

For the F$_2$ generation, the law of segregation requires that each gamete receive either an *R* allele or an *r* allele along with either a *Y* allele or a *y* allele. The law of independent assortment states that a gamete into which an *r* allele sorted would be equally likely to contain either a *Y* allele or a *y* allele. Thus, there are four equally possible gametes that can be formed when the *YyRr* heterozygote is self-crossed: *YR*, *Yr*, *yR*, and *yr*. Arranging these gametes along the top and left of a four × four Punnett square (Figure 9.8) gives us 16 equally likely genotypic

combinations. From these genotypes, we infer a phenotypic ratio of 9 round/yellow:3 round/green:3 wrinkled/yellow:1 wrinkled/green (Figure 9.8). These are the offspring ratios we would expect, assuming we performed the crosses with a large enough sample size. The law of independent assortment also indicates that a cross between yellow, wrinkled (*YYrr*), and green, round (*yyRR*) parents would yield the same F_1 and F_2 offspring as in the *YYRR* x *yyrr* cross.

The physical basis for the law of independent assortment can be explained by events that occur in meiosis I (Figure 9.9). Recall, during metaphase I of meiosis I the different homologous pairs line up arbitrarily on the metaphase plate, termed independent assortment. Which chromosome, paternal or maternal, will align on what side of the metaphase plate is unknown and leads to several different possible genetic arrangements (Figure 9.9). During anaphase I of meiosis I, homologous chromosomes are separated, and each gamete can contain any combination of both paternal and maternal chromosomes.
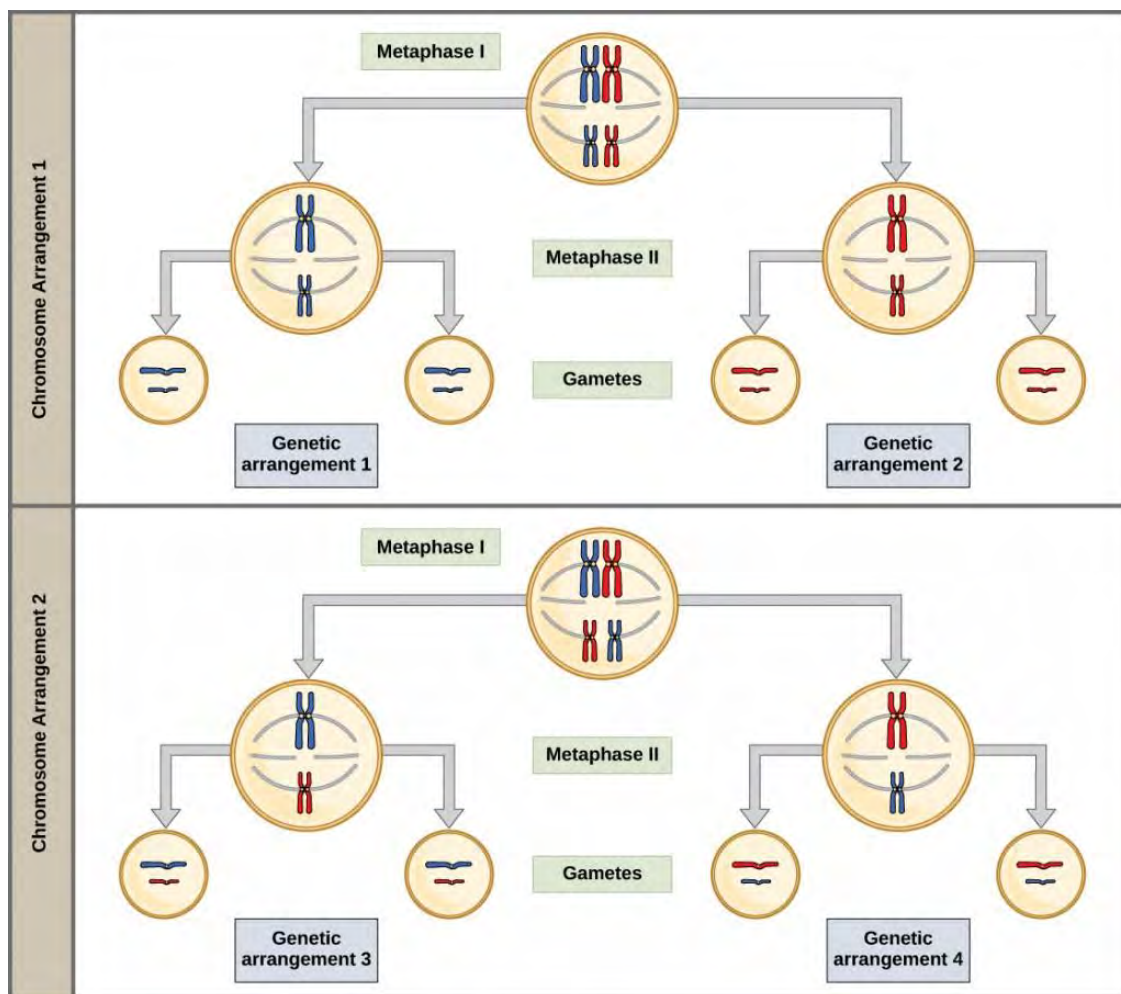
Figure 9.9 The random segregation into daughter nuclei that happens during the first division in meiosis can lead to a variety of possible genetic arrangements. (credit: Fowler et al. / Concepts of Biology OpenStax)

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.

Pedigrees

Mendel chose a model organism, the common garden pea plant, that he could easily manipulate through cross-fertilizations. This allowed him to observe and track different characteristics from one generation to the next. Humans also have characteristics that are genetically inherited. However, doing cross-fertilizations in humans is both unethical and impractical. Instead, geneticists can use a **pedigree** to study inheritance patterns of human genetic characteristics (Figure 9.10). A pedigree is chart used to study inheritance patterns of genetic characteristics.

How can a pedigree be used to study inheritance patterns? Let's look at an example of a recessive disorder, alkaptonuria, in which two amino acids, phenylalanine and tyrosine, are not properly metabolized (Figure 9.10). Individuals that have this condition may have darkened skin and brown urine. They may also suffer joint damage and other complications.

When looking at or generating a pedigree, phenotypic females are represented by circles, and phenotypic males are represented by squares. A horizontal line connecting a phenotypic male and a phenotypic female indicates a mating event. A vertical line represents any offspring that result from a mating event. In the pedigree below, individuals with the disorder are shown by solid blue circles or squares. Because we know the inheritance pattern of Alkaptonuria is autosomal recessive, we also know these affected individuals have the genotype *aa*. Unaffected individuals are indicated by unshaded or white circles or squares and have either genotype *AA* or *Aa*. Sometimes it is not possible using a pedigree to determine whether a person is *AA* or *Aa*, and in these cases, the genotype can be denoted as *A_* or by writing out both possibilities, "*AA* or *Aa*". Note that it is often possible to determine a person's genotype from the genotype of their offspring. For example, if neither parent has the disorder, but their child does, then both parents must be heterozygous for the gene to be passed down.
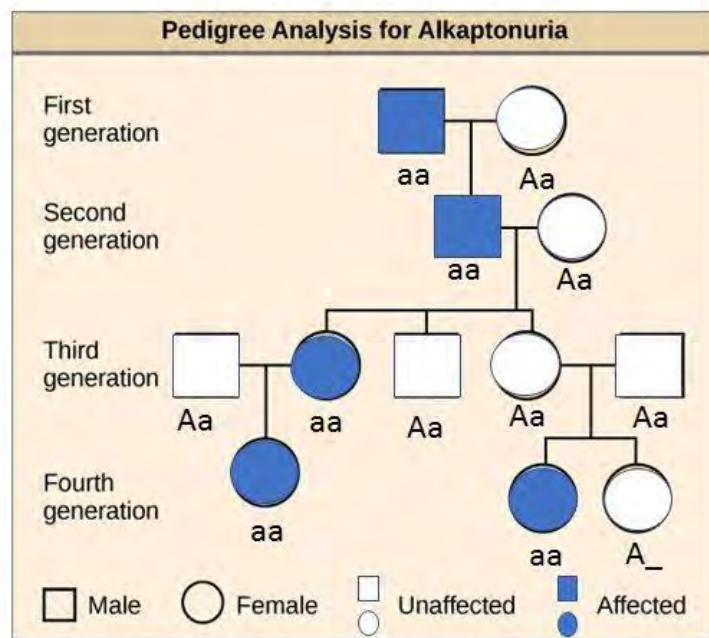
Figure 9.10 A pedigree is showing the recessive genetic disorder, alkaptonuria. (credit: Modified by Elizabeth O'Grady original work of Clark et al. / Biology 2E OpenStax)

Pedigrees can be generated by observing traits of individuals within a family or by looking for the gene using molecular biology techniques. In either case, pedigrees allow geneticists to look at patterns of inheritance within a family and predict genotypic probabilities.

Check your knowledge

In a pedigree, you are evaluating a filled in circle. Which best describes this person?
a. Phenotypic male who is unaffected
b. Phenotypic female who is unaffected
c. Phenotypic female who is affected
d. Phenotypic male who is affected

Punnet square: What is the genotype of the parents if all the offspring are dominant?

Answers: (c) and If all the offspring are dominant, at least one of the parents must be homozygous dominant for the trait. The second parent could be any genotype.

Section Summary

Working with garden pea plants, Mendel found that crosses between parents that differed by one trait produced F_1 offspring that all expressed the traits of one parent. Observable traits are referred to as dominant, and non-expressed traits are described as recessive. When the offspring 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 plant. Reciprocal crosses generated identical F_1 and F_2 offspring ratios. By examining sample sizes, Mendel showed that his crosses behaved reproducibly according to the laws of probability, and that the traits were inherited as independent events.

Mendel hypothesized that genes are inherited as pairs of alleles 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. Also, 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. A dihybrid cross demonstrates independent assortment when the genes in question are on different chromosomes or distant from each other on the same chromosome.

Exercises

1. The observable traits expressed by an organism are described as its _____.
   a. phenotype
   b. genotype
   c. alleles
   d. zygote
2. A recessive trait will only be observed in individuals that are _____ for that trait.
   a. heterozygous
   b. homozygous recessive
   c. homozygous dominant
   d. diploid
3. 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*
4. On a pedigree, how would an affected male be notated?
   a. Shaded / solid circle
   b. unshaded circle
   c. shaded/ solid square
   d. unshaded square
5. 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?
6. 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?

Answers

1. (a)
2. (2)
3. (3)
4. (3)
5. 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 2 tall:2 dwarf.
6. 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*.

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

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

gene: the basic unit of heredity

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 concerning 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

pedigree: to chart used to study inheritance patterns of genetic characteristics

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

9.3 Extensions of the Laws of Inheritance

> **Learning objectives**
>
> By the end of this section, you will be able to:
>
> - *Identify non-Mendelian inheritance patterns such as incomplete dominance, codominance, pleiotropy, polygenic inheritance, and environmental factors*
> - *Follow traits passed down through incomplete dominance and codominance using a monohybrid cross and be able to predict the genotypes and phenotype of the offspring*
> - *Be able to define and explain all bolded terms*

Mendel's experiments with pea plants suggested that: (1) two alleles exist for every gene (2) alleles maintain their integrity in each generation, and (3) in the presence of the dominant allele, the recessive allele is hidden and makes no contribution to the phenotype. Recessive alleles can be "carried" and not expressed by individuals. Mendel's work suggested that the presence of the dominant allele, independent of whether an individual had one copy or two, always resulted in the same phenotype, a concept referred to as **complete dominance**. The work put forth by Mendel forms the basis of classical, or Mendelian, genetics.

Not all traits are passed from parents to offspring according to Mendelian genetics. Further genetic studies in other plants and animals have shown that much more complexity exists. With that being said, the fundamental principles of Mendelian genetics still hold true. In this section, we consider modes of inheritance that differ from classical Mendelian genetics. If Mendel had chosen an experimental system that exhibited these genetic complexities, it's possible that he would not have understood what his results meant.

Incomplete Dominance

Mendel's results that traits are inherited as dominant and recessive pairs contradicted the view that offspring exhibited a blend of their parents' traits. However, the heterozygote phenotype occasionally does appear to be an intermediate phenotype between the two parents. For example, in the snapdragon, *Antirrhinum majus* (Figure 9.11), if a homozygous parent with white flowers (*rr*) is crossed with a homozygous parent with red flowers (*RR*) all offspring will have pink flowers (*Rr*). The heterozygous offspring has half as much red pigment as their red homozygous dominant parent. This pattern of inheritance is described as **incomplete dominance**.

Figure 9.11 These pink flowers of a heterozygote snapdragon result from incomplete dominance. (credit: RudLus02 / Wikimedia commons)
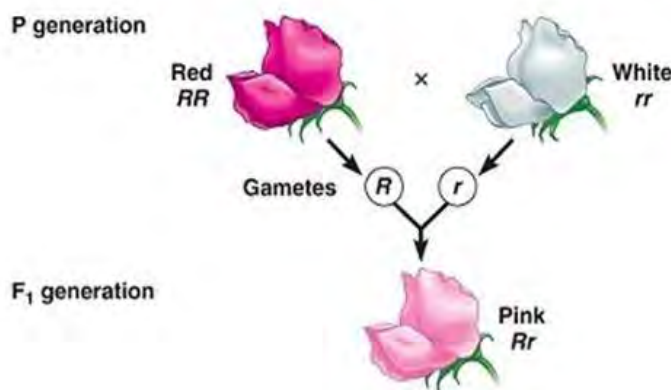
With incomplete dominance, heterozygous individuals have intermediate phenotypes. The allele for red flowers is incompletely dominant over the allele for white flowers. Although the pink intermediate phenotype would appear to support the blending hypothesis, this is not the case. Recall that if genes blended, the paternal phenotypes would not appear in future generations, which is not the case in snapdragons. The results of a heterozygote self-cross provide data that rejects the blending hypothesis with the reappearance of both the red and white phenotypes (Figure 9.12). In this case, the genotypic ratio would be 1 *RR*: 2 *Rr:* 1 *rr*, and the phenotypic ratio would be 1:2:1 for red: pink: white (Figure 9.12).

Figure 9.12 These pink flowers of a heterozygote snapdragon result from incomplete dominance. (credit: RudLus02 / Wikimedia commons)
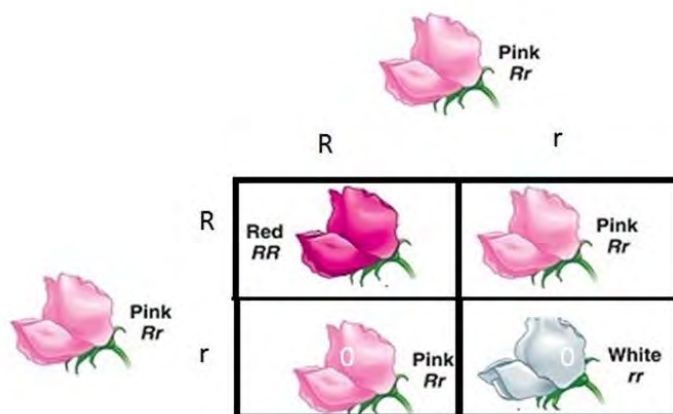
Codominance

Mendel implied that only two alleles, one dominant and one recessive, could exist for a given gene. For example, violet or white flowers and yellow or green seeds. We know now that this is an oversimplification in most cases. Many genes have more than just two different alleles. Human blood type is an example of a character that is determined by three different alleles (Figure 9.13). The alleles are notated as I^O, I^A, and I^B. Each person should have only two alleles for blood type, one from each parent. The two alleles a person inherits leads to one of four possible phenotypes: blood type A, B, AB, or O. The letters represent two different carbohydrates that can be found on the cell membrane of red blood cells. For example, someone who is type A has the A carbohydrate, whereas someone who is O has neither the A nor the B carbohydrates. Someone who is AB has both the A and the B carbohydrates on their red blood cells. To explain the AB blood type, we need to discuss codominance, which is another variation of Mendelian inheritance.
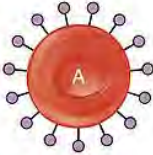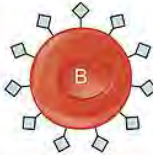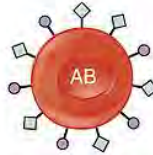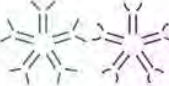
Figure 9.13 The four different ABO blood types. (credit: Betts et. al / Anatomy and Physiology OpenStax)

With **codominance**, both alleles for the same characteristic are simultaneously expressed in the heterozygote genotype. For example, a person that inherits the I^A allele from one parent and the I^B allele from the other parent will have the genotype $I^A I^B$ and the phenotype of AB blood type. Homozygotes ($I^A I^A$ and $I^B I^B$) express either the A or B blood type, respectively. Someone who is $I^A I^O$ or $I^B I^O$ will also express either the A or B blood type. Only individuals that receive an I^O allele from both parents will have the O blood type. If the genotypes of the parents are known, the Punnett square can still be used to predict the possible outcomes of the offspring's phenotype. For example, if a male has the genotype $I^A I^O$ and the female has the genotype $I^B I^O$ then they can produce offspring that have all four phenotypes, A, B, AB, or O (Figure 9.14).
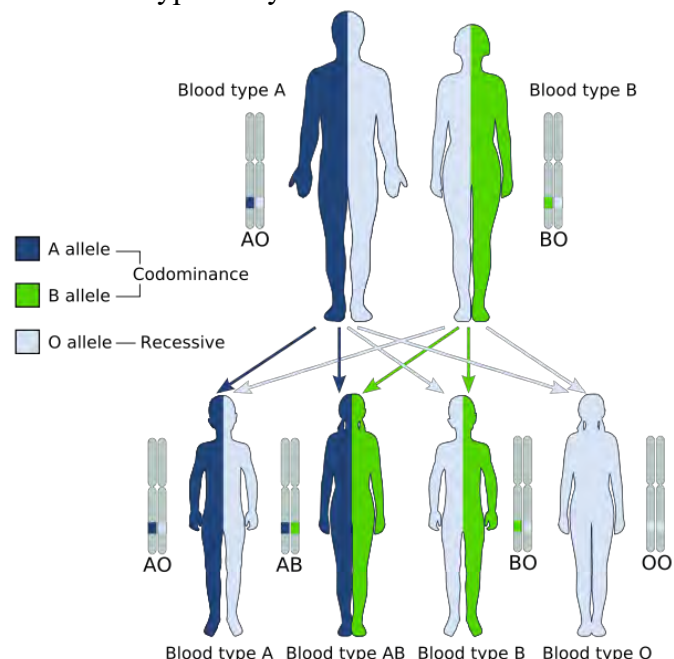
Figure 9.14 A blood typing genetic cross between a male with the genotype I^A I^O and the female with the genotype I^B I^O and the possible offspring they can produce. (credit: YassineMrabet / Wikimedia commons)

Pleiotropy

In pea plants, Mendel focused on how one gene is responsible for one characteristic. However, Mendel did notice with some characteristics, certain phenotypes tended to relate to one another. White flowering pea plants always had clear seed coverings, whereas violet flowering pea plants always had seed coverings that were brown. It is now understood that the gene that leads to flower color also impacts the color of the seed's cover. **Pleiotropy** is a pattern of inheritance where one gene controls two or more different characteristics (Figure 9.15).
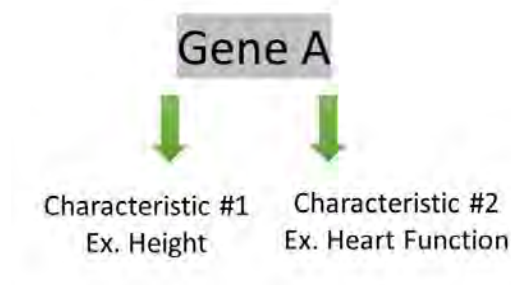
Figure 9.15 In this image, "gene A" affects multiple characteristics, both height, and heart function. This is an example of pleiotropy. (credit: Elizabeth O'Grady)

Fibrillin – 1 syndrome is an example of human pleiotropy and is caused by a single gene mutation. The gene mutation prevents individuals from making a necessary protein found in connective tissue. It can cause individuals to be abnormally tall and have digits, fingers and toes, that are long and thin, and they may have visual impairments. Individuals that have Fibrillin – 1 syndrome also often suffer from aortic aneurysms, a heart condition where the aorta bulges and can burst, leading to death. Although treatments are available to help with symptoms, there is no cure for Fibrillin – 1 syndrome.

Polygenic Inheritance

Mendel worked with traits that showed discontinuous variation. Recall that discontinuous variation is when each individual exhibit one of two easily distinguishable traits, such as violet or white flowers. However, at the time of Mendel many people supported the blending hypothesis because of what is commonly referred to as continuous variation. Continuous variation is when a character, such as height in humans, is influenced by several different genes. This also occurs with characteristics such as skin, hair, and eye color.

For example, when looking at eye color, it is evident that there are many different shades when it comes to blue and brown. In this case, there isn't just one gene that determines eye color, but rather many genes that contribute to this characteristic. Height can be just as complicated, with individuals ranging from very short to very tall. How does genetic inheritance lead to such variation? The answer lies in the fact that many different genes control characteristics such as height, skin color, and eye color. Each gene that an individual inherits has a small additive effect on the overall phenotype, a concept known as **polygenic inheritance**.

To see how polygenic inheritance has an additive effect on phenotype, click the link below to see how three genes, which are inherited separately, can lead to seven different wheat kernel colors (Figure 9.16).

 Figure 9.16 Wheat kernel color variation is a characteristic under the control of polygenic inheritance. (credit: unknown / Public Domain)

CONCEPTS IN ACTION- Visualize the polygenic inheritance at this link - Link on Polygenic Inheritance

Environmental Influences

Often an individual's phenotype is impacted by environmental factors. Using height as an example, this characteristic is not only influenced by the number and type of genes inherited; it also depends on environmental factors. For instance, if a child does not receive the proper nutrients, including calcium for bone growth, he or she may be stunted or delayed in growth. Exercise and proper sleep quantities also influence a person's overall growth and stature. As you can see, genetics alone cannot always explain an individual's phenotype.

Many characteristics are thought to be dependent on both genetic and environmental factors; a concept often referred to as nature vs. nurture. Most humans are born with the physiological ability to make sound; however, the language that an individual learns to speak is heavily influenced by the environment in which they are raised. It is yet to be determined and agreed upon on how much of an organism's characteristics are based on genetics versus environmental factors. Most agree that an individual's phenotype is a result of some combination of both.

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 represents the simultaneous expression of both alleles in the heterozygous genotype. Pleiotropy is the term used to describe when one gene controls two or more different characteristics. Polygenic inheritance represents when multiple genes each have a small additive effect on the overall phenotype. Examples of polygenic inheritance include skin color, height, and eye color. Also, an individual's phenotype is impacted by environmental factors.

Exercises

1. If you cross a male who is $I^A I^A$ and a female who is $I^B I^B$ for blood type, what are the possible blood types of their offspring?
   a. AB and O
   b. only A or B
   c. only AB
   d. Only O
2. If black true-breeding mice are mated with white true-breeding mice, 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
3. Characteristics such as height are only influenced by your genetic makeup.
   a. TRUE
   b. FALSE
4. _____ is when each gene that an individual inherits has a small additive effect on the overall phenotype.
   a. Polygenic inheritance
   b. Pleiotropy
   c. Complete dominance
   d. Incomplete dominance
5. Could an individual with blood type O (genotype $I^O I^O$) be a legitimate child of parents in which one parent had blood type A and the other parent had blood type B?

Answers

1. (c)
2. (d)
3. (b)
4. (a)
5. 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 $I^A I^O$, and the type b parent had to have genotype $I^B I^O$.

Glossary

codominance: in a heterozygote, complete and simultaneous expression of both alleles for the same characteristic

complete dominance: in a heterozygote the dominant allele masks the effect of the recessive allele

incomplete dominance: in a heterozygote, expression of two contrasting alleles such that the individual displays an intermediate phenotype

pleiotropy: describes when one gene controls two or more different characteristics

polygenic inheritance: describes when each gene that an individual inherits has a small additive effect on the overall phenotype

9.4 Chromosomal Basis of Inheritance

Learning objectives

By the end of this section, you will be able to:

- *Discuss the Chromosomal Theory of Inheritance*
- *Explain the effect of linkage and recombination on gamete genotypes*
- *When multiple alleles exist for a gene, know the difference between the wild type and variants*
- *Be able to define and explain all bolded terms*

Long before scientists visualized chromosomes under a microscope, the father of modern genetics, Gregor Mendel, began studying heredity in 1843. With improved microscopic techniques during the late 1800s, cell biologists could stain and visualize subcellular structures with dyes and observe their actions during cell division and meiosis. With each cell division, chromosomes replicated, condensed, and migrated to separate cellular poles. These advancements allowed scientists to connect inheritance with the physiological events of cell division.

Chromosomal Theory of Inheritance

The speculation that chromosomes might be the key to understanding heredity led several scientists to examine Mendel's publications and reevaluate his model in terms of chromosome behavior during mitosis and meiosis. In 1902, Theodor Boveri observed that sea urchin embryonic development does not occur unless chromosomes are present. That same year, Walter Sutton observed chromosome separation into daughter cells during meiosis. Together, these observations led to the **Chromosomal Theory of Inheritance**. The Chromosomal Theory of Inheritance states that genes are found at specific locations on chromosomes and that it is the chromosomes that independently assort and segregate during metaphase I and anaphase I of meiosis I (Figure 9.17).
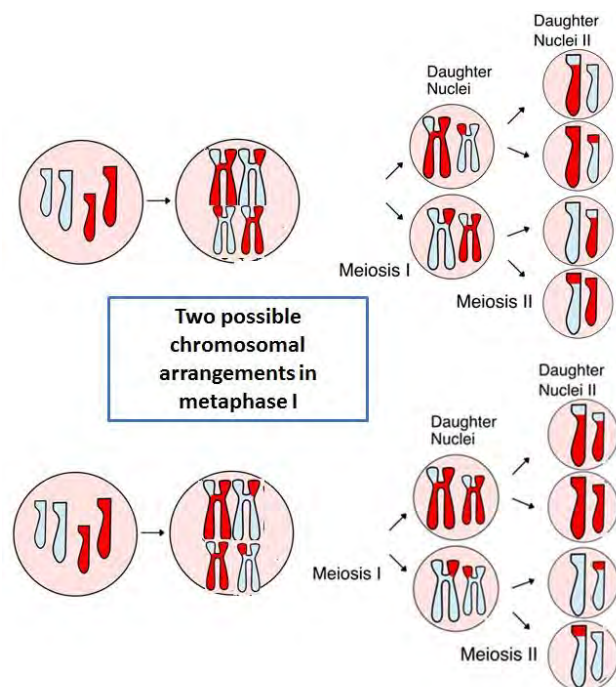
Figure 9.17: Shows how chromosomes are separated, or segregated, during meiosis. (credit: Modified by Elizabeth O'Grady original work of Rdbickel / Wikimedia commons)

The Chromosomal Theory of Inheritance was consistent with Mendel's laws. The following observations supported the connection between the two:

- During meiosis, homologous chromosome pairs migrate as discrete structures that are independent of other chromosome pairs.
- Chromosome sorting from each homologous pair into gametes appears to be random.
- Each parent synthesizes gametes that contain only half their chromosomal number.
- Even though male and female gametes, sperm and egg, differ in size and shape, they have the same number of chromosomes, suggesting equal genetic contributions from each parent.
- The chromosomes found in each gamete come together during fertilization to produce offspring with the same chromosome number as their parents.

Scientists proposed the Chromosomal Theory of Inheritance long before there was any direct evidence that chromosomes carried traits. Critics pointed out that individuals had far more independently segregating traits than they had chromosomes. It was only after several years of carrying out cross fertilizations with the fruit fly, *Drosophila melanogaster*, that Thomas Hunt Morgan provided experimental evidence to support the Chromosomal Theory of Inheritance.

Linked Genes Violate the Law of Independent Assortment

Although all of Mendel's pea characteristics behaved according to the law of independent assortment (Figure 9.3), we now know that some allele combinations are not inherited independently of each other. Genes that are located on separate non-homologous chromosomes will always sort independently. However, each chromosome contains hundreds or thousands of genes, organized linearly on chromosomes like beads on a string. The segregation of alleles into gametes can be influenced by **linkage**, in which genes that are located physically close to each other on the same chromosome are more likely to be inherited as a pair. However, because of the process of recombination, or "crossover," it is possible for two genes on the same chromosome to behave independently, or as if they are not linked. To understand this, let's consider the biological basis of gene linkage and recombination.

Homologous chromosomes possess the same genes in the same linear order. The alleles may differ on homologous chromosome pairs, but the genes to which they correspond do not. In preparation for the first division of meiosis, homologous chromosomes replicate and form tetrads. Genes on the homologous pairs align with each other. At this stage, segments of homologous chromosomes exchange linear segments of genetic material (Figure 9.18). This process, called *recombination* or crossing over, 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.
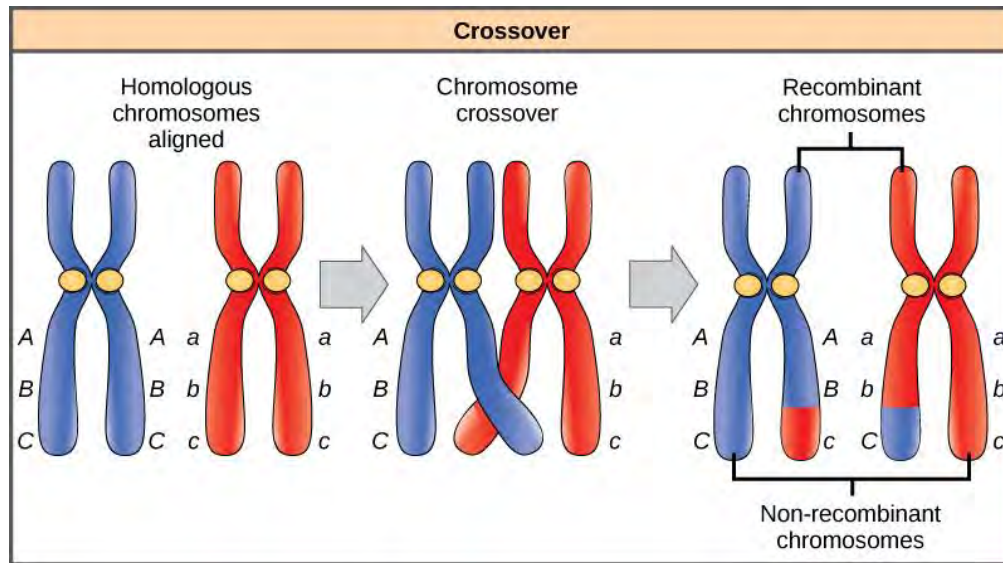
Figure 9.18 The process of crossover, or recombination, occurs when two homologous chromosomes align during meiosis and exchange a segment of genetic material. Here, the alleles for gene C were exchanged. The result is two recombinant and two non-recombinant chromosomes. (credit: Clark et al. / Biology 2E OpenStax)

When two genes are located in close proximity on the same chromosome, they are considered linked, and their alleles tend to be passed through meiosis together. To demonstrate this, imagine a dihybrid cross involving flower color and plant height in which the genes are next to each other on the chromosome. If one homologous chromosome has alleles for tall plants and red flowers, and the other chromosome has genes for short plants and yellow flowers, then when the gametes are formed, the tall and red alleles will go together into gametes, and the short and yellow alleles will go into other gametes. However, because the genes are linked, there will be no gametes with tall and yellow alleles and no gametes with short and red alleles. If you create the Punnett square with these gametes, you will see that the classical Mendelian prediction of a 9:3:3:1 outcome of a dihybrid cross would not apply. As the distance between two genes increases, the probability of one or more crossovers between them increases, and the genes behave more like they are on separate chromosomes. Geneticists have used the proportion of recombinant gametes, the ones not like the parents, as a measure of how far apart genes are on a chromosome. Using this information, they have constructed elaborate maps of genes on chromosomes for well-studied organisms, including humans. Mendel's 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 hypothesis. 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.

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. For any given gene, multiple alleles may exist at the population level. Different combinations of alleles lead to different observed phenotypes. Note that when many alleles exist for the same gene, the convention is to denote the most common phenotype or genotype among wild organisms as the **wild type**, often abbreviated "+"; this is considered the standard or norm. All other phenotypes or genotypes are considered **variants** of this standard, meaning that they deviate from the wild type. The variant may be recessive or dominant to the wild-type allele.

An example of multiple alleles is coat color in rabbits (Figure 9.19). Here, four alleles exist for the c gene. The wild-type version, C^+C^+, is expressed as brown fur. The chinchilla phenotype, $c^{ch}c^{ch}$, is expressed as black-tipped white fur. The Himalayan phenotype, c^hc^h, has black fur on the extremities and white fur elsewhere. Finally, the albino, or "colorless" phenotype, cc, is expressed as white fur. In cases of multiple alleles, dominance hierarchies can exist. In this case, the wild-type allele is dominant over all the others, chinchilla is incompletely dominant over Himalayan and albino, and Himalayan is dominant over albino. This hierarchy, or allelic series, was revealed by observing the phenotypes of each possible heterozygote offspring.

The complete dominance of a wild-type phenotype over all other mutants often occurs as an effect of "dosage" of a specific gene product. The wild-type allele supplies the correct amount of gene product, whereas the mutant alleles cannot. For the allelic series in rabbits, the wild-type allele may supply a given dosage of fur pigment, whereas the mutants supply a lesser dosage or none at all. Interestingly, the Himalayan phenotype is the result of an allele that produces a temperature-sensitive gene product that only produces pigment in the cooler extremities of the rabbit's body.

Figure 9.19 Four different alleles exist for the rabbit coat color (C) gene. (credit: Clark et al. / Biology 2E OpenStax)

Mendel's work identified the fundamental principles of heredity; however, as you have now learned, genetics are much more complicated. Had he used a different model organism or investigated both linked and unlinked genes, it would have been much more difficult for him to create a unified model of his data based on probability. Researchers who have since mapped the traits that Mendel investigated have confirmed that all the genes he examined are either on separate chromosomes or are sufficiently far apart as to be statistically unlinked. Some have suggested that Mendel was enormously lucky in both his choice of model organism and that he selected only unlinked genes. Others question whether Mendel discarded any data suggesting linkage. Regardless, Mendel and his data helped build the foundation for modern genetics.

Section Summary

Sutton and Boveri's Chromosomal Theory of Inheritance states that chromosomes are the vehicles of genetic heredity. Neither Mendelian genetics nor gene linkage apply to inheritance of all characteristics. Instead, chromosome behavior involves segregation, independent assortment, and occasionally, linkage. Sturtevant devised a method to assess recombination frequency and infer linked genes' relative positions and distances on a chromosome based on the average number of crossovers in the intervening region between the genes. Sturtevant correctly presumed that genes are arranged in serial order on chromosomes and that recombination between homologs can occur anywhere on a chromosome with equal likelihood. Whereas linkage causes alleles on the same chromosome to be inherited together, homologous recombination biases alleles toward an independent inheritance pattern.

Exercises

1. The Chromosomal Theory of Inheritance was consistent with Mendel's laws. Provide two observations that supported the connection between the two.
2. When many alleles exist for the same gene, the convention is to denote the most common phenotype or genotype among individuals as the:
   a. variant
   b. wild type
   c. dosage
   d. none of the above
3. When two genes are located in close proximity on the same chromosome, they are considered linked, and their alleles tend to be passed through meiosis together.
   a. TRUE
   b. FALSE

Answers

1. (1) During meiosis, homologous chromosome pairs migrate as discrete structures that are independent of other chromosome pairs. (2) Chromosome sorting from each homologous pair into gametes appears to be random. (3) Each parent synthesizes gametes that contain only half their chromosomal number. (4) Even though male and female gametes, sperm and egg, differ in size and morphology, they have the same number of chromosomes, suggesting equal genetic contributions from each parent. (5) The chromosomes found in each gamete come together during fertilization to produce offspring with the same chromosome number as their parents.
2. (b)
3. (a)

Glossary

Chromosomal Theory of Inheritance: a theory proposing that chromosomes are the genes' vehicles and that their behavior during meiosis is the physical basis of the inheritance patterns that Mendel observed

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

variants: genotypes or phenotype that deviate from the wild type

wild type: the most commonly occurring genotype or phenotype for a given characteristic found in a population

9.5 Patterns of Inheritance

Chromosomes carry genes necessary to maintain homeostasis. Thanks to the work of many scientists, it is now understood that chromosomes, not just individual genes, are the heritable units that are passed on from one generation to the next. Recall from chapter eight that both human males and females have twenty-two pairs of homologous chromosomes called autosomes. **Autosomes** are chromosome pairs one through twenty-two and do not determine a person's sex. The twenty-third pair of chromosomes are referred to as the **allosomes** and determine whether an individual will physiologically develop as a male or female.

Human Genetic Disorders

Some human disorders are genetically inherited. These conditions are caused by faulty genes located on chromosomes that often code for non-functional proteins. Genetic disorders can be classified based on whether the gene is located on autosomes or the allosomes. Disorders can be further classified as dominant or recessive, depending on whether a dominant or recessive allele causes the disorder. Most genetic disorders fall into one of three inheritance patterns: autosomal dominant, autosomal recessive, or X (sex) -linked disorders.

Autosomal Dominant Disorders

Autosomal dominant disorders occur when an individual inherits a mutated or faulty dominant allele on an autosome. The person may have one faulty dominant allele and one functional recessive allele (Aa) or two defective dominant alleles (AA). Regardless of whether the individual is homozygous dominant or heterozygous, they will have the genetic condition. Only individuals that are homozygous recessive (aa) will not be affected.

An example of an autosomal dominant disorder is neurofibromatosis type I, a disease that induces tumor formation within the nervous system and leads to skin and skeletal deformities. Consider a couple in which one parent is heterozygous (*Nn)* and has the disorder neurofibromatosis, and the other person (*nn)* is healthy and does not have the disorder. The heterozygous parent would have a 50 percent chance of passing the dominant allele for this disorder to his or her offspring, and the homozygous parent would always pass on the normal/functional allele. Therefore, four possible offspring genotypes are equally likely to occur: *Nn*, *Nn*, *nn*, and *nn*. Every child of this couple would have a 50 percent chance of inheriting neurofibromatosis. This inheritance pattern is shown in Figure 9.20.
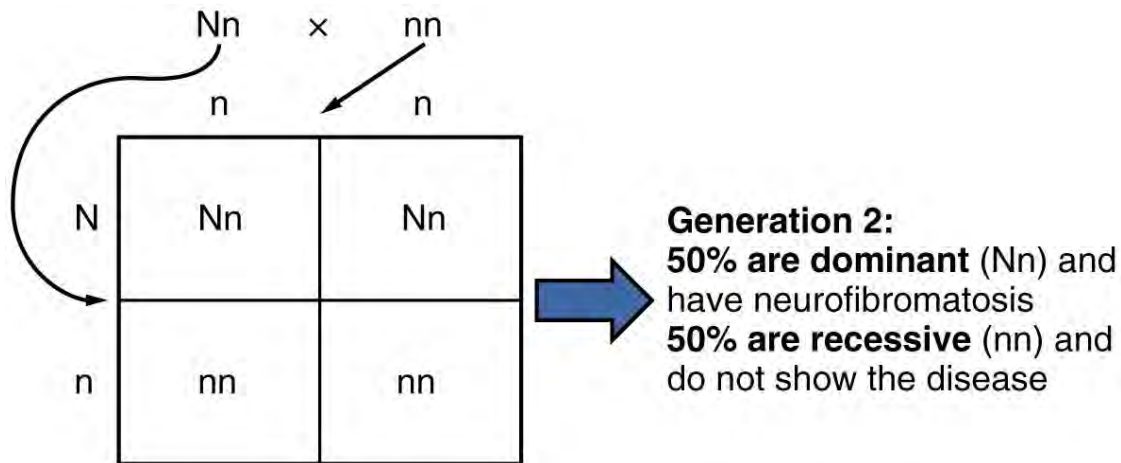
Figure 9.20 Autosomal Dominant Inheritance pattern of an autosomal dominant disorder, such as neurofibromatosis, is shown in a Punnett square. (credit: Betts et al. / Anatomy and Physiology OpenStax)

Other genetic diseases that are inherited in this pattern are achondroplasty dwarfism, Fibrillin – 1 syndrome, and Huntington disease. Because autosomal dominant disorders are expressed by the presence of just one allele, parents that do not have the autosomal dominant condition cannot pass the faulty allele on to their offspring. However, if an offspring has the condition, then at least one of their parents must have at least one defective allele and therefore also has the condition.

Autosomal Recessive Disorders

Autosomal recessive disorders occur when the gene is located on an autosome and the faulty allele which causes the disorder is recessive. When a genetic disorder is inherited in an autosomal recessive inheritance pattern, the condition corresponds to the homozygous recessive genotype. Heterozygous individuals will not display symptoms of this disorder because their functional dominant allele will be expressed. Heterozygous individuals are called "**carriers**." Carriers for an autosomal recessive disorder do not themselves have signs or symptoms of the condition, but they can pass the faulty allele on to their offspring. The carrier may never know they have a defective allele unless they have a child with the condition, or they have their genome sequenced. Only recessive disorders can have carriers since heterozygous individuals with autosomal dominant disorders will always show the disease.

An example of an autosomal recessive disorder is cystic fibrosis (CF). CF is characterized by the chronic accumulation of thick, tenacious mucus in the lungs and digestive tract. Decades ago, children with CF rarely lived to adulthood. With advances in medical technology, the average lifespan in developed countries has increased into middle adulthood. CF is a relatively common disorder that occurs in approximately 1 in 2000 Caucasians. A child born to two CF carriers would have a 25 percent chance of inheriting the disease. This is the same 3:1 dominant: recessive ratio that Mendel observed in his pea plants. Figure 9.21 shows what the probability is of having an offspring with an autosomal recessive condition if two carriers mate.

On the other hand, someone who is homozygous dominant (AA), with two functional alleles, would have a zero percent probability of passing on an autosomal recessive condition to their offspring. Other examples of autosome recessive conditions include the blood disorder sickle-cell anemia, the fatal neurological disorder Tay–Sachs disease, and the metabolic disorder phenylketonuria.
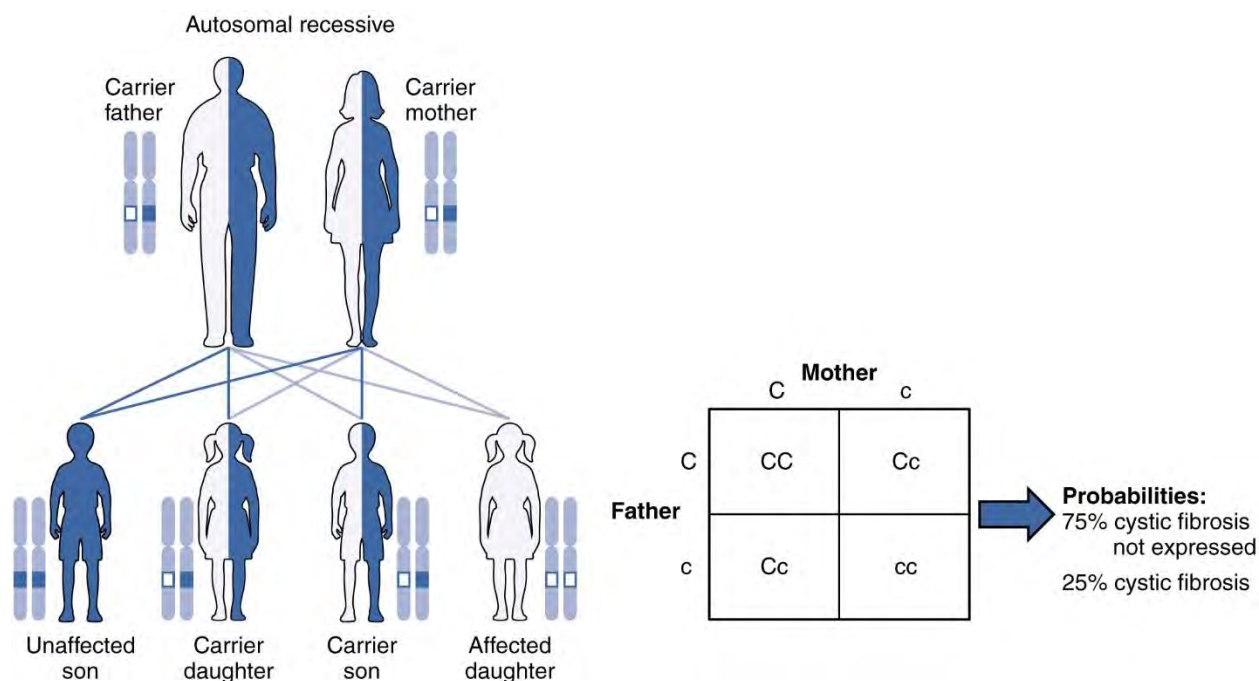
Figure 9.21 Autosomal Recessive Inheritance The inheritance pattern of an autosomal recessive disorder with two carrier parents reflects a 3:1 probability of expression among offspring. (credit: U.S. National Library of Medicine / Anatomy and Physiology OpenStax)

Sex-linked Disorders

A **X (sex)-linked** inheritance pattern involves genes located on the X chromosome of the 23rd pair (Figure 9.22). Recall that a male has one X and one Y chromosome. When a father transmits a Y chromosome, the child is male, and when he transmits an X chromosome, the child is female. A mother can transmit only an X chromosome, as both her allosomes are X chromosomes. Any male that has a X-linked condition received the faulty allele from his mother.

When an abnormal allele for a gene that occurs on the X chromosome is dominant over the recessive, functional allele, the pattern is described as **X-linked dominant**. This is the case with vitamin D resistant rickets. For example, an unaffected mother and an affected father have children. The affected father would pass the faulty gene on the X chromosome to all of his daughters, but none of his sons. He can only donate the Y chromosome to his sons (see Figure 9.22a). If it is the mother who is affected and she is homozygous dominant for the faulty allele, all her children, male or female, would have the condition. If the mother is heterozygous for the faulty allele, her sons and daughters have a 50 percent chance of inheriting the disorder (see Figure 9.2b).
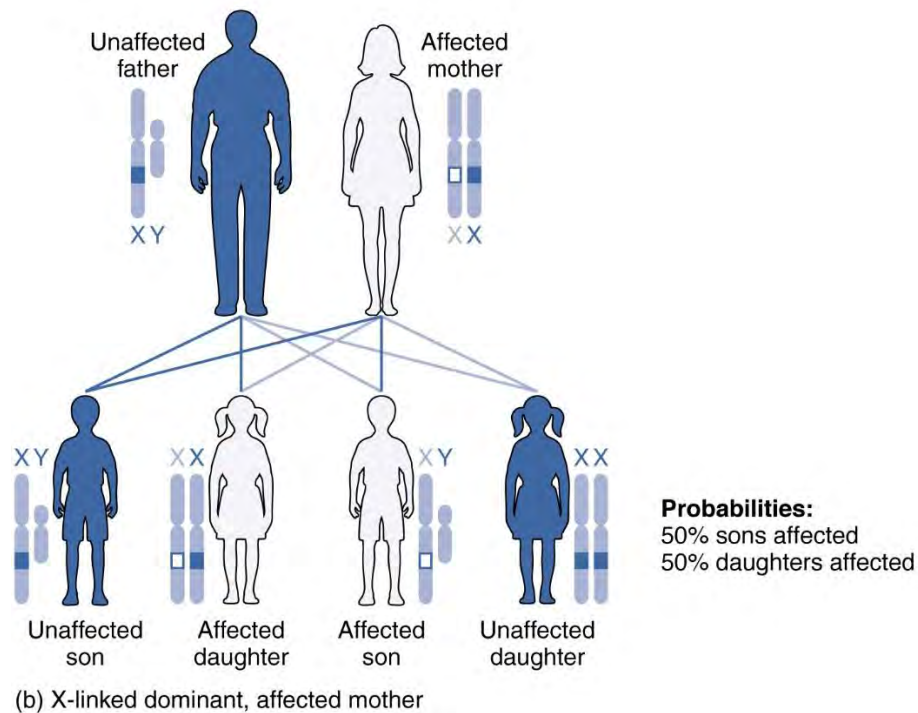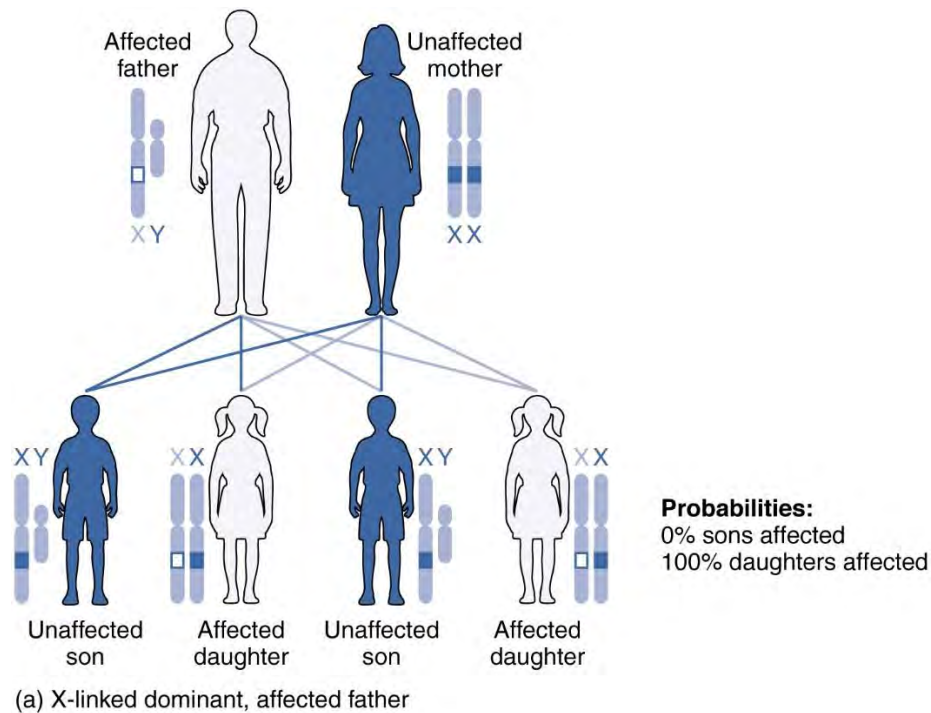
Figure 9.22 X-Linked Patterns of Inheritance A chart of X-linked dominant inheritance patterns differ depending on whether (a) the father or (b) the mother is affected with the disease. (credit: U.S. National Library of Medicine / Anatomy and Physiology OpenStax)

The **X-linked recessive** inheritance pattern is much more common because females can be carriers of the disease yet still have a normal phenotype. X-linked recessive conditions include red-green color blindness, the blood-clotting disorder hemophilia, and some forms of muscular dystrophy. For an example of X-linked recessive inheritance, consider parents in which the mother is an unaffected carrier, and the father does not have the condition. None of the daughters would have the condition because they receive a functional allele from their father. However, they have a 50 percent chance of receiving the faulty allele from their mother and becoming a carrier. In contrast, 50 percent of the sons would be affected (Figure 9.23).

With X-linked recessive conditions, males either have the condition or they do not; they cannot be carriers. Also recall, males always get the sex-linked recessive condition from their mothers. Females, however, may not have the condition but may carry the faulty allele and therefore pass it on to their offspring. A daughter that has an X-linked recessive condition had to get the faulty alleles from both her mother and her father. As you can imagine, X-linked recessive disorders affect many more males than females. For example, color blindness affects at least 1 in 20 males, but only about 1 in 400 females.
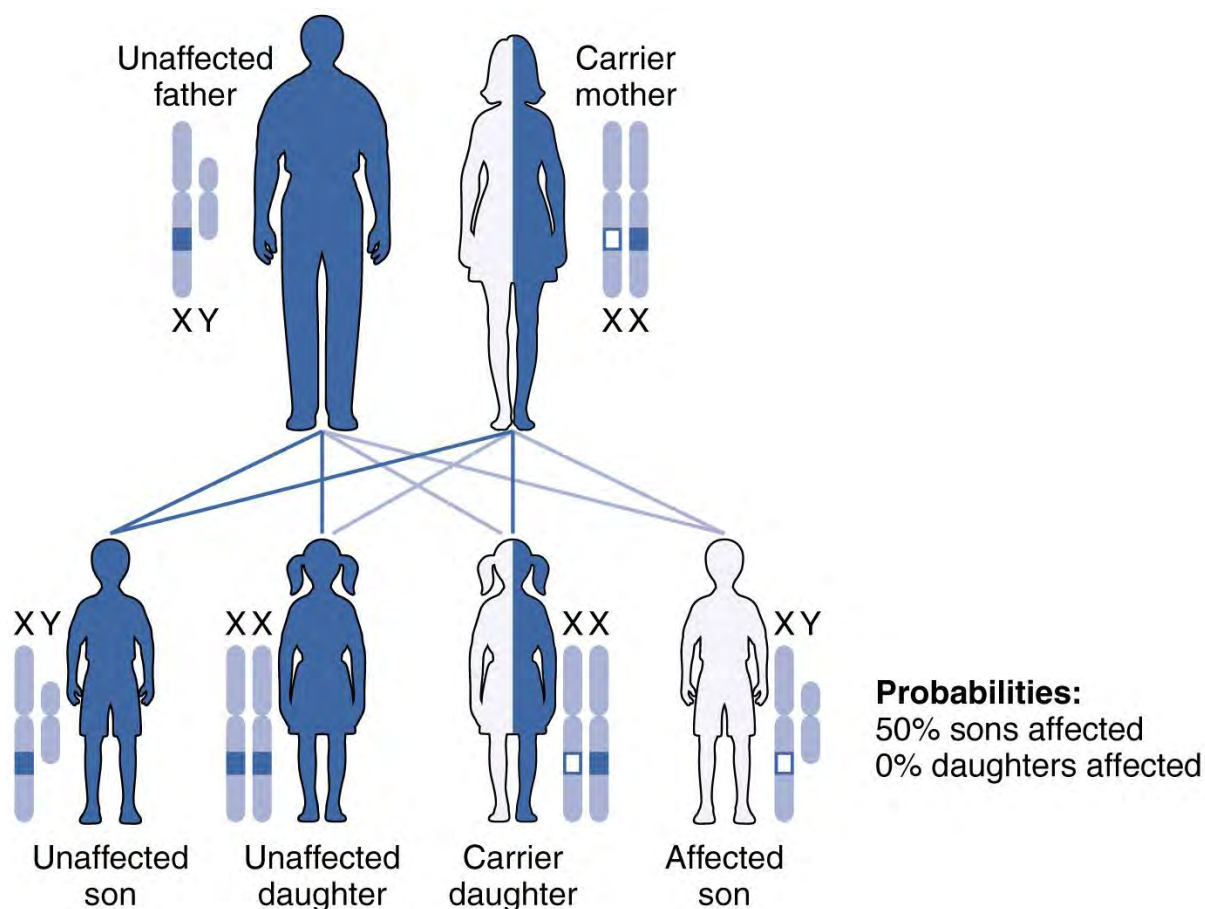
Figure 9.23 X-Linked Recessive Inheritance Given two parents in which the father is normal, and the mother is a carrier of an X-linked recessive disorder, a son would have a 50 percent probability of being affected with the disorder. In contrast, daughters would either be carriers or entirely unaffected. (credit: U.S. National Library of Medicine/ Anatomy and Physiology OpenStax)

CAREER CONNECTION - Genetic Counselor

Given the intricate orchestration of gene expression, cell migration, and cell differentiation during prenatal development, it is amazing that the vast majority of newborns are healthy and free of major birth defects. When a woman over 35 is pregnant or intends to become pregnant, or her partner is over 55, or if there is a family history of a genetic disorder, she and her partner may want to speak to a genetic counselor to discuss the likelihood that their child may be affected by a genetic or chromosomal disorder. A genetic counselor can interpret a couple's family history and estimate the risks to their future offspring.

For many genetic diseases, a DNA test can determine whether a person is a carrier. For instance, carrier status for Fragile X, an X-linked disorder associated with mental retardation, or for cystic fibrosis can be determined with a simple blood draw to obtain DNA for testing. A genetic counselor can educate a couple about the implications of such a test and help them decide whether to undergo testing. For chromosomal disorders, the available testing options include a blood test, amniocentesis (in which amniotic fluid is tested), and chorionic villus sampling (in which tissue from the placenta is tested). Each of these has advantages and drawbacks. A genetic counselor can also help a couple cope with the news that either one or both partners are a carrier of a genetic illness, or that their unborn child has been diagnosed with a chromosomal disorder or other birth defects.

To become a genetic counselor, one needs to complete a 4-year undergraduate program and then obtain a Master of Science in Genetic Counseling from an accredited university. Board certification is attained after passing examinations by the American Board of Genetic Counseling. Genetic counselors are essential professionals in many branches of medicine, but there is a particular demand for preconception and prenatal genetic counselors.

CONCEPTS IN ACTION- Visit the National Society of Genetic Counselors website for more information about genetic counselors. Visit the American Board of Genetic Counselors, Inc. website for more information about genetic counselors.

Section Summary

Human genetics focuses on identifying different alleles and understanding how they express themselves. Medical researchers are especially interested in the identification of inheritance patterns for genetic disorders, which provides the means to estimate the risk that a given couple's offspring will inherit a genetic disease or disorder. Patterns of inheritance in humans include autosomal dominance, autosomal recessive, X-linked dominance, and X-linked recessive.

Exercises

1. Hemophilia is a X-linked recessive disorder. A woman who has hemophilia and an unaffected (healthy) male have a son; what is the probability that their son will have hemophilia?
    a. 25%
    b. 50%
    c. 75%
    d. 100%
2. Cystic fibrosis is an autosomal recessive disorder. Two heterozygous carriers have an offspring; what is the probability that they will have an offspring with cystic fibrosis?
    a. 25%
    b. 50%
    c. 75%
    d. 100%
3. Marfan syndrome is inherited in an autosomal dominant pattern. Which of the following is true?
    a. Female offspring are more likely to be carriers of the disease.
    b. Male offspring are more likely to inherit the disease.
    c. An affected offspring must have at least one affected parent.
    d. Female offspring are more likely to inherit the disease.
4. Can a male be a carrier of red-green color blindness?

Answers

1. (d)
2. (a)
3. (c)
4. No, males can only express color blindness and cannot carry it because an individual needs two X chromosomes to be a carrier.

Glossary

allosomes: chromosome pair twenty-three in humans and plays a role in a person's sex

autosomal dominant inheritance: pattern of dominant inheritance that corresponds to a gene on one of the 22 autosomal chromosomes

autosomal recessive inheritance: pattern of recessive inheritance that corresponds to a gene on one of the 22 autosomal chromosomes

autosome: chromosome pairs one through twenty-two and does not determine a person's sex

carriers: a heterozygous individual who does not display symptoms of a recessive genetic disorder but can transmit the disorder to his or her offspring

X (sex)-linked: pattern of inheritance in which an allele is carried on the X chromosome of the 23rd pair

X-linked dominant inheritance: pattern of dominant inheritance that corresponds to a gene on the X chromosome of the 23rd pair

X-linked recessive inheritance: pattern of recessive inheritance that corresponds to a gene on the X chromosome of the 23rd pair

Chapter 10: DNA replication and Protein Synthesis

Figure 10.1 This photo shows Dolly the sheep. Dolly the sheep was the first clone of a mammal. (credit: Clark et al. / Biology 2E OpenStax)

DNA, deoxyribonucleic acid, is found in every living cell. It can be isolated from single-celled organisms like bacteria, or multicellular organisms like plants and animals. Each organism's DNA is unique, making it an excellent tool for species identification.

The field of molecular biology, which was developed in the last half-century, has enabled us to both isolate and sequence DNA. These techniques allow us to look more closely at the history of life and to understand the relationships between different living organisms. Thousands of species have had their entire genomes sequenced. These sequences allow us to understand inheritance, evolutionary relationships, and much more.

10.1 The Structure of DNA

Learning objectives

By the end of this section, you will be able to:

- *Briefly explain the history and work of Watson, Crick, Franklin, and Wilkins*
- *Describe the structure of DNA including locations of covalent and hydrogen bonds, base pairing, and the major components of a nucleotide*
- *Compare DNA and RNA*
- *Be able to define and explain all bolded terms*

In the 1950s, many different scientists were working to answer the following question: what does the structure of DNA look like? Research supported that DNA was the heritable material being passed from parent to offspring. It was also understood that if cells were going to divide, the DNA needed to be replicated. However, to understand DNA synthesis or how DNA leads to specific phenotypes, the molecular structure of DNA needed to be determined.

Francis Crick and James Watson, both students at the University of Cambridge, England, worked together to determine the structure of DNA; however, they did not do it alone. They depended on the work and research of other scientists, including Rosalind Franklin and Maurice Wilkins. Maurice Wilkins and Rosalind Franklin were working in the same laboratory when Franklin developed an improved technique of X-ray crystallography to understand the structure of DNA (Figure 10.2). X-ray crystallography was a process that involved shooting X-rays through a crystal of a substance and then observing the patterns that were formed. The patterns give important information about the structure of the molecule of interest. Wilkins shared Franklin's X-ray crystallography data with Watson and Crick without her permission. With the help of her data, they were able to piece together the structure of DNA.

Figure 10.2 Rosalind Franklin provided X-ray crystallography data leading to the discovery of the structure of DNA. "Photo 51" led to a new understanding of DNA structure. (credit: Rosalind Franklin image MRC Laboratory of Molecular Biology/ Wikimedia Commons SA 4.0 (credit: X-ray crystallography image modification of work by NIH / Biology 2E OpenStax)

Watson and Crick also used information published by the researcher Erwin Chargaff. Chargaff was an Austrian biochemist who examined the content of DNA in different species and found that the amounts of pyrimidines (cytosine and thymine) were not found in equal quantities. Likewise, purines (adenine and guanine) were also not found in equal quantities (Figure 10.3). He found that the relative concentrations of the four nucleotide bases varied from species to species. He also discovered that the amount of adenine equaled the amount of thymine, and the amount of cytosine equaled the amount of guanine; that is, A = T and G = C. These observations became known as Chargaff's rules. Chargaff's findings proved immensely useful when Watson and Crick were getting ready to propose their DNA double helix model.
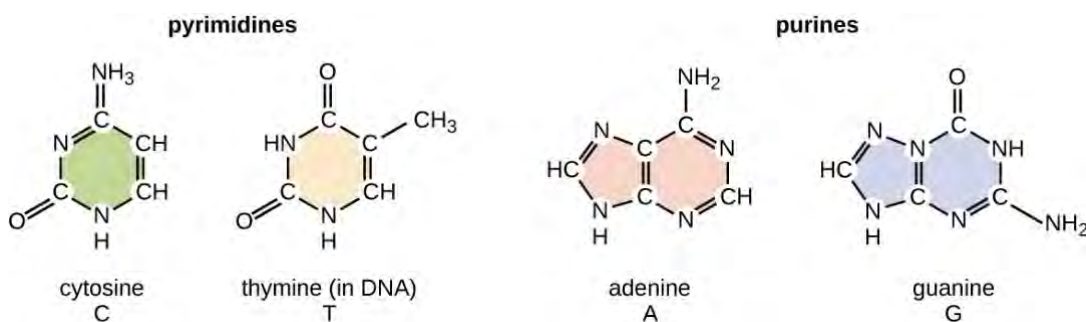
Figure 10.3 Nitrogenous bases within DNA are categorized into the two-ringed purines, adenine and guanine, and the single-ringed pyrimidines, cytosine and thymine. Thymine is unique to DNA. (credit: Parker et al. / Microbiology OpenStax)

Thanks in part to the work done by Rosalind Franklin and others, such as Erwin Chargaff, Watson and Crick were able to determine the structure of DNA (Figure 10.4). Watson and Crick proposed that DNA is made up of two strands that are twisted around each other to form a right-handed **double helix**, and that in the interior base pairing takes place between a purine and pyrimidine (A-T or G-C), as was suggested by Chargaff's Rules.

Figure 10.4 Pioneering scientists (a) James Watson and Francis Crick are pictured here with American geneticist Maclyn McCarty. (Biology 2E OpenStax) (b) Double helix DNA model. (credit: Zephyris/ CC BY-SA 3.0)

a.

b.
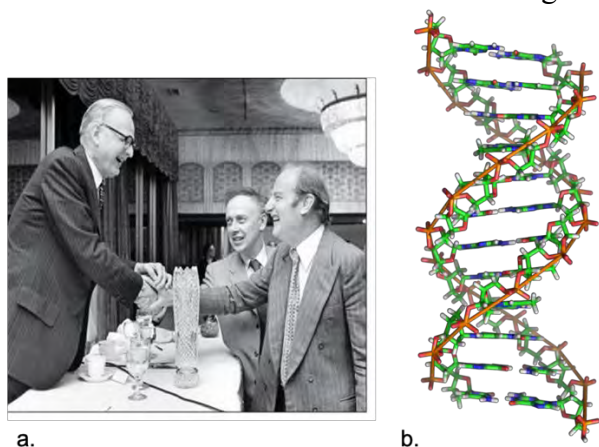
In 1962, James Watson, Francis Crick, and Maurice Wilkins were awarded the Nobel Prize in Medicine for their work in determining the structure of DNA. Rosalind Franklin died of ovarian cancer in 1958 at the age of 37. As a result, she was not awarded the Nobel Prize for her contribution in the discovery of the DNA structure because it is not given posthumously.

Nucleic Acids

In chapter three, students learned about nucleic acids, one of the four different biologically important molecules found in all living cells. Recall that there are two important polymers of nucleic acids, **deoxyribonucleic acid** (DNA) and **ribonucleic acid** (RNA). Although both DNA and RNA are made up of nucleotides, they function differently within the cell. DNA stores the genetic information needed to build proteins required for maintaining homeostasis. RNAs, on the other hand, are molecules that are involved in protein synthesis. Currently, cells use DNA as a template to assemble RNA. This process will be covered in sections 10.3 and 10.4.

Figure 10.5 (a) Each nucleotide is made up of a sugar, a phosphate group, and a base. (b) Cytosine, thymine, and uracil are pyrimidines. Guanine and adenine are purines. (credit: Fowler et al. / Concepts of Biology OpenStax)
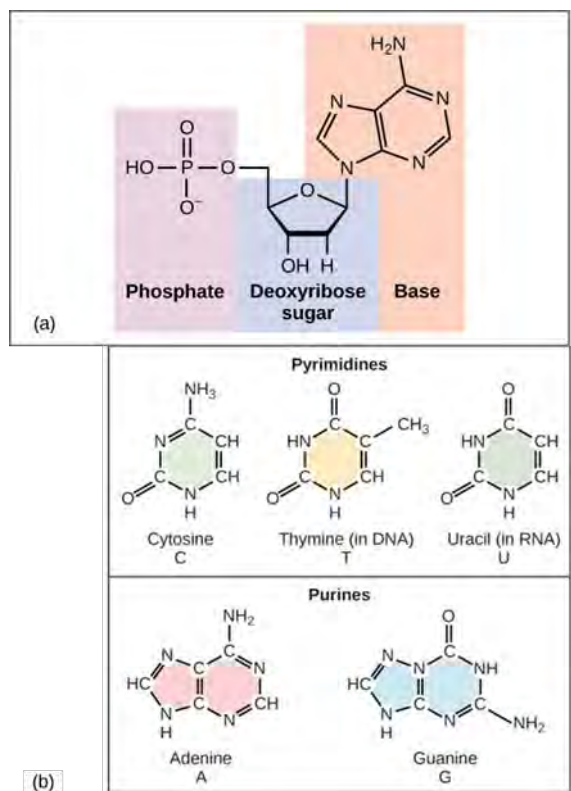
The Structure of DNA

All nucleic acids are made up of monomers called nucleotides. A **nucleotide** has three parts: a 5-carbon sugar, a phosphate group, and a **nitrogenous base** (Figure 10.5). DNA nucleotides contain the 5-carbon sugar **deoxyribose** and four types of nitrogenous bases: adenine (A), guanine (G), cytosine (C), and thymine (T).

Long polymers of DNA are formed when the phosphate group of one nucleotide bonds covalently with the sugar molecule of the next nucleotide (Figure 10.6). The sugar–phosphate groups line up and form a "backbone" for each strand of DNA. The nitrogenous bases stick out from each backbone and the bases on opposite DNA strands can base pair through hydrogen bonding (Figure 10.6).
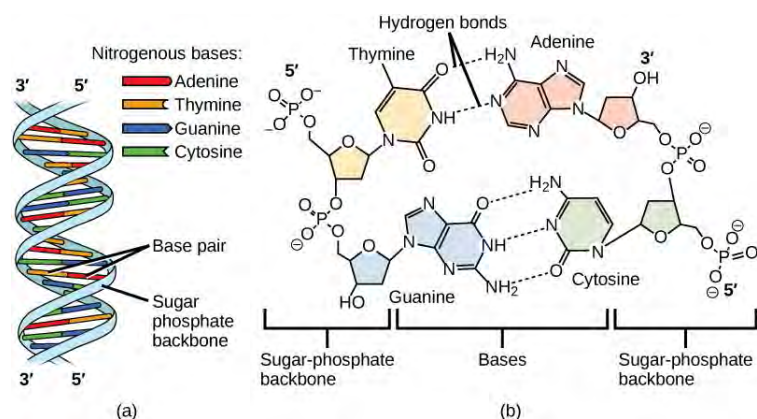
Figure 10.6 DNA (a) forms a double stranded helix, and (b) adenine pairs with thymine and cytosine pairs with guanine. (credit a: modification of work by Jerome Walker, Dennis Myts/ Concepts of Biology OpenStax)

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") (Figure 10.7a). The phosphate group is attached to the 5' carbon of one nucleotide and the 3' carbon of the next nucleotide (Figure 10.7b). Each DNA strand has a 5' carbon at one end and a 3' carbon at the other end. In its natural state, each DNA molecule is composed of two single DNA strands held together by hydrogen bonds between the nitrogenous bases.
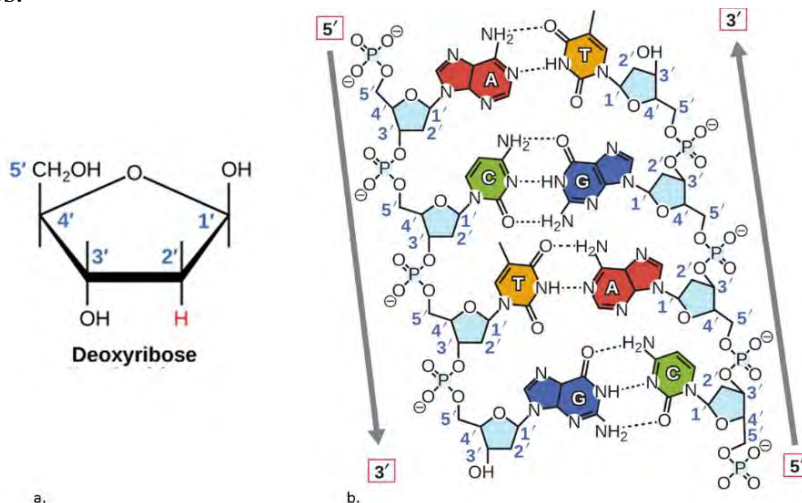
Figure 10.7 a. The carbon atoms of the five-carbon sugar are numbered clockwise from the oxygen as 1', 2', 3', 4', and 5' (1' is read as "one prime"). (credit: Fowler et al. / Concepts of Biology OpenStax) b. The direction of each strand is identified by numbering the carbons (1 through 5) in each sugar molecule. (credit: Parker et al. / Microbiology OpenStax)

It has long since been confirmed that base-pairing takes place between specific purines and pyrimidines. Adenine always base pairs with thymine and cytosine always base pairs with guanine. Adenine and thymine are connected by two hydrogen bonds, and cytosine and guanine are connected by three hydrogen bonds (Figure 10.6b). The two strands of DNA 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 3' carbon in the "downward" position (Figure 10.7b).

The Structure of RNA

Like DNA, RNA is also a polymer composed of nucleotides. RNA nucleotides also contain a 5-carbon sugar, a phosphate group, and a nitrogenous base. RNA nucleotides are made of the five-carbon sugar **ribose**, unlike the deoxyribose found in DNA. Ribose has a hydroxyl group at the 2' carbon, unlike deoxyribose, which has only a hydrogen atom (Figure 10.8).
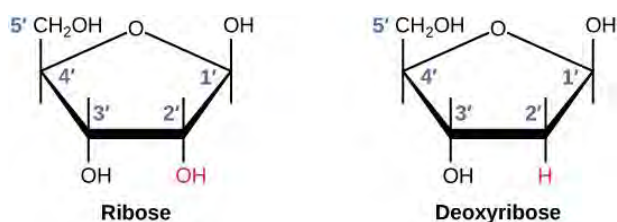
Figure 10.8 The difference between the ribose found in RNA and the deoxyribose found in DNA is that ribose has a hydroxyl group at the 2' carbon. (credit: Fowler et al. / Concept of Biology OpenStax)

RNA nucleotides also have a nitrogenous base; however, the four types of RNA nitrogenous bases are: adenine (A), uracil (U), cytosine (C), and guanine (G). Note, RNA does not use the nitrogenous base thymine, which is found in DNA. RNA is also different than DNA in that it is a single-stranded molecule rather than a double-stranded helix (Figure 10.9). Molecular biologists have named several different kinds of RNA based on their function. These include messenger RNA (mRNA), transfer RNA (tRNA), and ribosomal RNA (rRNA). All three types of RNA molecules are involved in protein synthesis and will be discussed in sections 10.3 and 10.4.
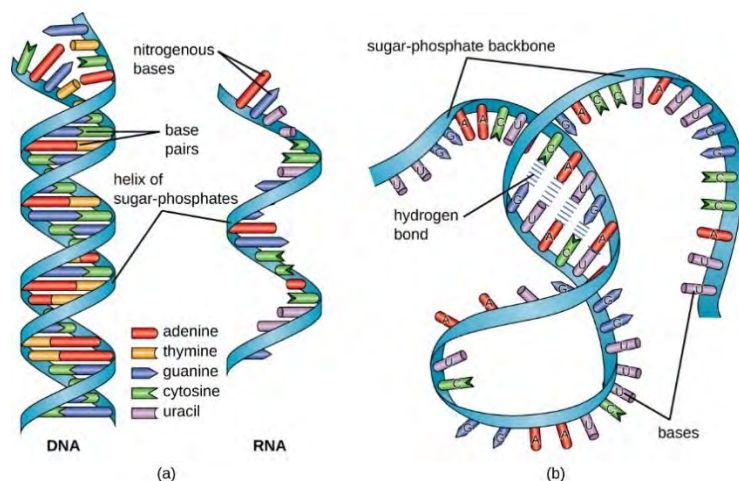
Figure 10.9 (a) DNA is typically double stranded, whereas (b) RNA is typically single stranded. Although it is single stranded, RNA can fold upon itself, with the folds stabilized by short areas of complementary base pairing within the molecule, forming a three-dimensional structure. (credit: Parker et al. / Microbiology OpenStax)

Answer: DNA nucleotides contain the 5-carbon sugar deoxyribose and four types of nitrogenous bases, adenine (A) and guanine (G), and cytosine (C) and thymine (T). The nucleotides that make up RNA contain the 5-carbon sugar ribose. RNA nucleotides also have nitrogenous bases, however the four types of RNA nitrogenous bases are: adenine (A) and uracil (U), and cytosine (C) and guanine (G). RNA exists as shorter single-stranded molecules rather than long double-stranded helices like DNA. There are several kinds of RNA including messenger RNA (mRNA), transfer RNA (tRNA), and ribosomal RNA (rRNA). All three RNA molecules are involved in the production of proteins from the DNA. DNA stores the genetic information needed to build and control the cell.

CONCEPTS IN ACTION– See more about comparing DNA and RNA in this video.

Section Summary

The model of the double-helix structure of DNA was proposed by Watson and Crick with the assistance of information from Franklin, Wilkins, and Chargaff. 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. Nitrogenous bases extend from the sugar-phosphate backbone. 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.

Exercises

1. Which of the following does cytosine pair with?
    a. guanine
    b. thymine
    c. adenine
    d. a pyrimidine
2. Whose x-ray crystallography data was used to determine the structure of DNA?
    a. James Watson
    b. Francis Crick
    c. Erwin Chargaff
    d. Rosalind Franklin
3. Describe the structure and complementary base pairing of DNA.

Answers

1. (a)
2. (d)
3. 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 for 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.

Glossary

deoxyribonucleic acid (DNA): stores the genetic information needed to build and control the cell.

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

nucleotide: monomers of nucleic acids. Consist of a five-carbon sugar, phosphate group, and nitrogenous base

ribonucleic acid (RNA): RNA molecules are involved in the production of proteins from the DNA.

ribose: a five-carbon sugar molecule with hydroxyl group in the 2' position; the sugar component of RNA nucleotides

10.2 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 interphase in the cell cycle, before the cell enters mitosis or meiosis.
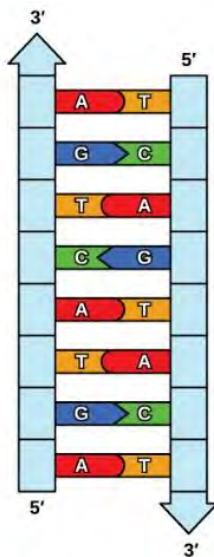
The structure of the double helix provided a hint as to how DNA is copied. Recall that adenine nucleotides pair with thymine nucleotides, and cytosine with guanine. This means that the two strands are complementary to each other. For example, a strand of DNA with a nucleotide sequence of AGTCATGA will have a complementary strand with the sequence TCAGTACT (Figure 10.10).

Figure 10.10 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. (credit: Fowler et al. / Concepts of Biology OpenStax)

Because of the complementarity of the two strands, having one strand means that it is possible to recreate the other strand. The double-helix model 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. What was not clear was how the replication took place. There were three models suggested (Figure 10.11): *conservative, semi-conservative, and dispersive*.

In conservative replication, the "old" parental DNA strands remains together, and the newly formed DNA strands come together to form the second helix (Figure 10.11). The **semi-conservative method** suggests that each of the two "old" parental DNA strands acts as templates. The two "new" complement strands of DNA are synthesized using the "old" template strands; after replication, each DNA helix consists of one parental or "old" strand and one "new" complement strand (Figure 10.11). In the dispersive model, both DNA helices have double-stranded segments of parental DNA and newly synthesized DNA interspersed (Figure 10.11).
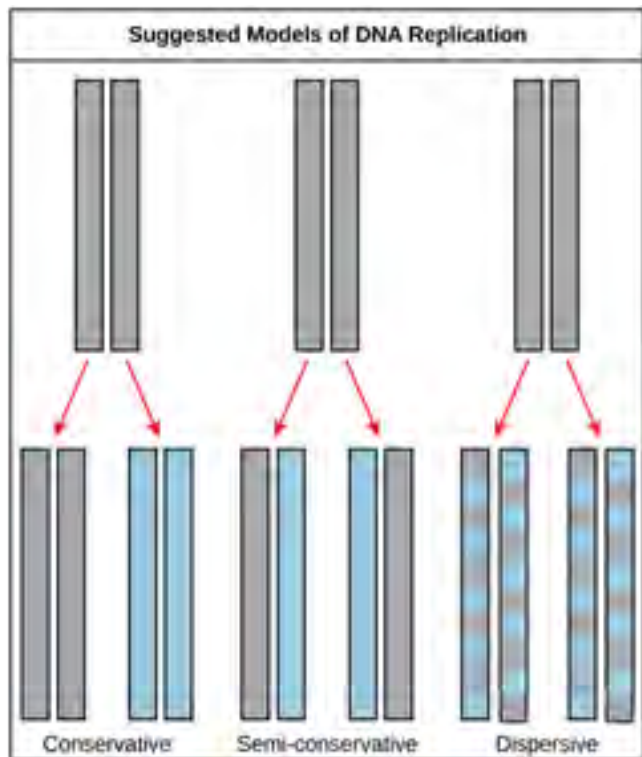
Figure 10.11 The three suggested models of DNA replication. Gray indicates the original DNA strands, and blue indicates newly synthesized DNA. (credit: Modified by Jason Cashmore original work by Clark et al. / Biology 2E OpenStax)

To address these different models, scientists Matthew Meselson and Franklin Stahl carried out experiments using *E. coli* grown in different environments containing different isotopes of nitrogen. Recall that each nucleotide has a nitrogenous base, therefore nitrogen is necessary for DNA replication. Their work provided the necessary data that supported the semi-conservative replication model (Figure 10.12).

Figure 10.12 Meselson and Stahl experimented with *E. coli* grown first in heavy nitrogen (^{15}N) then in ^{14}N. DNA grown in ^{15}N (red band) is heavier than DNA grown in ^{14}N (orange band), and sediments to a lower level in cesium chloride solution in an ultracentrifuge. (credit: modification of work by Mariana Ruiz Villareal/ Biology 2E OpenStax)
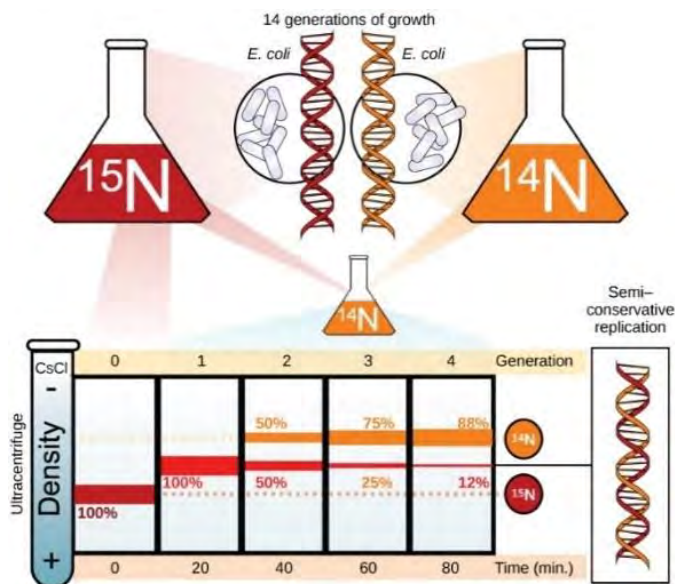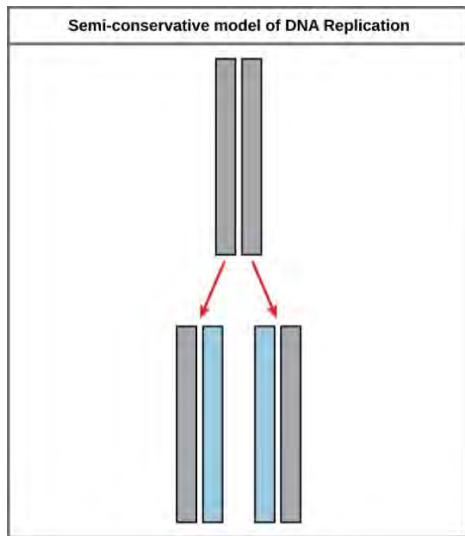
Based on the research of Meselson and Stahl and several others, it is understood that during DNA replication, each of the two "old" parental DNA strands serve as templates from which two "new" complement DNA strands are made. The two "new" strands will be complementary to the parental or "old" strands. Once DNA replication is complete, each new helix will consist of one "old" template strand and one "new" complement strand (Figure 10.13).

Figure 10.13 The semiconservative model of DNA replication is shown. Gray indicates the original DNA strands, and blue indicates newly synthesized DNA. (credit: Fowler et al. / Concepts of Biology OpenStax)

CONCEPTS IN ACTION – Paul Anderson explains DNA replication in this video.

DNA Replication in Eukaryotes

Because eukaryotic genomes are very complex, DNA replication is a very complicated process that involves several enzymes and additional proteins. It occurs in three main stages: initiation, elongation, and termination.
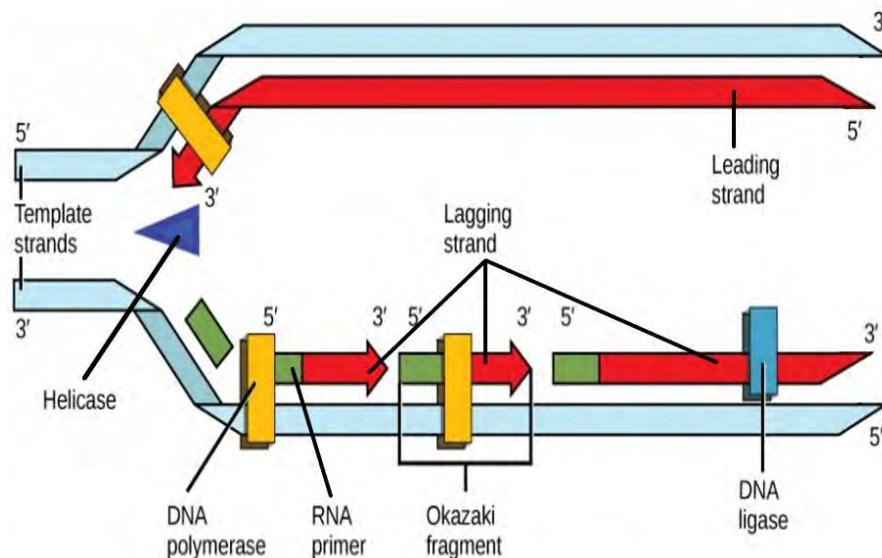
Figure 10.14 Helicase opens the DNA double helix and exposes replication forks. RNA primers are added by RNA polymerase. DNA polymerase then starts attaching DNA nucleotides to the 3' end of the primers. For the leading strand, DNA polymerase will continue adding nucleotides to make a single, uninterrupted strand. The lagging strand is constructed in short segments called Okazaki fragments as helicase exposes more of the template strand. DNA ligase then connects the fragments. (credit: Modified by Jason Cashmore original work by Fowler et al. / Concepts of Biology OpenStax)

Recall that eukaryotic DNA is wound around histone proteins that then coil and form structures called nucleosomes. During initiation, DNA must be unwound in order to make it accessible to binding proteins and enzymes necessary for DNA replication. 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 where replication begins. Replication binding proteins attach to the origin of replication and an enzyme called **helicase** unwinds and opens the DNA helix (Figure 10.14). As the DNA double-helix opens, Y-shaped structures called **replication forks** are formed (Figure 10.14). Two replication forks are formed at the origin of replication, and these extend in both directions. There are multiple origins of replication on eukaryotic chromosomes. This allows replication to occur simultaneously from several places within the genome.

Once initiation has occurred with the help of helicase, the DNA is now accessible. The next step of DNA replication, elongation, can now occur.
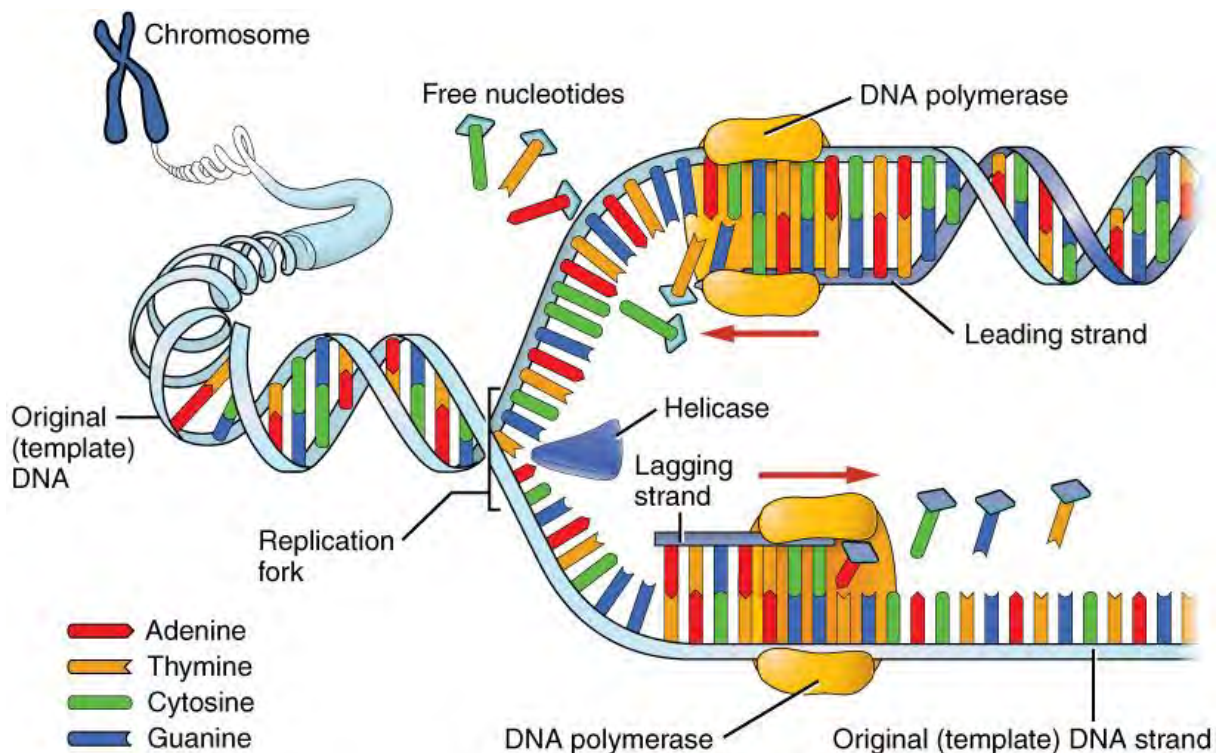
Figure 10.15 In DNA replication, DNA polymerase adds complementary base pairs. (credit: Betts et al. / Anatomy and Physiology OpenStax)

During elongation, an enzyme called **DNA polymerase** adds nucleotides one-by-one to the growing DNA strand which is complementary to the "old" parent template strand (Figure 10.15). DNA polymerase has two important restrictions. First, DNA polymerase can only add nucleotides in the 5' to 3' direction. This means, new DNA strands can only be extended or made in the 5' to 3' direction (Figure 10.14). Second, DNA polymerase requires a free 3'-OH group to which it can add nucleotides. Where does the free 3'-OH group come from? An enzyme called **RNA primase** adds a small five to ten nucleotide RNA segments, which provides the necessary

free 3'-OH end. Because this RNA sequence primes the DNA synthesis, it is appropriately called the **RNA primer**. DNA polymerase can now extend the RNA primer, adding nucleotides one-by-one that are complementary to the template strand. This primer is later removed, and the RNA nucleotides are replaced with DNA nucleotides.

The two template DNA strands have opposing orientations: one strand is in the 5' to 3' direction and the other is oriented in the 3' to 5' direction (Figure 10.10 and 10.14). Only one new DNA strand, the one that is complementary to the 3' to 5' parental DNA strand, can be synthesized continuously towards the replication fork. This continuously synthesized strand is known as the **leading strand** (Figure 10.15). The other strand, complementary to the 5' to 3' parental DNA, is extended away from the replication fork, in small fragments known as **Okazaki fragments**. Each Okazaki fragment requires an RNA primer to start the DNA synthesis (Figure 10.14). Okazaki fragments are named after the Japanese scientists, Tsuneko and Reiji Okazaki, who first discovered them. The strand with the Okazaki fragments is known as the **lagging strand**. As synthesis proceeds, each RNA primer is removed and replaced with DNA nucleotides. Gaps between the Okazaki fragments are filled in and sealed by an enzyme called **DNA ligase**. Termination is said to have occurred when each of the two original strands are bound to their own, finished, complementary strands.

The process of DNA replication can be summarized as follows:

1. DNA unwinds at the origin of replication with the help of specialized binding proteins.
2. Helicase opens up the DNA, forming replication forks. Each replication fork is extended in one direction.
3. RNA Primase synthesizes RNA primers complementary to the DNA strand.
4. DNA polymerase adds new nucleotides complementary to the DNA strand. The leading strand is made continuously, while the lagging strand is made in segments called Okazaki fragments.
5. RNA primers are removed, new DNA nucleotides are put in place of the RNA primers and the backbone is sealed by DNA ligase.

Check your knowledge

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

CONCEPTS IN ACTION – Observe DNA replication in this video.

Telomere Replication

As you have learned, the DNA polymerase 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, once the end of the chromosome is reached there is no place for a RNA primer to be added. 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**. Telomeres have repetitive sequences that do not code for a gene. They are important because they prevent chromosomes from arbitrarily fusing with one another and protect the DNA from becoming damaged.

It is the 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 10.16) helped explain how chromosome ends are maintained. The **telomerase** carries its own RNA primer which can base pair to the end of the DNA strand. The telomerase can then add DNA nucleotides to the end of the chromosome, elongating it. Once the template strand is sufficiently elongated, DNA polymerase can then add nucleotides that are complementary to the ends of the chromosomes. Thus, the ends of the chromosomes are maintained in germline cells, adult stem cells, and some cancer cells.
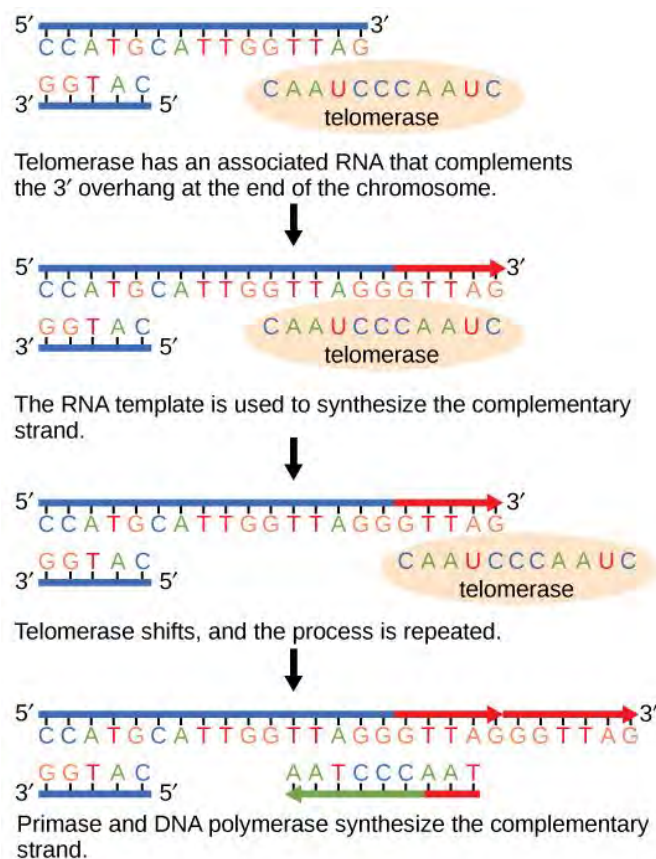
Figure 10.16 The ends of linear chromosomes are maintained by the action of the telomerase enzyme. (credit: Fowler et al. / Concepts of Biology OpenStax)

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. For her discovery of telomerase and its action, Elizabeth Blackburn (Figure 10.17) received the Nobel Prize for Medicine and Physiology in 2009.

Figure 10.17 Elizabeth Blackburn, 2009 Nobel Laureate, was the scientist who discovered how telomerase works. (credit: U.S. Embassy, Stockholm, Sweden / Concepts of Biology OpenStax)

DNA Replication in Prokaryotes

While both eukaryotes and prokaryotes share many similarities when it comes to the process of DNA replication, the structural differences in the chromosomes necessitate some modifications. Recall that prokaryotes typically have one circular chromosome compared to the multiple linear chromosomes found in eukaryotic cells. We will only briefly discuss prokaryotic replication in this chapter, but students that take microbiology will have the opportunity to look more closely at this process.

DNA replication has been extremely well-studied in prokaryotes, primarily because of the small size of the genome and large number of strains that exist and are readily available. *Escherichia coli* has 4.6 million base pairs in a single circular chromosome. The entire chromosome gets replicated in approximately 42 minutes. The process begins from a single origin of replication and proceeds around the chromosome in both directions. Many of the same enzymes used in eukaryotic DNA replication are also used by prokaryotes, including helicase, DNA polymerase, and ligase. As DNA replication proceeds, approximately 1000 nucleotides are added per second. The process of DNA replication is much more rapid in prokaryotes than in eukaryotes. This results in a higher mutation rate in prokaryotes.

Table 10.1 Differences between Prokaryotic and Eukaryotic Replications (credit: Fowler et al. / Concepts of Biology OpenStax)

Property	Prokaryotes	Eukaryotes
Origin of replication	Single	Multiple
Rate of replication	1000 nucleotides/sec	50 to 100 nucleotides/sec
Chromosome structure	Circular	Linear
Telomerase	Not needed	Present

DNA Repair

Because DNA polymerase can make mistakes while adding nucleotides, it is important that the enzyme goes back and edits the DNA by proofreading every newly added base. Incorrect bases are removed and replaced by the correct base before the process continues (Figure 10.18 **a**).

(a) Proofreading

(b) Mismatch Repair

(c) Nucleotide Excision
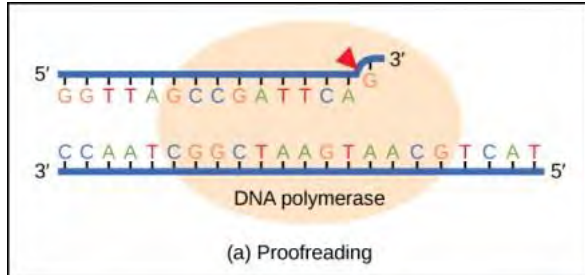
Most mistakes are corrected during replication, but some are not. When mismatched bases are not caught, the mismatch repair mechanism is employed. Mismatch repair enzymes recognize the wrongly incorporated base and cuts it from the DNA. The enzymes then replace the mismatched base with the correct base (Figure 10.18 **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 then replaced with the help of the DNA polymerase (Figure 10.18 **c**).
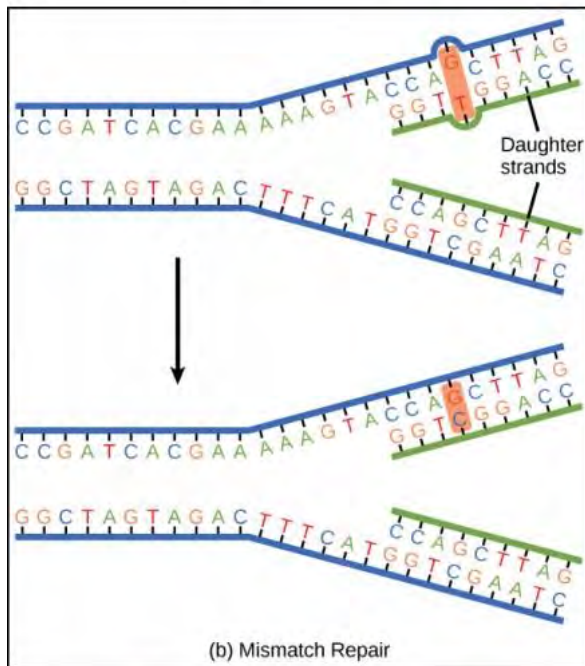
Nucleotide excision repair is particularly important in correcting thymine dimers, which are primarily caused by ultraviolet light. A thymine dimer occurs when two thymine nucleotides adjacent to one another, covalently bond to each other rather than their complementary bases. If the dimer is not removed and repaired, it will lead to a mutation. Individuals with flaws in their nucleotide excision repair genes show extreme sensitivity to sunlight and often develop skin cancers early in life.
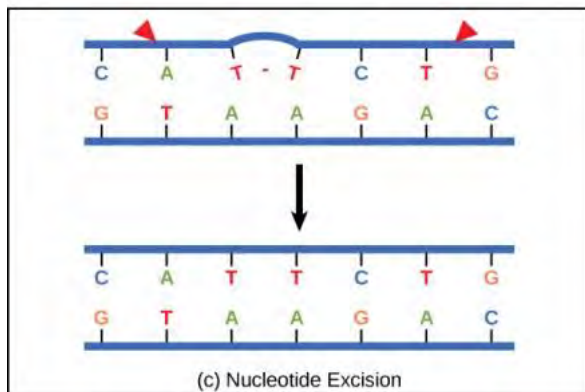
Figure 10.18 Proofreading by DNA polymerase (a) corrects errors during replication. In mismatch repair (b), the incorrectly added base is detected after replication. Nucleotide excision (c) repairs thymine dimers. When exposed to UV, two thymines lying adjacent to each other can form thymine dimers. In normal cells, they are excised and replaced. (credit: Fowler et al. / Concepts of Biology OpenStax)

DNA Mutation

As mentioned, most mistakes are caught and corrected; however, if they are not, they may result in a **mutation.** A mutation is defined as a permanent change in the DNA sequence. Changes in the DNA sequence can have effects on the protein products, which can be either beneficial or detrimental.

Evolution, the genetic change in a population over time, is heavily dependent on mutation. Mutations in the DNA lead to variations among individuals which can lead to new or different traits within a population. These new or different traits can be beneficial to individuals within the population and can provide advantages, for example increased reproductive success, when compared to others in the population. Without genetic changes to the DNA, evolution would not occur. This topic will be discussed more in chapter 11.

Mutations can also be detrimental. Changes in the DNA sequence can lead to the inability to properly synthesize proteins. Changes in the DNA sequence can lead to changes in the amino acid sequence of a protein. If the amino acid sequence of a protein changes, the protein usually does not function properly.

There are several different types of mutations that can occur. One type, **point mutations,** occur when a single nucleotide is permanently changed in the DNA sequence. Point mutations may occur when one base is substituted for another. For example, when an adenine (A) gets replaced by a cytosine (C) (Figure 10.19). This change may cause a change in the amino acid sequence which would cause a change in the protein's structure. Sometimes the point mutation may be silent where the substitution of a base causes no change in the amino acid or amino acid sequence. These silent mutations are thought to have no detrimental impacts. All individuals are thought to have some silent mutations in their genomes.
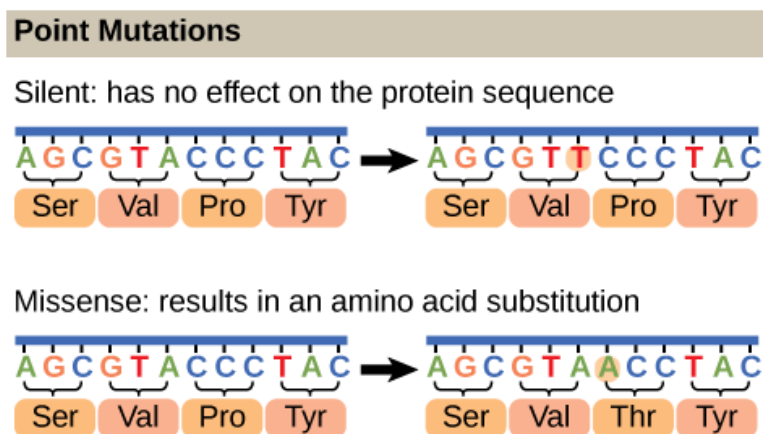
Figure 10.19 Mutations in the DNA can lead to a change in the protein sequence. (credit: Modified by Elizabeth O'Grady original work of Parker et al. / Microbiology OpenStax)

Mutations can be caused by several different factors. As discussed, errors by DNA polymerase during replication can cause mutations. Mutations can also occur because the DNA is damaged in some way. Such mutations are classified as being induced or spontaneous. Induced mutations are those that result from exposure to chemicals, UV rays, x-rays, or some other environmental agent. Spontaneous mutations occur without any exposure to any environmental agent; they are a result of natural reactions taking place within the body.

Mutations in repair genes have been known to cause cancer. Many mutated repair genes have been implicated in certain forms of pancreatic cancer, colon cancer, and colorectal cancer. Mutations can affect either somatic cells or germline cells.

Mutations can affect either somatic cells or germline cells. Recall that human somatic cells contain 46 chromosomes and these cells do not lead to the formation of gametes. Most cells that make up the human body are somatic cells. If mutations accumulate in a somatic cell, they may lead to problems such as the uncontrolled cell division observed in cancer. Somatic cell mutations can be extremely dangerous to the individual organism, but are not passed on to their offspring, therefore they are not heritable.

Germline cells, also called gametes, have half the number of chromosomes compared to a somatic cell. If a mutation takes place in germline cells, the mutation will be passed on to the next generation, and therefore is considered a heritable mutation. Hemophilia, a condition that effects an individual's ability to form blood clotting proteins, is an example of a germline mutation.

Check your knowledge

A mutation occurs in the leaf of a plant. Will the offspring of the plant be affected?

A mutation occurs in the ovary and eggs of a plant. Will the offspring of the plant be affected?

Answers: No, the leaf is a made of somatic cells that will not be passed on to the next generation. It is not heritable. The eggs, on the other hand, are gametes and germline cells. These will be heritable.

Section Summary

DNA replicates by a semi-conservative method in which each of the two "old" parental DNA strands act as templates for the two "new" complement DNA strands. After replication, each DNA helix has one parental or "old" strand, and one "new" complement 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 including an enzyme called helicase. This forms replication forks. RNA primase synthesizes an RNA primer to initiate DNA synthesis by DNA polymerase. DNA polymerase can add nucleotides in only one direction, the 5' to 3' 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 fragments are joined together with DNA ligase.

The ends of eukaryotic chromosomes pose a problem, as DNA polymerase is unable to extend them without a primer. Telomerase, an enzyme with an inbuilt RNA primer, extends the ends by copying the RNA primer and extending the "lagging" end of the chromosome. DNA polymerase can then extend the DNA using the RNA 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. Most mistakes are caught and corrected; however, if they are not, they may result in a mutation. A mutation is defined as a permanent change in the DNA sequence. Changes in the DNA sequence can have effects on the protein products, which can be either beneficial or detrimental.

Exercises

1. DNA replicates by which of the following models?
    a. conservative
    b. semiconservative
    c. dispersive
    d. none of the above
2. The initial mechanism for repairing nucleotide errors in DNA is _____.
    a. mismatch repair
    b. DNA polymerase proofreading
    c. nucleotide excision repair
    d. thymine dimers
3. How do the linear chromosomes in eukaryotes ensure that its ends are replicated completely?
4. Mutations can be either beneficial or detrimental.
    a. TRUE
    b. FALSE

Answers

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

mutation: a permanent variation in the nucleotide sequence of a genome

Okazaki fragments: the DNA fragments that are synthesized in short stretches on the lagging strand

point mutation: occur when a single nucleotide is permanently changed in the DNA sequence

RNA primase: an enzyme that can base pair with the DNA and add a short stretch of RNA nucleotides called a primer. The primer is required to initiate DNA replication

RNA primer: short sequence of RNA nucleotides which DNA polymerase can add DNA nucleotides to

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

Footnotes

1 Mariella Jaskelioff, et al., "Telomerase reactivation reverses tissue degeneration in aged telomerase-deficient mice," *Nature*, 469 (2011):102–7.

10.3 Transcription

In both prokaryotes and eukaryotes, DNA contains the information necessary for the cell to build proteins. Most structural components of the cell are made up, at least in part, by proteins. Virtually all the functions that a cell carries out are completed with the help of proteins. In order to make proteins, the DNA is "read" or **transcribed** into an mRNA molecule. The mRNA then leaves the nucleus and provides the information necessary to synthesize the protein through a process called **translation**. This section will focus on the details of transcription.

The Central Dogma: DNA Encodes RNA; RNA Encodes Protein

The flow of genetic information in cells from DNA to RNA to protein is described by the **central dogma** (Figure 10.20). The central dogma states that genes specify the sequences of RNAs, which in turn specify the sequences of proteins. Recall, that a gene is a functional segment of DNA that provides the genetic information necessary to build a protein.
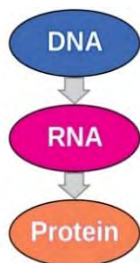
Figure 10.20 The central dogma states that DNA encodes RNA, which in turn encodes protein. (credit: Fowler et al. / Concepts of Biology OpenStax)

The copying of DNA to mRNA is relatively straightforward. During transcription, mRNA is synthesized with the help of many enzymes. RNA nucleotides complementary base pair with DNA nucleotides forming the RNA transcript. The translation to protein is more complex and will be discussed in the next section. Before taking a closer look at the process of transcription, let's first review the three types of RNA introduced in section 10.1: mRNA, tRNA, and rRNA.

Types of RNA

As mentioned, ribonucleic acid, or RNA, is mainly involved in the process of protein synthesis. RNA is usually single-stranded and is comprised of nucleotides that are linked by phosphodiester bonds. A nucleotide in the RNA chain contains the sugar ribose, one of the four nitrogenous bases (adenine, uracil, guanine, and cytosine), and a phosphate group. There are three major types of RNA: messenger RNA (mRNA), ribosomal RNA (rRNA), and transfer RNA (tRNA).

Messenger RNA

The first type, **messenger RNA** (mRNA), carries the message encoded in the DNA on how to build proteins (Figure 10.21). If a cell needs to synthesize a certain protein, the gene for this protein "turns on" and the messenger RNA is transcribed.

Ribosomal RNA

Ribosomal RNA (rRNA) is a major constituent of ribosomes (Figure 10.21). The rRNA ensures the proper alignment of the mRNA and the ribosomes. The ribosome's rRNA also has an enzymatic activity and catalyzes peptide bond formation between two aligned amino acids.

Transfer RNA

Transfer RNA (tRNA) is one of the smallest of the four types of RNA, usually 70–90 nucleotides long. It carries the correct amino acid to the site of protein synthesis within the ribosome(Figure 10.21). It base-pairs with the mRNA and allows for the correct amino acid to insert itself in the polypeptide chain.

Figure 10.21 A eukaryotic cell showing mRNA, rRNA, and tRNA. (credit: Modified by Elizabeth O'Grady original work of Betts et al./ Anatomy and Physiology OpenStax)
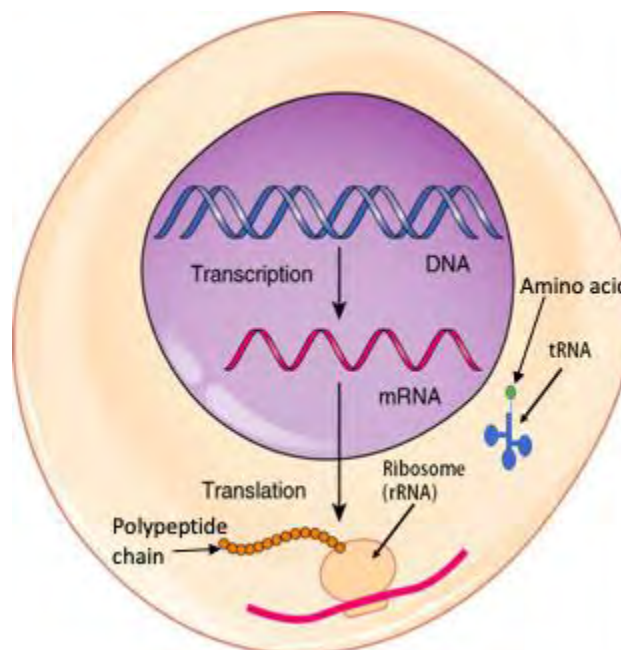
Check your knowledge

In the following list, determine if each is a characteristic of rRNA, mRNA, tRNA.
- Carries code from DNA
- Carries the amino acid
- Made in the nucleolus
- Joins enzymes to form the ribosome
- Found in cytoplasm

Distinguish the difference between transcription and translation.

Answers: mRNA, tRNA, rRNA, rRNA, all are found in the cytoplasm during translation.

Transcription must occur before translation. In transcription, DNA is coded into mRNA. The mRNA is then coded into an amino acid sequence in translation.

Transcription: from DNA to mRNA

Both prokaryotes and eukaryotes perform fundamentally the same process of transcription, with one very important difference. In eukaryotes, transcription occurs in the membrane-bound nucleus. In prokaryotes, transcription occurs in the nucleoid region; recall that prokaryotes lack membrane bound organelles. Once the mRNA is formed in eukaryotic cells it must be transported to the cytoplasm. Because the mRNA of prokaryotes does not need to be transported anywhere, translation can immediately follow.

In both prokaryotes and eukaryotes, transcription occurs in three main stages: initiation, elongation, and termination.
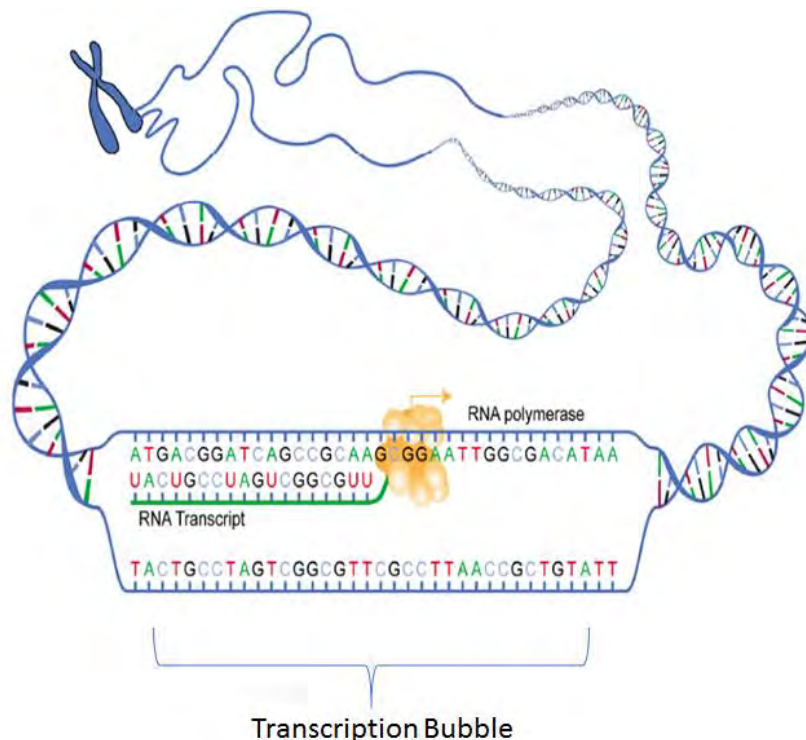
Figure 10.22 Transcription: from DNA to mRNA. (credit: Betts et al. / Anatomy and Physiology OpenStax)

Initiation

Transcription requires a small part of the DNA double helix to partially unwind. The DNA must unwind to allow enzymes and additional proteins to access specific genes which will then be used to make mRNA. The region of the DNA that is unwound is called the **transcription bubble** (Figure 10.22). Several proteins and enzymes bind to a region at the beginning of the gene called a **promoter**, a particular sequence of nucleotides that triggers the start of transcription (Figure 10.23). In most cases, promoters exist upstream, or in front 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.
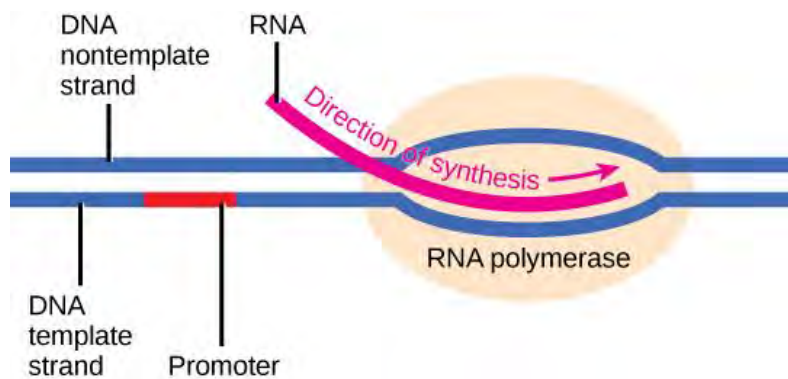
Figure 10.23 The initiation of transcription begins when DNA is unwound, forming a transcription bubble. Enzymes and other proteins involved in transcription bind at the promoter. (credit: Fowler et al. / Concepts of Biology OpenStax)

Elongation

Transcription always proceeds from one of the two DNA strands, which is called the template strand. The mRNA is complementary to the template strand and is almost identical to the other DNA strand, called the non-template strand. The two big exceptions are that RNA nucleotides contain the sugar ribose while DNA nucleotides contain the sugar deoxyribose, and that RNA contains the nitrogenous base uracil (U) instead of the thymine (T) found in DNA. During elongation, an enzyme called **RNA polymerase** proceeds along the DNA template adding RNA nucleotides by base pairing with the DNA template in a manner similar to DNA replication. As elongation proceeds, the DNA is continuously unwound ahead of the enzyme and then rewound behind it (Figure 10.24).
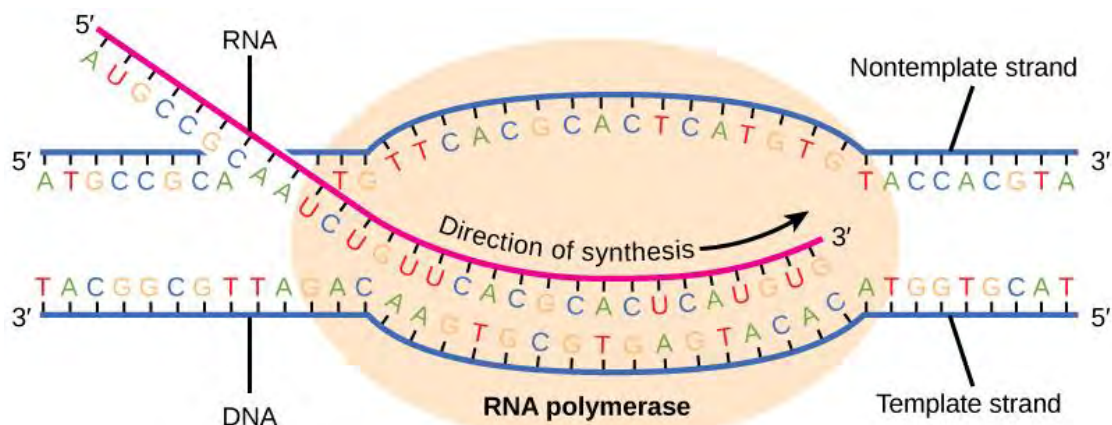
Figure 10.24 During elongation, RNA polymerase tracks along the DNA template, synthesizes mRNA in the 5' to 3' direction, and unwinds then rewinds the DNA as it is read. (credit: Fowler et al. / Concepts of Biology OpenStax)

Termination

When the polymerase has reached the end of the gene, the RNA polymerase needs to be instructed to dissociate, or separate, from the DNA template strand. Once the RNA polymerase

dissociates, the newly made mRNA transcript is released. Depending on the gene being transcribed, there are two kinds of termination signals, but both involve repeated nucleotide sequences in the DNA template. These repeated sequences cause the RNA polymerase to stall, separate from the DNA template, and free the newly synthesized mRNA.

At the end of termination, the process of transcription is complete. In a prokaryotic cell, by the time termination occurs, the mRNA is already being used to synthesize numerous copies of the encoded protein. This is possible because prokaryotic cells do not have their DNA enclosed in membrane bound nuclei. As soon as the mRNA is partially synthesized, ribosomes attach and begin generating the protein (Figure 10.25). Because of their nucleus, this is not possible for eukaryotic cells. Once the mRNA has been synthesized and undergoes modifications it must first be moved out of the nucleus and into the cytoplasm before translation can begin. This prevents simultaneous transcription and translation in eukaryotic cells.
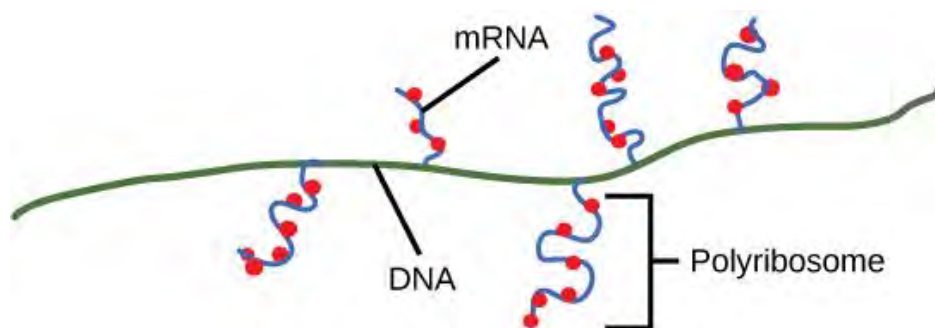
Figure 10.25 Multiple polymerases can transcribe a single bacterial gene while numerous ribosomes concurrently translate the mRNA transcripts into polypeptides. (credit: Fowler et al. / Concepts of Biology OpenStax)

CONCEPTS IN ACTION – Observe transcription at this site.

Eukaryotic RNA Processing

The newly transcribed eukaryotic mRNAs are referred to as primary transcripts. These primary transcripts must undergo several processing steps before they can be transferred from the nucleus to the cytoplasm and then 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 mRNA transcript is still being synthesized and involves adding a special nucleotide "cap" to the 5' end of the growing transcript (Figure 10.26). 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 nucleotides to the 3' end, called the poly-A tail (Figure 10.26). This modification further protects the mRNA transcript from degradation and signals that the mRNA transcript is ready to be exported to the cytoplasm.
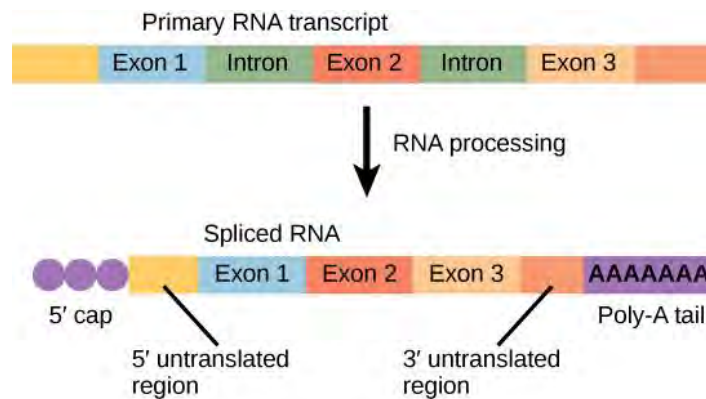
Figure 10.26 Eukaryotic mRNA contains introns that must be spliced out. A 5' cap and 3' tail are also added. (credit: Fowler et al. / Concepts of Biology OpenStax)

Eukaryotic DNA, and thus complementary mRNA, contains long non-coding regions that do not code for amino acids. Their function is still not well understood, but the process called **splicing** removes these non-coding regions, called **introns**, from the mRNA transcript (Figure 10.27). The non-coding regions are called introns because they are *int*ervening sequences. The coding regions are called **exons**; *ex*on signifies that they are *ex*pressed.

A **spliceosome**, a structure composed of various proteins and other molecules, attaches to the mRNA transcript and "splices" or cuts out the non-coding, introns. The remaining exons are pasted together to form the mature mRNA which will then be transported to the cytoplasm.

Figure 10.27 Splicing DNA in the nucleus, a structure called a spliceosome cuts out introns (noncoding regions) within a pre-mRNA transcript and reconnects the exons. (credit: Betts et al. / Anatomy and Physiology OpenStax)
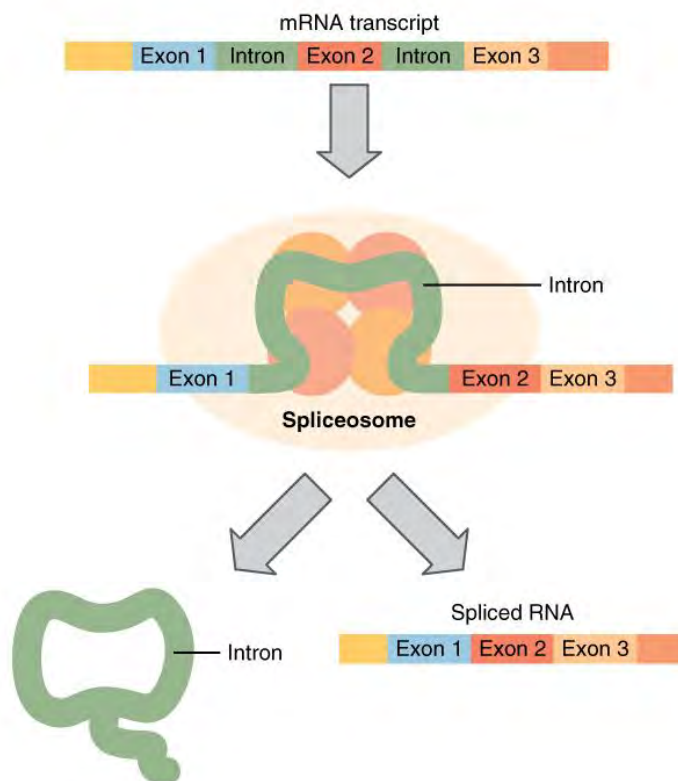
Some of the segments that are removed from mRNA during splicing are not always non-coding. When different coding regions of mRNA are **alternatively spliced** out, different variations of the protein will result, with differences in structure and function (Figure 10.28). This process results in a much larger variety of possible proteins and protein functions from a given genome. Humans, for example, have just over 20,000 genes, yet the human body produces over 80,000 different proteins.
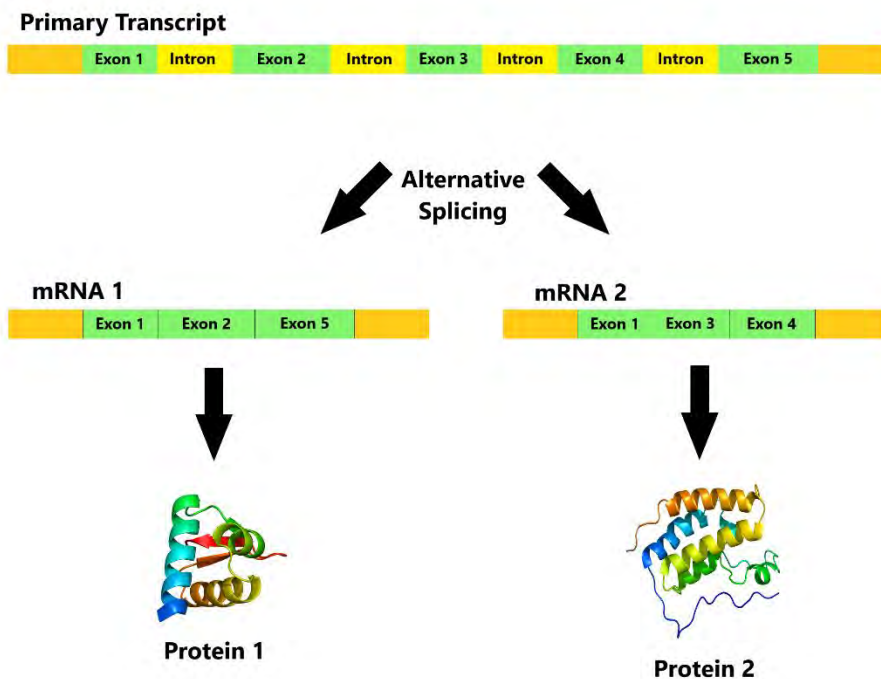
Figure 10.28 Alternative splicing of an mRNA primary transcript produces two different mRNA sequences, each of which results in a different protein. (credit: Jason Cashmore)

CONCEPTS IN ACTION – Observe alternate splicing in this video.

Section Summary

Cells use the genetic code stored within DNA to build proteins, which ultimately determine the structure and function of the cell. This genetic code lies in the particular sequence of nucleotides that make up each gene. To "read" this code, the cell must perform two sequential steps. In the first step, transcription, the DNA code is converted into an RNA code. mRNA synthesis is initiated at a promoter sequence on the DNA template. Elongation synthesizes a new mRNA transcript, and termination frees the mRNA. 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. Only finished mRNAs are exported from the nucleus to the cytoplasm.

Exercises

1. 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
2. Portions of eukaryotic mRNA sequence that are removed during RNA processing are _____.
   a. exons
   b. caps
   c. poly-A tails
   d. introns
3. Which enzyme is used to synthesize RNA?
4. Compare and contrast the three types of RNA.

Answers

1. (a)
2. (d)
3. RNA polymerase
4. All RNA is made up of nucleotides that consist of the sugar ribose, a phosphate group and a nitrogenous base. All RNA's use the bases adenine, uracil, guanine, and cytosine. All RNA's are synthesized in the nucleus. mRNA is used to carry the instructions on how to make protein from the nucleus to the cytoplasm. rRNA helps form ribosomes where proteins will be built in the cytoplasm. tRNA carry amino acids, the monomers of proteins, to the ribosome where the protein will be made.

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

central dogma: The flow of genetic information in cells from DNA to mRNA to protein

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

messenger RNA (mRNA): a form of RNA that carries the nucleotide sequence code for a protein sequence that is translated into a polypeptide sequence

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

ribosomal RNA (rRNA): molecules of RNA that combine to form part of the ribosome

spliceosome: a structure composed of various proteins and other molecules, which attaches to the mRNA transcript and "splices" or cuts out the non-coding, introns

splicing: the process of removing introns and reconnecting exons in a pre-mRNA

transcription: the synthesis of a strand of mRNA that is complementary to the gene of interest.

transcription bubble: the region of locally unwound DNA that allows for transcription of mRNA

transfer RNA (tRNA): 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

translation: the process of synthesizing a chain of amino acids called a polypeptide chains or proteins

10.4 Translation

Learning objectives

By the end of this section, you will be able to:

- *Describe the different steps involved in translation*
- *Discuss the role of rRNA, mRNA, and tRNA in protein synthesis*
- *Describe the genetic code and how the nucleotide sequence determines the amino acid sequence of a protein*
- *Be able to take an mRNA sequence and transcribe and translate the corresponding protein*
- *Be prepared to define and explain all bolded terms*

Proteins perform a wide variety of functions in a cell and are necessary to maintain homeostasis. Protein synthesis is one of a cell's most energy-consuming metabolic processes. The process of **translation**, or protein synthesis, involves "decoding" a mRNA molecule with the purpose of forming a polypeptide chain. Amino acids are linked together through covalent bonds to form polypeptide chains that range in lengths from approximately 50 amino acids to more than 1,000.

The Protein Synthesis Machinery

In addition to the mature mRNA, many other molecules contribute to the process of translation. Translation requires not only mRNA, but also ribosomes, tRNAs, and various other enzymes (Figure 10.29). Although each of these components is necessary, their composition may vary across species. For instance, ribosomes may consist of different **ribosomal RNA**s (rRNA) and enzymes depending on the organism. Prokaryotic and eukaryotic cells have distinctly different ribosomes that vary in size. Although living cells may have slight differences, the general structures and functions of the protein synthesis machinery are comparable (Figure 10.29).
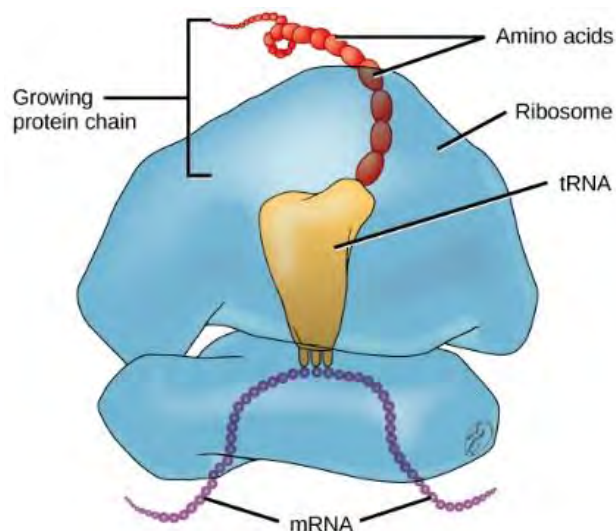
Figure 10.29 The protein synthesis machinery includes the large and small subunits of the ribosome, mRNA, and tRNA. (credit: modification of work by NIGMS, NIH / Concepts of Biology OpenStax)

Ribosomes

A ribosome is a complex macromolecule composed of structural and catalytic **rRNA**s. Ribosomes also consist of many distinct proteins, some of which have enzymatic properties. In eukaryotes, the nucleolus, a region found in the nucleus, is completely specialized for the synthesis and assembly of rRNAs.

Ribosomes are located in the cytoplasm in both prokaryotic and eukaryotic cells. In eukaryotes, ribosomes are also found attached to the rough endoplasmic reticulum. Ribosomes are made up of a large and small subunit that come together for translation. The small subunit is responsible for binding directly to the mRNA, whereas the large subunit sequentially binds transfer RNAs (Figure 10.30). **Transfer RNA (tRNA)** is a type of RNA molecule that brings amino acids to the growing polypeptide chain. Each mRNA is simultaneously translated by many ribosomes, all synthesizing the polypeptide chain in the same direction. Once the polypeptide chain is synthesized it must fold into its three-dimensional shape before it is functional. Once folded, the polypeptide chain is considered a protein.
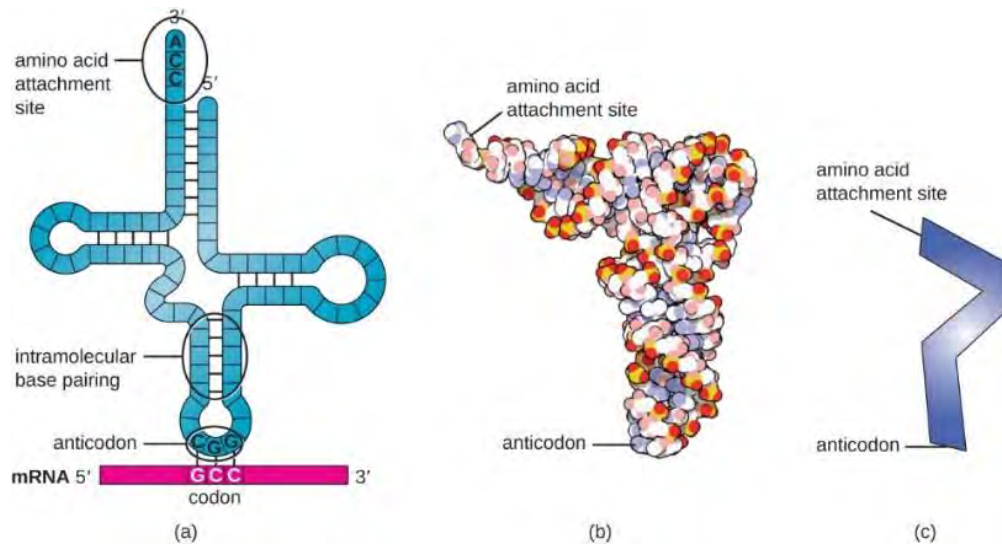
Figure 10.30 (a) After folding caused by intramolecular base pairing, a tRNA molecule has one end that contains the anticodon, which interacts with the mRNA codon, and the CCA amino acid binding end. (b) A space-filling model is helpful for visualizing the three-dimensional shape of tRNA. (c) Simplified models are useful when drawing complex processes such as protein synthesis. (credit: Parker et al. / Microbiology OpenStax)

Depending on the species, 40 to 60 types of tRNA exist in the cytoplasm. tRNA carrying a specific amino acid binds to sequences on the mRNA template and adds 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.

How is it that tRNA translates the mRNA nucleotide sequence into protein? To answer this question, we must first understand the **genetic code**, the relationship between the nucleotide sequence and the different amino acids that make up a protein.

The Genetic Code

To summarize what we know to this point, transcription generates messenger RNA from the DNA housed in the nucleus of eukaryotic cells. The mRNA is a mobile complement of one or more genes. mRNA is generated using the nitrogenous bases adenine, cytosine, guanine, and uracil.

During translation the mRNA nucleotide sequence is used to generate a protein. Proteins can be made up of as many as 20 different amino acids. 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. The three-nucleotide codon means that there is a total of 64 possible combinations (4^3), with four different nucleotides possible at each of the three different positions within the codon. This number is greater than the number of amino acids used to generate proteins. This means that some amino acids are encoded by more than one codon (Figure 10.31). This redundancy in the genetic code is called degeneracy. Typically, whereas the first two positions in a codon are important for determining which amino acid will be incorporated into a growing polypeptide, the third position, called the wobble position, is less critical. In many cases, if the nucleotide in the third position is changed, the same amino acid is still incorporated.

Figure 10.31 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 / Concepts of Biology OpenStax)

The codon AUG specifies the amino acid methionine and has a special function. AUG serves as the only **start codon.** The start codon is where a ribosome begins translation on that mRNA. Three of the 64 codons terminate protein synthesis and release the polypeptide chain from the ribosome. These triplets are called **stop codons;** they do not code for an amino acid. Once the stop codon is reached, no additional amino acids will be added to the polypeptide chain.

The genetic code is nearly universal. With a few exceptions, virtually all species use the same genetic code for protein synthesis. This is powerful evidence that all existing life on earth shares a common origin. However, there are some unusual amino acids such as pyrrolysine that have currently only been observed in archaea and bacteria. Research is being done to understand the relevance of this discovery.

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.

Protein synthesis begins with the formation of an initiation complex. In *E. coli*, this complex involves the small ribosome subunit, the mRNA, three initiation proteins, and a tRNA carrying the amino acid methionine (Figure 10.32). The tRNA has a region called the **anticodon**. The anticodon complements and interacts with the AUG start codon on the mRNA and delivers the first amino acid, methionine. Once the anticodon of tRNA base pairs with the AUG codon of the mRNA, the large ribosomal subunit binds to the complex. This step completes the initiation of translation.

The next step, elongation, takes place as the ribosome moves along the mRNA. Again, the basics of elongation are the same in both prokaryotes and eukaryotes, so we will review elongation from the perspective of *E. coli*. The large ribosomal subunit consists of three compartments: the A site, the P site, and the E site. The A site is responsible for binding incoming charged tRNAs. A charged tRNA is one that is attached to its specific amino acids. The P site binds charged tRNAs carrying the amino acids that are connected by peptide bonds. These amino acids are part of the growing polypeptide chain but have not yet dissociated from their corresponding tRNA (Figure 10.32).
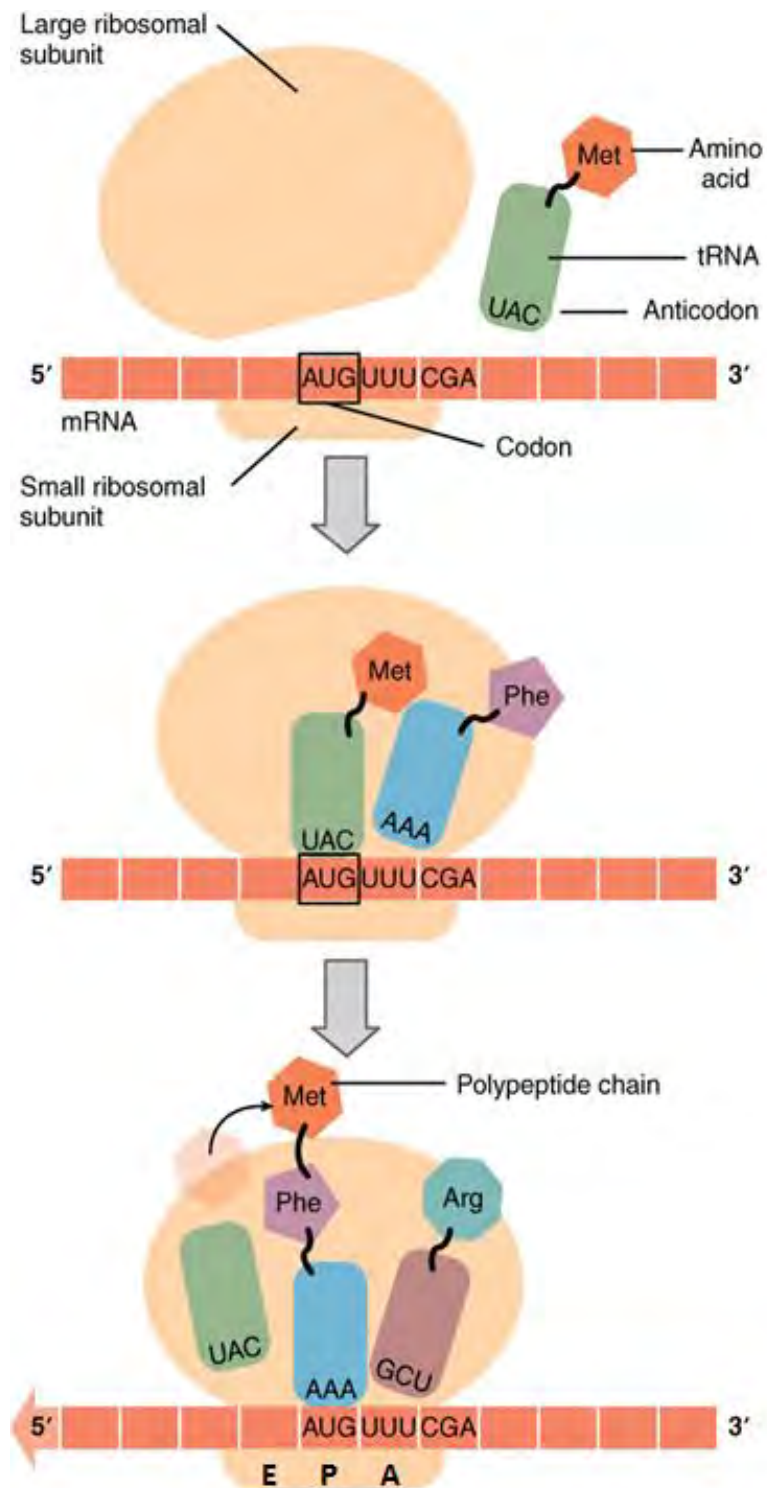
Figure 10.32 Translation begins when a tRNA anticodon recognizes a codon on the mRNA. The large ribosomal subunit joins the small subunit, and a second tRNA is recruited. As the mRNA moves relative to the ribosome, the polypeptide chain is formed. (credit: Modified by Elizabeth O'Grady original work of Betts et al. / Anatomy and Physiology OpenStax)

Peptide bonds are special covalent bonds that exist between the amino group of one amino acid and the carboxyl group of a second amino acid (Figure 10.33). The E site releases uncharged tRNAs so they can be recharged with free amino acids (Figure 10.32).
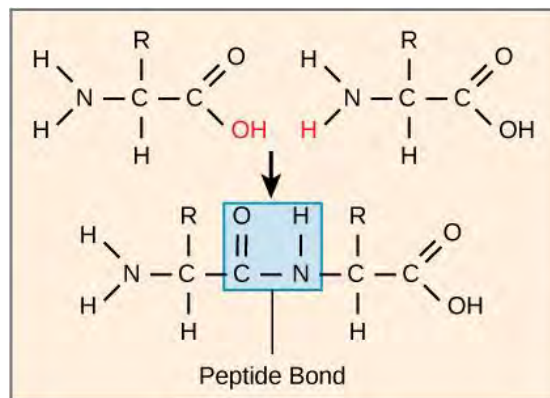
Figure 10.33 A peptide bond links the carboxyl end of one amino acid with the amino end of another, producing one water molecule during the process. This is a dehydration synthesis reaction. (credit: Clark et al. / Biology 2E OpenStax)

The ribosome shifts one codon at a time, catalyzing each process that occurs in the three sites (Figure 10.32). With each step, a charged tRNA enters the complex, the polypeptide chain 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.

Termination of translation occurs when a stop codon (UAA, UAG, or UGA) is encountered. When a stop codon enters the ribosome's A site 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.

CONCEPTS IN ACTION- Learn more by watching the video on translation.

Practice transcribing and translating genes by clicking on this link

Check your knowledge

The nucleotide code on a gene on DNA is GCT.
What is the mRNA codon?
What is the tRNA anticodon?
What amino acid is coded?

Answers: CGA, GCU, Arg (arginine)

Section Summary

The central dogma describes the flow of genetic information in the cell from DNA to RNA 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, which associates 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.

Translation includes the mRNA template, ribosomes, tRNAs, and various enzymatic proteins. The small ribosomal subunit binds to the mRNA template. Translation begins at the initiating AUG on the mRNA. The formation of peptide bonds occurs between sequential amino acids specified by the mRNA template according to the genetic code. The ribosome accepts charged tRNAs, and as it moves along the mRNA, it catalyzes bonding between the new amino acid and the end of the growing polypeptide chain. The entire mRNA is translated in three-nucleotide "steps" of the ribosome. When a stop codon is encountered, a protein binds allowing the translation components to separate and frees the new protein.

Exercises

1. The RNA components of ribosomes are synthesized in the _____.
    a. cytoplasm
    b. mitochondria
    c. nucleolus
    d. endoplasmic reticulum
2. How long would the peptide be that is translated from this mRNA sequence: 5'-AUGGGCUACCGAUAG-3'?
    a. 0
    b. 2
    c. 3
    d. 4
3. Transcribe and translate the following DNA sequence:
   5'-TACGCCGGTTATATTGCA-3'

Answers

1. (c)
2. (d)
3. The mRNA would be: 5'-AUG-CGG-CCA-AUA-UAA-CGU-3'. The protein would be: Meth-Arg-Pro-Ile. Even though there are six codons, the fifth codon corresponds to a stop, so the sixth codon would not be translated.

Glossary

anticodon: three consecutive nucleotides on tRNA that complement the codon on a mRNA

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

peptide bond: a covalent bond that exists between the amino group of one amino acid and the carboxyl group of a second amino acid

ribosomal RNA (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

translation: process of producing a protein from the nucleotide sequence code of an mRNA transcript

transfer RNA (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

10.5 How Genes Are Regulated

All organisms and cells control and regulate the transcription and translation of their DNA into protein. The process of turning on a gene to produce mRNA and then protein is called **gene expression**. All living cells control when and how its genes are expressed. For gene expression to occur, there must be mechanisms that control the following processes (1) when to turn on a gene to make mRNA and then protein (2) how much or what quantity of protein needs to be made, and (3) the ability to stop making that protein once it is no longer needed by the cell.

By regulating gene expression, cells can conserve energy and space. If an organism was to express every single gene at all times, it would require a significant amount of energy. It is much more energy efficient to only turn on the genes when they are required. In addition, only expressing a subset of genes in each cell saves space because DNA must be unwound from its tightly coiled structure to be transcribe and translated. Cells would have to be enormous if every gene were expressed in every cell all the time.

The control of gene expression is extremely complex and will only be covered briefly. To understand how gene expression is regulated, we must first understand how a gene codes for a functional protein in a cell. The process occurs in both prokaryotic and eukaryotic cells, just in slightly different manners.

Prokaryotic Gene Expression

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. This is primarily controlled by regulating transcription. Prokaryotic cells use a few methods to control gene expression at the transcriptional level.

One gene control example, the *lac* operon, was discovered using *E. coli* in the 1950s and 1960s by French researchers. The *lac* operon is a stretch of DNA that codes for proteins involved in absorption and metabolism of lactose, including the enzyme lactase. One promotor controls transcription of operon sequences. The *lac* operon is controlled using levels of lactose, a disaccharide, in *E. coli's* environment. When lactose is not present, transcription of the *lac* operon genes decreases, and the lactase translation slows. A repressor protein binds to the DNA preventing RNA polymerase from binding to the promoter. Thus, mRNA is not made and lactase translation is low. When lactose is present, the genes are transcribed at a higher rate and more

lactase is translated. The repressor protein is removed, and RNA polymerase can bind to the promotor, allowing the organism to make more lactase to metabolize the lactose (Figure 10.34).

In the absence of lactose, the *lac* repressor binds the operator, and transcription is blocked.

In the presence of lactose, the *lac* repressor is released from the operator, and transcription proceeds at a slow rate.

Figure 10.34 The three structural genes that are needed to degrade lactose in *E. coli* are located next to each other in the *lac* operon. RNA polymerase can bind to the promoter if a repressor is not present. (credit: Modified by Elizabeth O'Grady original work of Parker et al. / Microbiology OpenStax)

CONCEPTS IN ACTION – Learn more about operons in this video.

Eukaryotic Gene Expression

Eukaryotic cells, in contrast, have organelles and are therefore more complex. Recall that in eukaryotic cells, the DNA is contained inside the cell's nucleus where it is transcribed into mRNA. 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 occurs only outside the nucleus in the cytoplasm. The regulation of gene expression can occur before or during both transcription and translation.

Recall, that DNA in the nucleus is condensed by wrapping around histone proteins. When several histone proteins are wrapped together it forms bead like structures called a nucleosome. Nucleosomes can control how accessible the DNA is to transcription proteins, a type of regulation referred to as epigenetic control. For example, if a gene is to be transcribed, the histone proteins and DNA in the chromosomal region encoding that gene are modified in a way that opens the promoter region to allow RNA polymerase and other transcription proteins to bind and initiate transcription. If a gene is to remain turned off, or silenced, the histone proteins and DNA have different modifications that signal a closed chromosomal configuration. In this closed configuration, the RNA polymerase and transcription factors do not have access to the DNA and transcription cannot occur (Figure 10.35).
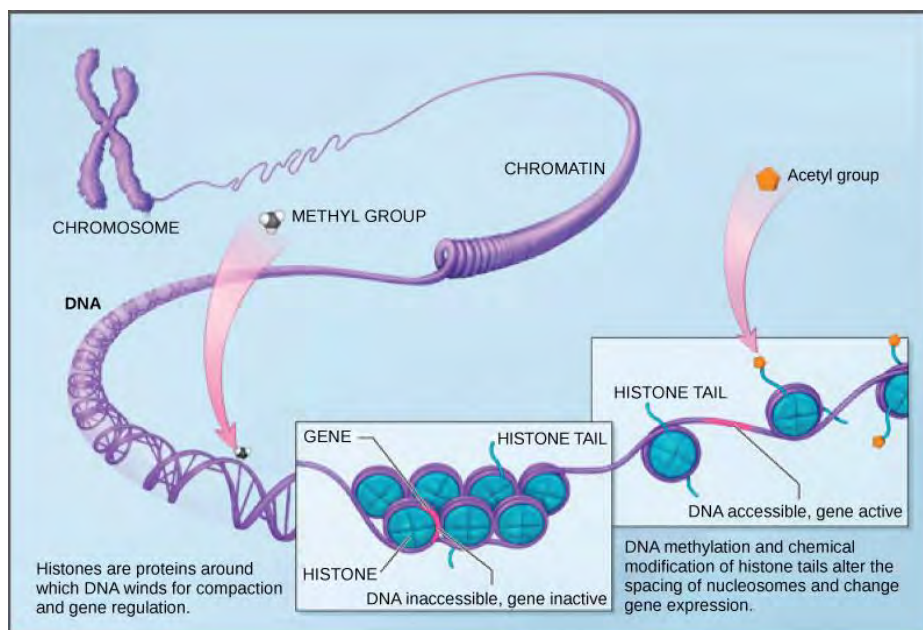
Figure 10.35 Histone proteins and DNA nucleotides can be modified chemically. Modifications affect nucleosome spacing and gene expression. (credit: Modified by Elizabeth O'Grady original work of NIH / Biology 2E OpenStax)

Gene expression can also be controlled when the mRNA is transcribed (transcriptional regulation) or when the mRNA is processed and exported to the cytoplasm after it is transcribed (post-transcriptional regulation). Recall from section 10.3 that mRNA transcripts undergo 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 10.28). Alternative splicing can be haphazard, but more often it is controlled and acts as a mechanism of post-transcriptional gene regulation. The frequency of different splicing alternatives is controlled by the cell as a way to control the production of different proteins.

CONCEPTS IN ACTION – Learn more about alternate splicing at this site.

Gene expression can also be controlled as the mRNA is translated into protein (translational regulation) or after the protein has been made (post-translational regulation). Like transcription, translation is controlled by proteins that bind and initiate the process (Figure 10.36). For example, an initiation protein must bind to the small sub-unit of the ribosome to allow translation (Figure 10.36). If that protein is phosphorylated, translation will be blocked, and the protein cannot be made. This is an example of translational gene regulation. Chemical modifications such as phosphorylation can occur in response to external stimuli such as stress, the lack of nutrients, heat, or ultraviolet light exposure.
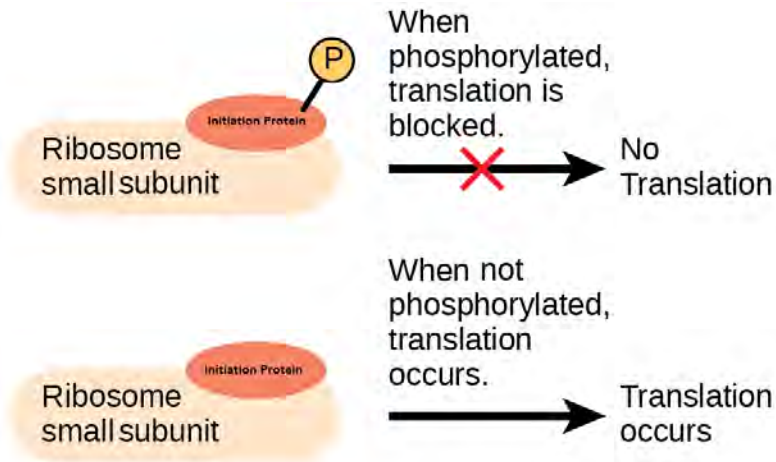
Figure 10.36 Gene expression can be controlled by chemical modifications of proteins needed to initiate translation. (credit: Modified by Elizabeth O'Grady original work of Clark et al. / Biology 2E OpenStax)

Section Summary

All organisms and cells control and regulate the transcription and translation of their DNA into protein. The process of turning on a gene to produce mRNA and then protein is called gene expression. 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.

Exercises

1. 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
2. Prokaryotic cells lack a nucleus. Therefore, the genes in prokaryotic cells are:
   a. all expressed, all of the time
   b. transcribed and translated almost simultaneously
   c. translated and then transcribed into proteins
   d. Transcribed and translated in the cytoplasm on the rough endoplasmic reticulum
3. Explain why it is important that cells are able to regulate gene expression.

Answers

1. (d)
2. (b)
3. By regulating gene expression, cells can conserve energy and space. If an organism was to express every single gene at all times, it would require a significant amount of energy. It is much more energy efficient to only turn on the genes when they are required. In addition, only expressing a subset of genes in each cell saves space because DNA must be unwound from its tightly coiled structure to be transcribe and translated. Cells would have to be enormous if every protein were expressed in every cell all the time.

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

gene expression: processes that control whether a gene is expressed

Chapter 11: Introduction Evolution

Figure 11.1 The diversity of life on Earth is the result of evolution, a continuous process that is still occurring. (credit "wolf": modification of work by Gary Kramer, USFWS; credit "coral": modification of work by William Harrigan, NOAA; credit "river": modification of work by Vojtěch Dostál; credit "protozoa": modification of work by Sharon Franklin, Stephen Ausmus, USDA ARS; credit "fish" modification of work by Christian Mehlführer; credit "mushroom", "bee": modification of work by Cory Zanker; credit "tree": modification of work by Joseph Kranak / Concepts of Biology OpenStax)

All living organisms, from the bacteria on our skin to the trees in our yards, have evolved at some point. Although it may seem that living organisms stay the same from generation to generation, that is not the case: evolution is ongoing. Evolution can be defined as a process through which allele and genotype frequencies change over time in a population, leading to changes in phenotype frequencies. Sometimes the changes are so dramatic that organisms within the population can no longer mate with one another. If this happens, a **speciation** event has occurred leading to the formation of a new species.

The theory of evolution is the unifying theme of biology, meaning it is the framework within which biologists ask questions about the living world. The Ukrainian-born American geneticist Theodosius Dobzhansky famously wrote that "nothing makes sense in biology except in the light of evolution."[1] All life is thought to have evolved and diversified from a common ancestor. This principle is the foundation from which we understand all other questions in biology. This chapter will explain some of the mechanisms for evolutionary change and the kinds of questions that biologists can and have answered using evolutionary theory.

Footnotes

1 Theodosius Dobzhansky. "Biology, Molecular and Organismic." *American Zoologist* 4, no. 4 (1964): 449.

11.1 Discovering How Populations Change

The theory of evolution by natural selection describes a mechanism for genetic changes in populations over time. Charles Darwin is given credit as the first to explain the mechanism of natural selection, however, many other individuals before Darwin had observed that species change overtime. Darwin not only explained the mechanism of how genetic change occurred (natural selection), but also provided data that supported that change.

The view that species were static and unchanging was based on the writings of Plato. Other ancient Greeks at the time of Plato did not agree and expressed ideas that organisms changed or were altered with time. In the eighteenth century, ideas about the evolution of animals were reintroduced by the naturalist Georges-Louis Leclerc and even by Charles Darwin's grandfather, Erasmus Darwin. During this time, it was accepted that there were species that had gone extinct. In spite of this, many still felt that living organisms did not change from one generation to the next.

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**. Lamarck hypothesized that an individual could change or be modified based on the environment in which it lives. These changes or modifications could then be inherited by its offspring, which would then bring about changes in a population over time. While this mechanism for evolutionary change as described by Lamarck was not accurate, Lamarck's ideas were an important influence on evolutionary thought.

Natural Selection is Discovered

The actual mechanism for evolution was independently conceived and described by two naturalists, Charles Darwin and Alfred Russell Wallace, in the mid-nineteenth century. Both individuals spent time, separately, 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 (Figure 11.2). Wallace traveled to Brazil to collect insects in the Amazon rainforest from 1848 to 1852 and to the Malay Archipelago from 1854 to 1862. Both Darwin's and Wallace's journeys included stops at several island chains.
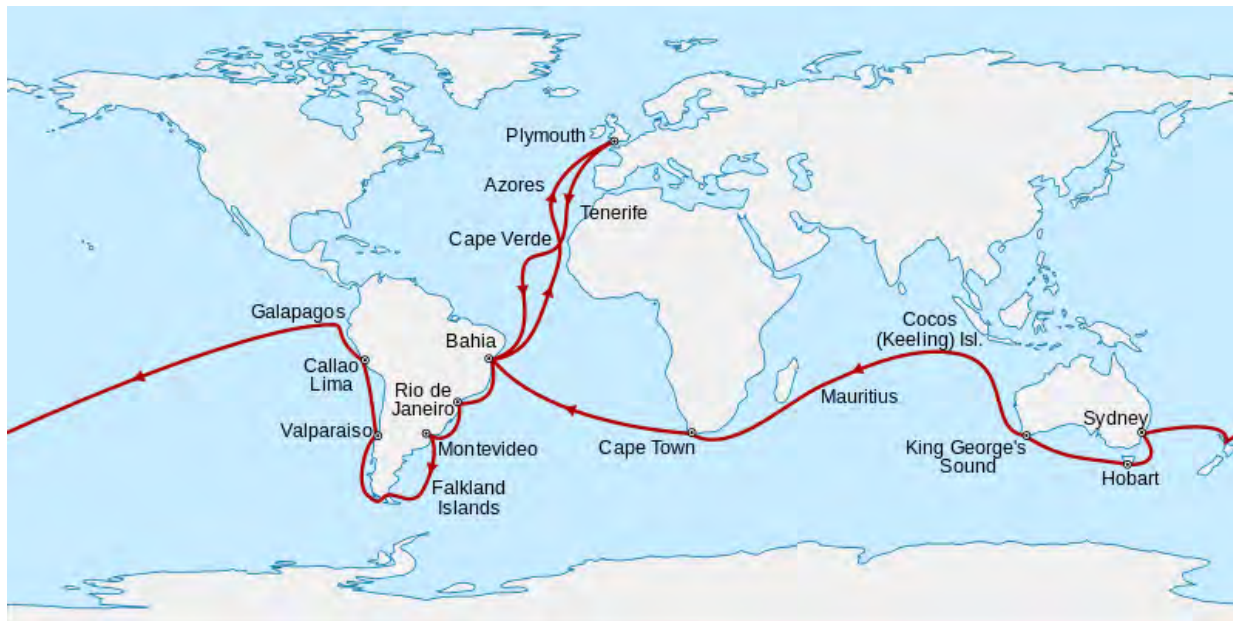
Figure 11.2 Darwin's voyage on the Beagle (credit: Semhur / Wikimedia commons SA)

Darwin's exploration of the Galápagos Islands, located west of Ecuador, led to many observations which helped provide data that supports the theory of evolution. On these islands, Darwin observed organisms that were clearly similar yet had distinct differences. For example, Darwin observed many different species of ground finches inhabiting the Galápagos Islands. Although they shared similarities, Darwin noted that each species had a different beak size and shape. (Figure 11.3). Darwin also realized that the finches on the Galápagos Islands closely resembled another finch species located on the mainland of South America. Darwin hypothesized that the island species might all be descendants from one original mainland species. He hypothesized that the beak of the ancestral species would have changed over time due to different environmental conditions. These adaptations allowed the finches to acquire different food sources on the islands and explained the differences he was seeing in beak size and shape. 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."[2]

Figure 11.3 Darwin observed that beak shape varies among finch species. 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). (credit: Fowler et al. / Concepts of Biology OpenStax)
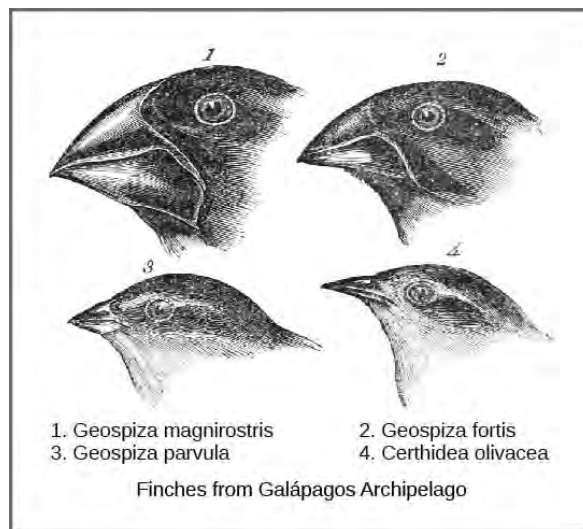
Both Alfred Wallace and Charles Darwin independently observed similar patterns of change in different organisms. Based on their observations, each independently conceived a mechanism to explain how and why such changes could occur. Darwin called this mechanism natural selection. **Natural selection**, Darwin argued, was an inevitable outcome based on three principles that he felt were occurring in nature. First, the characteristics of organisms are inherited, or passed from parent to offspring. Second, more offspring are produced than are able to survive. In other words, resources for survival and reproduction are limited. The capacity for reproduction in all organisms exceeds the availability of resources to support their numbers. Thus, there is a competition for those resources in each generation. Third, offspring vary among each other in regard to their characteristics and those variations are inherited. Out of these three principles, Darwin and Wallace reasoned that offspring with inherited characteristics that allow them to best compete for limited resources would be able to survive and have more offspring than those individuals with variations that are less able to compete. Because characteristics are inherited, the traits of the successful individuals will be represented in a higher proportion in the next generation. This will lead to changes in populations over generations in a process that Darwin called "descent with modification."

Darwin and Wallace (Figure 11.4) both wrote papers presenting their ideas on natural selection. Their papers 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.

Figure 11.4 (a) Charles Darwin and (b) Alfred Wallace wrote scientific papers on natural selection that were presented together before the Linnean Society in 1858. (credit: Fowler et al. / Concepts of Biology OpenStax)

Darwin's finishes are one of the best documented examples of evolution. The work done by Darwin in the 1830's was continued by two scientists by the names of Peter and Rosemary Grant. The Grants and their colleagues have studied Galápagos finch populations every year since 1976 and have provided important examples of the process of natural selection. The Grants observed evolutionary events in which the beak shape of the medium ground finch changed from one generation to the next. 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 Galápagos Island of Daphne Major. 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. When the Grants measured beak sizes in the year following the drought, they found that the average bill size was larger (Figure 11.5). This was clear evidence that supported evolution by natural selection. Based on the availability of seed sizes, finches with larger beak sizes were being naturally selected for. Continued research done by the Grants over several decades demonstrated additional natural selection events. These events led to the subsequent evolution of bill size in response to changing conditions on the island.
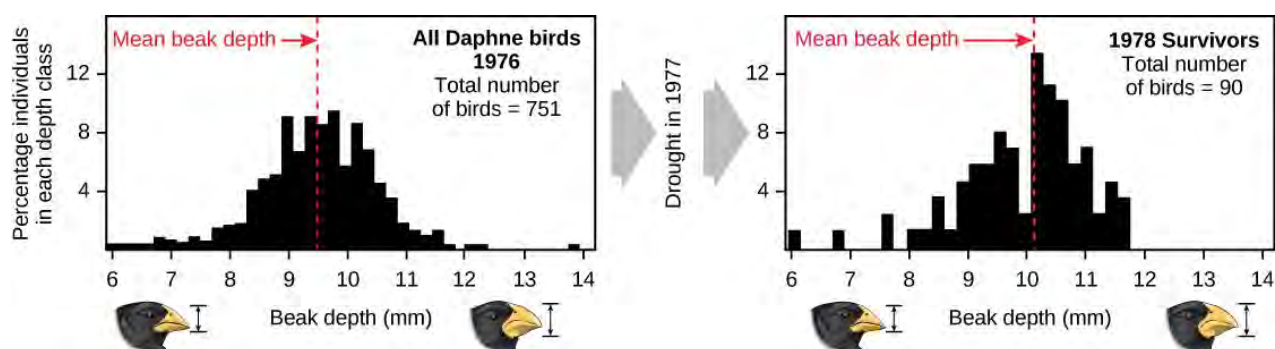
Figure 11.5 A drought on the Galápagos island of Daphne Major in 1977 reduced the number of small seeds available to finches, causing many of the small-beaked finches to die. This caused an increase in the finches' average beak size between 1976 and 1978. (credit: Fowler et al. / Concepts of Biology OpenStax)

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. For example, when it comes to variation in height, environmental factors such as better nutrition can also have an impact on this characteristic.

Genetic diversity in a population ultimately comes from mutation. **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' phenotype:

- A mutation may affect the phenotype of the organism in such a way that it reduces fitness. In an evolutionary context, fitness is a relative measure of how well individuals with a certain trait will survive and produce viable offspring relative to other traits.
- A mutation may produce a phenotype with a beneficial effect on fitness.
- Many mutations, called neutral mutations, will have no effect on fitness.

When a heritable trait that aids the survival and reproduction of an organism in its present environment becomes more frequent in a population, that is called an **adaptation**. For example, camouflage coloration patterns are adaptations. Frogs that can blend into their environment have a better chance of avoiding predation. Survival means a greater chance to reproduce and pass those heritable traits onto the next generation. Slight variations still often exist amongst the color patterns, however. This means that depending on the environmental conditions, different phenotypes can be favored at any given time.

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 and often do change. For example, finches with large bills were benefited in one climate, while finches with small bills were at a disadvantage. In a different climate, the relationship may be 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**. This process can be seen in the shape of a flowering plant's reproductive organs. Although they share the same basic anatomical organs, these organs can look very different because of divergent evolution (Figure 11.6). One cause of divergent evolution is when populations or species are found in different environments. Because the conditions are different in each environment, natural selection will favor different traits in each.
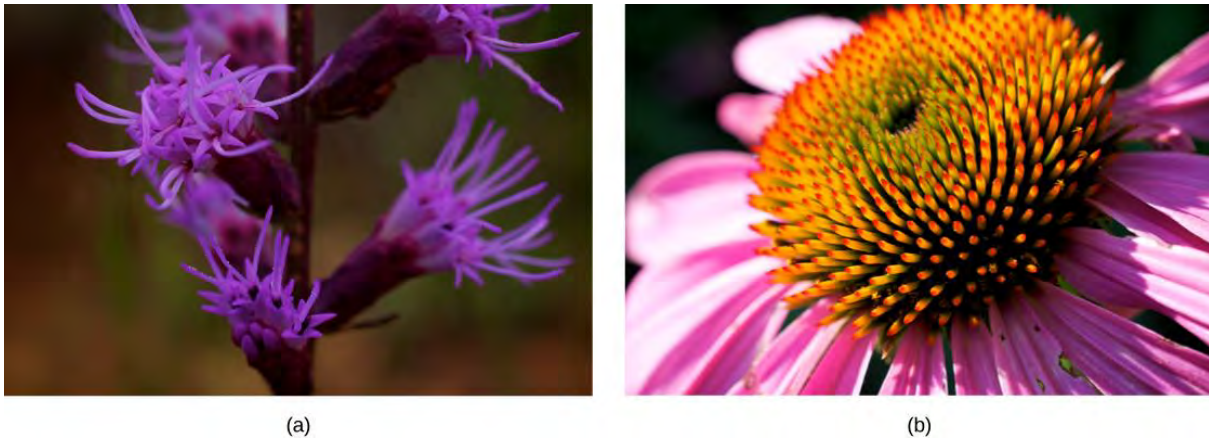
Figure 11.6 Flowering plants evolved from a common ancestor. Notice that the (a) dense blazing star and (b) purple coneflower vary in appearance, yet both share a similar basic morphology. (credit: modification of work by Cory Zanker / Concepts of Biology OpenStax)

In other cases, similar phenotypes evolve independently in distantly related species. For example, flight has evolved independently in both bats and insects. Both have structures that we refer to as wings, which are adaptations to flight. The wings of bats and insects, however, evolved from very different structures and as a result are quite different. For example, the wings of insects do not have bones, but the wings of bats do. 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 they were not inherited from a recent common ancestor. Instead, they evolved independently in two separate lineages. The wings of a hummingbird and an ostrich are homologous structures. **Homologous structures** are inherited from a common ancestor. As a result, they share similarities even though they look and function very different. Their differences result from divergent evolution.

The Modern Synthesis

The mechanisms of inheritance and genetics were not understood at the time when 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 hypothesis at that time. This made it difficult to understand how natural selection might operate. Darwin and Wallace were unaware of the work done by Gregor Mendel on inheritance, 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, and it was at this time geneticists began to understand the basics of inheritance. Initially, the newly discovered nature of genes made it difficult for biologists to understand how gradual evolution could occur. However, over the next few decades genetics and evolution were integrated in what became known as the modern synthesis. 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. The theory also connects the gradual change of a population over time, called **microevolution**.

Sometimes major evolutionary events happen at the level of the individual species, a concept called **macroevolution**. Major evolutionary events can lead to **speciation** events, the formation of two species from one original species. 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.

Population Genetics

Recall that a gene may have several different versions, or alleles, that code for different traits associated with that characteristic. For example, blood type in humans is determined by three different alleles: I^A, I^B, and I^0. For diploid organisms, each individual in a population can only carry two alleles for a particular gene, even though there may be more than two alleles present in 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 over time. This field of study is known as **population genetics**. Using human blood-type 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 gene in the population. For example, a study in Jordan found the frequency of I^A to be 26.1 percent.[3] The frequency of I^B and I^0 alleles made up 13.4 percent and 60.5 percent of the alleles respectively. All three frequencies together add up to 100 percent. A change in these frequencies over time would constitute an evolutionary change 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 results in 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." If an allele becomes "fixed," it means that every individual of the population will carry that allele. Similarly, detrimental alleles may be swiftly eliminated from the gene pool. The **gene pool** represents 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. This can give scientists clues regarding the selective forces that may be operating on a given population. For example, as the Industrial Revolution caused trees to darken from soot, darker colored peppered moths were better camouflaged than the lighter colored moths. The dark colored peppered moths were predated less, had more reproductive success, and passed on their dark color traits to their offspring more often than their lighter colored counterparts. This event led to a shift in color within this population. The changes in wing coloration in the peppered moths is a classic example of studying evolution in natural populations (Figure 11.7).
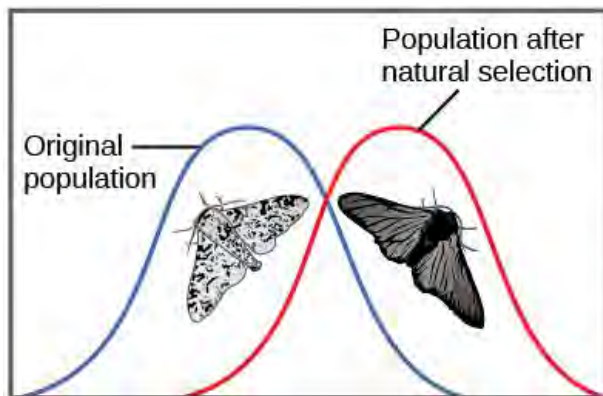
Figure 11.7 As the Industrial Revolution caused trees to darken from soot, darker colored peppered moths were better camouflaged than the lighter colored ones, which caused there to be more of the darker colored moths in the population. (credit: Fowler et al. / Concepts of Biology OpenStax)

In the early twentieth century, many questioned why a "dominant" allele, one that masks a recessive allele, would not increase in frequency in a population until it eliminated all the other alleles. English mathematician Godfrey Hardy and German physician Wilhelm Weinberg independently provided explanations for this somewhat counterintuitive concept. Hardy, who was not even a biologist, pointed 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 **Hardy-Weinberg equilibrium** states that a population's allele and genotype frequencies are inherently stable unless some kind of evolutionary force is acting on the population. In other words, the population would carry the same alleles in the same proportions generation after generation if evolution was not occurring. Individuals would look essentially the same and this would be unrelated to whether the alleles were dominant or recessive.

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. They can then compare evolving populations and infer what evolutionary forces might be at play. The population is evolving if the frequencies of alleles or genotypes deviate from the expected values calculated using the Hardy-Weinberg principle.

Footnotes

- 2 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.
- 3 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

Section 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 understanding 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.

Exercises

1. Which scientific concept did Charles Darwin and Alfred Wallace independently discover?
    a. mutation
    b. overbreeding
    c. natural selection
    d. sexual reproduction
2. Which of the following situation is not an example of natural selection?
    a. One plant grows larger than another plant because its leaves contain more chlorophyll.
    b. Two types of fish eat the same kind of food, and one is better able to gather food than the other.
    c. One male lion earns the right to mate with the females because he is larger than all the other males.
    d. A hurricane wiping out half of a population.
3. Explain the Hardy-Weinberg principle of equilibrium.

Answers

1. (c)
2. (d)
3. The Hardy-Weinberg equilibrium states that a population's allele and genotype frequencies are inherently stable unless some kind of evolutionary force is acting on the population. In other words, the population would carry the same alleles in the same proportions' generation after generation. Individuals would look essentially the same and this would be unrelated to whether the alleles were dominant or recessive.

Glossary

adaptation: a heritable trait or behavior in an organism that aids in its survival in its present environment

allopatric speciation: a speciation that occurs via a geographic separation

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

Hardy-Weinberg equilibrium: a principle that states a population's allele and genotype frequencies are inherently stable unless some kind of evolutionary force is acting on the population

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)

modern synthesis: the overarching evolutionary paradigm that took shape by the 1940s and is generally accepted today

mutation: a permanent variation in the nucleotide sequence of a genome

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

speciation: a formation of a new species

sympatric speciation: a speciation that occurs in the same geographic space

variation: the variety of alleles in a population

11.2 Mechanisms of Evolution

The four most important evolutionary forces that will disrupt 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 based on preference rather than at random.

Natural Selection

Natural selection acts on the population's heritable traits. **Natural selection** selects for beneficial alleles that allow for environmental adaptation, which leads to the frequency of the beneficial alleles increasing in the population. Deleterious alleles are selected against and thereby decrease in frequency in the population. Natural selection selects for organisms as a whole, not on an individual allele within the organism. An individual may carry a very beneficial genotype with a resulting phenotype that, for example, increases the ability to reproduce (fecundity). However, if that same individual also carries an allele that results in a fatal childhood disease, that fecundity phenotype will not pass to the next generation because the individual will not live long enough to reproduce. Natural selection selects for individuals with alleles that allow them to survive better and reproduce more. Scientists call this an organism's evolutionary (Darwinian) fitness.

Sexual Selection

Darwin identified a special case of natural selection that he called sexual selection. In **sexual selection** the fitness of certain traits is determined by different levels of reproductive success. Sexual selection leads to the evolution of dramatic traits that often appear maladaptive in terms of survival but persist because they allow greater reproductive success. Sexual selection occurs in two ways: through male–male competition for mates and through female selection of mates. Male–male competition occurs when males fight or compete for the opportunity to mate with a female(s). These competitions 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 over generations in the males.

It is thought that sexual selection can only proceed to a certain point. This is because natural selection eventually prevents further enhancement of a characteristic due to negative impacts on the male's ability to survive. For example, colorful feathers or an elaborate display make the male more obvious to predators. If a male peacock's tail feathers, for example, become too long and he cannot escape predation, then it doesn't matter that he is more attractive to a female. Because of his long feathers, he is more likely to be predated and therefore not able to reproduce and pass on his traits. There is a delicate balance between having enough enhancements to attract a mate but not so much that it results in being predated.

Mutation

Mutation creates a new allele from an existing allele by changing the DNA sequence. A mutation may produce an allele that is beneficial, harmful, or neutral in the current environment. Harmful mutations may be removed from the population by natural selection and will generally only be found in very low frequencies equal to the mutation rate. Beneficial mutations will spread through the population due to natural selection. 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. New alleles, and therefore new genetic variations, arise through mutation.

CONCEPTS IN ACTION – Learn more about mutations in this video.

Check your knowledge

True or false: All mutations result in evolution.

Dandelions produce over a hundred seeds from one flower. Those seeds than blow through the environment and out compete the grass found in our yards. Is this an example of natural selection, sexual selection, or mutation?

Answers: False. While mutations can cause evolution, some mutations will result in no effect on a population at all. Many affect an individual in somatic cell mutations and not whole populations.
This is natural selection. Dandelions are very adapted to survive in many environments and their tiny seeds can root almost anywhere there is a bit of soil.

Genetic Drift

Another way a population's allele frequencies can change is **genetic drift**, which is simply due to random chance. Genetic drift is most important in small populations. Drift would be completely absent in a population with an infinite number of individuals; however, no population is that large. Genetic drift occurs because the alleles in the F_1 generation are a random sample of the alleles in the parental 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 participating in fertilizations (Figure 11.8).
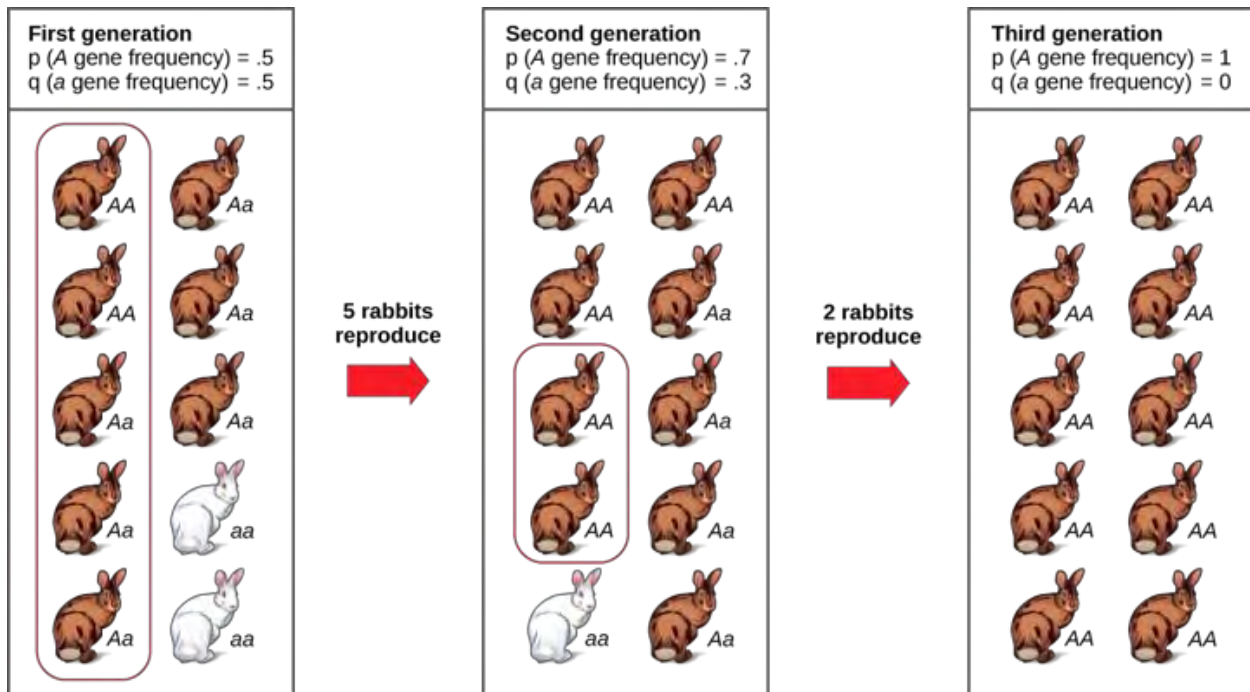
Figure 11.8 Genetic drift in a population can lead to the elimination of an allele from a population by chance. In each generation, a random set of individuals reproduces to produce the next generation. The frequency of alleles in the next generation is equal to the frequency of alleles among the individuals reproducing. (credit: Fowler et al. / Concepts of Biology OpenStax)

If one individual in a population of ten individuals happens to die before it leaves any offspring, all of its genes, a tenth of the population's gene pool, will be suddenly lost (Figure 11.9). In a population of 100, that 1 individual represents only 1 percent of the overall gene pool; therefore, it has much smaller impact on the population's genetic makeup and is unlikely to remove all copies of an allele (Figure 11.9).
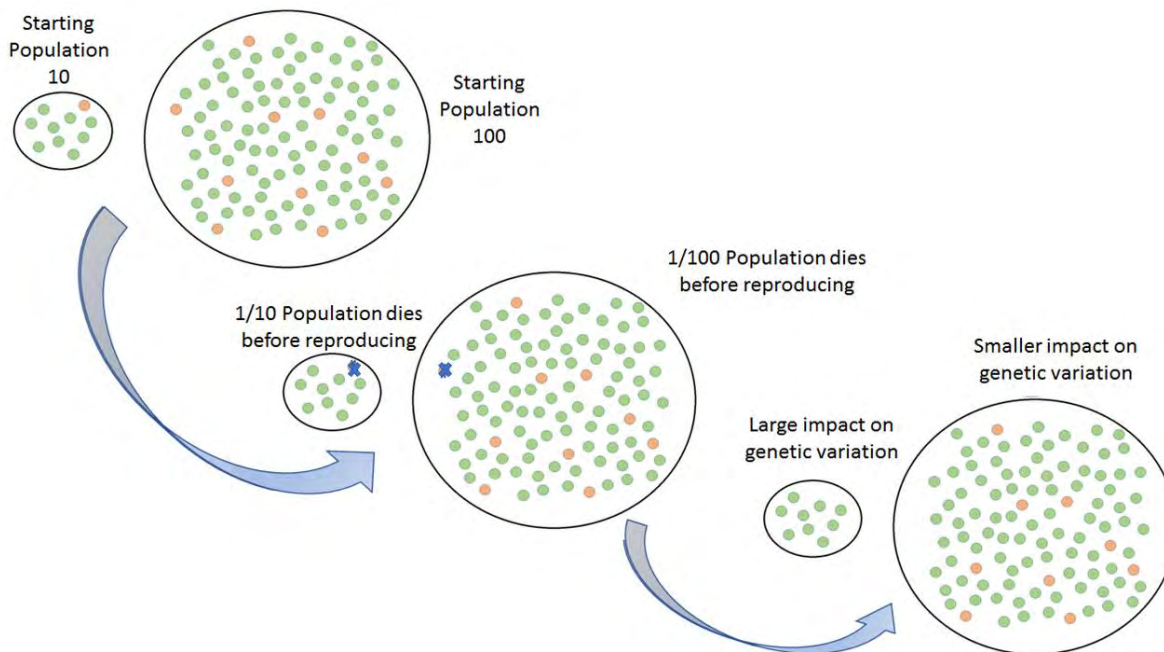
Figure 11.9 Genetic drift has less of an impact on a large population vs. a small population. (credit: Elizabeth O'Grady)

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. The result of this type of event is known as the **bottleneck effect** (Figure 11.10). After the event, the survivors now represent the whole population, and their genetic makeup is the population's gene pool. This genetic makeup may be very different from the pre-disaster population. In order for a disaster to be categorized as a bottleneck effect and genetic drift, it 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 tolerance. The result of such an event would be natural selection, not a bottleneck effect.

Figure 11.10 A chance event or catastrophe can reduce the genetic variability within a population. (credit: Fowler et al. / Concepts of Biology OpenStax)

Populations might also experience genetic drift if a portion of a 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 these situations, the genetic makeup of those individuals is unlikely to be representative of the original population's gene pool. This results in a founder effect. A **founder effect** occurs when there is a change or reduction in genetic variation in the new smaller population as compared to that of the original larger population (Figure 11.11). The founder effect is believed to have been a key factor in the genetic history of the Afrikaner community. The Afrikaner community is a South African ethnic group that descend from Dutch settlers. A small group of primarily Dutch settlers was first thought to have arrived in the Cape of Good Hope in the 17th century. The descendants of this small Dutch group, called the Afrikaner population, have unique mutations that are rare in most other African populations. The original Dutch colonists that settled in South Africa were only a small sample of the total Dutch population; however, just by chance, those that arrived had a higher-than-normal proportion of these rare faulty alleles. As a result, the population expresses unusually high incidences of Huntington disease (HD) and Fanconi anemia (FA), a genetic disorder known to cause bone marrow and congenital abnormalities, and even cancer.[4]
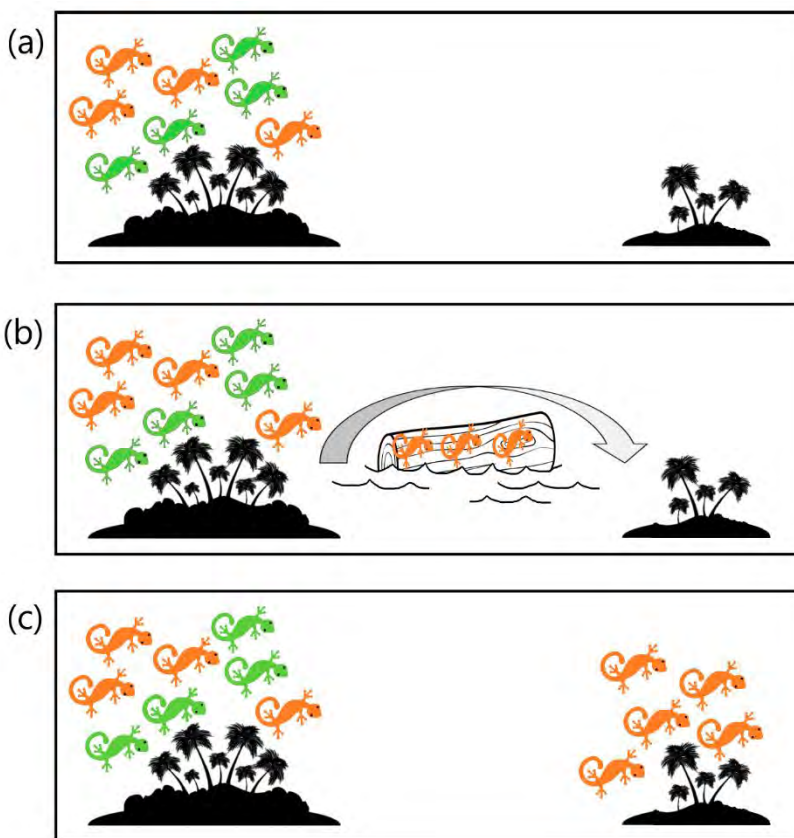
Figure 11.11 Due to the founder effect, the genetic makeup of new populations may be different than the original population. (a) A population of geckos with both green and orange variants is found on an island. (b) A branch with several orange geckos on it is knocked down in a storm and floats to a neighboring island. (c) Those geckos reproduce, founding a new population on the second island. Because all the founder geckos were orange, this population only consists of orange geckos. (credit: Jason Cashmore)

CONCEPTS IN ACTION – Visit this site to learn more about genetic drift and run simulations of allele changes caused by drift.

Gene Flow

Another important evolutionary force is **gene flow**, or the flow of alleles into and out of a population resulting from the **migration** of individuals or their gametes (Figure 11.12). While some populations are fairly stable, others experience more flux. Many plants, for example, send their seeds far and wide, by using the wind or in the digestive tracts of animals. These seeds may introduce new alleles common in the source population to a new population in which they are rare.

Figure 11.12 Gene flow can occur when an individual travels from one geographic location to another and joins a different population of the species. (a) In the example shown here, there are two populations of a beetle. One population has 100% green alleles and the other has 100% brown alleles. (b) Some beetles migrate from the brown population to the green population. (c) The genetic makeup of the brown population is unchanged, but the other population now has mostly green alleles with some brown alleles. (credit: Modified by Jason Cashmore original work by Fowler et al. / Concepts of Biology OpenStax)
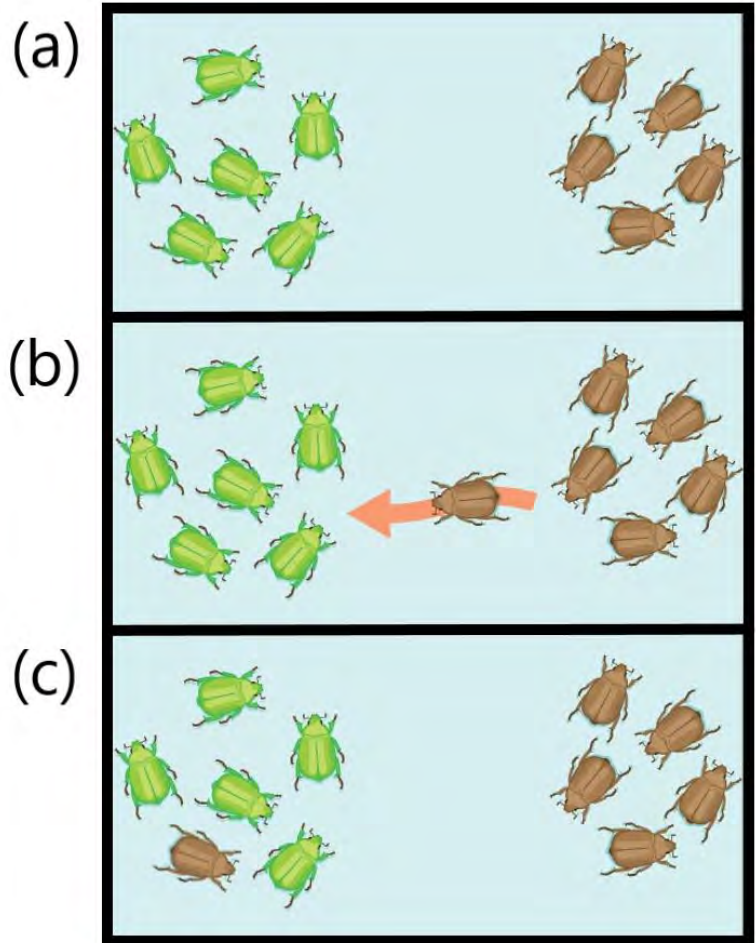
Footnotes

- 4 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.

Section 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.

Exercises

1. One of the original Amish colonies originated from a single ship of colonists that came from Europe. The ship's captain, who had polydactyly, a rare dominant trait, was one of the original colonists. Today, we see a much higher frequency of polydactyly in the Amish population. This is an example of:
    a. Natural selection
    b. Founder effect
    c. Bottleneck effect
    d. Mutation

2. When male lions reach sexual maturity, they leave their group in search of a new pride. This can alter the allele frequencies of the population through which of the following mechanisms?
    a. Natural selection
    b. Gene flow
    c. Population bottleneck
    d. Random mating

Answers

1. (b)
2. (b)

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

genetic drift: the effect of chance on a population's gene pool

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

mutation: a change in the DNA sequence

natural selection: the greater relative survival and reproduction of individuals in a population that have favorable heritable traits, leading to evolutionary change

speciation: a formation of a new species

11.3 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. In this section students will learn about data that supports the theory of evolution.

Fossils

Fossils provide solid evidence that organisms from the past are not the same as those found today; they show a progression of evolution. Fossils are mineralized, or preserved remains of organisms from the past. Scientists can determine the age of fossils and then categorize them to determine when organisms lived relative to each other. The resulting fossil record tells the story of the past and shows the evolution of form over millions of years. For example, both whales and modern horses have highly detailed fossil records (Figure 11.13).

The fossil record of horses in North America is especially rich and contains many transition fossils. Transitional fossils are those showing intermediate anatomy between earlier and later forms. The fossil record extends back to a dog-like ancestor some 55 million years ago. This dog-like ancestor gave rise to the first horse-like species 42 to 55 million years ago in the genus *Eohippus*. The series of fossils tracks the change in anatomy, which was most likely a result of changing environmental conditions. A gradual drying trend is thought to have changed the landscape from forests to prairies. Successive fossils show the evolution of teeth size, feet shapes, and leg anatomy. For example, *Mesohippus* found from 30 to 40 million years ago had adaptations, such as longer limbs compared to earlier ancestors. This would have been useful when evading predators in open environments, such as prairies. Later species showed gains in size, such as those of *Hipparion*, which existed from about 2 to 23 million years ago. The fossil record shows several adaptive radiations in the horse lineage, which is now reduced to only one genus, *Equus*, with several different species.
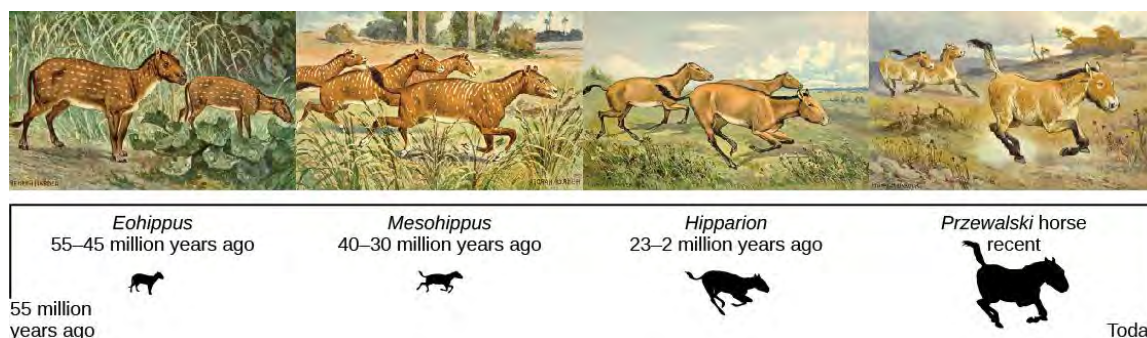
Figure 11.13 This illustration shows an artist's renderings of these species derived from fossils of the evolutionary history of the horse and its ancestors. The species depicted are only four from a very diverse lineage that contains many branches, dead ends, and adaptive radiations. (credit: Fowler et al. / Concepts of Biology OpenStax)

Anatomy and Embryology

Structures

Another piece of evidence that supports evolution is the presence of structures in organisms that share the same basic anatomy. For example, the bones found in the appendages of a human, dog, bird, and whale all share the same overall construction (Figure 11.14). That similarity results from a shared common ancestor. Over time, evolution led to changes in the shapes and sizes of these bones in different species. However, 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 "leftovers" from a past ancestor. For example, some snakes have pelvic bones despite having no legs. This can be explained by understanding that snakes 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, leaves on some cacti, traces of pelvic bones in whales, and the sightless eyes of cave animals.

Figure 11.14 The similar construction of these appendages indicates that these organisms share a common ancestor. (credit: Fowler et al. / Concepts of Biology OpenStax)
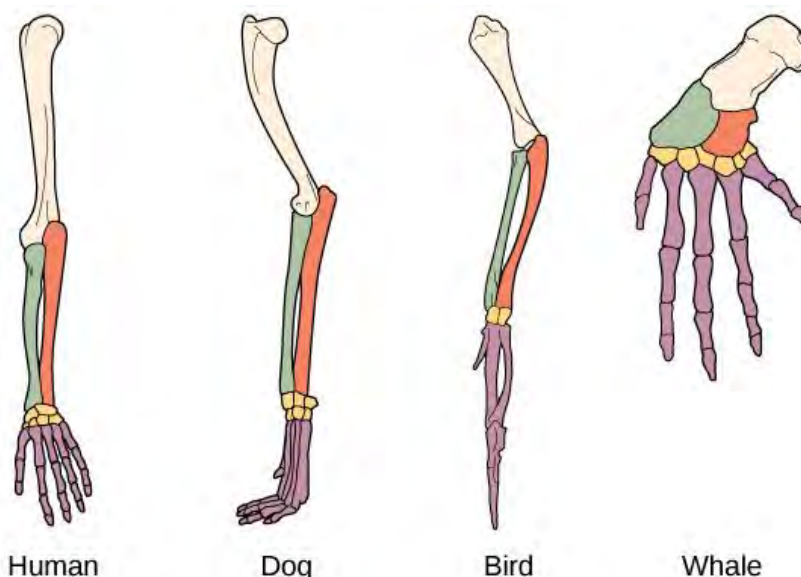
CONCEPTS IN ACTION – Click through the activities at this interactive site to guess which bone structures are homologous and which are analogous, and to see examples of all kinds of evolutionary adaptations that illustrate these concepts.

Similar environments

Another piece of evidence that supports the theory of evolution is the convergence of anatomical forms found in organisms that share similar environments. For example, unrelated animals, such as the arctic fox and ptarmigan, a type of bird, both live in arctic regions. Both have temporary white coverings during the winter to help them blend in with the snow and ice (Figure 11.15). The similarity occurs not because of common ancestry; keep in mind one has fur while the other has feathers. Rather, it is a result of similar selection pressures. They both benefit if they can blend into their environments to avoid being seen by predators.

(a)   (b)

Figure 11.15 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 / Concepts of Biology OpenStax)
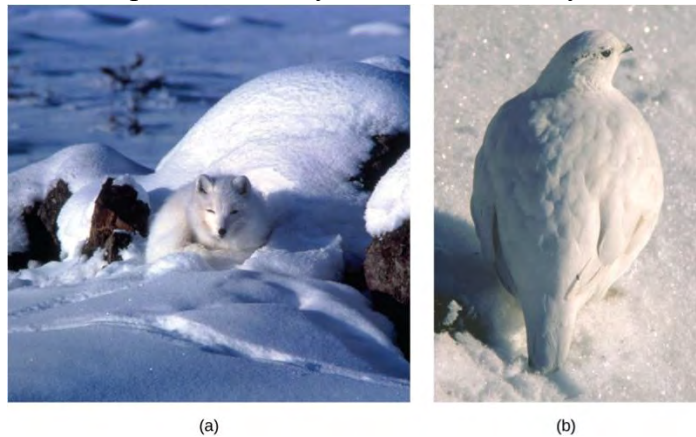
Embryology

Embryology, the study an organism's development from a zygote to its adult form, also provides evidence of relatedness between divergent groups of organisms. Structures that are absent in some groups often appear in their embryonic forms and then 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 (Figure 11.16). These disappear in the adults of terrestrial groups, but are maintained in adult forms of aquatic groups, such as fish and some

Fish Salamander Tortoise   Chick   Hog   Calf   Rabbit Human

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.
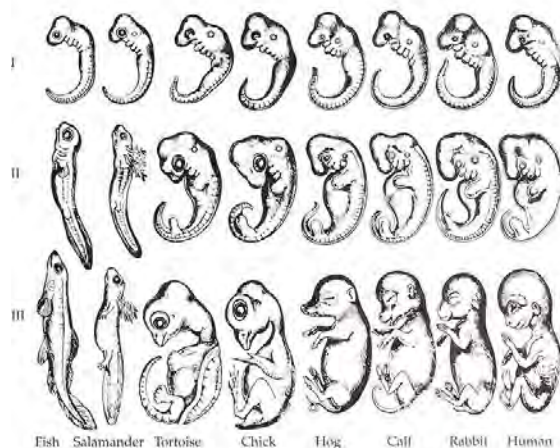
Figure 11.16 Embryo comparison. (credit: Romanes copy of Ernst Heaeckel / Public Domain)

Biogeography

The geographic distribution of organisms follows patterns that are best explained by examining evolution as it relates to 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 later, after the breakup, appear only in certain 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 plants such as macadamia, a member of the family 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 11.17).

Proteacea flower
Banksia spinulosa

Gondwana 220 million years ago
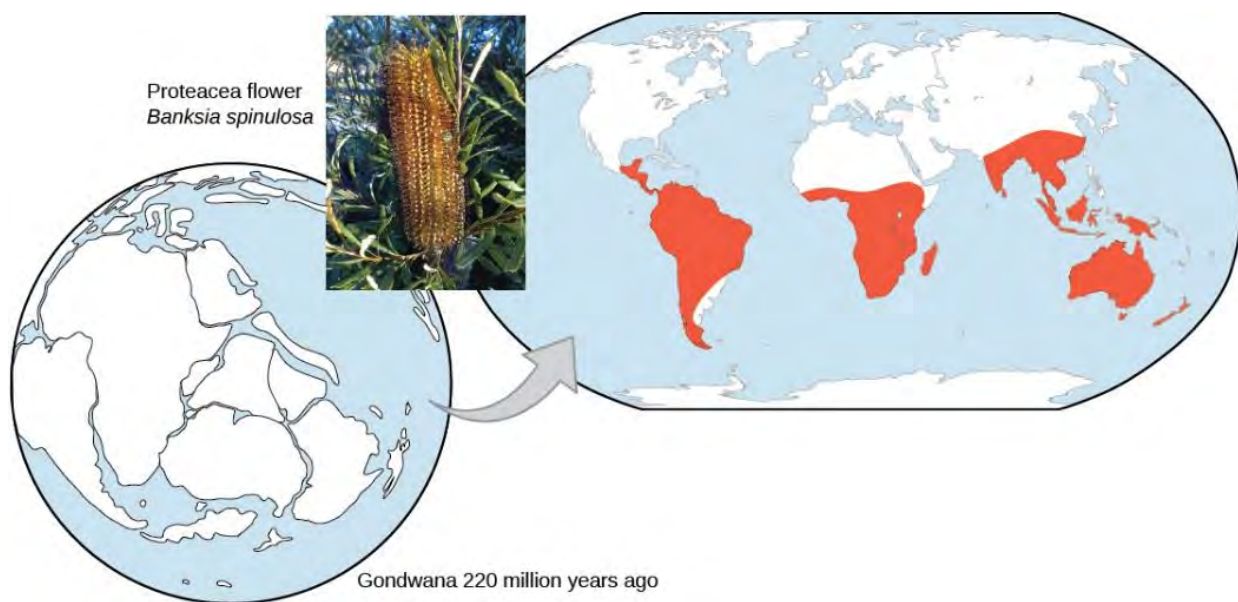
Figure 11.17 The Proteacea family of plants evolved before the supercontinent Gondwana broke up. Today, members of this plant family are found throughout the southern hemisphere (shown in red). (credit: "Proteacea flower": modification of work by "dorofofoto"/Flickr / Concepts of Biology OpenStax)

The great diversification of the marsupials in Australia and the absence of other mammals can best be explained by the fact that Australia has been isolated from other continents for many years. Australia has an abundance of endemic species, species found nowhere else, which is typical of island populations. Islands such as Australia or Hawaii are isolated by large expanses of water which prevents migration of species to other regions. Over time, these species diverge evolutionarily into new species that look very different from their ancestors. The marsupials of Australia, the finches on the Galápagos, and many species on the Hawaiian Islands are all found nowhere else yet display distant relationships to ancestral species on continental main lands.

Molecular Biology

Like anatomical structures, an organism's genetic material also reflects descent with modification. Evidence of a common ancestor for all of life is reflected in the universality of DNA as the genetic material, the near universal genetic code, similar enzymes used in all DNA replication, and the expression of genes. Fundamental divisions in life between the three domains are reflected in major structural differences. However, some structures such as ribosomes and the structures of membranes have been conserved in all cells. In general, the relatedness of groups of organisms is reflected in the similarity of their DNA sequences.

DNA sequences 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 in the genome. These duplications allow one copy to be modified by mutation, selection, and drift, while the second copy continues to produce a functional protein. Due to evolutionary forces, the duplicated copy may at some point result in a new or unique function.

Check your knowledge

In anatomy and physiology, you will learn that humans have 7 neck bones called cervical vertebrae. Based on the concept of homologous structures, how many do you think mice and giraffes have?

Explain why many mammals and birds in Northern Illinois are brown?

Answers: Both mice and giraffes also have 7 vertebrae. Obviously MUCH different in size and even function but humans, giraffes, and mice are all mammals with homologous structures. Many organisms in Illinois are brown because the environment put similar pressures on them. Much of the environment is brown so animals camouflage in the brown landscape.

Section Summary

The evidence for evolution is supported by fossils. Fossils provide evidence for the evolutionary change through now extinct forms that led to modern species. 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.

Exercises

1. The wing of a bird and the arm of a human are examples of _____.?
    a. Vestigial structure
    b. Molecular structure
    c. Homologous structure
    d. Analogous structure
2. The fact that DNA sequences are more similar in more closely related organisms is evidence of what?
    a. Fossils
    b. Optimal design of organisms
    c. Decent from a common ancestor with modification
    d. Mutation
3. Explain how homologous structures support the theory of evolution.

Answers

1. (c)
2. (c)
3. That similarity of homologous structures results from a shared common ancestor. Over time, evolution led to changes in the shapes and sizes of structures in different species. However, they have maintained the same overall layout, evidence of descent from a common ancestor.

Glossary

embryology: the study an organism's development from a zygote to its adult form

fossils: mineralized or preserved remains of organisms found in the past

homologous structure: a structure that is similar because of descent from a common ancestor

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

11.4 Misconceptions about Evolution

The theory of evolution initially generated some controversy. However, within 20 years of the publication of *On the Origin of Species* by Charles Darwin, the theory of evolution was almost universally accepted by biologists. Although the theory of evolution has been repeatedly supported by vast amounts of data, misconceptions still exist. In addition, there are those that reject it as an explanation for the diversity of life.

Misconception 1 - Evolution Is Just a Theory

Critics of the theory of evolution dismiss its importance by purposefully trying to confuse people. Critics have stated that evolution is "just a theory." The everyday common usage of the word "theory" by individuals not in science means a guess or suggested explanation for something. This meaning is more akin to the concept of a "hypothesis" used by scientists. Recall a **hypothesis** is a tentative testable explanation to a scientific question. When critics of evolution say evolution is "just a theory," they are implying that there is little evidence supporting it and that it is still in the process of being rigorously tested. This is a mischaracterization.

In science, a "**theory**" is understood to be a concept that has been extensively tested and supported with a lot of data over time. Several theories exist including the evolution theory, cell theory, the theory of gravity, and the theory of relativity. Each of these theories have been rigorously tested and describe what scientists understand at this time to be true about each of these concepts. A theory in science has survived significant efforts to discredit it. It is a culmination of the work done by many different scientists and the conclusions drawn have been verified and repeated numerous times. While theories can sometimes be overturned or revised, this does not lessen their weight but simply reflects the constantly evolving state of scientific knowledge.

Misconception 2 - Individuals Evolve

An individual is born with a specific set of genes; these genes do not change as the individual ages. Therefore, an individual cannot evolve. Evolution is the change in genetic makeup of a *population* over time, specifically over generations. Evolution results from differential reproduction of individuals with certain alleles. Individuals do change over their lifetime, but this is called development. Development involves changes programmed by the set of genes the individual acquired at birth in coordination with the individual's environment. When thinking

about the evolution of a characteristic, it is best to think about the change of the characteristic in the population over time. For example, natural selection does not cause individual bill-size of adult finches to change within their lifetime. If one measures the average bill size among all individuals in the population at one time, and then measures the average bill size in the population several years later after there has been a strong selection pressure, this average value may be different as a result of evolution. Note the changes are observed in the population, not just one individual.

Misconception 3 - Evolution Explains the Origin of Life

It is a common misunderstanding that evolution explains the origin of life. The theory of evolution explains how populations change over time and how life diversifies, not how life came to exist. It does not explain how life began or how the first cells originated. How life first originated on Earth is very difficult to address because it occurred a very long time ago, and the event most likely only occurred once. The early stages of life most likely included the formation of organic molecules such as carbohydrates, amino acids, or nucleotides. The early stages of life also would have included complex accumulations of molecules into enclosed structures. A boundary, like the cell membrane, would have formed at some point allowing for an internal environment to be separated from the external conditions.

Once DNA or RNA, a mechanism of inheritance, formed within a cell or within a pre-cell, these cells would have been subject to natural selection. More effective reproducers would increase in frequency. While evolution does not explain the origin of life, it may have contributed to why some metabolic processes exist in living cells.

Misconception 4 - Organisms Evolve on Purpose

Statements such as "populations will evolve in response to a change in an environment," are quite common. This statement is misleading for two different reasons. First, some interpret the statement to mean that evolution is somehow intentional. When environmental changes occur, some individuals in the population may be more successful than others based on their phenotype. Evolution does not intentionally favor one phenotype or another; rather individuals with phenotypes that provide the most beneficial properties will survive better and produce proportionately more offspring. Assuming the phenotype is a result of heritable genes, overtime the frequency of those genes will change in the population.

The second misunderstanding is the idea that evolution will automatically occur, if needed. It is important to understand that natural selection works on variation that already exists in a population. Variation does not arise in response to an environmental change. For example, exposing a population of bacteria to antibiotics will, over time, select for bacteria that are antibiotic resistant. The resistance, which is caused by a gene, did not arise by mutation because of the application of the antibiotic. The gene for resistance was already present in the gene pool of the bacteria, likely at a low frequency. The antibiotic, which kills the bacterial cells without

the resistance gene, strongly selects for individuals that have the gene and are therefore resistant. Experiments have demonstrated that mutations for antibiotic resistance do not arise as a result of antibiotic application.

In a larger sense, evolution is also not goal directed. Species do not become "better" over time. Organisms best suited for an environment have adaptations that maximize their reproduction in that particular environment at that particular time. Evolution has no goal of making faster, bigger, more complex, or even smarter species. What characteristics are selected for is a function of the genetic variation present in the population and the environment that they live in. Both genetics and the environment are constantly changing in a non-directional way. What trait is beneficial in one environment at one time may later be fatal.

Misconception 5 - Evolution Is Thought to Be Controversial among Scientists

The theory of evolution was controversial when it was first proposed in 1859, yet within 20 years virtually every biologist had accepted evolution as the explanation for the diversity of life. The rate of acceptance was extraordinarily fast, partly because Darwin had amassed an impressive body of evidence. The early controversies involved both scientific arguments against the theory and arguments from the general public. The number of scientists who reject the theory of evolution, or question its validity, is small. A Pew Research poll in 2009 found that 97 percent of the 2500 scientists polled believe species evolve.[5] The support for the theory is reflected by the fact that there are no experimental results that have been found to contradict the theory of evolution. There are also no peer-reviewed articles published in scientific journals that refute the theory of evolution. Evolution has been supported with both evidence and data and as a result it is accepted by the scientific community. The arguments of scientists were resolved relatively quickly. Through education and communication, the arguments from the general public are decreasing.

CONCEPTS IN ACTION – This website addresses some of the main misconceptions associated with the theory of evolution.

Footnotes

- [5] Pew Research Center for the People & the Press, *Public Praises Science; Scientists Fault Public, Media* (Washington, DC, 2009), 37.

Section Summary

The theory of evolution by natural selection describes the mechanism for genetic changes in a population over time. There are critics of the theory of evolution and several misconceptions about evolution exist. The factual nature of evolution is often challenged by wrongly associating the scientific meaning of a theory with the vernacular meaning. Evolution is sometimes mistakenly interpreted to mean that individuals evolve, when in fact only populations can evolve as their gene frequencies change over time. Evolution is often assumed to explain the origin of life, which it does not speak to. It is often spoken in goal-directed terms by which organisms change intentionally. Evolution is often characterized as being controversial among scientists; however, it is accepted by the vast majority of scientists.

Exercises

1. Which of the following is true?
    a. Evolution is intentional.
    b. Evolution is not well supported by the scientific community.
    c. There are no experimental results that have been found to contradict the theory of evolution.
    d. Evolution is just a theory therefore not well supported.
2. Evolution explains the origin of life.
    a. True
    b. False

Answers

1. (c)
2. (b)

Glossary

hypothesis: a testable explanation to a scientific question

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

Glossary

A

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)

acid: a substance that donates hydrogen ions and therefore lowers pH

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

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

active transport: the method of transporting materials into or out of a cell that requires energy

adaptation: a heritable trait or behavior in an organism that aids in its survival in its present environment

adenosine triphosphate (ATP): is the primary energy currency of all living cells

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

aerobic cellular respiration: the use of oxygen as an electron acceptor to complete metabolism

alcohol fermentation: the steps that follow the partial oxidation of glucose via glycolysis to regenerate NAD+ and produces the products ethanol and carbon dioxide

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

allopatric speciation: a speciation that occurs via a geographic separation

allosomes: chromosome pair twenty-three and determines a person's sex

allosteric activation: the mechanism for activating 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, allowing binding with the substrate

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

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

amino acid: a monomer of a protein

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

anaerobic cellular respiration: the use of an electron acceptor other than oxygen to complete metabolism

anaerobic: process in which organisms do not require oxygen

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

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

aneuploid: an individual with an error in chromosome number; includes deletions and duplications of chromosome segments

anion: a negative ion formed by gaining electrons

anticodon: three consecutive nucleotides on tRNA that complement the codon on a mRNA

aquaporin: channel protein that allows water through the membrane at a very high rate

asexual reproduction: produces genetically identical clones to the parent organism

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

atomic number: the number of protons in an atom

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

ATP: adenosine triphosphate; the cell's energy currency

autosomal dominant inheritance: pattern of dominant inheritance that corresponds to a gene on one of the 22 autosomal chromosomes

autosomal recessive inheritance: pattern of recessive inheritance that corresponds to a gene on one of the 22 autosomal chromosomes

autosome: chromosome pairs one through twenty-two and does not determine a person's sex

autotroph: an organism that can make its own food from materials in its environment

B

base: a substance that absorbs hydrogen ions and therefore raises pH

binary fission: the process of prokaryotic cell division

biology: the study of life

biosphere: a collection of all ecosystems on Earth

blending hypothesis of inheritance: states that when two individuals made an offspring, their original parental traits were lost because their traits blended together when the offspring was formed

bottleneck effect: the magnification of genetic drift as a result of natural events or catastrophes

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

C

Calvin cycle: the reactions of photosynthesis that use the energy stored by the light-dependent reactions to form glucose and other carbohydrate molecules

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

carriers: a heterozygous individual who does not display symptoms of a recessive genetic disorder but can transmit the disorder to his or her offspring

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

catalyst: substances that speed up the rate of chemical reactions

cation: a positive ion formed by losing electrons

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

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

cell plate: a structure formed during plant-cell cytokinesis by Golgi vesicles fusing at the

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

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

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

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

Central dogma: The flow of genetic information in cells from DNA to mRNA to protein

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

centrosomes: specialized microtubules that pull chromosomes to their poles during cell division and also give rise to the mitotic spindle

characteristic: different heritable, physical features

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

chemical energy: type of potential energy that exists within chemical bonds

chemical reactions: occur when two or more atoms bond together to form molecules or when bonded atoms break apart

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

chemoautotrophs: an organism capable of producing its own food by extracting energy from inorganic chemical compounds

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

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

chlorophyll a: the form of chlorophyll that absorbs violet-blue and red light

chlorophyll b: the form of chlorophyll that absorbs blue and red-orange light

chlorophyll: the green pigment that captures the light energy that drives the reactions of photosynthesis

chloroplast: a plant cell organelle that carries out photosynthesis

cholesterol: a lipid that plays an important role in membrane fluidity

chromatin: DNA wound around proteins forming long fiber-like strands

Chromosomal Theory of Inheritance: a theory proposing that chromosomes are the genes' vehicles and that their behavior during meiosis is the physical basis of the inheritance patterns that Mendel observed

chromosome: structures made of chromatin that are visible when the cell is dividing

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

citric acid cycle: a series of enzyme-catalyzed chemical reactions of central importance in all living cells that harvest 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

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

codominance: in a heterozygote, complete and simultaneous expression of both alleles for the same characteristic

codon: three consecutive nucleotides in mRNA that specify the addition of a specific amino acid or the release of a polypeptide chain during translation

coenzyme: small organic molecules, such as a vitamin or its derivative, which is required to enhance an enzyme's activity

cofactor: inorganic ion, such as iron and magnesium ions, required for optimal enzyme activity regulation

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

community: a set of populations inhabiting a particular area

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

complete dominance: in a heterozygote the dominant allele masks the effect of the recessive allele

compound: are made up of different types of atoms held together by chemical bonds

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

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

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

convergent evolution: an evolution that results in similar forms on different species

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

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

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

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 maintain 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

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

D

dehydration synthesis: a reaction where monomers combine with the help of water (and often an enzyme) to form polymers

deletion: a part of a chromosome is lost or removed

denaturation: loss of shape in a protein that may be a result of changes in temperature, pH, or chemical exposure

denature: loss of shape in a protein that may be a result of changes in temperature, pH, or chemical exposure

deoxyribonucleic acid (DNA): a double-stranded polymer of nucleotides that carries the hereditary information of the cell

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

dependent variable: the variable that will change when the independent variable is altered; this is what the researcher will measure or observe during the experiment

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

diffusion: a passive process of transport where solutes move from an area of high concentration to an area of low concentration until equilibrium is met

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

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

disaccharide: two sugar monomers that are linked together by a peptide bond

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

divergent evolution: an evolution that results in different forms in two species with a common ancestor

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

domain: the highest level of the taxonomic hierarchy; includes the Eukarya, Archaea, and Bacteria

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

double helix: the molecular shape of DNA in which two strands of nucleotides wind around each other in a spiral shape

duplication: a part of a chromosome is duplicated and either inserted into a different position on the same chromosome or a completely different chromosome

E

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

egg (ovum): the female gamete; a haploid cell

electron transfer: the movement of electrons from one element to another

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

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

electronegativity: an atom's ability to attract a shared pair of electrons more closely to its own nucleus

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

embryology: the study an organism's development from a zygote to its adult form

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

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

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

endosymbiosis: a relationship in which one organism lives inside the other

endosymbiotic theory: a theory that explains how mitochondria and chloroplasts originated

energy coupling: energy released from exergonic processes is used to support or transferred to endergonic processes

energy: the ability to do work or to create change

entropy: the measure of randomness or disorder within a system

enzyme: a molecule that catalyzes a biochemical reaction; speeds up a chemical reaction by lowering the amount of activation energy need to initiate a chemical reaction

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

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

euploid: an individual with the appropriate number of chromosomes for their species

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

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

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

exocytosis: a process of passing material out of a cell

exon: a sequence present in protein-coding mRNA after completion of pre-mRNA splicing

experimental group: the group where the independent variable is applied

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

F

F1: the first filial generation in a cross; the offspring of the parental generation

F2: the second filial generation produced when F1 individuals are self-crossed or fertilized with each other

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

falsifiable: it can be shown to be false by experimental results

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

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

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

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

first law of thermodynamics: states that the total amount of energy in the universe is constant and conserved

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

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

fossils: mineralized or preserved remains of organisms found in the past

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

free energy: usable energy or energy that is available to do work

functional group: groups of atoms that occur within molecules and confer specific chemical properties to those molecules

G

G0 phase: a cell-cycle phase distinct from the G1 phase of interphase; a cell in G0 is not preparing to divide

G1 phase: (also, first gap) a cell-cycle phase; the first phase of interphase centered on cell growth during mitosis

G2 phase: (also, second gap) a cell-cycle phase; third phase of interphase where the cell undergoes the final preparations for mitosis

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

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

gene expression: processes that control whether a gene is expressed

gene flow: the flow of alleles in and out of a population due to the migration of individuals or gametes

gene pool: all of the alleles carried by all of the individuals in the population

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

genetic code: the amino acids that correspond to three-nucleotide codons of mRNA

genetic drift: the effect of chance on a population's gene pool

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

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

germline cell: specialized cell line that produces gametes, such as eggs or sperm

glycocalyx: a fuzzy-appearing coating around the cell formed from glycoproteins and other carbohydrates attached to the cell membrane.

glycogen: a storage carbohydrate in animals

glycolipid: a combination of carbohydrates and lipids

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

glycoprotein: a combination of carbohydrates and proteins

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

granum: a stack of thylakoids located inside a chloroplast

guard cells: specialized plant cells that control the opening and closing of the stomata

H

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

Hardy-Weinberg equilibrium: a principle that states a population's allele and genotype frequencies are inherently stable unless evolutionary force(s) is acting on the population

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

helicase: an enzyme that helps to open up the DNA helix during DNA replication by breaking the hydrogen bonds

heterotroph: an organism that cannot make its own food and must consume other organisms to obtain its energy

heterotroph: an organism that cannot make its own food and must consume other organisms to obtain its energy

heterotroph: an organism that consumes other organisms for food

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

homeostasis: the ability of an organism to maintain constant internal conditions

homologous chromosomes: the randomness of how the homologous chromosome pairs align at the metaphase plate during metaphase I of meiosis I

homologous structure: a structure that is similar because of descent from a common ancestor

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

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

hybridization/cross-fertilization: the process of mating two individuals that differ, to achieve a certain characteristic in their offspring

hydrocarbon: organic molecules consisting entirely of carbon and hydrogen

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

hydrolysis reactions: a reaction where a water molecule (and usually an enzyme) is used to break a chemical bond within a polymer

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

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

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

hypothesis: a testable explanation to a scientific question

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

I

incomplete dominance: in a heterozygote, expression of two contrasting alleles such that the individual displays an intermediate phenotype

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

independent variable: is the variable that is being altered or changed by the researcher; it is the variable being tested

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

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

integral protein: protein integrated into the membrane structure that interacts extensively with the membrane lipids' hydrocarbon chains and often spans the membrane

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

intermediate filaments: fibers of the cytoskeleton that are of intermediate diameter and have structural functions, such as maintaining the shape of the cell and anchoring organelles

interphase: the period of the cell cycle leading up to mitosis; includes G1, S, and G2 phases; the interim between two consecutive cell divisions

intron: non–protein-coding intervening sequences that are spliced from mRNA during processing

inversion: the detachment, 180° rotation, and reinsertion of a chromosome arm

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

isomers: molecules that share the same chemical formula but differ in the placement (structure) of their atoms and or chemical bonds

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

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

K

karyogram: the photographic image of a karyotype

karyotype: the number and appearance of an individual's chromosomes, including the size, banding patterns, and centromere position

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

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

L

lactic acid fermentation: the steps that follow the partial oxidation of glucose via glycolysis to regenerate NAD+ and produces the products lactic acid

lagging strand: during replication of the 3' to 5' strand, the strand that is replicated in short fragments and away from the replication fork

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 concerning 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

leading strand: the strand that is synthesized continuously in the 5' to 3' direction that is synthesized in the direction of the replication fork

light-dependent reaction: the first stage of photosynthesis where visible light is absorbed to form two energy-carrying molecules (ATP and NADPH)

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

lipids: a class of macromolecules that are nonpolar and insoluble in water

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

locus: the position of a gene on a chromosome

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

M

macroevolution: a broader scale of evolutionary changes seen over paleontological time

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

mass number: the number of protons plus neutrons in an atom

matter: anything that has mass and occupies space

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

mesophyll: the middle layer of cells in a leaf

messenger RNA: messenger RNA; a form of RNA that carries the nucleotide sequence code for a protein sequence that is translated into a polypeptide sequence

metabolic pathway: a series of related chemical reactions is referred to as a

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

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

microevolution: the changes in a population's genetic structure (i.e., allele frequency)

microfilaments: the thinnest of the cytoskeletal fibers and function in moving cellular components and maintaining cell structure

microscope: the instrument that magnifies an object

microtubules: the thickest fibers that make up the cytoskeleton and can dissolve and reform quickly.

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

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

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

modern synthesis: the overarching evolutionary paradigm that took shape by the 1940s and is generally accepted today

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

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

monomers: the single subunits, or building blocks that make up polymers

monosaccharide: a single unit or monomer of carbohydrates

monosomy: an otherwise diploid genotype in which one chromosome is missing

mutation: a permanent variation in the nucleotide sequence of a genome

N

natural selection: the greater relative survival and reproduction of individuals in a population that have favorable heritable traits, leading to evolutionary change

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

nitrogenous base: a nitrogen-containing molecule that acts as a base; often referring to one of the purine or pyrimidine components of nucleic acids

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

nondisjunction: the failure of synapsed homologs to completely separate and migrate to separate poles during the first cell division of meiosis

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

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

nuclear pores: control the passage of ions, molecules, and RNA between the nucleus and the cytoplasm

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

nucleoid: a central region in a prokaryotic cell where DNA is found

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

nucleotide: monomers of nucleic acids. Consist of a five-carbon sugar, phosphate group, and nitrogenous base

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

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

O

oil: an unsaturated fat that is a liquid at room temperature

Okazaki fragments: the DNA fragments that are synthesized in short stretches on the lagging strand

orbital: an area where an electron is most likely to be found its

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

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

organelle: a membrane-bound compartment or sac within a cell

organic molecule: any carbon-containing liquid, solid, or gas

organism: an individual living entity

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. Water also moves from an area of low solutes to an area of high solutes until equilibrium is met.

oxidation reaction: a chemical reaction that consists of an electron being donated by an atom

oxidative phosphorylation: production of ATP using the process of chemiosmosis in the presence of oxygen

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

P

P: the parental generation in a cross

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

pedigree: to chart used to study inheritance patterns of genetic characteristics

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

peptide bond: a covalent bond that exists between the amino group of one amino acid and the carboxyl group of a second amino acid

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

peripheral protein: protein at the plasma membrane's surface either on its exterior or interior side

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

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

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

phenotype: the observable traits expressed by an organism

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

phosphorylation: addition of a high-energy phosphate to a molecule, usually a metabolic intermediate, a protein, or ADP

photoautotroph: an organism capable of synthesizing its own food molecules (storing energy), using the energy of light

photon: a distinct quantity or "packet" of light energy

photorespiration: when oxygen is in a higher concentration than carbon dioxide, rubisco will fix oxygen to RuBP

photosynthesis: a multi-step chemical reaction that requires light energy, carbon dioxide, and water and produces sugar and oxygen

photosystem: a group of proteins, chlorophyll, and other pigments that are used in the light-dependent reactions of photosynthesis to absorb light energy and convert it into chemical energy

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

pigment: a molecule that is capable of absorbing light energy

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

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

pleiotropy: describes when one gene controls two or more different characteristics

point mutation: occur when a single nucleotide is permanently changed in the DNA sequence

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

polygenic inheritance: describes when each gene that an individual inherits has a small additive effect on the overall phenotype

polymers: larger molecules that are formed by combining monomers using covalent bonds

polypeptide chain: a long chain of amino acids linked by peptide bonds

polyploid: an individual with an incorrect number of chromosome sets

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

population genetics: the study of how selective forces change the allele frequencies in a population over time

population: all individuals within a species living within a specific area

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

predictions: statements that describe what should happen if the hypothesis is supported

primary structure: a linear sequence of amino acids in a protein

products: the substances that are formed at the end of a chemical reaction (usually on the right side of a chemical equation

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

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

promoter: a sequence on DNA to which RNA polymerase and associated factors bind and initiate transcription

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

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

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

pseudoscience: claims or beliefs that are portrayed as scientific fact but cannot be evaluated using the scientific method

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

Q

qualitative data: data that is descriptive

quantitative data: data that is numerical

quaternary structure: association of different polypeptide chains in a protein

R

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

reactants: the substances used at the beginning of a chemical reaction (usually on the left side of a chemical equation)

reactivity: the ability of elements to combine and chemically bond with each other

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

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

redox reaction: a chemical reaction that consists of the coupling of an oxidation reaction and a reduction reaction

reduction reaction: a chemical reaction that consists of an electron being gained by an atom

replication fork: the Y-shaped structure formed during the initiation of replication

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

ribose: a five-carbon sugar molecule with hydroxyl group in the 2' position; the sugar component of RNA nucleotides

ribosomal RNA (rRNA): ribosomal RNA; molecules of RNA that combine to form part of the ribosome

RNA polymerase: an enzyme that synthesizes an RNA strand from a DNA template strand

RNA primase: an enzyme that can base pair with the DNA and add a short stretch of RNA nucleotides called a primer. The primer is required to initiate DNA replication

RNA primer: short sequence of RNA nucleotides which DNA polymerase can add DNA nucleotides to

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

S

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

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

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

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

second law of thermodynamics: states that every energy transfer or transformation increases the universe's entropy

secondary structure: structure that proteins form by hydrogen bonding between the oxygen atom of one amino acid, and the hydrogen attached to the nitrogen atom of another amino acid

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

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

septum: a partition formed between two bacterial daughter cells

sexual reproduction: requires that two different gametes (egg and sperm) come together to form a zygote

simple diffusion: a process where solutes move directly through the membrane from an area of high concentration to an area of low concentration until equilibrium is met

sister chromatids: two identical chromosomes attached to one another at a location called the centromere region

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

solute: a substance being dissolved in another to form a solution

solution: a homogeneous mixture made of two or more components

solvent: a substance capable of dissolving another substance

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

speciation: a formation of a new species

sperm: the male gamete; a haploid cell

spliceosome: a structure composed of various proteins and other molecules, which attaches to the mRNA transcript and "splices" or cuts out the non-coding, introns

splicing: the process of removing introns and reconnecting exons in a pre-mRNA

standardized variable: variables that must be kept consistent otherwise they can affect the outcome or results of the experiment

starch: a storage carbohydrate in plants

start codon: the AUG (or, rarely GUG) on an mRNA from which translation begins; always specifies methionine

steroid: a type of lipid composed of four fused hydrocarbon rings

stoma: the opening that regulates gas exchange and water regulation between leaves and the environment; plural: stomata

stop codon: one of the three mRNA codons that specifies termination of translation

stroma: the fluid-filled space surrounding the grana inside a chloroplast where the Calvin cycle reactions of photosynthesis take place

substrate-level phosphorylation: production of ATP from ADP using the excess energy from a chemical reaction and a phosphate group from a reactant

substrate: a reactant that binds to a specific enzyme

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

sympatric speciation: a speciation that occurs in the same geographic space

T

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

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

temperature: a measure of molecular motion

tertiary structure: a protein's three-dimensional conformation, including interactions between secondary structural elements

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

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

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

thylakoid: a disc-shaped membranous structure inside a chloroplast where the light-dependent reactions of photosynthesis take place using chlorophyll embedded in the membranes

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

tissue: a group of similar cells carrying out the same function

tonicity: the amount of solute in a solution

trait: a variation in an inherited characteristic

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

transcription bubble: the region of locally unwound DNA that allows for transcription of mRNA

transcription: the process of making mRNA from DNA

transfer RNA (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

translation: process of making a protein from the nucleotide sequence code of an mRNA transcript

translocation: the process by which one segment of a chromosome dissociates and reattaches to a different, nonhomologous chromosome

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

trisomy: an otherwise diploid genotype in which one entire chromosome is duplicated

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

V

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

valence shell: the outermost electron shell

variants: genotypes or phenotype that deviate from the wild type

variation: the variety of alleles in a population

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

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

W

wavelength: the distance between consecutive points of a wave

waxes: a type of lipid made up of a hydrocarbon chain with an alcohol (–OH) group and a fatty acid

wild type: the most commonly occurring genotype or phenotype for a given characteristic found in a population

X

X (sex)-linked: pattern of inheritance in which an allele is carried on the X chromosome of the 23rd pair

X-linked dominant inheritance: pattern of dominant inheritance that corresponds to a gene on the X chromosome of the 23rd pair

X-linked recessive inheritance: pattern of recessive inheritance that corresponds to a gene on the X chromosome of the 23rd pair

Z

zygote: a fertilized egg produced when a sperm and egg fuse

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Figure 6.3	Elizabeth O'Grady			
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Figure 6.5	Clark et al.	Biology 2E OpenStax	Creative Commons Attribution License v4.0	https://openstax.org/books/biology-2e/pages/7-1-energy-in-living-systems#fig-ch07_01_01
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Figure 6.24	Jason Cashmore			
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Figure 7.22	Elizabeth O'Grady			

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Figure 9.11	RudLus02	Wikimedia Commons	Creative Commons Attribution-Share Alike 4.0 International	https://commons.wikimedia.org/wiki/File:09_11aIncompleteDominance-L.jpg
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Figure 10.3	Parker et al.	Microbiology OpenStax	Creative Commons Attribution License v4.0	https://openstax.org/resources/b1b534f14389e0faa4f275ead517f1812126c3e3
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Figure 10.30	Parker et al.	Microbiology OpenStax	Creative Commons Attribution License v4.0	https://openstax.org/resources/31c6a39f4f53b07fee9b5636c0421b86a363fc62
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Figure 10.33	Clark et al.	Biology 2E OpenStax	Creative Commons Attribution License v4.0	https://openstax.org/books/biology-2e/pages/3-4-proteins#fig-ch03_04_03
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