

Unit 2

CHAPTERS

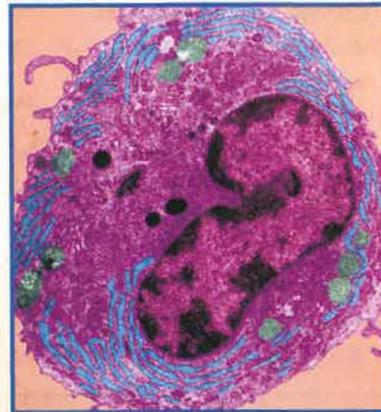
- 4 *Structure and Function of the Cell*
- 5 *Homeostasis and Transport*
- 6 *Photosynthesis*
- 7 *Cellular Respiration*
- 8 *Cell Reproduction*

CELLS

“The cell is the natural granule of life in the same way as the atom is the natural granule of simple, elemental matter. If we are to take the measure of the transit to life and determine its precise nature, we must try to understand the cell.”

From "The Advent of Life" from *The Phenomenon of Man* by Pierre Teilhard de Chardin. Copyright © 1955 by Editions de Seuil. English translation copyright © 1959 by William Collins Sons & Co. Ltd., London and Harper & Row Publishers, Inc., New York. Reprinted by permission of HarperCollins Publishers, Inc.

Eukaryotic cells contain a number of complex internal structures.



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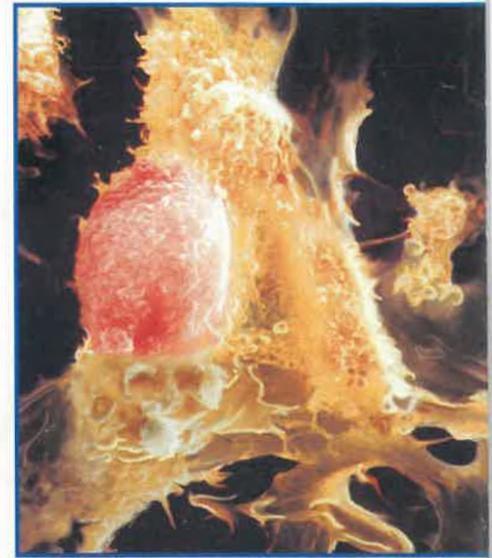
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located throughout this
unit.

Most cells are very small, but these frog eggs can be seen with the unaided eye.



White blood cells



The orange-stained immune-system cell shown above is attacking and ingesting the red-stained tumor cell. Mitochondria, below left, provide cells with the energy necessary for life.



CHAPTER 4

STRUCTURE AND FUNCTION OF THE CELL



This human bone cell has a complex internal structure. (TEM 17,938×)

FOCUS CONCEPT: *Cell Structure and Function*

As you read, find examples of how cell structures vary with their functions.



Unit 1—Cell Transport
and Homeostasis
Topics 1–2

4-1 Introduction to the Cell

4-2 Parts of the Eukaryotic Cell

4-3 Multicellular Organization

INTRODUCTION TO THE CELL

*Both living and nonliving things are composed of molecules made from chemical elements such as carbon, hydrogen, oxygen, and nitrogen. The organization of these molecules into cells is one feature that distinguishes living things from all other matter. A **cell** is the smallest unit of matter that can carry on all of the processes of life.*

DISCOVERY OF THE CELL

Every living thing—from the tiniest bacterium floating in a drop of water to the largest whale—is made of one or more cells. How did scientists come to this conclusion? The discovery of cells was made possible by the development of the microscope in the early seventeenth century.

In 1665, the English scientist Robert Hooke (1635–1703) used a microscope to examine a thin slice of cork. Hooke wrote, “I could exceedingly plainly perceive it to be all perforated and porous,” and he further described it as consisting of “a great many little boxes.” When he turned his microscope to the stems of elder trees, carrots, and ferns, Hooke found that each showed a similar formation. These “little boxes” reminded him of the small rooms in which monks lived, so he called them cells.

What Hooke had observed were actually the remains of dead plant cells. The first person to observe living cells was a Dutch microscope maker, Anton van Leeuwenhoek (1632–1723). Although van Leeuwenhoek’s microscope was rather simple, in 1673 it was powerful enough to enable him to open up a whole new world—the world of microscopic organisms, which had never before been seen.

The Cell Theory

About 150 years passed before scientists began to organize the observations begun by Hooke and van Leeuwenhoek into a unified theory known as the **cell theory**. This theory has three parts:

- All living things are composed of one or more cells.
- Cells are the basic units of structure and function in an organism.
- Cells come only from the reproduction of existing cells.

SECTION

4-1

OBJECTIVES

▲ Outline the discoveries that led to the development of the cell theory.

● State the cell theory.

■ Identify a limiting factor on the size of cells.

◆ Describe the relationship between cell shape and cell function.

▲ Distinguish between prokaryotes and eukaryotes.

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TOPIC: Cell theory
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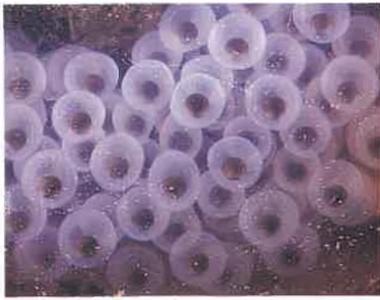


FIGURE 4-1

Although most cells are extremely small, some are large enough to be seen without a microscope. These frog egg cells, for instance, measure about 1.5 mm (0.1 in.) in diameter. Even larger are chicken eggs, which are several centimeters across. The egg cells of both frogs and chickens consist mainly of yolk, which serves as a stored nutrient for the developing embryo.

Early evidence for the cell theory was provided by a trio of German scientists. In 1838, the botanist Matthias Schleiden (1804–1881) concluded that all plants are composed of cells. A year later, the zoologist Theodor Schwann (1810–1882) came to the same conclusion about animals. In 1855, Rudolf Virchow (1821–1902), a physician who had been studying how disease affects living things, reasoned that cells come only from other cells. Over the years, modern scientists have gathered much additional evidence that strongly supports the cell theory.

CELL DIVERSITY

Not all cells are alike. Even cells within the same organism may show enormous diversity in size, shape, and internal organization. Your body, for example, contains at least 200 different cell types.

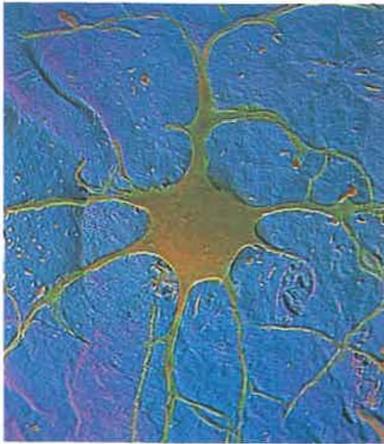
Size

A few types of cells, such as those shown in Figure 4-1, are large enough to be seen by the unaided eye. The nerve cells that extend down a giraffe's leg, for instance, can be up to 2 m (about 6½ ft) long. However, most plant and animal cells are only about 10 to 50 µm (0.002 in.) in diameter, and some bacterial cells are only 0.2 µm (0.000008 in.) in diameter. Therefore, most cells are visible only with a microscope.

Cells are limited in size by the ratio between their outer surface area and their volume. Table 4-1 shows how growth affects this ratio. For a cuboidal cell, volume increases with the *cube* of the side length, but surface area increases with the *square* of the side length. This means that if a cell keeps the same shape as it grows, its volume will increase more rapidly than its surface area. This trend is important because the nutrients, oxygen, and other materials a cell requires must enter through its surface. Thus, as a cell grows larger, at some point its surface area becomes too small to allow these materials to enter the cell quickly enough to meet the cell's needs.

TABLE 4-1 Surface Areas and Volumes of Cubes

	Side Length	Surface Area	Volume	Surface Area/Volume Ratio
	1 mm	6 mm ²	1 mm ³	6:1
	2 mm	24 mm ²	8 mm ³	3:1
	3 mm	54 mm ²	27 mm ³	2:1



NERVE CELL



SKIN CELLS



WHITE BLOOD CELL

Shape

Cells come in a variety of shapes. This diversity of form reflects a diversity of function. Examine the three human cells shown in Figure 4-2. The long extensions that reach out in various directions from the nerve cell enable the cell to receive and transmit nerve impulses. In contrast, the flat shape of dead skin cells is well suited to their function of covering the body surface. Some white blood cells can change shape, leave the blood, and enter the areas surrounding blood vessels. This allows them to move through narrow openings and to isolate, engulf, and destroy bacteria that invade the body.

Internal Organization

The micrographs in Figures 4-3 and 4-4 show that cells contain a variety of internal structures called **organelles**. An organelle is a cell component that performs specific functions for the cell. Just as the organs of a multicellular organism carry out the organism's life functions, the organelles of a cell maintain the life of the cell.

FIGURE 4-2

These photographs taken with a scanning electron microscope show three different types of cells that are found in the human body. Each cell type has a structure that enables it to perform its function effectively. (left 17,385 \times , middle 330 \times , right 23,250 \times)



TEM

Cell membrane

Nucleus

FIGURE 4-3

This plant cell, like other eukaryotic cells, is filled with membrane-bound organelles. The most prominent organelle is the nucleus. The entire cell is surrounded by a membrane. (TEM 105,661 \times)



Quick Lab

Comparing Surface Cells

Materials microscope, prepared slides of animal (human) skin and plant (dicot) stem, pencil, paper

Procedure Examine slides using medium magnification (100 \times).

Observe and draw the outer surface cells of the plant stem and the animal skin.

Analysis How do the surface cells of each organism differ from the cells beneath them? What is the function of these outer surface cells? Explain how the shape of surface cells are suited to their function.

In Figure 4-3, notice that the entire cell is surrounded by a thin membrane, called the **cell membrane**. Inside the cell are a variety of organelles, most of which are surrounded by their own membranes. The large organelle near the center of the cell is the **nucleus**. It contains the majority of the cell's genetic information and directs most of the activities of the cell. Organisms whose cells contain a membrane-bound nucleus and other organelles are called **eukaryotes** (yoo-KAR-ee-OHTS).

The cell shown in Figure 4-4 is a bacterium. It, too, has a cell membrane, but none of the organelles inside a bacterium are surrounded by a membrane. Although the genetic information of a bacterium may be concentrated in one part of the cell, a bacterium has no membrane-bound nucleus like that of a eukaryotic cell. Unicellular organisms that lack a membrane-bound nucleus and other organelles are called **prokaryotes** (proh-KAR-ee-OHTS). The difference between prokaryotes and eukaryotes is such an important distinction that prokaryotes are placed in two kingdoms, separate from eukaryotes.

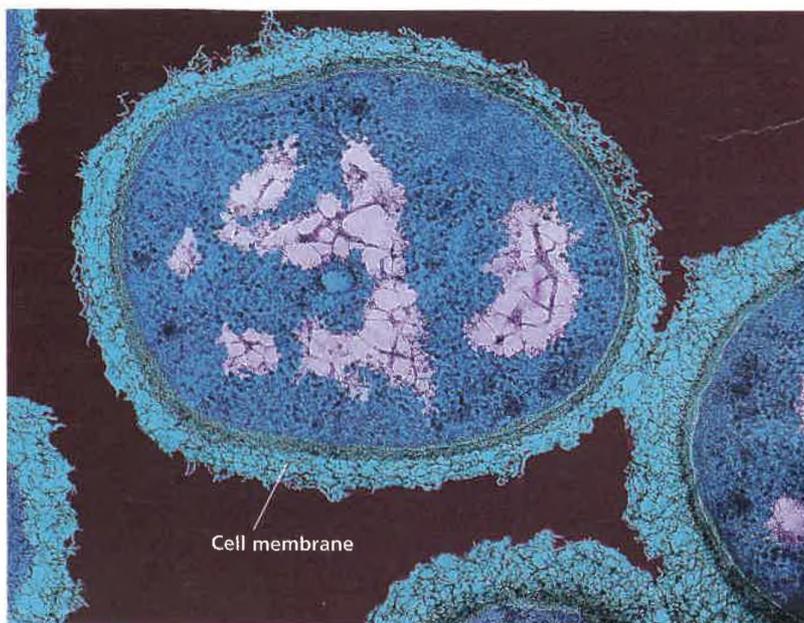


FIGURE 4-4

This bacterial cell is surrounded by a membrane, but it has no nucleus or other membrane-bound organelles. (TEM 84,721 \times)

SECTION 4-1 REVIEW

1. What is the cell theory?
2. What single factor limits the size that most cells are able to attain?
3. Give two examples of how cells' shapes are suited to their functions.
4. What is an organelle?
5. How can you determine whether a unicellular organism is a prokaryote or a eukaryote?
6. **CRITICAL THINKING** The observations that led to the formation of the cell theory occurred within a 17-year period. Why do you think that more than one scientist made critical observations about cells within this period?

PARTS OF THE EUKARYOTIC CELL

The structures that make up a eukaryotic cell are determined by the specific functions carried out by the cell. Thus, there is no typical eukaryotic cell. Nevertheless, eukaryotic cells generally have three main components: a cell membrane, a nucleus, and other organelles.

CELL MEMBRANE

A cell cannot survive if it is totally isolated from its environment. All cells must take in nutrients and other materials, and they must also dispose of the wastes they produce. Therefore, both nutrients and wastes must pass through the cell membrane. The cell membrane controls the ease with which substances pass into and out of the cell—some substances easily cross the membrane, while others cannot cross at all. For this reason, the cell membrane is said to be **selectively permeable**.

The structure of the cell membrane depends on the functions the cell performs. In a multicellular organism, for example, some cells secrete materials into their environment for use elsewhere in the organism. Other cells recognize potentially harmful “invaders” and destroy them before they cause any damage. In each case, the cells are surrounded by membranes specialized for that task. No matter what the task, however, all cell membranes are made primarily of lipids and proteins.

Membrane Lipids

One of the major types of lipids in the cell membrane is phospholipid. Recall from Chapter 3 that each phospholipid molecule has a polar “head” and two nonpolar “tails.” Because of its hydrophilic nature, the head of a phospholipid will orient itself so that it is as close as possible to water molecules. In contrast, the hydrophobic tails will tend to orient themselves away from water.

Cells are bathed in an aqueous, or watery, environment. Since the inside of a cell is also an aqueous environment, both sides of the cell membrane are surrounded by water molecules. These water molecules cause the phospholipids of the cell membrane to form two layers—a lipid bilayer. As you can see in Figure 4-5,

SECTION

4-2

OBJECTIVES

Describe the structure, composition, and function of the cell membrane.

Name the major organelles found in a eukaryotic cell, and describe their functions.

Describe the structure and function of the nucleus.

Describe three structures characteristic of plant cells.

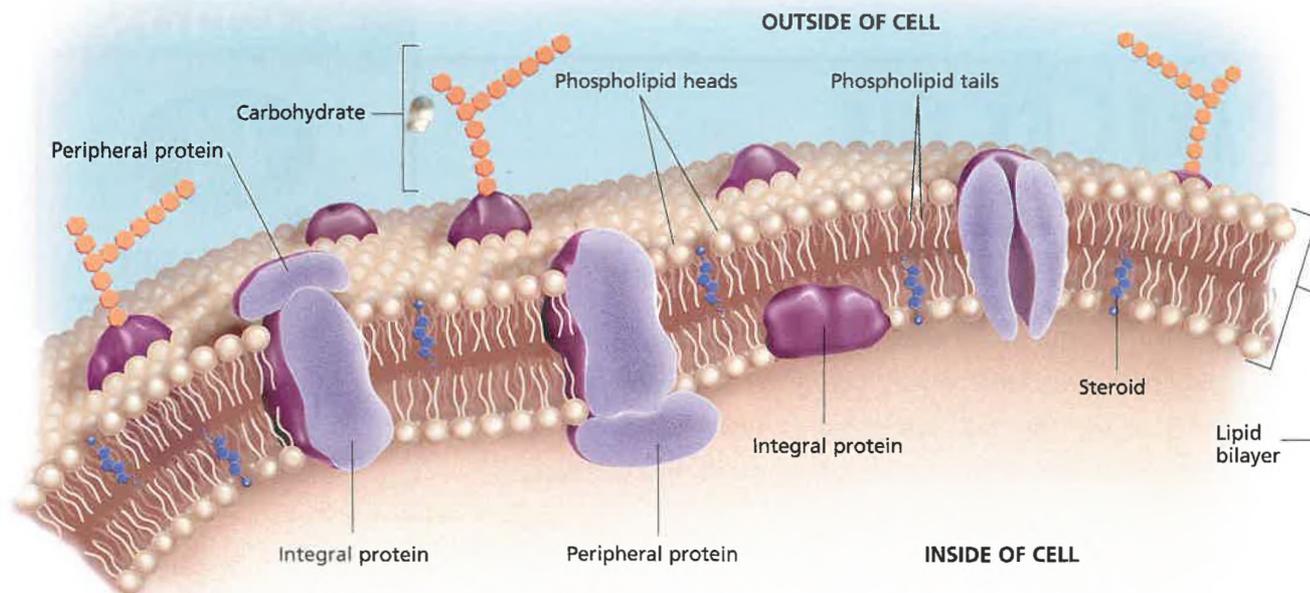


FIGURE 4-5

Cell membranes are composed mostly of a lipid bilayer and two types of proteins. Integral proteins are embedded within the membrane. Peripheral proteins are attached to both surfaces of the membrane.

the phospholipids are arranged so that their heads point outward, while their tails are confined to the interior of the membrane.

Figure 4-5 indicates that eukaryotic cell membranes also contain steroids, another type of lipid you encountered in Chapter 3. In membranes, the steroid molecules fit between the tails of the phospholipids. The major membrane steroid in animal cells is cholesterol. Other steroids are found in the cell membranes of plants.

Membrane Proteins

Some proteins are attached to the surfaces of the cell membrane. As shown in Figure 4-5, these **peripheral proteins** are located on both the interior surface and the exterior surface of the cell membrane. Weak bonds link peripheral proteins to membrane lipids or to other proteins that are embedded in the lipid bilayer. The proteins that are embedded in the bilayer are called **integral proteins**. Figure 4-5 shows that some integral proteins extend across the entire cell membrane and are exposed to both the inside of the cell and the exterior environment. Others extend either only to the inside or only to the exterior surface.

Notice in Figure 4-5 that the integral proteins exposed to the cell's external environment often have carbohydrates attached to them. These carbohydrates may hold adjoining cells together, or they may act as sites where viruses or chemical messengers such as hormones can attach.

Because the cell membrane is selectively permeable, cells must have mechanisms for transporting molecules through the lipid bilayer. Membrane proteins play an important role in this process. For example, some integral proteins form channels or pores through which certain substances can pass. Other proteins bind to a substance on one side of the membrane and carry it to the other side of the membrane. You will learn more about how substances cross the cell membrane in Chapter 5.

Fluid Mosaic Model of Cell Membranes

For many years, scientists thought that the molecular arrangement of lipids and proteins in the cell membrane was relatively static. But with the development of new techniques and instruments, including the scanning electron microscope, scientists have discovered that cell membranes are actually very dynamic. Today scientists use the **fluid mosaic model** to describe the cell membrane. According to this model, the lipid bilayer behaves more like a fluid than a solid. Because of this fluidity, the membrane's lipids and proteins can move laterally within the lipid bilayer, as indicated in Figure 4-6. As a result of such lateral movement, the pattern, or "mosaic," of lipids and proteins in the cell membrane is constantly changing.

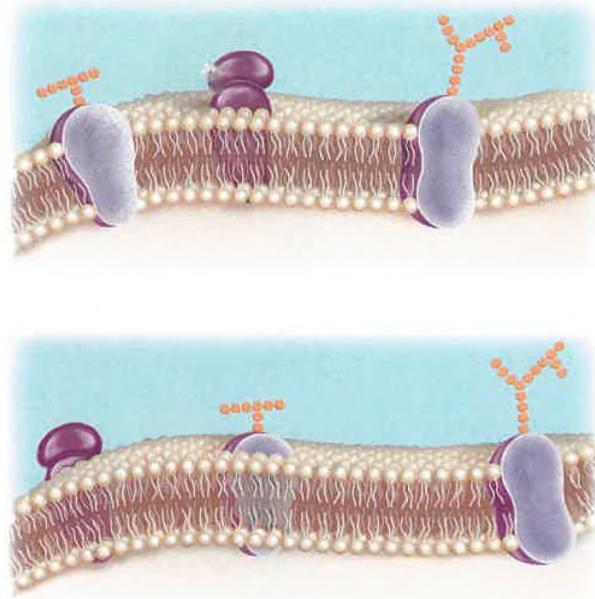


FIGURE 4-6

The cell membrane is a dynamic structure, with both lipids and proteins moving laterally within the lipid bilayer. Scientists therefore describe the structure of the cell membrane in terms of a fluid mosaic model.

ORGANELLES

Between the cell membrane and the nucleus lies the **cytoplasm** (SIET-oh-PLAZ-uhm), which contains the various organelles of the cell. The organelles are bathed in a gelatin-like aqueous fluid called the **cytosol** (SIET-oh-SAWL). Dissolved in the cytosol are salts, minerals, and organic molecules. The major organelles are summarized in Table 4-2, and those that are found in animal cells are illustrated in Figure 4-7.

TABLE 4-2 Organelles

Organelle	Function
Mitochondrion	transfers energy from organic compounds to ATP
Ribosome	organizes the synthesis of proteins
Endoplasmic reticulum (ER)	prepares proteins for export (rough ER); synthesizes steroids, regulates calcium levels, breaks down toxic substances (smooth ER)
Golgi apparatus	processes and packages substances produced by the cell
Lysosome	digests molecules, old organelles, and foreign substances
Microfilaments and microtubules	contribute to the support, movement, and division of cells
Cilia and flagella	propel cells through the environment; move materials over the cell surface
Nucleus	stores hereditary information in DNA; synthesizes RNA and ribosomes
Cell wall*	supports and protects the cell
Vacuole*	stores enzymes and waste products
Plastid*	stores food or pigments; one type (chloroplast) transfers energy from light to organic compounds

*Cell walls, large vacuoles, and plastids are found in the cells of plants and some other eukaryotes, but not in the cells of animals.

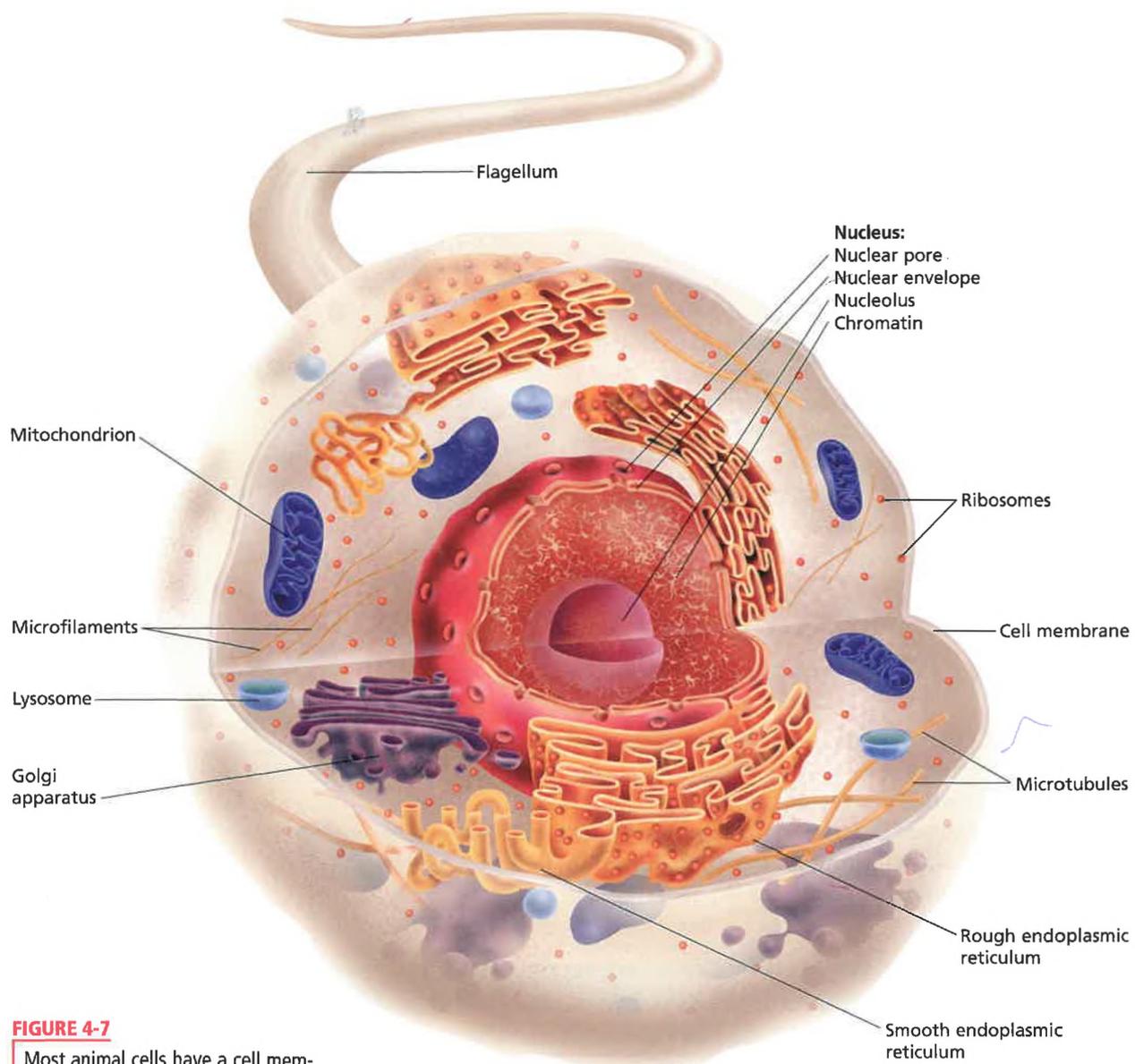


FIGURE 4-7

Most animal cells have a cell membrane, a nucleus, and a variety of other organelles.

Word Roots and Origins

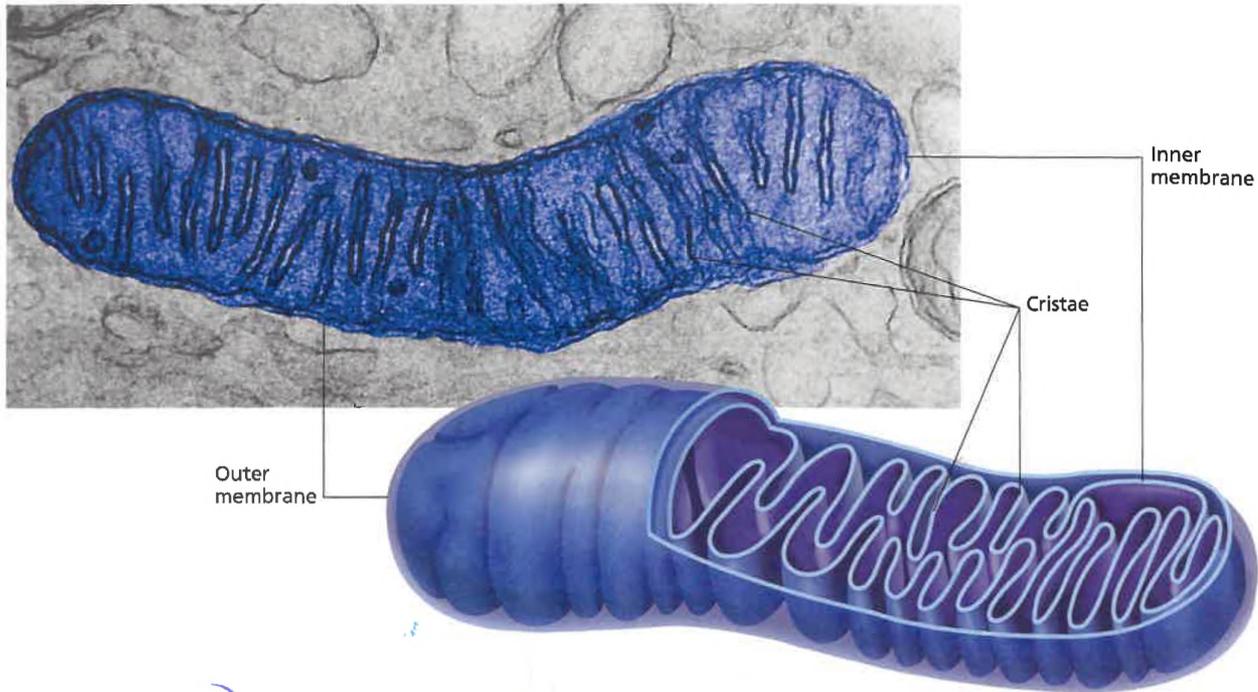
mitochondrion

from the Greek *mitos*, meaning "thread," and *chondrion*, meaning "grain"

Mitochondria

Scattered throughout the cytosol are relatively large organelles called **mitochondria** (MIET-oh-KAHN-dree-uh), illustrated in Figure 4-8. Mitochondria are the sites of chemical reactions that transfer energy from organic compounds to ATP. Remember from Chapter 3 that ATP is the molecule that most cells use as their main energy currency. The energy of ATP ultimately drives most of the chemical reactions that occur in a cell. Therefore, mitochondria are usually more numerous in cells that have a high energy requirement. Liver cells, for instance, carry out a host of biochemical activities, and each cell may contain as many as 2,500 mitochondria. Muscle cells also contain many mitochondria.

If you look closely at Figure 4-8, you will notice that a mitochondrion is surrounded by two membranes. The smooth *outer* membrane serves as a boundary between the mitochondrion and



the cytosol. The *inner* membrane has many long folds, known as **cristae** (KRIS-tee). The cristae greatly enlarge the surface area of the inner membrane, providing more space for the chemical reactions that occur in the mitochondrion.

Mitochondria have their own DNA, and new mitochondria arise only when existing ones grow and divide. These observations have led to a theory, discussed further in Chapter 15, that mitochondria developed from prokaryotic cells that lived inside eukaryotic cells. According to this theory, the prokaryotes may have gained protection by living inside the eukaryotes and, in turn, produced energy for the eukaryotes.

Ribosomes

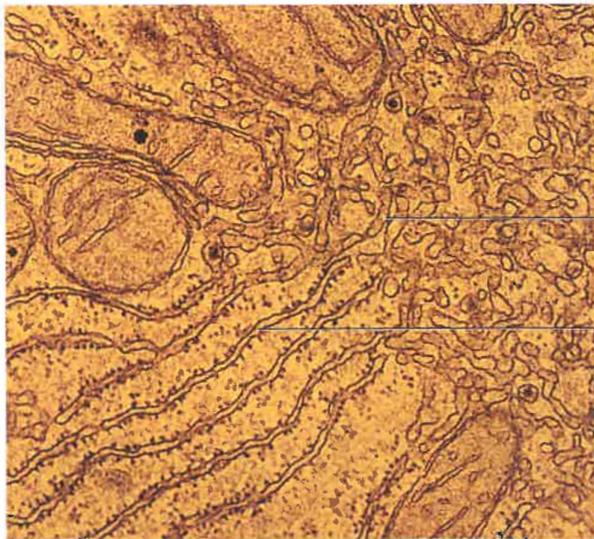
The most numerous organelles in many cells are the **ribosomes** (RIE-buh-SOHMZ). Unlike most other organelles, ribosomes are not surrounded by a membrane. Each ribosome is an assemblage of two organic compounds—proteins and RNA. Inside the cell's nucleus, proteins and RNAs are packaged into ribosomes, which are then transported to the cytosol. Some ribosomes remain free within the cytosol, while others become attached to an organelle called the endoplasmic reticulum. You can see both free and attached ribosomes if you examine Figure 4-9 closely.

Ribosomes play important roles in the synthesis of proteins. Proteins to be used within the cytosol are produced on the ribosomes that are free in the cytosol. Proteins to be inserted into membranes or exported from the cell are produced on the ribosomes that are attached to the endoplasmic reticulum.

FIGURE 4-8

Mitochondria are surrounded by a double membrane. The inner membrane is composed of many folds called cristae. (TEM 232,000×)

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Smooth ER

Rough ER

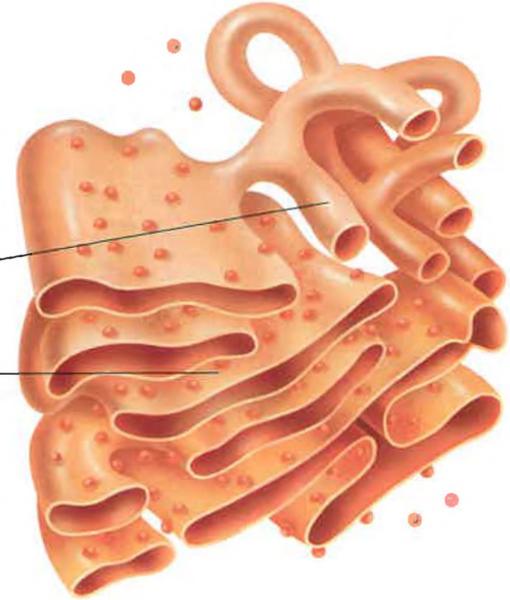


FIGURE 4-9

The small dark dots in this cell are ribosomes. Some are free in the cytosol, while others are attached to the rough ER. The smooth ER lacks attached ribosomes. (TEM 240,000 \times)

Endoplasmic Reticulum

The **endoplasmic reticulum** (EN-doh-PLAZ-mik ri-TIK-yuh-luhm), abbreviated ER, is a system of membranous tubules and sacs. The dark lines that you see in Figure 4-9 represent the membranes of the ER, while the lighter areas are the channels inside it. The ER functions primarily as an intracellular highway, a path along which molecules move from one part of the cell to another. The amount of ER inside a cell fluctuates, depending on the cell's activity.

A cell usually contains two types of ER, both of which are shown in Figure 4-9. One type appears to be covered with dark dots when viewed with an electron microscope. These dots are ribosomes, and they give the ER a rough appearance. Consequently, this type is known as **rough endoplasmic reticulum**, or rough ER. Rough ER is prominent in cells that make large amounts of proteins to be exported from the cell or inserted into the cell membrane.

The second type of ER is not covered with ribosomes. Because of their absence, this type of ER appears smooth and is therefore called **smooth endoplasmic reticulum**, or smooth ER. Smooth ER is involved in the synthesis of steroids in gland cells, the regulation of calcium levels in muscle cells, and the breakdown of toxic substances by liver cells. As you can see in Figure 4-9, rough ER and smooth ER may be continuous with each other.

Golgi Apparatus

The **Golgi** (GOHL-jee) **apparatus** is the processing, packaging, and secreting organelle of the cell. Like the endoplasmic reticulum, the Golgi apparatus is a system of membranes. Figure 4-10 shows that the Golgi apparatus appears as a series of flattened sacs with a characteristic convex shape in the cytosol. Working in close association with the endoplasmic reticulum, the Golgi apparatus modifies proteins for export by the cell. The role of the Golgi apparatus in protein synthesis will be discussed in Chapter 11.

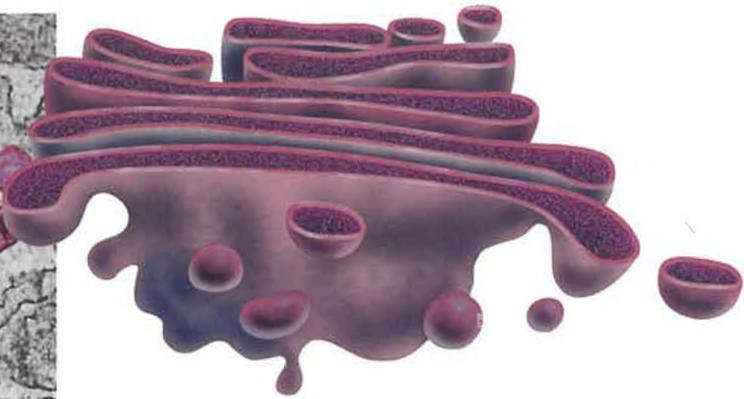
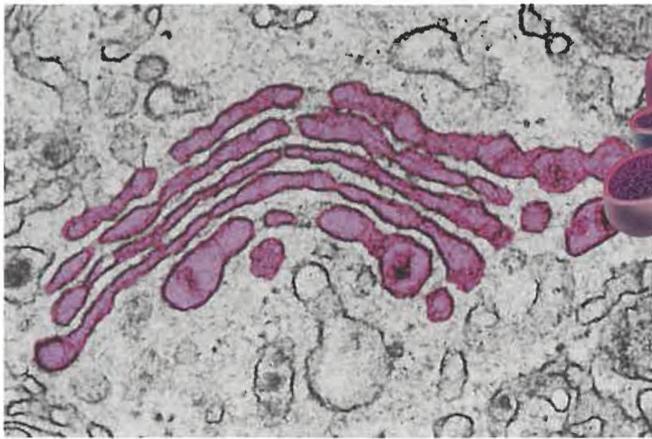


FIGURE 4-10

A collection of smooth, membrane-bound sacs isolated from the endoplasmic reticulum is known as the Golgi apparatus. Although separated from each other, the endoplasmic reticulum and Golgi apparatus work closely together in preparing materials for release by the cell. (TEM 237,250 \times)

Lysosomes

Lysosomes (LIE-suh-sohmz) are small, spherical organelles that enclose hydrolytic enzymes within single membranes. These enzymes can digest proteins, carbohydrates, lipids, DNA, and RNA. They may also digest old organelles as well as viruses and bacteria that have been ingested by a cell. Lysosomes are common in the cells of animals, fungi, and protists, but they are rare in plant cells. In some multicellular organisms, lysosomes play a role during early development. For example, the human hand begins as a solid structure in the embryo. As the embryo develops, lysosomal enzymes selectively destroy tissue to form the spaces between the fingers.

Cytoskeleton

Just as your body depends on your skeleton to maintain its shape and size, so a cell needs a structure to maintain its shape and size. In many cells, that structure is the **cytoskeleton**, a network of long protein strands located in the cytosol. Like ribosomes, these strands are not surrounded by membranes. In addition to providing support, the cytoskeleton participates in the movement of organelles within the cytosol. Two major components of the cytoskeleton are **microfilaments** and **microtubules**.

Microfilaments are threads made of a protein called **actin**. Each microfilament consists of many actin molecules that are linked together to form a polymer chain. Microfilaments constitute the smallest strands that make up the cytoskeleton. They contribute to cell movement and play a role in the contraction of muscle cells.

The largest strands of the cytoskeleton are hollow tubes known as **microtubules**. In many cells, microtubules extend outward from a central point near the nucleus to various sites near the cell membrane. When a cell is about to divide, bundles of microtubules come together and extend across the cell. These bundles, known as **spindle fibers**, are thick enough to be visible with a light microscope, as you can see in Figure 4-11. Spindle fibers assist in the movement of chromosomes during cell division. When cell division is complete, the spindle fibers are disassembled, and the microtubules resume their task of providing support to the cell.

FIGURE 4-11

This cell is dividing in two. Its chromosomes, stained orange by a fluorescent dye, are moving to opposite ends of the cell. They are being pulled by the spindle fibers, which are stained green. (LM 3,696 \times)

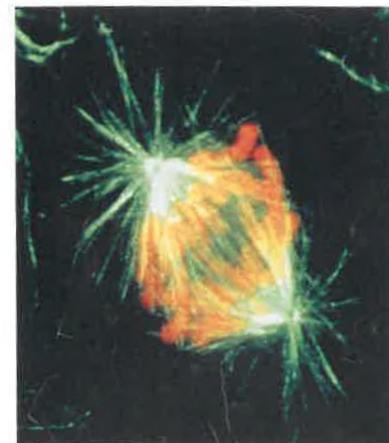


FIGURE 4-12

Sperm cells propel themselves by moving a long flagellum back and forth. (LM 3,350 \times)



Cilia and Flagella

Cilia (SIL-ee-uh) and **flagella** (fluh-JEL-uh) are hairlike organelles that extend from the surface of the cell, where they assist in movement. Because of the variety of roles they play, cilia and flagella can be found in many eukaryotic cells.

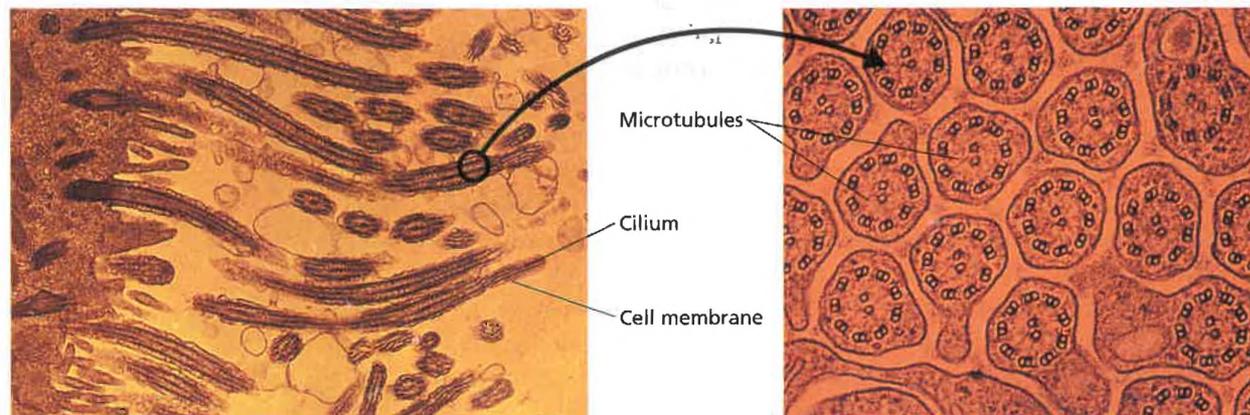
When these organelles are short and present in large numbers on a cell, they are called cilia. The external surfaces of many unicellular organisms are covered with cilia. The movements of the cilia propel these tiny organisms through the water as they search for food or escape from predators. Cilia are also found on the surfaces of cells in multicellular organisms. The cells lining your respiratory tract, for example, bear numerous cilia that trap particles and debris from the air you inhale. As these cilia move, they sweep the trapped materials back up to your throat, where they are removed from your respiratory tract when you swallow.

When the hairlike organelles are long and less numerous on a cell, they are called flagella. On many cells, including the sperm cells illustrated in Figure 4-12, only one flagellum is present. By whipping back and forth, flagella can swiftly propel unicellular organisms or specialized cells in multicellular organisms, such as sperm cells.

Cilia and flagella have a similar internal structure. Notice in Figure 4-13 that both organelles are composed of nine pairs of microtubules arranged around a central pair.

FIGURE 4-13

Microtubules are important components of cilia and flagella. A cross section of a cilium shows that it consists of nine pairs of microtubules that surround a central pair. A flagellum has a similar structure. (TEM 38,000 \times left, 396,000 \times right)



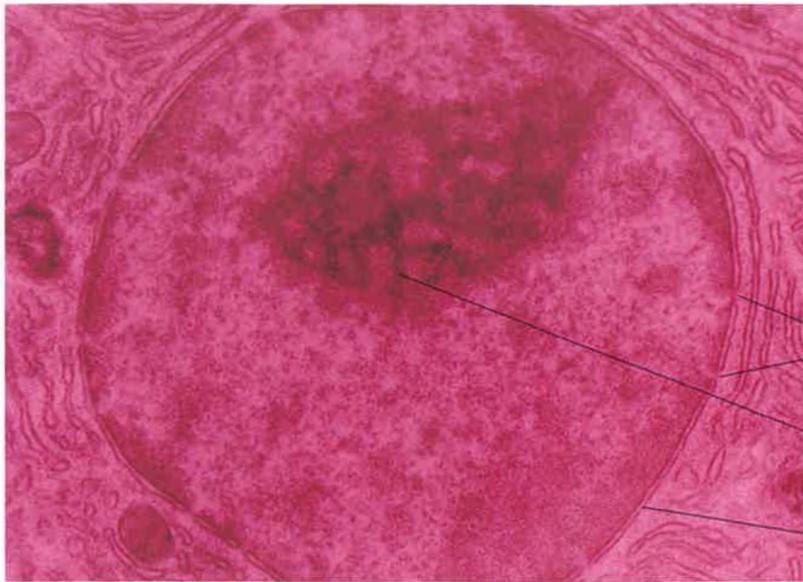


FIGURE 4-14

The most prominent organelle in most eukaryotic cells is the nucleus, which is surrounded by a double membrane perforated with pores. These pores allow materials to be exchanged between the nucleus and the cytosol. Inside the nucleus is the nucleolus, where ribosomes are made before they are transported to the cytosol. (TEM 360,734×)

Nuclear pores

Nucleolus

Nuclear envelope

NUCLEUS

The nucleus is often the most prominent structure within a eukaryotic cell. It maintains its shape with the help of a protein skeleton known as the **nuclear matrix**. As indicated in Figure 4-14, the nucleus is surrounded by a double membrane called the **nuclear envelope**. Inside the nuclear envelope are fine strands of **chromatin**, a combination of DNA and protein. When a cell is about to divide, the chromatin strands coil up and become densely packed, forming **chromosomes**.

The nucleus stores hereditary information in its DNA. The nucleus is also the site where RNA is copied from DNA. In turn, RNA directs the synthesis of proteins, a process that occurs in the cytosol, as you have read. This means that RNA must travel from the nucleus to the cytosol before it can direct protein synthesis. RNA makes this journey by passing through **nuclear pores**, small holes in the nuclear envelope. Most nuclei also contain at least one spherical area called the **nucleolus** (noo-KLEE-uh-luhs). The nucleolus is the site where ribosomes are synthesized and partially assembled before they pass through the nuclear pores to the cytosol. Both the nuclear pores and the nucleolus are visible in Figure 4-14.

Word Roots and Origins

chromosome

from the Greek *chroma*, meaning "color," and *soma*, meaning "body"

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PLANT CELLS

Most of the organelles and other parts of the cell just described are common to all eukaryotic cells. However, plant cells may have three additional kinds of structures—cell walls, vacuoles, and plastids—that are extremely important to plant function.

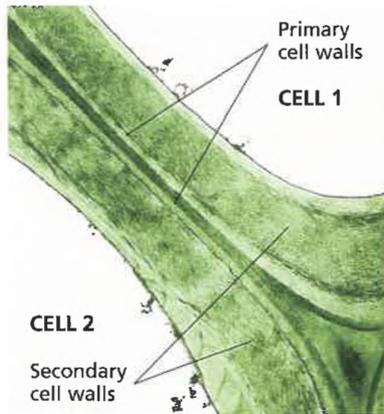


FIGURE 4-15

The two plant cells in this photograph each have their own primary and secondary cell walls. The primary walls are constructed first. Later, the secondary walls are formed inside the primary walls. (TEM 12,750 \times)

Cell Wall

Plant cells are covered by a rigid **cell wall** that lies outside the cell membrane. The rigidity of cell walls helps support and protect the plant. Cell walls contain long chains of cellulose, one of the complex carbohydrates you read about in Chapter 3. The cellulose is embedded in proteins and other carbohydrates that harden the entire structure. Pores in the cell wall allow ions and molecules to enter and exit the cell.

Figure 4-15 shows that cell walls are of two types—primary and secondary. While a plant cell is being formed, a primary cell wall develops just outside the cell membrane. As the cell expands in length, cellulose and other molecules are added, enlarging the cell wall. When the cell reaches its full size, a secondary cell wall may develop. As you can see in Figure 4-15, the secondary cell wall develops between the primary cell wall and the cell membrane. The secondary cell wall is tough and woody. Therefore, once it is completed, a plant cell can grow no further. When you pick up a piece of wood, you are holding secondary cell walls. The cells inside the walls have died and disintegrated.

Vacuoles

Vacuoles are a second common characteristic of plant cells. These fluid-filled organelles store enzymes and metabolic wastes. Often, as Figure 4-16 shows, they are quite large. In fact, some vacuoles may occupy 90 percent of a plant cell's volume, pushing all of the other organelles up against the cell membrane. Some of the wastes stored by vacuoles are toxic and must be kept away from the rest of the cell. The storage of these materials may be beneficial to a plant in other ways. For instance, the poisons that certain acacia trees have in their vacuoles provide a defense against plant-eating animals.

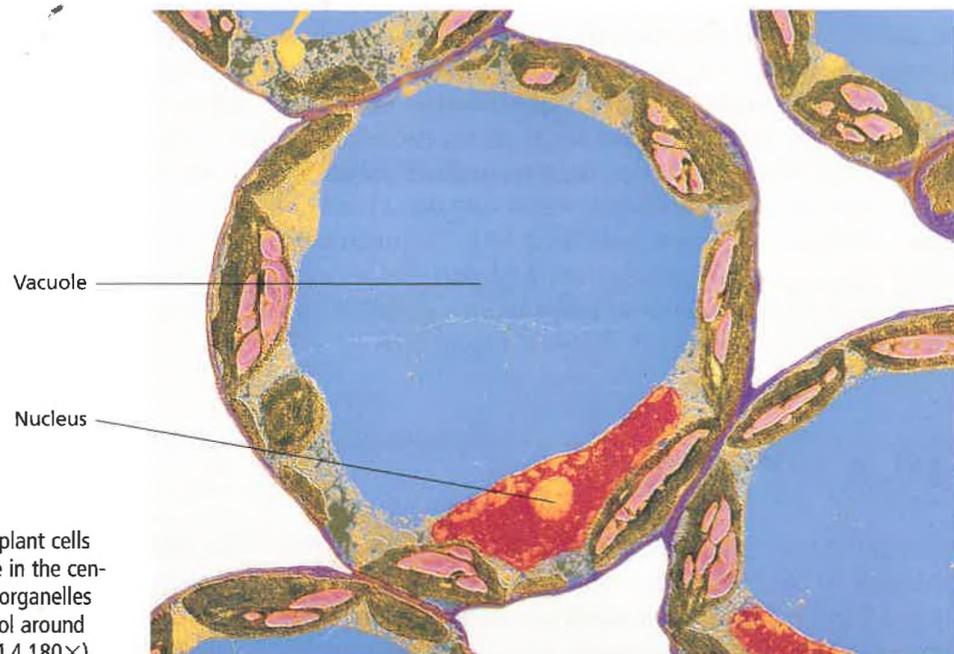


FIGURE 4-16

Much of the volume of these plant cells is occupied by a large vacuole in the center of the cell. The rest of the organelles are confined to a rim of cytosol around the periphery of the cell. (TEM 4,180 \times)

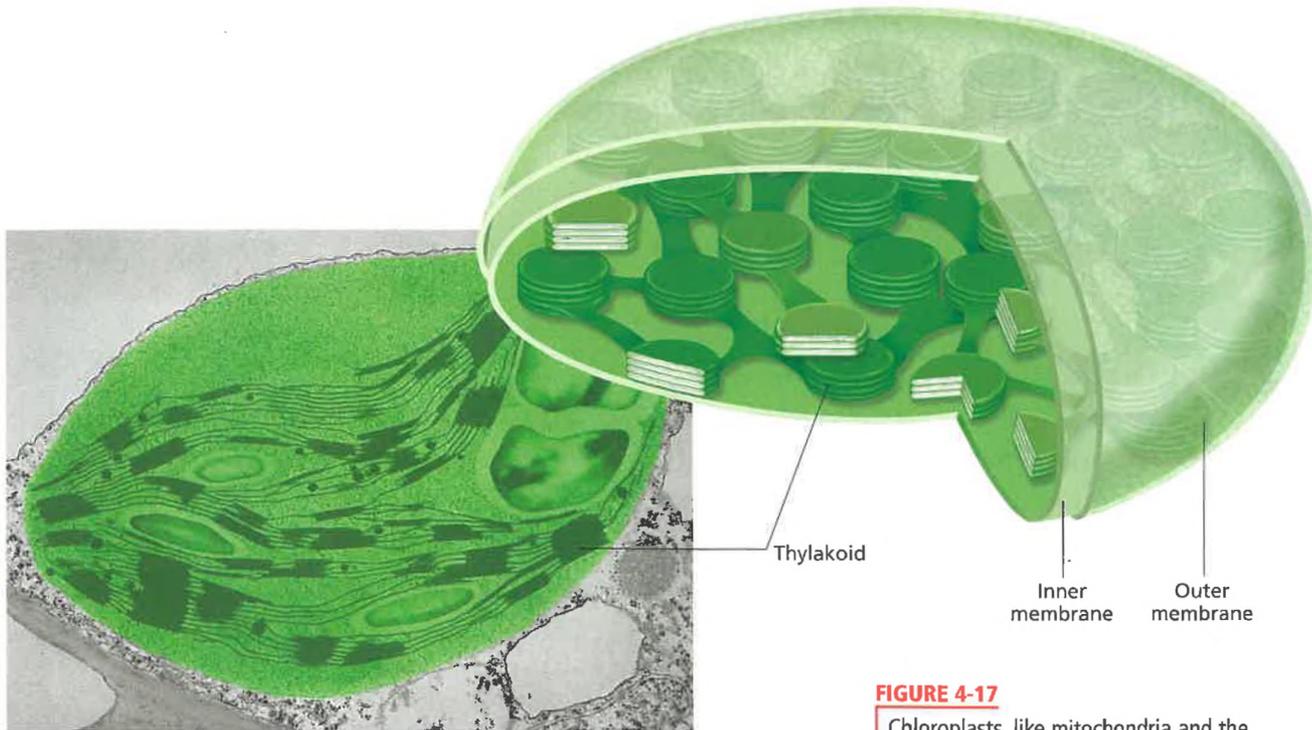


FIGURE 4-17

Chloroplasts, like mitochondria and the nucleus, are surrounded by a double membrane. The thylakoids inside each chloroplast contain pigments involved in photosynthesis. (TEM 14,648 \times)

Plastids

A third distinguishing feature of plant cells is the presence of **plastids**. Plastids are organelles that, like mitochondria and the nucleus, are surrounded by two membranes and contain DNA. Some plastids store starch or fats, while others contain compounds called pigments, which absorb visible light.

The most familiar type of plastid is the **chloroplast**, illustrated in Figure 4-17. Each chloroplast encloses a system of flattened, membranous sacs called **thylakoids**. Chloroplasts are the organelles in a plant cell in which the energy of sunlight is converted into chemical energy in organic compounds. This conversion occurs in the thylakoids during the process of photosynthesis, which you will study in Chapter 6. Chloroplasts contain large amounts of a green pigment that gives leaves their green color. Different pigments in other types of plastids are responsible for the colors of fruits and flowers.

SECTION 4-2 REVIEW

1. Name the three main components of a eukaryotic cell.
2. Summarize the fluid mosaic model of the cell membrane.
3. Distinguish between the nucleus and the nucleolus.
4. Which organelles are surrounded by two membranes?
5. What structural feature do cilia and flagella have in common?
6. **CRITICAL THINKING** Plant cells have cell walls, but animal cells do not. Why do you think that is so?

Discovering a New World

HISTORICAL PERSPECTIVE

The first microscopes, made around 1600, had a single lens and were much like a powerful magnifying glass. Compound microscopes, those with two or more lenses, produced greater enlargement but caused blurred images. This problem, known as chromatic aberration, was not solved until more than a century later. Meanwhile, Anton van Leeuwenhoek, who lived in Holland from 1632 to 1723, made hundreds of simple, high-quality microscopes. He was the first person to view and describe the amazing miniature world of protozoa and bacteria.

Toy or Tool?

About 25 years after van Leeuwenhoek began his work with microscopes, Robert Hooke, a fellow scientist, noted that few scientists besides van Leeuwenhoek considered the microscope an essential tool. "I hear of none that make any other use of that instrument, but for diversion and pastime," Hooke wrote. *Diversion* and *pastime* are not words we usually connect with the microscope, a tool so basic to scientific work today that we can hardly imagine scientists, or students of science, being without one.

Why weren't more scientists using microscopes? The main reason is that early microscopes were of poor quality, and only an unusually diligent and persistent person could find them useful. Van Leeuwenhoek was such a person.

A linendraper by trade, van Leeuwenhoek spent most of his time on his hobby—science—and for him the microscope was a valuable



Anton van Leeuwenhoek

instrument. He ground his own high-quality lenses, more than 400 in his lifetime, and mounted them between thin brass plates. They magnified objects by 50 to 300 times, and van Leeuwenhoek never tired of peering through the lenses and making discoveries about animals, plants, and microorganisms.

Over a 50-year period beginning in 1673, van Leeuwenhoek sent letters to the British Royal Society describing his microscopic observations. Most of his letters were published in the society's journal, *Philosophical Transactions*.

Van Leeuwenhoek's first letter described what he called *animalcules*, or "tiny animals," which we now know as protozoa. He explained that he had found them

"in rain, which had stood but a few days in a new tub. . . . I saw, after divers observations, that the bodies consisted of 5, 6, 7, or 8 very clear globules."

He said his animalcules sometimes "stuck out two little horns, which were continually moved, after the fashion of a horse's ears." Later, scientists would name them *Vorticella* and identify their "little horns" as *cilia*, or tiny hairs.

Father of Microbiology

Van Leeuwenhoek examined hundreds of objects, including the lenses of eyes, the striations of muscles, the mouthparts of insects, the detailed structures of plants, and many protozoa and bacteria found in rainwater, pond water, well water, saliva,

idea in his letter to the Royal Society by describing the flea's development with great precision.

Van Leeuwenhoek's remarkable powers of observation enabled him to make accurate judgments not only of an object's structure but also of its size. For example, he thought



In 1674, van Leeuwenhoek sent a piece of cork, along with other samples, to the British Royal Society. This photograph shows what the piece of cork would have looked like through van Leeuwenhoek's most powerful microscope.

and other liquids. He was the first person to accurately describe red blood cells.

Van Leeuwenhoek also examined human and animal spermatozoa and made correct guesses about the reproductive process of animals, even though fertilization would not be observed under the microscope until the 1800s. His observations disproved the long-held theory of spontaneous generation—the idea that life could grow out of nonliving substances. Some believed, for example, that fleas grew out of sand or dust, but van Leeuwenhoek refuted that

100 human red blood cells in a row would be nearly the width of a grain of coarse sand. That made each red cell about $8.5\mu\text{m}$ (0.0003 in.) in diameter, close to its actual measurement.

In addition to writing about his observations, van Leeuwenhoek drew sketches of what he saw. In fact, he was the first person to draw an image of bacteria; the drawing was published in *Philosophical Transactions* in 1683. Because of his studies of microorganisms, van Leeuwenhoek is often called the father of microbiology.

After van Leeuwenhoek

Even though van Leeuwenhoek had published reports about his many discoveries, the scientific community failed to recognize the microscope's significance for many years. In 1733, an amateur optician named Chester Moor Hall found a way to solve the persistent problem of chromatic aberration in compound lenses, and in 1774, the technique was applied to microscopes. By the 1820s, new types of microscopes were available, and the 1800s and 1900s brought frequent improvements. In 1931, the first electron microscope was invented, and in 1981, the scanning tunneling microscope began to reveal objects atom by atom. Today's work in microbiology, protozoology, bacteriology, and other fields depends on advanced microscopes, descendants of those simple lenses through which van Leeuwenhoek first saw his "animalcules."



Van Leeuwenhoek's microscope consisted of a single lens. He placed a small drop of liquid on the tip of a fine point and peered through the lens to observe the miniature world hidden in the liquid. By turning a screw, van Leeuwenhoek could move the point closer to the lens, bringing objects in the liquid into focus.

SECTION

4-3

OBJECTIVES

▲
Distinguish between tissues, organs, and organ systems.

●
Describe the features of a colonial organism.

MULTICELLULAR ORGANIZATION

In a unicellular organism, one cell carries out all of the functions of life. In contrast, most cells in a multicellular organism are specialized to perform one or a few functions. Because of cell specialization, the cells of multicellular organisms depend on other cells in the organism for their survival.

TISSUES, ORGANS, AND ORGAN SYSTEMS

In most multicellular organisms, cells are organized into **tissues**, or groups of cells that carry out a specific function. In animals, epithelial tissue consists of sheets of closely packed cells that form surface coverings, such as the outermost living layer of the skin and the inside lining of the nose. The loosely scattered cells of connective tissue serve mainly to support and link together other tissues. Cells that pull against one another by contracting make up muscle tissue. Cells that are specialized for transmitting messages rapidly make up nervous tissue.

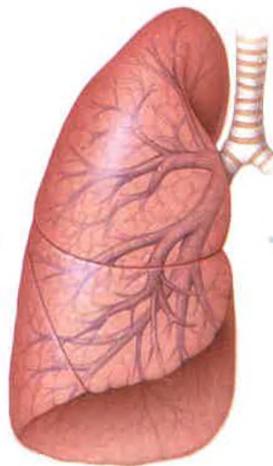
Several types of tissues that interact to perform a specific function form an **organ**. The stomach is one example of an organ. In the

FIGURE 4-18

Spongy tissue makes up the air sacs that in turn make up the lung, which is an organ. The lungs are part of the respiratory system.



TISSUE



ORGAN



ORGAN SYSTEM

stomach, muscle tissue causes movement, epithelial tissue secretes enzymes, connective tissue holds the stomach together, and nervous tissue transmits messages back and forth between the stomach and the brain. All but the simplest animals have organs.

An **organ system** is made up of a group of organs that work together to perform a set of related tasks. For instance, the mouth, esophagus, stomach, intestines, and several other organs make up the digestive system. Each of these organs performs a specific function in the complex process of digesting food. Figure 4-18 illustrates the relationship between tissues and organs in another organ system, the respiratory system.

The different organ systems in a multicellular organism interact to carry out the processes of life. The digestive system, for example, extracts nutrients from food, while the respiratory system obtains oxygen from the environment and eliminates waste carbon dioxide. None of the body's organ systems could survive without the others.

Plants also have tissues and organs, although they are arranged somewhat differently from those in animals. A dermal tissue system forms the outer layer of a plant. A ground tissue system makes up the bulk of roots and stems. A vascular tissue system transports water throughout the plant. The four plant organs are roots, stems, leaves, and flowers.

EVOLUTION OF MULTI-CELLULAR ORGANIZATION

Fossil evidence suggests that the earliest cells on Earth were simple prokaryotes similar to some present-day bacteria. Like most bacteria, they lacked the internal structures required to synthesize their own nutrients. Instead, they depended on organic nutrients in the environment. As they reproduced and their numbers increased, however, they began to compete for limited environmental resources. Because of the increasing competition, cells with adaptations evolved. Some of these cells were eukaryotic. You will learn more about the evolution of prokaryotes and eukaryotes in Chapter 15.

Colonial Organizations

Eventually, some of the early unicellular eukaryotes may have begun to live in temporary groups, or colonies, with other cells of the same kind. Some of the cells in these colonies may have specialized in performing certain functions, such as converting energy. Biologists refer to such associations of cells as **colonial organisms**. A colonial organism is a collection of genetically identical cells that live together in a closely connected group.

An example of a colonial organism that exists today is the green alga *Volvox*, shown in Figure 4-19. A hollow *Volvox* sphere contains

Eco Connection

The Impact of Single Cells

Most people are familiar with the kinds of effects humans and other multicellular organisms can have on their environment. But single-celled organisms can also produce major environmental changes through their activities. One of the most important examples of such a change occurred about 2.8 billion years ago, when certain types of bacteria began producing oxygen as a byproduct of photosynthesis. As oxygen entered the Earth's atmosphere, the composition of the atmosphere changed dramatically. That set the stage for the evolution of animals and other organisms that require oxygen to live.

Even today, unicellular organisms continue to have a profound ecological impact. For example, about half the organic material produced through photosynthesis is made by single-celled eukaryotes known as algae. These simple but important organisms provide food for countless other organisms in marine and freshwater environments.

FIGURE 4-19

New *Volvox* colonies are formed in the interior of older ones and are released when the old colony ruptures. (LM 105×)



500 to 60,000 cells, each of which maintains its own individual existence. Many of the cells, though, carry out specific functions that benefit the whole colony. The outer cells use their flagella to propel the colony through the water. A few of the other cells are specialized for reproduction. They produce offspring colonies, which you can see in Figure 4-19 as the large green spheres contained within the main sphere.

Colonial organisms, such as *Volvox*, appear to straddle the border between a collection of unicellular organisms and a true multicellular organism. Although they lack tissues and organs, they exhibit the principle of cell specialization, which is found in all multicellular organisms. Biologists may be able to learn how multicellular organisms evolved by studying *Volvox* and other colonial organisms.

Many biologists believe that animals, plants, and fungi probably evolved from different varieties of colonial organisms hundreds of millions of years ago. Initially, all of the cells in each type of colony may have been very similar. As these primitive colonial organisms evolved, however, their cells became more specialized and less capable of living independently.

SECTION 4-3 REVIEW

1. What is a tissue?
2. What is an organ?
3. Give an example of an organ system, and name some of the parts that form it.
4. Name the plant tissue systems and organs.
5. To what extent are the individual cells within a *Volvox* colony independent of one another?
6. **CRITICAL THINKING** Green algae, such as *Codium*, enlarge by dividing the nucleus but do not form cell walls between the parent and offspring cells. Would you call *Codium* a unicellular or a multicellular organism? Explain your answer.

CHAPTER 4 REVIEW

SUMMARY/VOCABULARY

- 4-1**
- A cell is the smallest unit that can carry on all of the processes of life. The development of the microscope enabled scientists to take their first close look at cells.
 - The cell theory states that (1) all living things are composed of one or more cells, (2) cells are the units of structure and function in an organism, and (3) cells come only from preexisting cells.

Vocabulary

cell (69)
cell membrane (72)

cell theory (69)
eukaryote (72)

- The ratio of surface area to volume determines how large a cell can get. Most plant and animal cells are only about 10 to 50 μm in diameter.
- A cell's shape reflects its function.
- Eukaryotic cells contain a nucleus and membrane-bound organelles, but prokaryotic cells have neither.

nucleus (72)
organelle (71)

prokaryote (72)

- 4-2**
- The cell membrane is selectively permeable and consists mostly of lipids and proteins. Both move constantly within the membrane, as described by the fluid mosaic model.
 - Mitochondria are organelles in which the energy in organic compounds is transferred to ATP. Mitochondria are surrounded by a double membrane.
 - Ribosomes are involved in the synthesis of proteins. Some ribosomes are free in the cytosol. Others are attached to the rough endoplasmic reticulum, which prepares proteins for export from the cell or insertion into the cell membrane. The smooth endoplasmic reticulum lacks ribosomes.
 - The Golgi apparatus is the cell's processing, packaging, and secreting organelle.
 - Lysosomes contain hydrolytic enzymes that digest organic compounds, old cell parts, and other materials.
 - The cytoskeleton includes microfilaments and microtubules, strands of protein that help cells move and maintain their shape.

Vocabulary

actin (79)
cell wall (82)
chloroplast (83)
chromatin (81)
chromosome (81)
cilium (80)
crista (77)
cytoplasm (75)
cytoskeleton (79)

cytosol (75)
endoplasmic reticulum (78)
flagellum (80)
fluid mosaic model (75)
Golgi apparatus (78)
integral protein (74)
lysosome (79)
microfilament (79)
microtubule (79)

- Cilia and flagella assist in cell movement. Both are made of nine pairs of microtubules arranged around a central pair.
- The nucleus is surrounded by a double membrane and contains chromatin, a combination of DNA and protein. DNA stores hereditary information and directs the synthesis of RNA. RNA directs the synthesis of proteins in the cytosol.
- Plant cells contain three structures not found in animal cells: cell walls, vacuoles, and plastids.
- A rigid cell wall covers the cell membrane in plant cells and provides support and protection.
- Large fluid-filled vacuoles store enzymes and waste products within plant cells.
- Plastids store starch, fats, and pigments in plant cells. One type of plastid, the chloroplast, is the site where light energy is converted into chemical energy during photosynthesis.

mitochondrion (76)
nuclear envelope (81)
nuclear matrix (81)
nuclear pore (81)
nucleolus (81)
peripheral protein (74)
plastid (83)
ribosome (77)

rough endoplasmic reticulum (78)
selectively permeable membrane (73)
smooth endoplasmic reticulum (78)
spindle fiber (79)
thylakoid (83)
vacuole (82)

- 4-3** ■ The cells in most multicellular organisms are organized into tissues, organs, and organ systems.
- The earliest cells on Earth were probably single-celled prokaryotes. Unicellular eukaryotes evolved later, followed by multicellular organisms.

Vocabulary

colonial organism (87)

organ (86)

- A colonial organism is a group of genetically identical cells that live together in closely connected groups. Some of the cells that make up a colonial organism are specialized to perform certain tasks, like movement or reproduction.

organ system (87)

tissue (86)

REVIEW

Vocabulary

- The word part *eu-* means “true,” *pro-* means “before,” and *kary-* means “nucleus.” With this information, explain why the words *prokaryote* and *eukaryote* are good terms for the organisms they describe. What do the terms suggest about the evolution of these organisms?
- Compare cell membranes with cell walls in terms of their structure and function.
- Explain the meaning of the terms *cytoplasm*, *cytosol*, and *cytoskeleton*.
- Explain the relationship between microtubules, cilia, and flagella.
- Choose the term that does not belong in the following group, and explain why it does not belong: Golgi apparatus, endoplasmic reticulum, chromatin, and mitochondria.

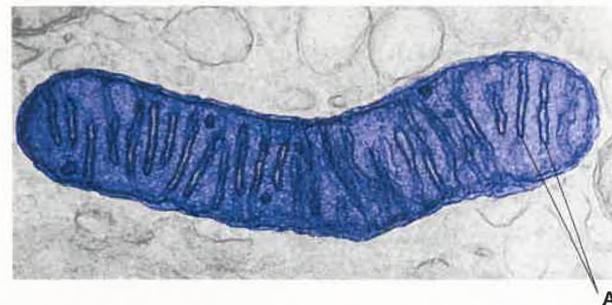
Multiple Choice

- A prokaryote has (a) a nucleus (b) a cell membrane (c) membrane-bound organelles (d) all of the above.
- The growth of cells is limited by the ratio between (a) volume and surface area (b) organelles and surface area (c) organelles and cytoplasm (d) nucleus and cytoplasm.
- The major components of cell membranes are (a) lipids (b) proteins (c) nucleic acids (d) lipids and proteins.
- The function of the Golgi apparatus is to (a) synthesize proteins (b) release energy (c) modify proteins for export (d) synthesize lipids.

- Mitochondria (a) transport materials (b) release energy (c) make proteins (d) control cell division.
- Ribosomes are (a) surrounded by a double membrane (b) manufactured in the cytosol (c) composed of proteins and RNA (d) attached to the smooth endoplasmic reticulum.
- Lysosomes function in cells to (a) recycle cell parts (b) destroy viruses and bacteria (c) shape developing body parts (d) all of the above.
- The nucleolus is (a) the control center of the cell (b) the storehouse of genetic information (c) the site where ribosomes are synthesized (d) none of the above.
- Plastids (a) store pigments (b) store membranes (c) synthesize proteins (d) secrete proteins.
- The stomach is an example of (a) a tissue (b) an organ (c) an organ system (d) none of the above.

Short Answer

- Explain how microscopes have been helpful in the study of cells.
- Identify the organelle illustrated in the micrograph below, and name the structures labeled *A* inside the organelle. Explain the significance of the shape of these structures.

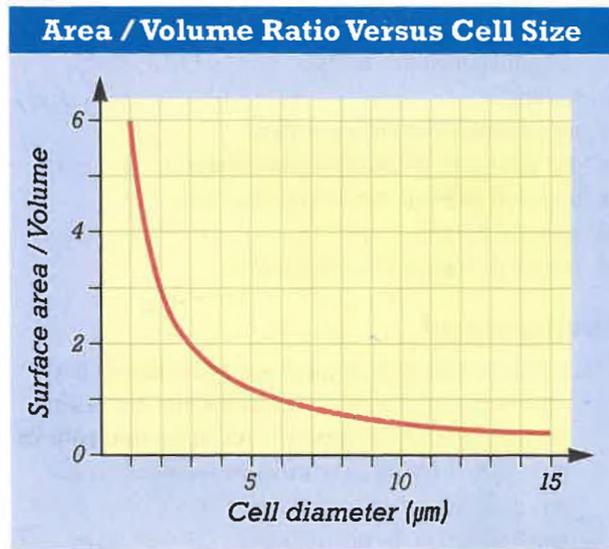


18. What limits the maximum size of cells? Explain your answer.
19. How is the structure of cell membranes influenced by the reaction of phospholipids to water?
20. Why is the cell membrane said to be selectively permeable?
21. If a cell has a high energy requirement, would you expect it to have many or few mitochondria? Explain your answer.
22. Explain how the ribosomes, endoplasmic reticulum, and Golgi apparatus function together in protein synthesis.
23. **Unit 1—Cell Transport and Homeostasis**
 Write a report summarizing the roles of different types of cell-membrane proteins in the preservation of body organs donated for transplant.

CRITICAL THINKING

1. A mature human red blood cell has no nucleus or mitochondria. It consists primarily of a membrane surrounding hemoglobin, the protein molecule that carries oxygen. Suggest an advantage of the simple organization of human red blood cells.
2. The coils of a radiator provide a large surface area from which heat is radiated into a room. Which cell organelles have a structure similar to that of a radiator? How is their

- structure related to their function?
3. What characteristic of eukaryotic cells gives them a greater capacity for specialization than prokaryotic cells have? Explain your answer.
4. Livestock in the western United States often die after eating a locoweed, such as *Astragalus toanus*. The chemical that the plant contains is also poisonous to plants. How does locoweed keep from poisoning itself?
5. The graph below illustrates how the ratio between surface area and volume changes as a spherical cell's diameter increases. By what percentage does this ratio change when a cell grows from 1 μm to 2 μm in diameter? What is the maximum diameter the cell could



EXTENSION

1. Read "The Nobel Prizes for 1999" in *Scientific American*, January 2000, on page 16. Prepare an oral report on how Günter Blobel, a scientist at Rockefeller University, won the Nobel Prize for Physiology or Medicine.
2. Use the resources in your school or public library to learn more about the work of Schleiden, Schwann, or Virchow. Write a brief report summarizing the processes that the researcher used to arrive at his conclusions about cells.
3. Place a sprig of the aquarium plant *Elodea* in water, and shine a bright light on it for an hour. Then examine a leaf under a light microscope, and make a drawing that indicates the direction of chloroplast movement. How do you think the movement of these organelles in response to light helps the cell to function?

CHAPTER 4 INVESTIGATION

Comparing Animal and Plant Cells

OBJECTIVE

- Examine the similarities and differences between the structure of cells in animals and the structure of cells in plants.

PROCESS SKILLS

- hypothesizing
- classifying
- observing

MATERIALS

- lab apron
- safety goggles
- compound light microscope
- forceps
- microscope slides and coverslips
- dropper bottle of Lugol's iodine solution
- prepared slides of human epithelial cells
- sprigs of *Elodea*
- prepared slides of three unknowns

Background

1. In this investigation, you will use a compound light microscope to observe cells from animals and plants. First you will view a prepared slide of human epithelial cells taken from the skin lining the mouth. Then you will make your own slide of a leaf from *Elodea*, a pond weed shown in the photograph on the next page.



2. Based on your observations of human epithelial cells and *Elodea* leaf cells, you will be asked to classify three slides of unknown cells as either animal or plant cells.
3. Before you examine any cells, list the structural characteristics that distinguish animal cells from plant cells.

PART A Animal Cells

1.  **CAUTION** Handle glass microscope slides carefully. Dispose of broken glass separately in a container designated by your teacher.
2.  **CAUTION** Do not use electrical equipment with wet hands or near water.
3. Examine a prepared slide of epithelial cells under low power. Locate cells that are separate from each other and place them in the center of the field of view. Examine the cells under high power. Adjust the diaphragm to reduce the light intensity and achieve greater clarity.
4. In your lab report, make a drawing of two or three cells as they appear under high power. Identify and label the cell membrane, the cytoplasm, the nuclear envelope, and the nucleus of one of the cells in your drawing.

PART B Plant Cells

5. Carefully tear off a small leaf near the top of an *Elodea* sprig. Using forceps, place the whole leaf in a drop of water on a slide. Place a coverslip on top of the leaf.
6. Observe the leaf under low power. The outermost part of the cell is the cell wall. The many small, green organelles in the cells are chloroplasts.
7. Locate a cell that you can see clearly, and move the slide so that the cell is in the center of the field of view. Examine this cell under high power, and use the fine adjustment to bring the cell into focus.
8. Find an *Elodea* cell that is large enough to allow you to see the cell wall and the chloroplasts clearly. In your lab report, make a drawing of this cell. Label the cell wall and at least one chloroplast in your drawing.



9. The chloroplasts may be moving in some of the cells. If you observe no movement, warm the slide in your hand or shine a bright lamp on it for a minute or two. Then reexamine the slide under high power, and look for the movement of the cell's contents. This movement is called cytoplasmic streaming.
10. Because the cell membrane is pressed against the cell wall, you may not see it. Also, the abundance of chloroplasts may hide other organelles in the cells. You can make the cell membrane, vacuole, nucleus, and nucleolus more visible by making a stained wet-mount slide of *Elodea*.
11.  Put on a lab apron and safety goggles. Prepare a wet-mount slide of *Elodea* as you did in step 4, but substitute Lugol's iodine solution for the water. Allow the iodine solution to diffuse throughout the leaf.

12. Observe the stained cells under low and high power. Make a drawing of a stained *Elodea* cell in your lab report. Label the central vacuole, nucleus, nucleolus, chloroplasts, cell wall, and cell membrane if they are visible.

PART C Identifying Unknown Cells

13. Make a data table like the one below to record your observations of the unknown specimens.
14. Obtain prepared slides of three unknown specimens from your teacher.
15. Observe each specimen under low and high power. In your data table, record the code number assigned to each unknown, each specimen's classification as plant or animal, and your reasons for classifying each specimen.
16.  Clean up your materials and wash your hands before leaving the lab.

Analysis and Conclusions

- According to your observations in this investigation, list several ways that plant and animal cells are structurally similar and several ways that they are different.
- What do you think might be the function of cytoplasmic streaming in a plant cell? Lugol's iodine solution causes cytoplasmic streaming to stop. Why do you think this happens?
- Which organelles that you read about in Chapter 4 did you not see in this investigation? Why do you think you were unable to see these organelles in your slides?

Further Inquiry

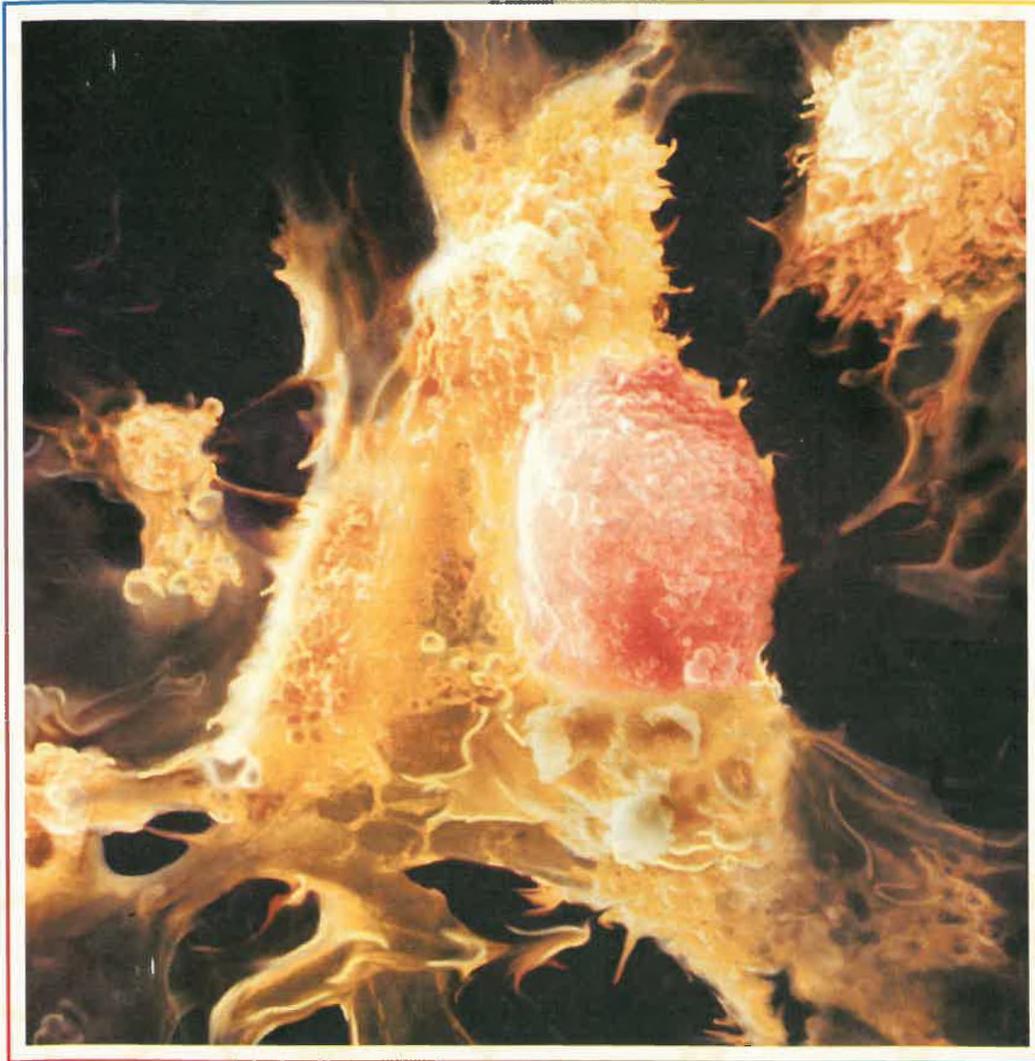
Use library resources to locate electron micrographs of cell structures that you were unable to see with the compound light microscope.

CLASSIFICATION OF UNKNOWN SPECIMENS

Unknown (code number)	Classification (plant or animal)	Reasons for classification

CHAPTER 5

HOMEOSTASIS AND TRANSPORT



A macrophage engulfs a human tumor cell. (SEM 3,520 \times)

FOCUS CONCEPT: *Stability and Homeostasis*

As you read, look for the ways that cells regulate the movement of materials across their membranes and thereby maintain internal balance despite changes in their environment.



Unit 1—*Cell Transport
and Homeostasis*
Topics 3–6

5-1 *Passive Transport*

5-2 *Active Transport*

SECTION

5-1

OBJECTIVES

▲ Explain how an equilibrium is established as a result of diffusion.

● Distinguish between diffusion and osmosis.

■ Explain how substances cross the cell membrane through facilitated diffusion.

◆ Explain how ion channels assist the diffusion of ions across the cell membrane.

PASSIVE TRANSPORT

Cell membranes help organisms maintain homeostasis by controlling what substances may enter or leave cells. Some substances can cross the cell membrane without any input of energy by the cell. The movement of such substances across the membrane is known as **passive transport**.

DIFFUSION

The simplest type of passive transport is diffusion. **Diffusion** is the movement of molecules from an area of higher concentration to an area of lower concentration. This difference in the concentration of molecules across a space is called a **concentration gradient**.

Consider what happens when you add a sugar cube to a beaker of water. As shown in Figure 5-1, the sugar cube sinks to the bottom of the beaker. That makes the concentration of sugar molecules much greater at the bottom of the beaker than at the top. As the cube dissolves, the sugar molecules begin to diffuse slowly through the water, moving from the bottom of the beaker to the top.

Diffusion is driven entirely by the kinetic energy the molecules possess. Because of their kinetic energy, molecules are in constant motion. They move randomly, traveling in a straight line until they hit an object, such as another molecule. When they hit something, they rebound and move off in a new direction, traveling in another straight line. If no object blocks their movement, they continue on their path. Thus, molecules tend to move “down” their concentration gradient, from areas where they are more concentrated to areas where they are less concentrated.

Equilibrium

In the absence of other influences, diffusion will eventually cause the concentration of molecules to be the same throughout the space the molecules occupy. When the concentration of the molecules of a substance is the same throughout a space, a state of **equilibrium** exists. Returning to the example in Figure 5-1, if the beaker of water is left undisturbed, at some point the concentration of sugar molecules will be the same throughout the beaker. The sugar concentration will then be at equilibrium.



FIGURE 5-1

Sugar molecules, initially in a high concentration at the bottom of a beaker, will move about randomly through diffusion. At equilibrium, the sugar concentration will be the same throughout the beaker. Diffusion occurs naturally because of the kinetic energy the molecules possess.



Quick Lab

Observing Diffusion

Materials disposable gloves, lab apron, safety goggles, 600 mL beaker, 25 cm dialysis tubing, 15 mL starch solution (10 percent), 20 drops IKI, 300 mL water, 100 mL graduated cylinder, 20 cm piece of string (2)

Procedure



1. Put on your disposable gloves, lab apron, and safety goggles.
2. Pour 300 mL of water in the 600 mL beaker.
3. Add 20 drops of IKI to the water.
4. Open the dialysis tubing, and tie one end tightly with a piece of string.
5. Using the funnel, pour 15 mL of 10 percent starch solution into the dialysis tubing.
6. Tie the other end of the dialysis tubing tightly with the second piece of string, forming a sealed bag around the starch solution.
7. Place the bag into the solution in the beaker, and observe the setup for a color change.

Analysis What happened to the color in the bag? What happened to the color of the water around the bag? Explain your observations.

It is important to understand that even at equilibrium the random movement of molecules continues. But because there is no concentration gradient, molecules are just as likely to move in one direction as in any other. The random movements of many molecules in many directions balance one another, and equilibrium is maintained.

Diffusion Across Membranes

You learned in Chapter 4 that cell membranes allow some molecules to pass through, but not others. If a molecule can pass through a cell membrane, it will diffuse from an area of higher concentration on one side of the membrane to an area of lower concentration on the other side.

The ability of a molecule to diffuse across a cell membrane depends on the size and type of the molecule and on the chemical nature of the membrane. Remember from Chapter 4 that a membrane is made, in part, of a lipid bilayer and that certain proteins can form pores in the membrane. Molecules that can dissolve in lipids may pass through the membrane by diffusion. For example, because of their nonpolar nature, both carbon dioxide and oxygen dissolve in lipids. Molecules that are very small but not soluble in lipids may diffuse across the membrane by moving through the pores in the membrane.

OSMOSIS

Recall from Chapter 2 that a solution is composed of a solute dissolved in a solvent. In the sugar water described earlier, the solute was sugar and the solvent was water, and the solute molecules diffused through the solvent. It is also possible for solvent molecules to diffuse. In the case of cells, the solutes are organic and inorganic compounds, and the solvent is water. The process by which water molecules diffuse across a cell membrane from an area of higher concentration to an area of lower concentration is called **osmosis** (ahz-MOH-suhs). Because water moves down its concentration gradient, osmosis does not require cells to expend energy. Osmosis, therefore, is a type of passive transport.

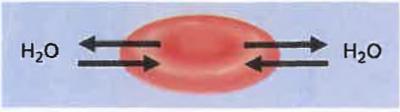
Direction of Osmosis

The net direction of osmosis depends on the relative concentration of solutes on the two sides of the membrane. Examine Table 5-1. When the concentration of solute molecules outside the cell is *lower* than the concentration in the cytosol, the solution outside is **hypotonic** to the cytosol. In this situation, water diffuses *into* the cell until equilibrium is established. When the concentration of solute molecules outside the cell is *higher* than the concentration in the cytosol, the solution outside is **hypertonic** to the cytosol. In this situation, water diffuses *out of* the cell until equilibrium is established. When the concentrations of solutes outside and inside

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NSTA

TOPIC: Osmosis
GO TO: www.scilinks.org
KEYWORD: HM096

Condition	Net movement of water
External solution is hypotonic to cytosol	into the cell 
External solution is hypertonic to cytosol	out of the cell 
External solution is isotonic to cytosol	none 

the cell are equal, the outside solution is said to be **isotonic** to the cytosol. Under these conditions, water diffuses into and out of the cell at equal rates, so there is no net movement of water.

Notice that the prefixes *hypo-*, *hyper-*, and *iso-* refer to the relative solute concentrations of two solutions. Thus, if the solution outside the cell is *hypotonic* to the cytosol, then the cytosol must be *hypertonic* to that solution. Conversely, if the solution outside is *hypertonic* to the cytosol, then the cytosol must be *hypotonic* to the solution. Water tends to diffuse from hypotonic solutions to hypertonic solutions.

How Cells Deal with Osmosis

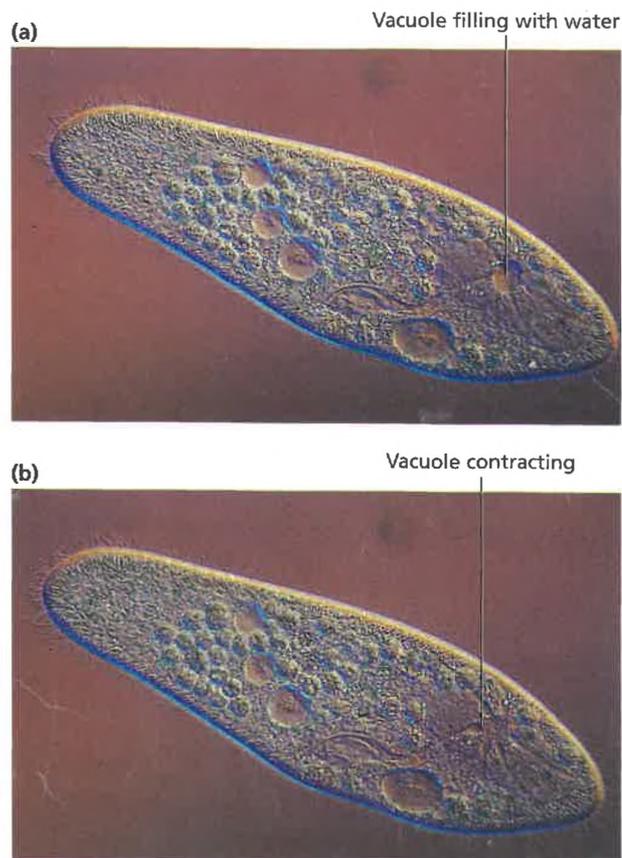
Cells that are exposed to an isotonic external environment usually have no difficulty keeping the movement of water across the cell membrane in balance. This is the case with the cells of vertebrate animals on land and of most other organisms living in the sea.

In contrast, many cells function in a hypotonic environment. Such is the case for unicellular freshwater organisms. Water constantly diffuses into these organisms. Because they require a relatively lower concentration of water in the cytosol to function normally, unicellular organisms must rid themselves of the excess water that enters by osmosis. Some of them, such as the paramecia shown in Figure 5-2, do this with **contractile vacuoles**, which are organelles that remove water. Contractile vacuoles collect the excess water and then contract, pumping the water out of the cell. Unlike diffusion and osmosis, this pumping action requires the cell to expend energy.

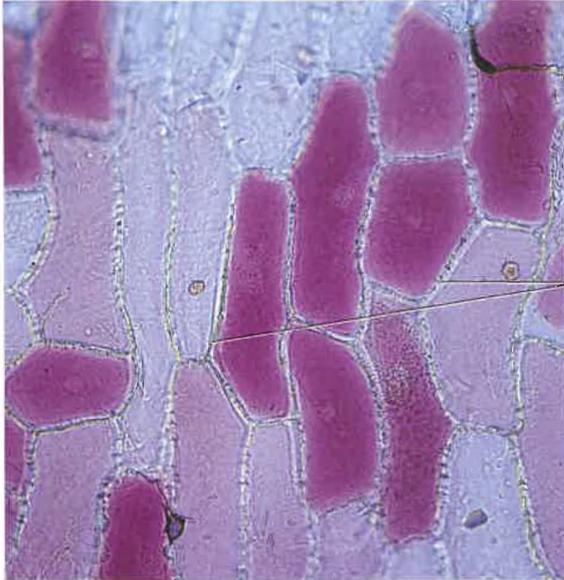
Other cells, including many of those in multicellular organisms, respond to hypotonic environments by pumping solutes out of the cytosol. This

FIGURE 5-2

The paramecia shown below live in fresh water, which is hypotonic to their cytosol. (a) Contractile vacuoles collect excess water that moves by osmosis into the cytosol. (b) The vacuoles then contract, returning the water to the outside of the cell. (LM 315 \times)



(a) Hypotonic



(b) Hypertonic



Cell walls

FIGURE 5-3

These two photographs show cells in the skin of a red onion. (a) In a hypotonic environment, the cells are pressed against the cell walls (LM 90 \times). (b) In a hypertonic environment, the cells contract and pull away from the cell walls (LM 98 \times).

lowers the solute concentration in the cytosol, bringing it closer to the solute concentration in the environment. As a result, water molecules are less likely to diffuse into the cell.

Most of the time, plant cells also live in a hypotonic environment. In fact, the cells that make up plant roots may be surrounded by water. Water, therefore, moves by osmosis into plant cells, which swell as they fill with water. The swelling stops when the cell membrane is pressed against the inside of the cell wall, as Figure 5-3a shows. The cell wall is strong enough to resist the pressure exerted by the water inside the expanding cell. The pressure that water molecules exert against the cell wall is called **turgor pressure**.

In a hypertonic environment, water leaves the cells through osmosis. As shown in Figure 5-3b, the cells shrink away from the cell walls, and turgor pressure is lost. This condition is called **plasmolysis** (plaz-MAHL-uh-suhs). Plasmolysis is the reason that plants wilt if they don't receive enough water.

Some cells cannot compensate for changes in the solute concentration of their environment. Red blood cells in humans, for instance, lack contractile vacuoles, solute pumps, and cell walls. As you can see in Figure 5-4, these cells lose their normal shape when they are placed in an environment that is not isotonic to their

FIGURE 5-4

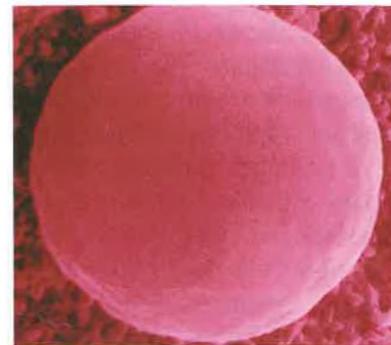
(a) In an environment that is isotonic to the cytosol, a human red blood cell keeps its normal shape—round and dimpled (SEM 37,125 \times). (b) In a hypertonic environment, the cell loses water and becomes shriveled (SEM 39,762 \times). (c) In a hypotonic environment, the cell gains water and swells (SEM 37,125 \times).



(a) Isotonic



(b) Hypertonic



(c) Hypotonic

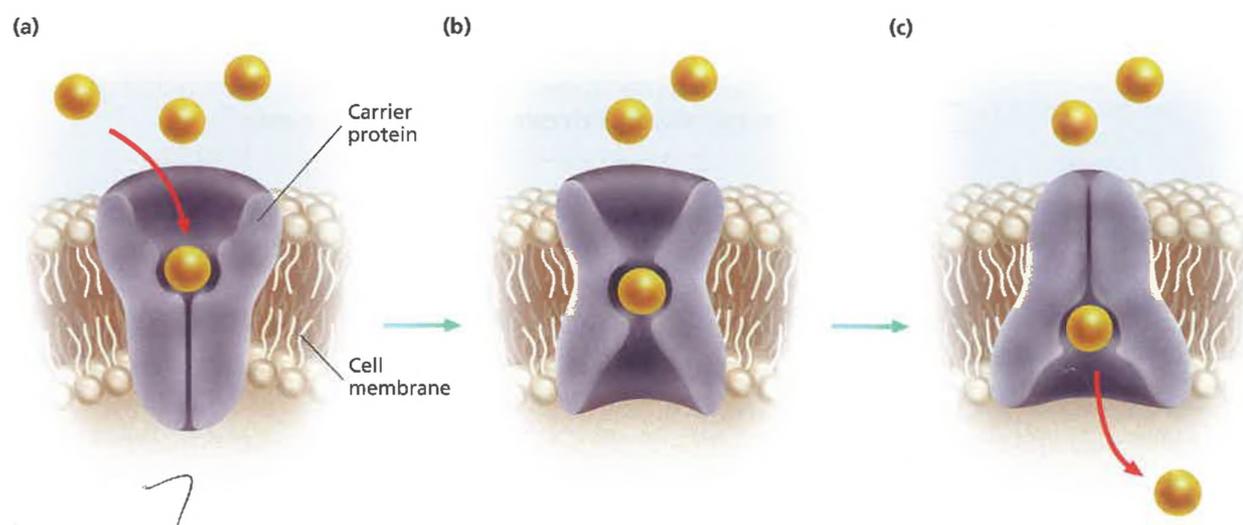
cytosol. In a hypertonic environment, water leaves the cells, making them shrink and shrivel. In a hypotonic environment, water diffuses into the cells, causing them to swell and eventually burst. The bursting of cells is called **cytolysis** (sie-TAHL-uh-suh).

FACILITATED DIFFUSION

Another type of passive transport is called **facilitated diffusion**. This process is used for molecules that cannot diffuse rapidly through cell membranes, even when there is a concentration gradient across the membrane. Such molecules may not be soluble in lipids, or they may be too large to pass through the pores in the membrane. In facilitated diffusion, the movement of these kinds of molecules across the cell membrane is assisted by specific proteins in the membrane. These proteins are known as **carrier proteins**.

The carrier proteins that serve in facilitated diffusion transport molecules from an area of higher concentration on one side of the membrane to an area of lower concentration on the other side. Because the molecules are moving down their concentration gradient, facilitated diffusion is passive transport. The cell does not have to supply additional energy to make it happen.

Figure 5-5 shows a model of how facilitated diffusion is thought to work. According to the model, a carrier protein binds to the molecule it transports. As soon as the carrier protein binds to the molecule, the carrier protein changes shape. This altered shape may shield the molecule from the hydrophobic interior of the lipid bilayer. Once shielded, the molecule can be transported across the cell membrane. On the other side of the membrane, the molecule is released from the carrier protein, which then returns to its original shape.



Word Origins

cytolysis

from the Greek *kytos*, meaning "hollow vessel," and *lysis*, meaning "loosening"

FIGURE 5-5

Facilitated diffusion occurs in three steps. (a) A carrier protein binds to a molecule on one side of the cell membrane. (b) The carrier protein changes shape, shielding the molecule from the interior of the membrane. (c) The molecule is released on the other side of the membrane.

Eco

Purifying Water with Membranes

The tendency for water molecules to diffuse across membranes can be used to extract pure water from a mixture of water and solutes. If a dilute solution is separated from a more concentrated solution by a selectively permeable membrane, osmosis will occur, as water molecules diffuse from the dilute solution to the concentrated solution. However, if enough external pressure is applied to the concentrated solution, the opposite will happen: water molecules will diffuse from the concentrated solution to the dilute solution. This process, called reverse osmosis, effectively moves most of the water to one side of the membrane and leaves most of the solutes on the other side.

Reverse osmosis was initially developed for desalination plants, which produce fresh water from sea water. It is now also used to purify polluted water from a variety of sources, including manufacturing facilities and sanitary landfills. After the polluted water from these sources is purified through reverse osmosis, it is clean enough to be returned safely to the environment.

A good example of facilitated diffusion is the transport of glucose. As you learned in Chapter 3, many cells depend on glucose for much of their energy needs. But glucose molecules are too large to diffuse quickly across cell membranes. When the level of glucose within a cell is lower than the level of glucose outside the cell, carrier proteins accelerate the movement of glucose into the cell.

The transport of glucose illustrates two important properties of facilitated diffusion. First, facilitated diffusion can help substances move either into or out of a cell, depending on the concentration gradient. Thus, when the level of glucose is higher inside a cell than it is outside the cell, facilitated diffusion speeds the diffusion of glucose out of the cell. Second, the carrier proteins involved in facilitated diffusion are each specific for one type of molecule. For example, the carrier protein that helps with the diffusion of glucose and other simple sugars does not assist with the diffusion of amino acids.

DIFFUSION THROUGH ION CHANNELS

Another type of passive transport involves membrane proteins known as **ion channels**. Ions such as sodium (Na^+), potassium (K^+), calcium (Ca^{2+}), and chloride (Cl^-) are important for a variety of cell functions. Because they are not soluble in lipids, however, ions cannot diffuse across the lipid bilayer without assistance. Ion channels provide small passageways across the cell membrane through which ions can diffuse. Each type of ion channel is usually specific for one type of ion. Thus, most Na^+ ion channels will allow Na^+ ions to pass through them, but they will not accept Ca^{2+} or Cl^- ions.

Some ion channels are always open. Others have “gates” that open to allow ions to pass or close to stop their passage. The gates may open or close in response to three kinds of stimuli: stretching of the cell membrane, electrical signals, or chemicals in the cytosol or external environment. These stimuli therefore control the ability of specific ions to cross the cell membrane.

SECTION 5-1 REVIEW

1. Toward what condition does diffusion eventually lead, in the absence of other influences?
2. How is osmosis related to diffusion?
3. If the concentration of solute molecules outside a cell is lower than the concentration in the cytosol, is the external solution hypotonic, hypertonic, or isotonic to the cytosol?
4. What role do carrier proteins play in facilitated diffusion?
5. How is facilitated diffusion similar to diffusion through ion channels?
6. **CRITICAL THINKING** Sea water has a higher concentration of solutes than do human body cells. Why might drinking large amounts of sea water be dangerous for humans?

SECTION

5-2

OBJECTIVES

▲
Distinguish between passive transport and active transport.

●
Explain how the sodium-potassium pump operates.

■
Compare and contrast endocytosis and exocytosis.

ACTIVE TRANSPORT

*In many cases, cells must move materials up their concentration gradient, from an area of lower concentration to an area of higher concentration. Such movement of materials is known as **active transport**. Unlike passive transport, active transport requires a cell to expend energy.*

CELL MEMBRANE PUMPS

Carrier proteins not only assist in passive transport but also help with some types of active transport. The carrier proteins that serve in active transport are often called cell membrane “pumps” because they move substances up their concentration gradients. In other respects, the carrier proteins involved in facilitated diffusion and those involved in active transport are very similar. In both, the protein first binds to a specific kind of molecule on one side of the cell membrane. Once it is bound to the molecule, the protein changes shape, shielding the molecule from the hydrophobic interior of the lipid bilayer. The protein then transports the molecule across the membrane and releases it on the other side.

Sodium-Potassium Pump

One example of active transport in animal cells involves a carrier protein known as the **sodium-potassium pump**. As its name suggests, this protein transports Na^+ ions and K^+ ions up their concentration gradients. To function normally, many types of animal cells must have a higher concentration of Na^+ ions outside the cell and a higher concentration of K^+ ions inside the cell. The sodium-potassium pump works to maintain these concentration differences.

Follow the steps in Figure 5-6 to see how the sodium-potassium pump operates. First, three Na^+ ions bind to the carrier protein on the cytosol side of the membrane, as shown in Figure 5-6a. At the same time, the carrier protein splits a phosphate group from a molecule of ATP. As you can see in Figure 5-6b, the phosphate group also binds to the carrier protein. Figure 5-6c shows how the splitting of ATP supplies the energy needed to change the shape of the carrier protein. With its new shape, the protein carries the three Na^+ ions across the membrane and then releases them outside the cell.

At this point, the carrier protein has the shape it needs to bind two K^+ ions outside the cell, as Figure 5-6d shows. When the K^+ ions bind, the phosphate group is released, as indicated in Figure 5-6e, and the carrier protein changes shape again. This time, the change

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TOPIC: Active transport
GO TO: www.scilinks.org
KEYWORD: HM101

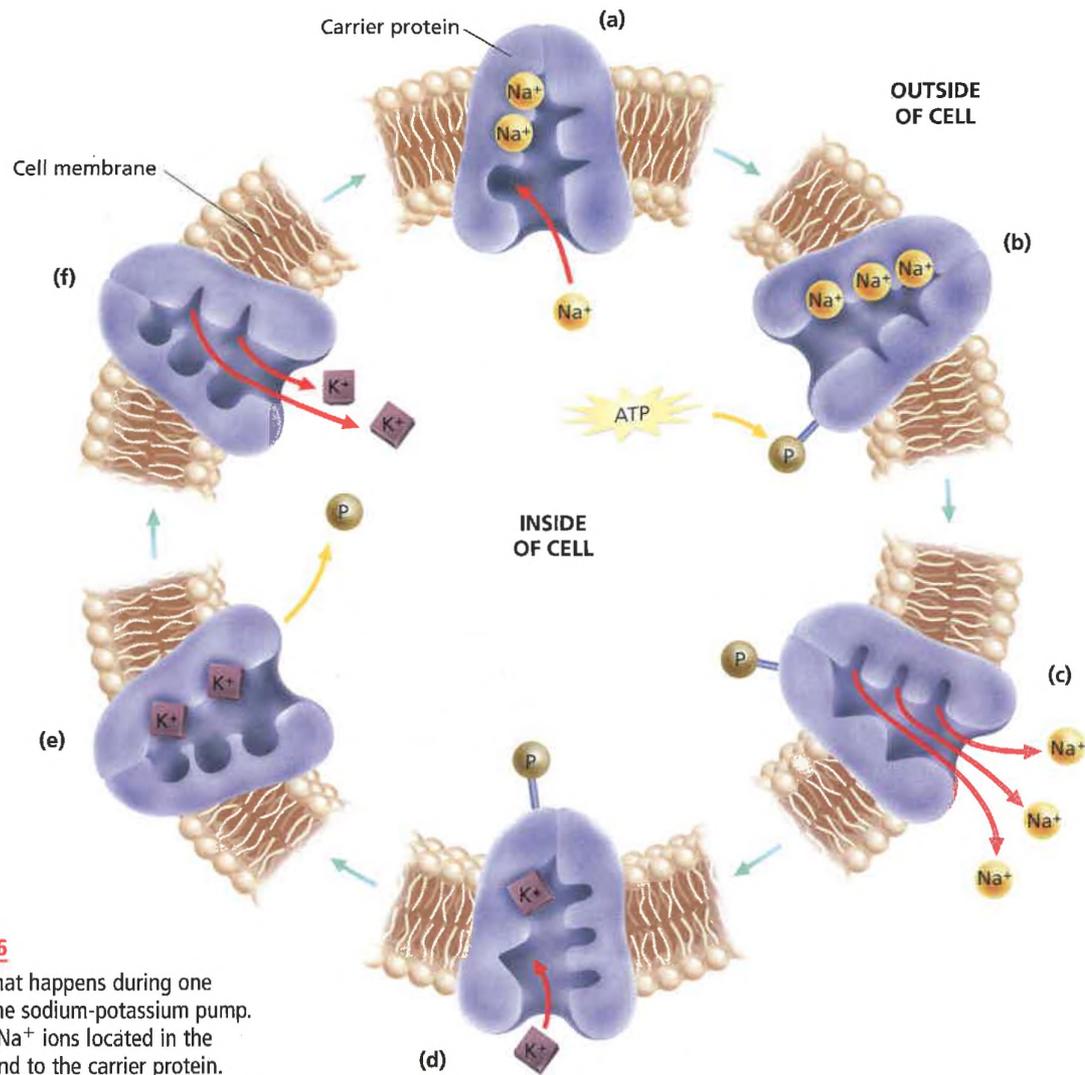


FIGURE 5-6

Follow what happens during one cycle of the sodium-potassium pump. (a) Three Na^+ ions located in the cytosol bind to the carrier protein. (b) A phosphate group, represented by the letter P in the diagram, is removed from ATP and bound to the carrier protein. (c) The binding of the phosphate group changes the shape of the carrier protein, allowing the three Na^+ ions to be released into the cell's environment. (d) Two K^+ ions located outside the cell bind to the carrier protein. (e) The phosphate group is released, changing the shape of the carrier protein again. (f) The two K^+ ions are released into the cytosol, and the cycle is ready to repeat.

in shape causes the carrier protein to release the two K^+ ions inside the cell. As you can see in Figure 5-6f, at this point the carrier protein is ready to begin the process again. Thus, a complete cycle of the sodium-potassium pump transports three Na^+ ions outside the cell and two K^+ ions inside the cell. At top speed, the sodium-potassium pump can transport about 450 Na^+ ions and 300 K^+ ions per second.

The exchange of three Na^+ ions for two K^+ ions creates an electrical gradient across the cell membrane. That is, the outside of the membrane becomes positively charged and the inside of the membrane becomes negatively charged. In this way, the two sides of the cell membrane are like the positive and negative terminals of a battery. This difference in charge is important for the conduction of electrical impulses along nerve cells, as you will learn in Chapter 50. The sodium-potassium pump is only one example of a cell membrane pump. Other pumps work in similar ways to transport important metabolic materials across cell membranes.

ENDOCYTOSIS AND EXOCYTOSIS

Some substances, such as macromolecules and food particles, are too large to pass through the cell membrane by the transport processes you have studied so far. Cells employ two other transport mechanisms—endocytosis and exocytosis—to move such substances across their membranes. Endocytosis and exocytosis are also used to transport large quantities of small molecules into or out of cells at a single time. Both endocytosis and exocytosis require cells to expend energy. Therefore, they are types of active transport.

Endocytosis

Endocytosis (EN-doh-sie-TOH-suhs) is the process by which cells ingest external fluid, macromolecules, and large particles, including other cells. As you can see in Figure 5-7, these external materials are enclosed by a portion of the cell, which folds into itself and forms a pouch. The pouch then pinches off from the cell membrane and becomes a membrane-bound organelle called a **vesicle**. Some of the vesicles fuse with lysosomes, and their contents are digested by lysosomal enzymes. Other vesicles that form during endocytosis fuse with other membrane-bound organelles.

Biologists distinguish two types of endocytosis, based on the kind of material that is taken into the cell: **pinocytosis** (PIN-oh-sie-TOH-suhs) involves the transport of solutes or fluids, while **phagocytosis** (FAG-oh-sie-TOH-suhs) is the movement of large particles or whole cells. Many unicellular organisms feed by phagocytosis. In addition, certain cells in animals use phagocytosis to ingest bacteria and viruses that

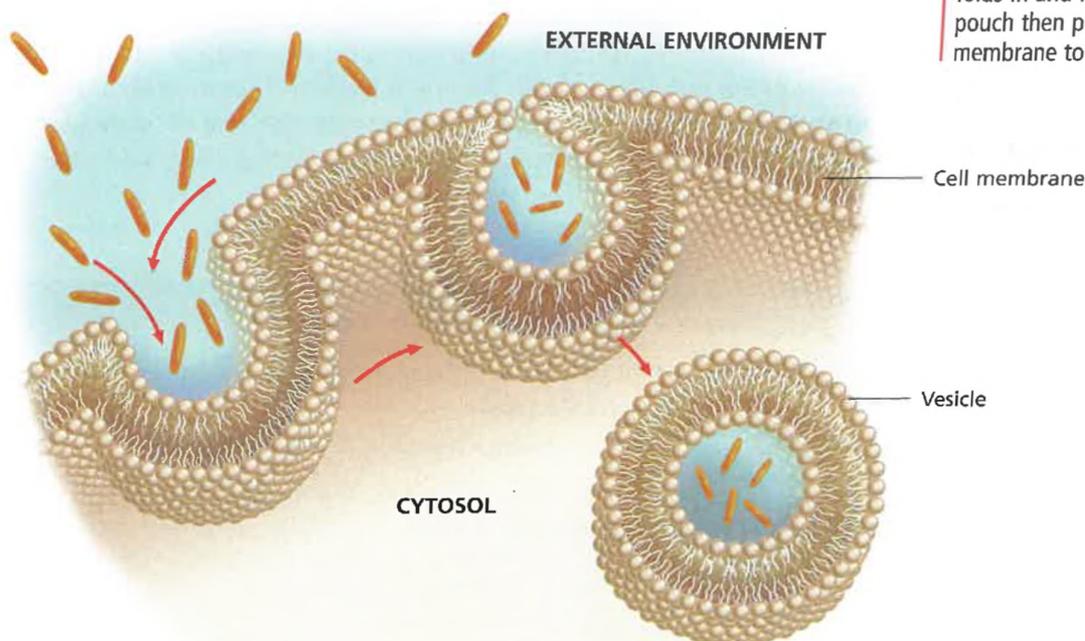


FIGURE 5-7

During endocytosis, the cell membrane folds in and forms a small pouch. The pouch then pinches off from the cell membrane to become a vesicle.

FIGURE 5-8

During exocytosis, a vesicle moves to the cell membrane, fuses with it, and then releases its contents to the outside of the cell.

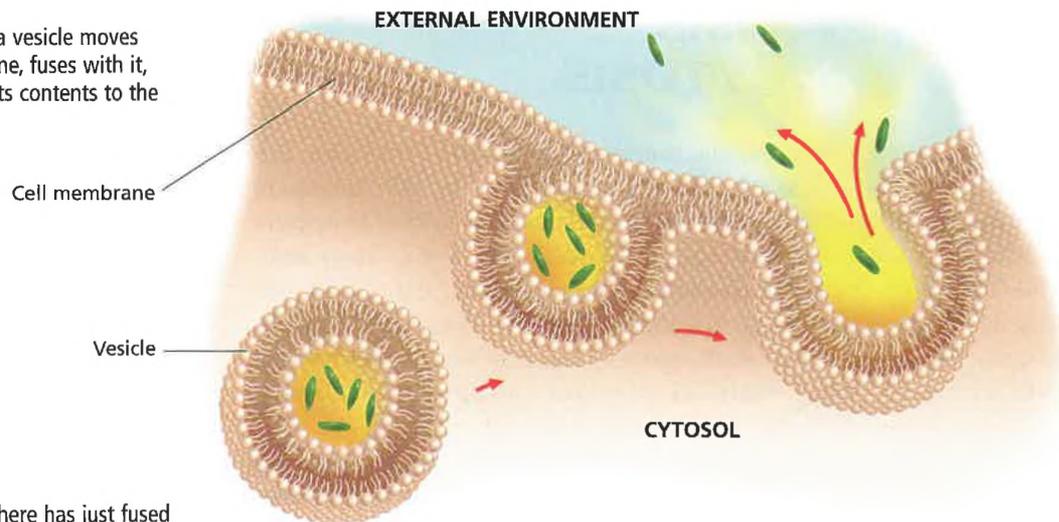
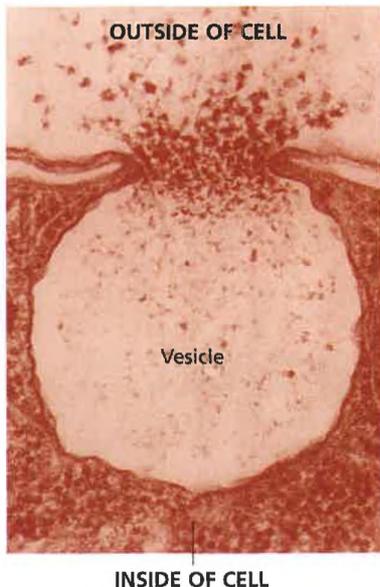


FIGURE 5-9

The vesicle shown here has just fused with the cell membrane, and the vesicle's contents are entering the external environment of the cell. (TEM, 71,250)



invade the body. These cells, known as **phagocytes**, allow lysosomes to fuse with the vesicles that contain the ingested bacteria and viruses. Lysosomal enzymes then destroy the bacteria and viruses before they can harm the animal.

Exocytosis

Exocytosis (EK-soh-sie-TOH-suhs), illustrated in Figure 5-8, is essentially the reverse of endocytosis. During exocytosis, vesicles in the cytoplasm fuse with the cell membrane, releasing their contents into the cell's external environment. Figure 5-9 shows a vesicle in the process of exocytosis. Cells may use exocytosis to release large molecules such as proteins. Recall that proteins are made on ribosomes and packaged into vesicles by the Golgi apparatus. The vesicles then move to the cell membrane and fuse with it, delivering the proteins outside the cell. As you'll learn in Chapters 50 and 51, cells in the nervous and endocrine systems also use exocytosis to release small molecules that control the activities of other cells.

SECTION 5-2 REVIEW

1. Explain the difference between passive transport and active transport.
2. What function do carrier proteins perform in active transport?
3. What provides the energy that drives the sodium-potassium pump? **ATP**
4. Explain the difference between pinocytosis and phagocytosis.
5. Describe the steps involved in exocytosis.
6. **CRITICAL THINKING** During intense exercise, potassium tends to accumulate in the fluid surrounding muscle cells. What membrane protein helps muscle cells counteract this tendency? Explain your answer.

CHAPTER 5 REVIEW

SUMMARY/VOCABULARY

- 5-1**
- Passive transport involves the movement of molecules across the cell membrane without an input of energy by the cell.
 - Diffusion is the movement of molecules from an area of higher concentration to an area of lower concentration, driven by the molecules' kinetic energy. It eventually leads to equilibrium, a condition in which the concentration of the molecules is the same throughout a space or on both sides of a membrane.
 - Molecules can diffuse across a cell membrane by dissolving in the lipid bilayer or by passing through pores in the membrane.
 - Osmosis is the diffusion of water across a membrane. The net direction of osmosis is determined by the relative solute concentrations on the two sides of the membrane.
 - When the solute concentration outside the cell is lower than that in the cytosol, the solution outside is hypotonic to the cytosol, and water will diffuse into the cell.

Vocabulary

carrier protein (99)	diffusion (95)
concentration gradient (95)	equilibrium (95)
contractile vacuole (97)	facilitated diffusion (99)
cytolysis (99)	hypertonic (96)

- When the solute concentration outside the cell is higher than that in the cytosol, the solution outside is hypertonic to the cytosol, and water will diffuse out of the cell.
- When the solute concentrations outside and inside the cell are equal, the solution outside is isotonic, and there will be no net movement of water.
- To remain alive, cells must compensate for the water that enters the cell in hypotonic environments and leaves the cell in hypertonic environments.
- In facilitated diffusion, a carrier protein binds to a molecule on one side of the cell membrane. The protein then changes its shape and transports the molecule down its concentration gradient to the other side of the membrane.
- Ion channels are proteins that provide small passageways across the cell membrane through which specific ions can diffuse.

hypotonic (96)	passive transport (95)
ion channel (100)	plasmolysis (98)
isotonic (97)	turgor pressure (98)
osmosis (96)	

- 5-2**
- Active transport moves molecules across the cell membrane from an area of lower concentration to an area of higher concentration. It requires cells to expend energy.
 - Some types of active transport are performed by carrier proteins called cell membrane pumps.
 - One example of a cell membrane pump is the sodium-potassium pump. It moves three Na^+ ions into the cell's external environment for every two K^+ ions it moves into the cytosol. ATP supplies the energy that drives the pump.
 - Endocytosis and exocytosis are active trans-

Vocabulary

active transport (101)	phagocyte (104)
endocytosis (103) ↗	phagocytosis (103) ↖
exocytosis (104)	pinocytosis (103) ↘

- port mechanisms in which large substances cross the membrane inside vesicles.
- In endocytosis, the cell membrane folds around something in the external environment and forms a pouch. The pouch then pinches off and becomes a vesicle in the cytoplasm. Endocytosis includes pinocytosis, in which the vesicle contains solutes or fluids, and phagocytosis, in which the vesicle contains large particles or cells.
- In exocytosis, vesicles made by the cell fuse with the cell membrane, releasing their contents into the external environment.

sodium-potassium pump (101)
vesicle (103) ↘

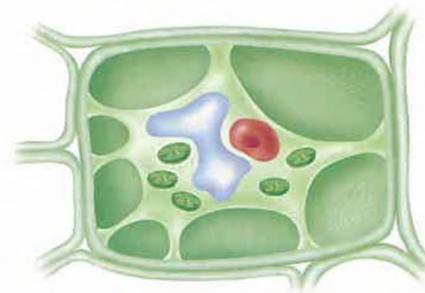
REVIEW

Vocabulary

1. Distinguish between diffusion and facilitated diffusion.
2. What does it mean to say that two solutions are isotonic?
3. How is plasmolysis related to turgor pressure in plant cells?
4. What is a contractile vacuole, and how does it function?
5. The word part *pino-* means “to drink,” *phago-* means “to eat,” and *cyto-* means “cell.” With this information, explain why the words *pinocytosis* and *phagocytosis* are good names for the processes they describe.

Multiple Choice

6. During diffusion, molecules tend to move (a) up their concentration gradient (b) down their concentration gradient (c) in a direction that doesn't depend on the concentration gradient (d) from an area of lower concentration to an area of higher concentration.
7. The part of a cell that functions to maintain homeostasis relative to the cell's environment is the (a) cytosol (b) Golgi apparatus (c) nucleus (d) cell membrane.
8. Ion channels aid the movement of (a) molecules up a concentration gradient (b) carrier proteins within the lipid bilayer (c) ions across a cell membrane (d) water across a cell membrane.
9. Glucose enters a cell most rapidly by (a) facilitated diffusion (b) diffusion (c) osmosis (d) phagocytosis.
10. When the cells in a plant have low turgor pressure, the plant (a) is rigid (b) dies (c) wilts (d) explodes.
11. The sodium-potassium pump transports (a) Na^+ into the cell and K^+ out of the cell (b) Na^+ out of the cell and K^+ into the cell (c) both Na^+ and K^+ into the cell (d) both Na^+ and K^+ out of the cell.
12. A cell must expend energy to transport substances using (a) cell membrane pumps (b) facilitated diffusion (c) ion channels (d) osmosis.
13. Some animal cells engulf, digest, and destroy invading bacteria through the process of (a) exocytosis (b) phagocytosis (c) pinocytosis (d) all of the above.
14. Carrier proteins are important in (a) osmosis (b) endocytosis (c) diffusion (d) facilitated diffusion.
15. The drawing below shows a plant cell after the solute concentration of its environment has been changed. The new external environment is most likely (a) isotonic (b) hypertonic (c) hypotonic (d) none of the above.



Short Answer

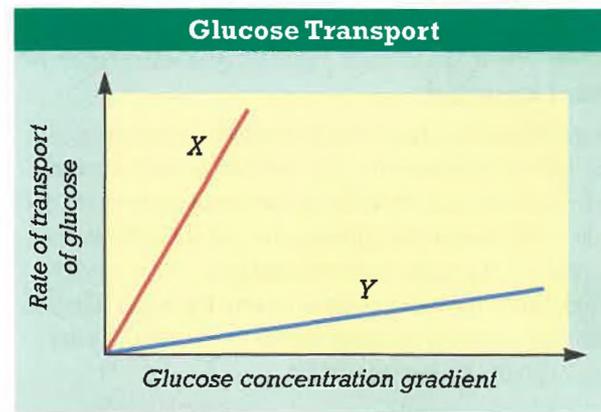
16. What does it mean to say that diffusion eventually results in equilibrium?
17. Can all molecules diffuse through all cell membranes? Explain your answer.
18. Describe three structures characteristic of plant cells. Explain the function of each.
19. What determines the direction of net movement of water across a cell membrane?
20. How does the lipid bilayer of a membrane form a barrier to molecules?
21. How can a cell that consumes glucose speed up its intake of glucose from the environment?
22. How is ATP involved in maintaining the sodium and potassium gradients across a cell membrane?
23. Distinguish between endocytosis and exocytosis.
24.  Write a report summarizing the roles of osmosis and diffusion in the preservation of body organs donated for transplants. Why must organs be preserved in special solutions prior to a transplant? Find out what kinds of substances these solutions contain.

CRITICAL THINKING

1. There is a higher concentration of air molecules inside an inflated balloon than there is outside the balloon. Because of their constant random motion, the molecules inside press against the balloon and keep it taut. How is the pressure exerted by these air molecules similar to turgor pressure? How is it different?
2. Sometimes water seeps through the concrete wall of a basement after a heavy rain, and the homeowner must remove it with a sump pump. How can this situation be compared to the action of a unicellular organism that lives in a pond?
3. When a cell takes in substances through endocytosis, the cell membrane forms an inside-out vesicle. That is, the outside of the cell membrane becomes the inside of the vesicle. What might this suggest about the structure of the cell membrane?
4. If a cell were exposed to a poison that blocked the cell's ability to manufacture ATP, what effect would that have on the cell membrane's transport processes?
5. Some plant cells have carrier proteins that transport sugar molecules and hydrogen ions (H^+) into the cytosol at the same time. These carrier proteins move sugar molecules up their gradient as hydrogen ions move down their gradient. How would the transport of sugar into these cells affect the pH of the

cells' external environment? What would happen to the transport of sugar if hydrogen ions were removed from the external environment?

6. A gelatin block is prepared with a chemical indicator that turns pink in the presence of a base. The block is enclosed in a membrane and placed in a beaker of ammonium hydroxide solution. After half an hour, the block begins to turn pink. Account for the gelatin's pink color.
7. The two curves below show the rate at which glucose is transported across a cell membrane versus the concentration gradient of glucose. One curve represents the diffusion of glucose through the lipid bilayer, and the other curve represents the transport of glucose by facilitated diffusion. Which curve corresponds to facilitated diffusion? Explain your reasoning.



EXTENSION

1. Read "Coming to Grips with the Golgi" in *Science*, December 18, 1999, on page 2169. Describe how the cisternal maturation model of the Golgi system differs from the vesicular transport model.
2. Kidney dialysis is the artificial filtering of blood to remove wastes in patients whose kidneys can no longer function well. Selectively permeable membranes are used in kidney dialysis and in other areas of medicine.

Consult your local hospital, and obtain information on how kidney dialysis is performed and on the medical condition of the people who receive dialysis treatment.

3. Examine a number of food items at a grocery store. Find at least four foods for which salt is listed as a preservative. Keeping in mind what you have learned about osmosis, explain why salt is often used to preserve food.

CHAPTER 5

INTERACTIVE EXPLORATION

Exploring the Role of Osmosis in Cystic Fibrosis

OBJECTIVES

- Simulate the effects of three different genotypes on the movement of water molecules and chloride ions through the cell membrane.
- Relate the symptoms of cystic fibrosis to the ability of water molecules and chloride ions to pass through the cell membrane.

MATERIALS

- computer with CD-ROM drive
- CD-ROM *Interactive Explorations in Biology: Human Biology*

Background

Cystic fibrosis is a fatal genetic disease that results from the failure of chloride ions (Cl^-) to pass through the cell membrane. As a result, chloride ions accumulate inside the cells of the body, drawing water into the cells. When this happens in the lungs, pancreas, and liver, a thick mucus builds up on the lining of these organs. The severe congestion that gradually develops usually causes death by the age of 30 in afflicted individuals.

FEEDBACK METERS

Cl^- Ion Transfer: the rate at which chloride ions move across the membrane

Mucus Buildup: how much mucus has accumulated on the cell

Exterior/Interior Cl^- Concentration: ratio of chloride ion concentration outside the cell to concentration inside the cell

Exterior/Interior Water Concentration: ratio of number of water molecules, outside the cell to number inside the cell

VARIABLE

Type of Mutation: allows you to select one of three genotypes: $+/+$, $cf/+$, or cf/cf

In this interactive exploration, you will examine the three possible pairs of genes that an individual can have: two normal genes, represented by $+/+$; one cystic fibrosis gene and one normal gene, represented by $cf/+$; and two cystic fibrosis genes, represented by cf/cf . Then you will explore how these genetic combinations affect the membrane proteins involved in transporting Cl^- ions through the cell membrane.

Prelab Preparation

1. Load and start the program Cystic Fibrosis. Click the Topic Information button on the Navigation palette. Read the focus questions, and review the following concepts: Transport Channels, Osmosis, Mutation, and Cystic Fibrosis.
2. Click the word *File* at the top left of the screen, and select Interactive Exploration Help. Listen to the instructions for operating the exploration. Click the Exploration button at the bottom right of the screen to begin the exploration. You will see an animated drawing like the one below.

The screenshot shows a 3D model of a cell membrane with various proteins and molecules. On the left, there are four feedback meters: **Cl^- Ion Transfer** (High), **Mucus Buildup** (Normal), **Exterior/Interior Cl^- Concentration** (Low), and **Exterior/Interior Water Concentration** (Clogged). At the bottom, there is a control panel with an **Elapsed Time** display (00:00 min sec), a **Type of Mutation** dropdown menu (set to $+/+$), buttons for $+/+$, $cf/+$, and cf/cf , **Start** and **Stop** buttons, **H₂O** and **Cl⁻** buttons, and a **Navigation** button.

CHLORIDE ION AND WATER CONCENTRATION INSIDE CELLS

Genetic makeup	Exterior/interior Cl ⁻ concentration	Exterior/interior water concentration	Mucus buildup
+/+	100%	normal	normal
cf/+	50%	normal	normal
cf/cf	20%	low	low

Procedure

Create a table like the one above for recording your data.

PART A Two Normal Genes (+/+)

1. Move the pointer to the Type of Mutation box, and click the +/+ button. The transport of Cl⁻ ions and water molecules in a person with this gene combination is normal. Note that water molecules and Cl⁻ ions are located both outside the cell (the portion of the screen above the cell membrane) and inside the cell (the portion of the screen below the cell membrane). Also note the position of the two CF proteins in the cell membrane.
2. Click the Start button to begin the simulation. Allow the simulation to run for two to three minutes. Describe how water molecules pass through the cell membrane. How does this differ from the passage of Cl⁻ ions through the membrane? What appears to be the function of the two CF proteins?
3. Click the Stop button. In your table, record the Exterior/Interior Cl⁻ Concentration, the Exterior/Interior Water Concentration, and the amount of mucus buildup outside the cell membrane.

PART B One Cystic Fibrosis Gene and One Normal Gene (cf/+)

4. Move the pointer to the Type of Mutation box, and click the cf/+ button. Describe what happens to the CF protein shown on the left and how this affects the Cl⁻ ion channel.
5. Click the Start button, and allow the simulation to run for two to three minutes. Describe the changes in the way water molecules and Cl⁻ ions move through the membrane. How will the change in the movement of water molecules and Cl⁻ ions affect the external surface of the cell?

6. Click the Stop button. In your table, record the same three variables that you recorded in step 3. On which side of the membrane are chloride ions at the higher concentration? On which side is water at the higher concentration? Compare the results with those you obtained in Part A, and explain any differences.

PART C Two Cystic Fibrosis Genes (cf/cf)

7. Move the pointer to the Type of Mutation box, and click the cf/cf button. An individual with this gene combination will be afflicted with cystic fibrosis. Describe what happens to both CF membrane proteins and how this affects the Cl⁻ ion channels.
8. Click the Start button, and allow the simulation to run for two to three minutes. Describe the changes in the movement of water molecules and Cl⁻ ions through the membrane. How will the external surface of the cell be affected?
9. Click the Stop button. Describe the difference between the cell's external environment and its internal environment. In your table, record the same variables that you recorded in steps 3 and 6. On which side of the membrane are chloride ions at the higher concentration? Compare the results with those you obtained in Parts A and B, and explain any differences.

Analysis and Conclusions

1. Why are the Cl⁻ ion channels, but not the water channels, said to have gates?
2. Use the term *hypotonic*, *hypertonic*, or *isotonic* to describe the cells that line the organs of individuals with cystic fibrosis.
3. How does an accumulation of chloride ions inside a cell result in a thickening of the mucus outside the cell?

CHAPTER 6

PHOTOSYNTHESIS



Through photosynthesis, these corn plants obtain energy from the sun and store it in organic compounds.

FOCUS CONCEPT: *Matter, Energy, and Organization*

As you read about photosynthesis, notice the mechanisms in cells that keep the process operating.

6-1 *Capturing the Energy in Light*

6-2 *The Calvin Cycle*



Unit 2—Photosynthesis
Topics 1–6

CAPTURING THE ENERGY IN LIGHT

*All organisms use energy to carry out the functions of life. Some organisms obtain this energy directly from sunlight. They capture part of the energy in light and store it within organic compounds. The process by which this energy transfer takes place is called **photosynthesis**.*

ENERGY FOR LIFE PROCESSES

You learned in Chapter 1 that organisms can be classified according to how they obtain energy. Organisms that manufacture their own food from inorganic substances and energy are autotrophs. Most autotrophs use photosynthesis to convert light energy from the sun into chemical energy, which they then store in various organic compounds, primarily carbohydrates. Plants are the most common example of photosynthetic organisms, but algae and some bacteria can also make their own organic compounds through photosynthesis.

Recall that animals and other organisms that cannot manufacture their own organic compounds from inorganic substances are called heterotrophs. Heterotrophs obtain food by eating autotrophs or by eating other heterotrophs that feed on autotrophs. For example, a caterpillar is a heterotroph that feeds directly on an autotroph, grass. A bird that eats caterpillars is also a heterotroph. The food that fuels the bird originates with autotrophs, but it passes *indirectly* to the bird through the caterpillars. In a similar way, all life ultimately depends on autotrophs.

Photosynthesis involves a complex series of chemical reactions, in which the product of one reaction is consumed in the next reaction. A series of reactions linked in this way is referred to as a **biochemical pathway**.

As you can see in Figure 6-1, autotrophs use the biochemical pathways of photosynthesis to manufacture organic compounds from carbon dioxide (CO₂) and water. During this conversion, molecular oxygen (O₂) is released.

Some of the energy stored in organic compounds is released by cells in another set of biochemical pathways, known as cellular

SECTION

6-1

OBJECTIVES

▲ Explain how the structure of the chloroplast relates to its function.

● Describe the role of chlorophylls and other pigments in photosynthesis.

■ Summarize the main events of electron transport.

◆ Describe what happens to a water molecule in photosynthesis.

▲ Explain how ATP is synthesized during the light reactions.

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TOPIC: Photosynthesis
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KEYWORD: HM111

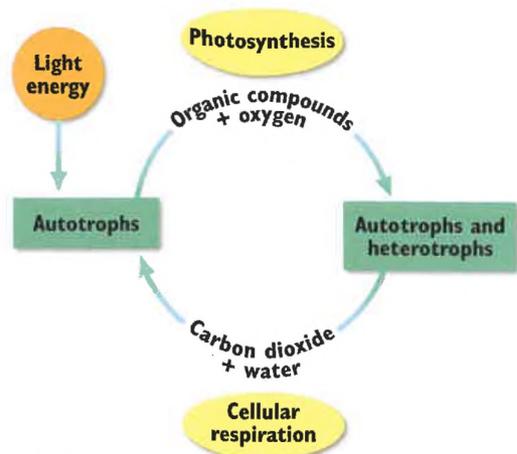


FIGURE 6-1

Many autotrophs produce organic compounds and oxygen through photosynthesis. Both autotrophs and heterotrophs produce carbon dioxide and water through cellular respiration.

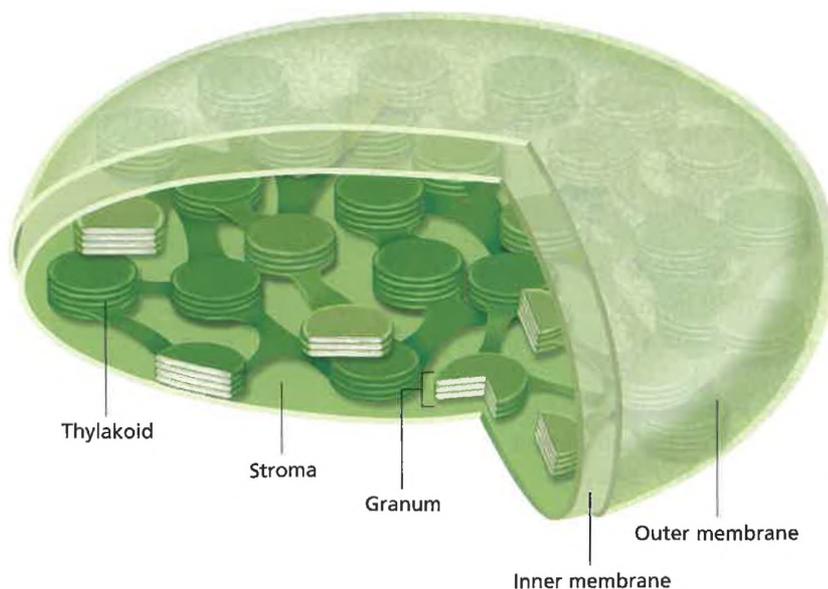
LIGHT ABSORPTION IN CHLOROPLASTS

In plants, the initial reactions in photosynthesis are known collectively as the **light reactions**. They begin with the absorption of light in chloroplasts. Remember from Chapter 4 that a chloroplast is an organelle found in the cells of plants and in unicellular eukaryotes known as algae. While some algae may contain a single large chloroplast, a cell in the leaf of a plant may have 50 or more chloroplasts.

Most chloroplasts are similar in structure, regardless of the organism in which they are found. As you learned in Chapter 4, each chloroplast is surrounded by a pair of membranes. Inside the inner membrane is another system of membranes, arranged as flattened sacs called thylakoids. Figure 6-2 shows that the thylakoids are interconnected and that some are layered on top of one another to form stacks called **grana** (GRAY-nuh). Surrounding the thylakoids is a solution called the **stroma** (STROH-muh).

FIGURE 6-2

Photosynthesis in eukaryotes occurs inside the chloroplasts. The light reactions of photosynthesis take place in the thylakoids, which are stacked to form grana.



Light and Pigments

To explain how chloroplasts absorb light in photosynthesis, it is important to understand some of the properties of light. Light from the sun appears white, but it is actually composed of a variety of colors. As Figure 6-3 demonstrates, you can separate white light into its component colors by passing the light through a prism. The resulting array of colors, ranging from red at one end to violet at the other, is called the **visible spectrum**.

Light travels through space as waves of energy. These waves are analogous to the waves that travel

across a body of water when an object hits the surface. Like water waves, light waves can be measured in terms of their **wavelength**, the distance between crests in a wave. You can see in Figure 6-3 that the different colors in the visible spectrum have different wavelengths.

When white light strikes an object, its component colors can be reflected, transmitted, or absorbed by the object. However, the various colors will react differently if the object contains a **pigment**, which is a compound that absorbs light. Most pigments absorb certain colors more strongly than others. By absorbing certain colors, a pigment subtracts those colors from the visible spectrum. Therefore, the light that is reflected or transmitted by the pigment no longer appears white. For example, the lenses in green-tinted sunglasses contain a pigment that reflects and transmits green light and absorbs the other colors. As a result, the lenses look green.

Chloroplast Pigments

Located in the membrane of the thylakoids are a variety of pigments, the most important of which are called **chlorophylls** (KLOHR-uh-FILZ). There are several different types of chlorophylls. The two most common types are designated chlorophyll *a* and chlorophyll *b*.

A slight difference in molecular structure between chlorophyll *a* and chlorophyll *b* causes the two molecules to absorb different colors of light. As Figure 6-4 shows, chlorophyll *a* absorbs less blue light but more red light than chlorophyll *b* absorbs. Neither chlorophyll *a* nor chlorophyll *b* absorbs much green light. Instead, they allow green light to be reflected or transmitted. That is why young leaves and other plant structures that contain large amounts of chlorophyll look green.

Only chlorophyll *a* is directly involved in the light reactions of photosynthesis. Chlorophyll *b* assists chlorophyll *a* in capturing light energy, and therefore chlorophyll *b* is called an **accessory pigment**. Other compounds found in the thylakoid membrane, including the yellow, orange, and brown **carotenoids** (kuh-RAHT-uhn-OYDZ), also function as accessory pigments. Looking again at Figure 6-4, notice that the pattern of light absorption of one of the carotenoids differs from the pattern of either type of chlorophyll. By absorbing colors that chlorophyll *a* cannot absorb, the accessory pigments enable plants to capture more of the energy in light.

In the leaves of a plant, the chlorophylls are much more abundant and therefore mask the colors of the other pigments. But in the nonphotosynthetic parts of a plant, such as fruits and flowers, the colors of the other pigments may be quite visible. During the fall, many plants lose their chlorophylls, and their leaves take on the rich hues of the carotenoids.

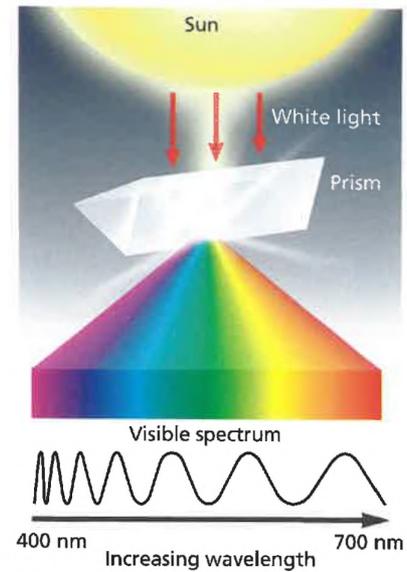
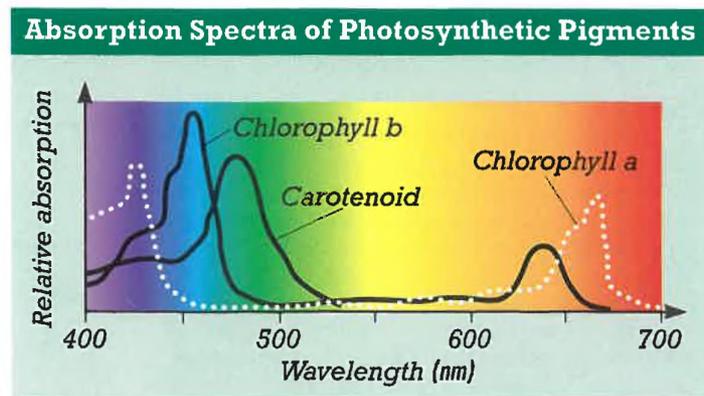


FIGURE 6-3

White light contains a variety of colors called the visible spectrum. Each color has a different wavelength, measured in nanometers.

FIGURE 6-4

The three curves on this graph show how three pigments involved in photosynthesis differ in the colors of light they absorb. Where a curve has a peak, much of the light at that wavelength is absorbed. Where a curve has a trough, much of the light at that wavelength is reflected or transmitted.



ELECTRON TRANSPORT

The chlorophylls and carotenoids are grouped in clusters of a few hundred pigment molecules in the thylakoid membrane. Each cluster of pigment molecules is referred to as a **photosystem**. Two types of photosystems are known: **photosystem I** and **photosystem II**. They are similar in terms of the kinds of pigments they contain, but they have different roles in the light reactions, as you'll soon see.

The light reactions begin when accessory pigment molecules in both photosystems absorb light. By absorbing light, those molecules acquire some of the energy that was carried by the light waves. In each photosystem, the acquired energy is passed quickly to other pigment molecules until it reaches a specific pair of chlorophyll *a* molecules. The events that occur from this point on can be divided into five steps. Refer to Figure 6-5 as you follow these steps.

Step 1. Light energy forces electrons to enter a higher energy level in the two chlorophyll *a* molecules of photosystem II. These energized electrons are said to be “excited.”

Step 2. The excited electrons have enough energy to leave the chlorophyll *a* molecules. Because they have lost electrons, the chlorophyll *a* molecules have undergone an oxidation reaction.

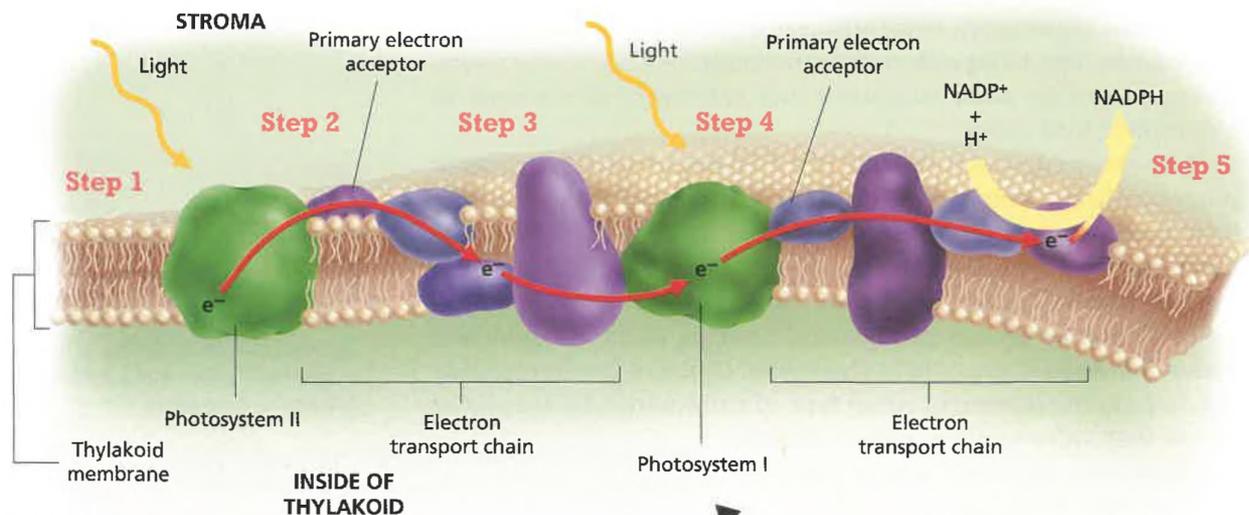


FIGURE 6-5

The light reactions take place in the thylakoid membrane and involve several steps. Step 1: Light excites electrons in chlorophyll *a* molecules of photosystem II. Step 2: These electrons move to a primary electron acceptor. Step 3: The electrons are then transferred along a series of molecules called an electron transport chain. Step 4: Light excites electrons in chlorophyll *a* molecules of photosystem I. As these electrons move to another primary electron acceptor, they are replaced by electrons from photosystem II. Step 5: The electrons from photosystem I are transferred along a second electron transport chain. At the end of this chain, they combine with NADP^+ and H^+ to make NADPH.

Remember from Chapter 2 that each oxidation reaction must be accompanied by a reduction reaction. This means that some substance must accept the electrons that the chlorophyll *a* molecules have lost. That substance is a molecule in the thylakoid membrane known as the **primary electron acceptor**.

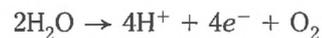
Step 3. The primary electron acceptor then donates the electrons to the first of a series of molecules located in the thylakoid membrane. This series of molecules is called an **electron transport chain**, because it transfers electrons from one molecule to the next in series. As the electrons pass from molecule to molecule in the electron transport chain, they lose most of the energy that they acquired when they were excited. The energy they lose is harnessed to move protons into the thylakoid.

Step 4. At the same time, light is absorbed by photosystem II, light is also absorbed by photosystem I. Electrons move from a pair of chlorophyll *a* molecules in photosystem I to another primary electron acceptor. The electrons that are lost by these chlorophyll *a* molecules are replaced by the electrons that have passed through the electron transport chain from photosystem II.

Step 5. The primary electron acceptor of photosystem I donates electrons to a different electron transport chain. This chain brings the electrons to the side of the thylakoid membrane that faces the stroma. There the electrons combine with a proton and **NADP⁺**. NADP⁺ is an organic molecule that accepts electrons during redox reactions. As you can see in Figure 6-5, this reaction causes NADP⁺ to be reduced to NADPH.

Restoring Photosystem II

You read in Step 4 that electrons from chlorophyll molecules in photosystem II replace the electrons that leave chlorophyll molecules in photosystem I. If the electrons from photosystem II were not replaced, both electron transport chains would stop, and photosynthesis would not occur. The replacement electrons are provided by water molecules. As Figure 6-6 shows, an enzyme inside the thylakoid splits water molecules into protons, electrons, and oxygen. The following equation summarizes the reaction:



For every two molecules of water that are split, four electrons become available to replace those lost by chlorophyll molecules in photosystem II. The protons that are produced are left inside the thylakoid, while the oxygen diffuses out of the chloroplast and can then leave the plant. Thus, oxygen can be regarded as a byproduct of the light reactions—it is not needed for photosynthesis to occur. However, as you will learn in Chapter 7, the oxygen that results from photosynthesis is essential for cellular respiration in most organisms, including plants themselves.

Eco Connection

Photosynthesis and the Global Greenhouse

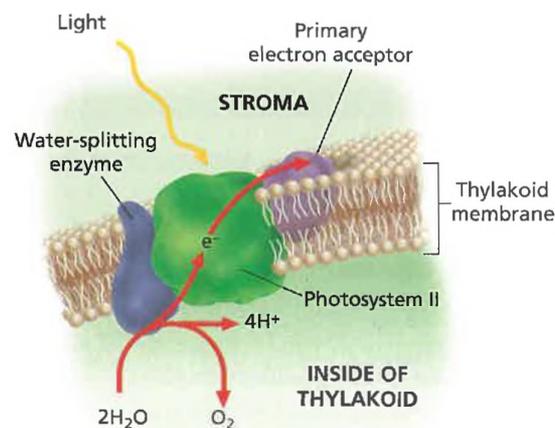
With the beginning of the Industrial Revolution around 1850, the atmospheric concentration of CO₂ started to increase. This increase has resulted largely from the burning of fossil fuels, which releases CO₂ as a byproduct. You might expect plants to benefit from the buildup of CO₂ in the atmosphere. In fact, the rise in CO₂ levels may harm photosynthetic organisms more than it helps them.

CO₂ and other gases in the atmosphere retain some of the Earth's heat, causing the Earth to become warmer. This warming could reduce the amount of worldwide precipitation, creating deserts that would be inhospitable to most plants.

Also, CO₂ in the atmosphere reacts with water to produce acid precipitation, which can kill plants.

FIGURE 6-6

The splitting of water inside the thylakoid releases electrons, which replace the electrons that leave photosystem II when it is illuminated.



Word Roots and Origins

chemiosmosis

from the Greek *chemeia*, meaning "alchemy," and *osmosis*, meaning "pushing"

CHEMIOSMOSIS

An important part of the light reactions is the synthesis of ATP through a process called **chemiosmosis** (KEM-ee-ahz-MOH-sühs). Chemiosmosis relies on a concentration gradient of protons across the thylakoid membrane. Recall that some protons are produced from the breakdown of water molecules inside the thylakoid. Other protons are pumped from the stroma to the interior of the thylakoid. The energy required to pump these protons is supplied by the excited electrons as they pass along the electron transport chain of photosystem II. Both of these mechanisms act to build up a concentration gradient of protons. That is, the concentration of protons is higher inside the thylakoid than in the stroma.

The concentration gradient of protons represents potential energy. That energy is harnessed by a protein called **ATP synthase**, which is located in the thylakoid membrane, as Figure 6-7 shows. ATP synthase makes ATP by adding a phosphate group to **adenosine diphosphate**, or ADP. The energy that drives this reaction is

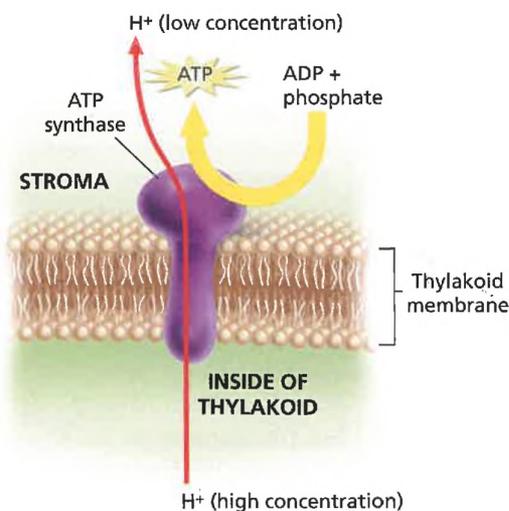
provided by the movement of protons from the inside of the thylakoid to the stroma. Thus, ATP synthase converts the potential energy of the proton concentration gradient into chemical energy stored in ATP. Remember from Chapter 3 that ATP is the main energy currency of cells.

As you learned earlier, some of the protons in the stroma are used to make NADPH from NADP^+ . Together, NADPH and ATP provide energy for the second set of reactions in photosynthesis, which are described in the next section.

ATP synthase is a multifunctional protein. By allowing protons to cross the thylakoid membrane, ATP synthase functions as a carrier protein. By catalyzing the synthesis of ATP from ADP, ATP synthase functions as an enzyme. You will encounter other examples of multifunctional proteins in later chapters.

FIGURE 6-7

During chemiosmosis, the movement of protons into the stroma of the chloroplast releases energy, which is used to manufacture ATP.



SECTION 6-1 REVIEW

- ✓ 1. Describe the structure and function of the thylakoids of a chloroplast.
- ✓ 2. What role do the accessory pigments play in photosynthesis?
- ✓ 3. What happens to the electrons that are lost by photosystem II? What happens to the electrons that are lost by photosystem I?
4. Name the three substances that are produced when water molecules are broken down during the light reactions.
5. How is ATP made in the light reactions?
6. **CRITICAL THINKING** Explain how the light reactions would be affected if there were no concentration gradient of protons across the thylakoid membrane.

SECTION

6-2

OBJECTIVES

Summarize the main events of the Calvin cycle.

Describe what happens to the compounds made in the Calvin cycle.

Distinguish between C_3 , C_4 , and CAM plants.

Explain how environmental factors influence photosynthesis.

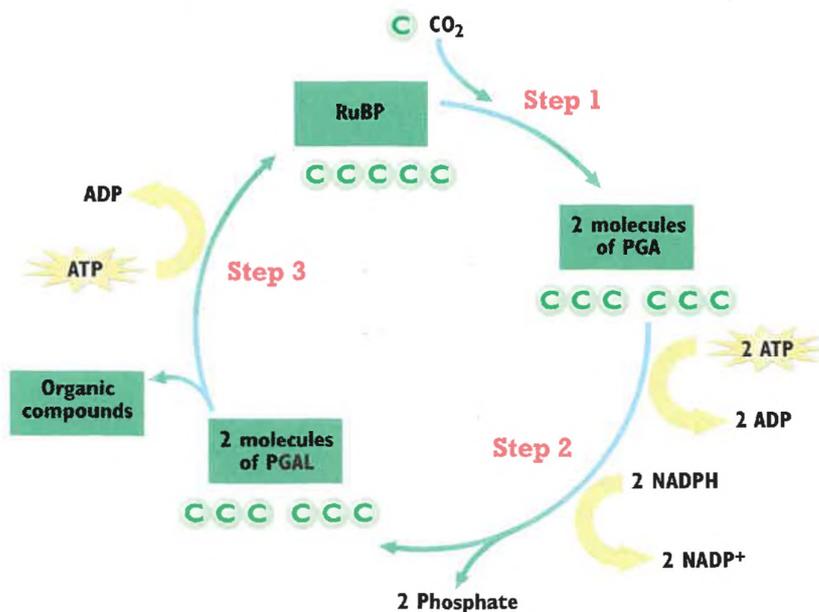
THE CALVIN CYCLE

The second set of reactions in photosynthesis involves a biochemical pathway known as the **Calvin cycle**. This pathway produces organic compounds, using the energy stored in ATP and NADPH during the light reactions. The Calvin cycle is named after Melvin Calvin (1911–1997), the American scientist who worked out the details of the pathway.

CARBON FIXATION BY THE CALVIN CYCLE

In the Calvin cycle, carbon atoms from CO_2 are bonded, or “fixed,” into organic compounds. This incorporation of CO_2 into organic compounds is referred to as **carbon fixation**. The Calvin cycle has three major steps, which occur within the stroma of the chloroplast. Refer to Figure 6-8 as you read the following summary of the steps in the Calvin cycle.

Step 1. CO_2 diffuses into the stroma from the surrounding cytosol. An enzyme combines a CO_2 molecule with a five-carbon carbohydrate called **RuBP**. The product is a six-carbon molecule that splits immediately into a pair of three-carbon molecules known as **PGA**.



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TOPIC: Calvin cycle
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FIGURE 6-8

The Calvin cycle takes place in the stroma of the thylakoid and involves three major steps. Step 1: CO_2 combines with RuBP to form two molecules of PGA. Step 2: Each molecule of PGA is converted into a molecule of PGAL. Step 3: Most of the PGAL is converted back into RuBP, but some PGAL can be used to make a variety of organic compounds.



Quick Lab

Analyzing Photosynthesis

Materials disposable gloves, lab apron, safety goggles, 250 mL Erlenmeyer flasks (3), bromothymol blue, 5 cm sprigs of *Elodea* (2), water, drinking straw, plastic wrap, 100 mL graduated cylinder

Procedure



1. Put on your disposable gloves, lab apron, and safety goggles.
2. Label the flasks "1," "2," and "3." Add 200 mL of water and 20 drops of bromothymol blue to each flask.
3. Put the drinking straw in flask 1 and blow into the blue solution until the solution turns yellow. Repeat this step with flask 2.
4. Put one *Elodea* sprig in flask 1. Do nothing to flask 2. Put the other *Elodea* sprig in flask 3.
5. Cover all flasks with plastic wrap. Place the flasks in a well-lighted location, and leave them overnight. Record your observations.

Analysis Describe your results. Explain what caused one of the solutions to change color. Why did the other solutions not change color? Which flask is the control in this lab?

Step 2. PGA is converted into another three-carbon molecule, **PGAL**, in a two-part process. First, each PGA molecule receives a phosphate group from a molecule of ATP. The resulting compound then receives a proton from NADPH and releases a phosphate group, producing PGAL. In addition to PGAL, these reactions produce ADP, NADP⁺, and phosphate. These three products can be used again in the light reactions to synthesize additional molecules of ATP and NADPH.

Step 3. Most of the PGAL is converted back into RuBP in a complicated series of reactions. These reactions require a phosphate group from another molecule of ATP, which is changed into ADP. By regenerating the RuBP that was consumed in Step 1, the reactions of Step 3 allow the Calvin cycle to continue operating. However, some PGAL molecules are not converted into RuBP. Instead, they leave the Calvin cycle and can be used by the plant cell to make other organic compounds, as explained in the next section.

The Balance Sheet for Photosynthesis

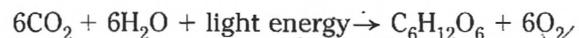
How much ATP and NADPH are required to make one molecule of PGAL from CO₂? Each turn of the Calvin cycle fixes one CO₂ molecule. Since PGAL is a three-carbon compound, it takes three turns of the cycle to produce each molecule of PGAL. For each turn of the cycle, two ATP molecules and two NADPH molecules are used in Step 2—one for each molecule of PGAL produced—and one more ATP molecule is used in Step 3. Therefore, three turns of the Calvin cycle use nine molecules of ATP and six molecules of NADPH.

Some of the PGAL and other molecules made in the Calvin cycle are built up into a variety of organic compounds, including amino acids, lipids, and carbohydrates. Among the carbohydrates are the monosaccharides glucose and fructose, the disaccharide sucrose, and the polysaccharides glycogen, starch, and cellulose. Most heterotrophs depend on the chemical energy that is stored in the organic compounds made by plants and other photosynthetic organisms.

Recall that water is split during the light reactions, yielding electrons, protons, and oxygen as a byproduct. Thus, the simplest overall equation for photosynthesis, including both the light reactions and the Calvin cycle, can be written as follows:



In the equation above, (CH₂O) represents the general formula for a carbohydrate. It is often replaced in this equation by the carbohydrate glucose, C₆H₁₂O₆, giving the following equation:



Keep in mind, however, that glucose is not actually produced by the pathways of photosynthesis. Glucose is included in the equation mainly to emphasize the relationship between photosynthesis and cellular respiration, which will be discussed in Chapter 7.

ALTERNATIVE PATHWAYS

The Calvin cycle is the most common pathway for carbon fixation. Plant species that fix carbon exclusively through the Calvin cycle are known as **C₃ plants** because of the three-carbon compound, PGA, that is initially formed. Other plant species fix carbon through alternative pathways and then release it to enter the Calvin cycle.

These alternative pathways are generally found in plants that evolved in hot, dry climates. Under such conditions, plants can rapidly lose water to the air. Most of the water loss from a plant occurs through small pores called **stomata** (STOH-muh-tuh), which are usually located on the undersurface of the leaves. As Figure 6-9 shows, plants can partially close their stomata when the air is hot and dry, thereby reducing water loss.

Stomata are also the major passageways through which CO₂ enters and O₂ leaves a plant. Thus, when a plant's stomata are partly closed, the level of CO₂ in the plant falls as CO₂ is consumed in the Calvin cycle. At the same time, the level of O₂ in the plant rises as the light reactions split water and generate O₂. Both of these conditions—a low CO₂ level and a high O₂ level—inhibit carbon fixation by the Calvin cycle. Plants with alternative pathways for carbon fixation have evolved ways of dealing with this problem.

The C₄ Pathway

One alternative pathway enables certain plants to fix CO₂ into four-carbon compounds. This pathway is therefore called the **C₄ pathway**, and plants that use it are known as C₄ plants. During the hottest part of the day, C₄ plants have their stomata partially closed. However, certain cells in C₄ plants have an enzyme that can fix CO₂ into four-carbon compounds even when the CO₂ level is low and the O₂ level is high. These compounds are then transported to other cells, where CO₂ is released and enters the Calvin cycle.

C₄ plants include corn, sugar cane, and crabgrass. Such plants lose only about half as much water as C₃ plants when producing the same amount of carbohydrate.

The CAM Pathway

Cactuses, pineapples, and certain other plants have a different adaptation to hot, dry climates. Such plants fix carbon through a pathway called **CAM**. Plants that use the CAM pathway open their stomata at night and close them during the day—just the opposite of what other plants do. At night, CAM plants take in CO₂ and fix it into a variety of organic compounds. During the day, CO₂ is released from these compounds and enters the Calvin cycle. Because CAM plants have their stomata open at night, when the temperature is lower, they grow fairly slowly. However, they lose less water than either C₃ or C₄ plants.

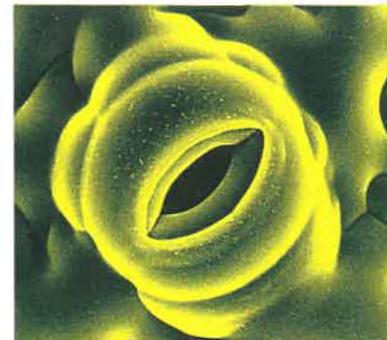
Word Roots and Origins

stoma

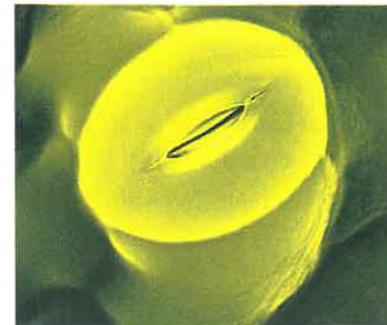
from the Greek *stoma*, meaning "mouth"

FIGURE 6-9

These SEMs show stomata in the leaf of a tobacco plant, *Nicotiana tabacum*. (a) When a stoma is open, water, carbon dioxide, and other gases can pass through it to enter or leave a plant (814×). (b) When a stoma is closed, passage through it is greatly restricted (878×).



(a) OPEN STOMA



(b) CLOSED STOMA

RATE OF PHOTOSYNTHESIS

The rate at which a plant can carry out photosynthesis is affected by the plant's environment. One of the most important environmental influences is light intensity. Figure 6-10a shows that as light intensity increases, the rate of photosynthesis initially increases and then levels off to a plateau. This plateau represents the maximum rate of photosynthesis. Higher light intensity causes more electrons in the chlorophyll molecules of both photosystems to become excited. As more electrons are excited, the light reactions occur more rapidly. At some light intensity, however, all of the available electrons are excited, and any further increase in light intensity will not increase the rate of photosynthesis.

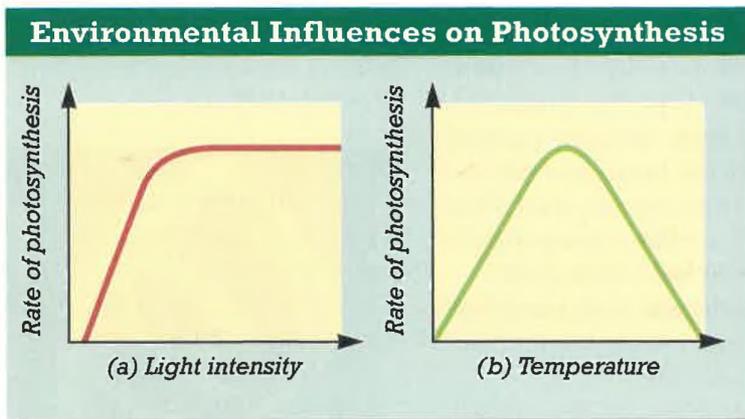
CO₂ is another important influence on photosynthesis. Like increasing light intensity, increasing levels of CO₂ around a plant stimulate photosynthesis until the rate of photosynthesis reaches a plateau. Thus, a graph of the rate of photosynthesis versus CO₂ concentration would resemble Figure 6-10a.

A third environmental factor affecting photosynthesis is temperature. Raising the temperature accelerates the various chemical reactions involved in photosynthesis. As a result, the rate of photosynthesis increases as temperature increases, over a certain range. This effect is illustrated by the left half of the curve in Figure 6-10b.

The rate of photosynthesis generally peaks at a certain temperature. At that temperature, many of the enzymes that catalyze the reactions in photosynthesis start to become unstable and ineffective. Also, the stomata begin to close, limiting water loss and CO₂ entry into the leaves. These conditions cause the rate of photosynthesis to decrease when the temperature is further increased, as shown by the right half of the curve in Figure 6-10b.

FIGURE 6-10

Environmental factors affect the rate of photosynthesis in plants. (a) As light intensity increases, the rate of photosynthesis increases and then levels off at a maximum. (b) As temperature increases, the rate of photosynthesis increases to a maximum and then decreases with further rises in temperature.



SECTION 6-2 REVIEW

1. In what part of a chloroplast does the Calvin cycle take place?
2. Describe what can happen to PGAL molecules made in the Calvin cycle.
3. How many turns of the Calvin cycle are needed to produce a molecule of PGAL? How many molecules of ATP and NADPH are used in the process?
4. What plant structures control the passage of water out of a plant and carbon dioxide into a plant?
5. What is a C₄ plant?
6. **CRITICAL THINKING** Why does the rate of photosynthesis increase and then reach a plateau as the concentration of CO₂ around a plant increases?

CHAPTER 6 REVIEW

SUMMARY/VOCABULARY

- 6-1**
- Photosynthesis converts light energy into chemical energy through complex series of reactions known as biochemical pathways. Autotrophs use photosynthesis to make organic compounds from carbon dioxide and water.
 - In plants and algae, photosynthesis occurs inside the chloroplasts.
 - White light from the sun is composed of an array of colors called the visible spectrum. Different colors in the visible spectrum have different wavelengths.
 - Pigments absorb certain colors of light and reflect or transmit the other colors.
 - The light reactions of photosynthesis begin with the absorption of light by chlorophyll *a* and accessory pigments in the thylakoids.
 - Accessory pigments absorb colors of light that aren't absorbed by chlorophyll *a*, and they transfer some of the energy in this light to chlorophyll *a*.
 - Excited electrons that leave chlorophyll *a* travel along two electron transport chains, resulting in the production of NADPH. The electrons are replaced when water is split into electrons, protons, and oxygen in the thylakoid. Oxygen is released as a byproduct of photosynthesis.
 - As electrons travel along the electron transport chains, a concentration gradient of protons builds up across the thylakoid membrane. The movement of protons down this gradient results in the synthesis of ATP through chemiosmosis.

Vocabulary

accessory pigment (113)	chemiosmosis (116)	NADP ⁺ (115)	primary electron acceptor (115)
adenosine diphosphate (ADP) (116)	chlorophyll (113)	photosynthesis (111)	stroma (112)
ATP synthase (116)	electron transport chain (115)	photosystem (114)	visible spectrum (112)
biochemical pathway (111)	granum (112)	photosystem I (114)	wavelength (113)
carotenoid (113)	light reactions (112)	photosystem II (114)	
		pigment (113)	

- 6-2**
- The ATP and NADPH produced in the light reactions drive the second part of photosynthesis, the Calvin cycle. In the Calvin cycle, CO₂ is incorporated into organic compounds, a process referred to as carbon fixation.
 - The Calvin cycle produces a compound called PGAL. Three turns of the Calvin cycle are needed to produce one PGAL molecule.
 - Most PGAL molecules are converted into another molecule that keeps the Calvin cycle operating. However, some PGAL molecules are used to make other organic compounds, including amino acids, lipids, and carbohydrates.
 - In the overall equation for photosynthesis, CO₂ and water are the reactants, and carbohydrate and O₂ are the products.
 - Some plants living in hot, dry climates supplement the Calvin cycle with the C₄ or CAM pathways. These plants carry out carbon fixation and the Calvin cycle either in different cells or at different times.
 - The rate of photosynthesis increases and then reaches a plateau as light intensity or CO₂ concentration increases. Below a certain temperature, the rate of photosynthesis increases as temperature increases. Above that temperature, the rate of photosynthesis decreases as temperature increases.

Vocabulary

C ₃ plant (119)	CAM (119)	PGAL (118)
C ₄ pathway (119)	carbon fixation (117)	RuBP (117)
Calvin cycle (117)	PGA (117)	stoma (119)

REVIEW

Vocabulary

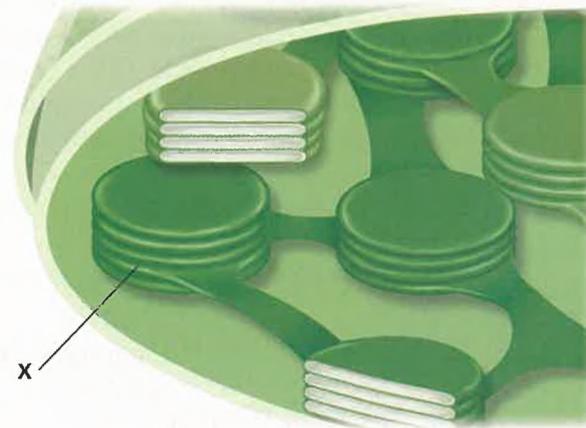
1. The prefix *chloro-* means “green.” With this information, explain why the chlorophylls are well named.
2. What is the difference between *stroma* and *stomata*?
3. Explain what is meant by the term *carbon fixation*.
4. What is a biochemical pathway?
5. Choose the term that does not belong in the following group, and explain why it does not belong: electron transport chain, chemiosmosis, Calvin cycle, and photosystem II.

Multiple Choice

6. A product in the overall equation for photosynthesis is (a) O_2 (b) CO_2 (c) H_2O (d) RuBP.
7. A reactant used in the Calvin cycle is (a) H_2O (b) glucose (c) CO_2 (d) O_2 .
8. Accessory pigments (a) add color to plants but do not absorb light energy (b) absorb colors of light that chlorophyll *a* cannot absorb (c) receive electrons from the electron transport chain of photosystem I (d) are not involved in photosynthesis.
9. C_4 plants (a) are usually found in cool, moist environments (b) lose more water than C_3 plants during photosynthesis (c) have no stomata (d) fix CO_2 into four-carbon compounds.
10. During photosynthesis, oxygen is produced when (a) PGA is converted into PGAL (b) CO_2 is fixed (c) water is split (d) ATP is converted into ADP.
11. The light reactions take place (a) on the outer membrane of the chloroplast (b) in the stroma (c) in the cytosol (d) on the thylakoid membrane.
12. During chemiosmosis, (a) ATP is synthesized from ADP (b) NADPH is synthesized from $NADP^+$ (c) water is broken down (d) electrons are removed from chlorophyll molecules.
13. Which of the following is NOT part of the light reactions? (a) splitting of water (b) electron transport (c) carbon fixation (d) absorption of light energy
14. Most of the PGAL made in the Calvin cycle is used to (a) synthesize carbohydrates (b) keep the cycle operating (c) convert light energy into chemical energy (d) drive the light reactions.
15. The reactions of the Calvin cycle take place (a) on the outer membrane of the chloroplast (b) in the stroma (c) in the cytosol (d) on the thylakoid membrane.

Short Answer

16. What is the difference between the roles of photosystems I and II in photosynthesis?
17. Explain how the Calvin cycle is an example of a biochemical pathway.
18. In what type of environment are most CAM plants found? How is the CAM pathway advantageous for that type of environment?
19. How is ATP made during photosynthesis?
20. Why do the leaves of some plants look green during the summer and then turn yellow, orange, or brown during the fall?
21. The diagram below shows a portion of a chloroplast. Identify the structure labeled X in the diagram. During photosynthesis, is the concentration of protons higher inside this structure or in the space surrounding it?



22. Unit 2—Photosynthesis



Many plants have stomata that take in CO_2 at night and release it during the day. Why is this form of photosynthesis an advantage for plants living in a hot, dry climate?

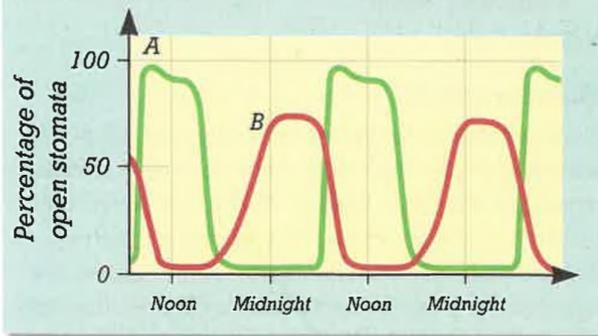
CRITICAL THINKING

1. A famous scientist once said that wherever in the universe life exists, some of those life-forms must be colored. Why would the scientist make such a statement?
2. One of the accessory pigments used in photosynthesis is beta-carotene, a carotenoid found in high concentration in carrots. When one molecule of beta-carotene is split by an enzyme, two molecules of vitamin A are produced. Removal of a hydrogen atom from vitamin A produces retinal, the pigment involved in vision. Explain why eating carrots is important for good vision.
3. When the CO_2 concentration in the cells of a C_3 plant is low compared with the O_2 concentration, an enzyme combines RuBP with O_2 rather than with CO_2 . What effect would this enzymatic change have on photosynthesis? Under what environmental conditions would it be most likely to occur?
4. All of the major components of the light reactions, including the pigment molecules clustered in photosystems I and II, are located in the thylakoid membrane. What is the advantage of having these components confined to the same membrane rather than dissolved in the stroma or the cytosol?
5. Cactuses and other CAM plants are very efficient at carrying out photosynthesis

while conserving water. Why aren't they more common in environments where water is plentiful?

6. Some bacteria conduct a type of photosynthesis that makes ATP but does not produce NADPH or split water. How might the evolution of cellular respiration have been different if this had been the only type of photosynthesis to evolve?
7. The graph below shows how the percentage of stomata that are open varies over time for two different kinds of plants. One curve represents the stomata of a geranium, and the other curve represents the stomata of a pineapple. Which curve corresponds to the pineapple stomata? Explain your reasoning.

Daily Cycle of Stomatal Opening



EXTENSION

1. Read "Lake of Dreams" in *New Scientist*, December 4, 1999, on page 35. Write a report describing Lake Vostok and the characteristics that make it so unusual. Explain why some scientists think the lake may be similar to the geothermal vents near the Galápagos Islands.
2. When the sun's rays are blocked by a thick forest, clouds, dust from a volcanic eruption, or smoke from a large fire, what effect do you think this has on photosynthesis? How might it affect the levels of atmospheric carbon dioxide and oxygen? What experiments could scientists conduct in the laboratory to test your predictions?
3. Collect a sample of algae from a local pond. Divide the sample into two covered bowls, and keep one bowl in the dark and the other in the light. Keep both bowls at the same temperature. Every other day for 10 days, observe the algae with a dissecting microscope. Draw and record the organisms and debris that you see. What do your observations tell you about the role of light in pond life?

CHAPTER 6

INTERACTIVE EXPLORATION

Examining the Rate of Photosynthesis

OBJECTIVES

- Simulate how the rate of photosynthesis is affected by variations in the intensity and wavelength of light.
- Relate the rate of photosynthesis to the production of ATP in a chloroplast.

MATERIALS

- computer with CD-ROM drive
- CD-ROM *Interactive Explorations in Biology: Cell Biology and Genetics*
- graph paper

Background

Photosynthesis is the process by which plants, algae, and some bacteria use the energy contained in light to make organic compounds, including carbohydrates. In the light reactions of photosynthesis, chlorophyll and other pigments absorb light, and electrons in these molecules are raised to higher energy levels. These excited electrons are passed through electron transport chains, resulting in the production of ATP and NADPH. In the Calvin cycle, ATP and

NADPH are used in the synthesis of carbohydrates from carbon dioxide. Because the Calvin cycle cannot occur without ATP, the overall rate of photosynthesis depends on the rate of ATP production in the light reactions. This interactive exploration allows you to see how varying the intensity and wavelength of light affects the rate of ATP production in photosynthesis.

Prelab Preparation

1. Load and start the program Photosynthesis. You will see an animated cross section of a thylakoid membrane like the one below. Click the Navigation button, and then click the Topic Information button. Read the focus questions and review these concepts: Photons, Pigments, and The Action Spectrum of Photosynthesis.
2. Click the word *Help* at the top left of the screen, and select How to Use This Exploration. Listen to the instructions that explain the operation of the exploration. Click the Interactive Exploration button on the Navigation Palette to begin the exploration.

FEEDBACK METERS

% Maximal ATP: ratio of number of ATP molecules produced to the maximum number that can be produced

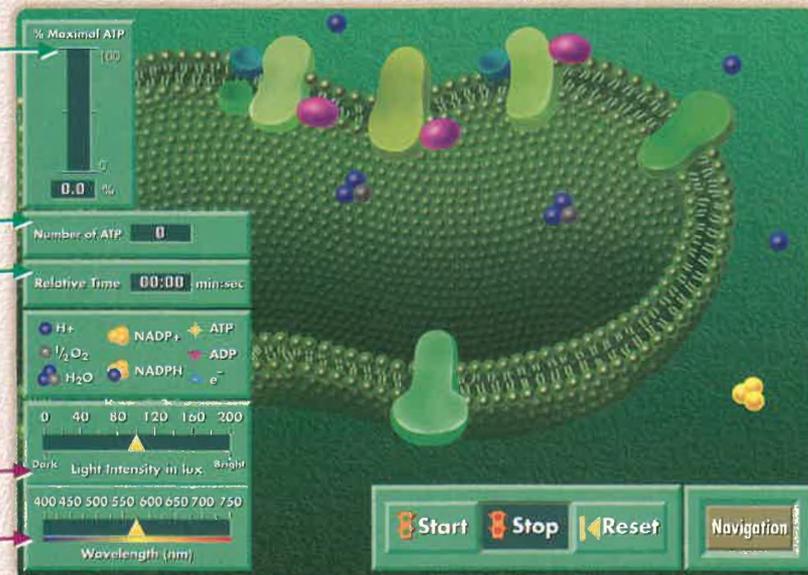
Number of ATP: the number of ATP molecules that have been synthesized

Relative Time: how long the investigation has been running

VARIABLES

Light Intensity: the amount of light

Wavelength of Light: the wavelength of the light



Procedure

PART A Effect of Light Intensity on the Rate of Photosynthesis

1. You will first investigate how varying light intensity affects the rate of photosynthesis. Create a data table like Table A shown below for recording your data.

TABLE A VARYING LIGHT INTENSITY AT A WAVELENGTH OF 650 NM

Light intensity (lux)	% Maximal ATP	Number of ATP
0		
40		
80		
120		
160		
200		

2. Click the word *Speed* at the top of the screen. Select Slow.
3. Click and slide the wavelength indicator to 650. Click and slide the light intensity indicator to 120 lux. A lux is a measure of light intensity.
4. Click the Start button. Observe the diagram of the protein at the bottom of the screen. What molecule is synthesized near this protein?
5. Allow the simulation to run for 30 seconds, as indicated on the relative time meter, and then click the Stop button. In your table, record the % Maximal ATP and the Number of ATP molecules that were produced.
6. Click the Reset button, and then click and slide the light intensity indicator to 160 lux.
7. Click the Start button and allow the simulation to run for 30 seconds, as indicated on the relative time meter.
8. Click the Stop button and record the % Maximal ATP and Number of ATP in your table.
9. Continue testing until you have evaluated all of the light intensities listed on your table.
10. Explain why the wavelength of light is kept constant in this series of steps.

PART B Effect of Wavelength on the Rate of Photosynthesis

11. Click the Reset button. Prepare a data table like Table B shown below.

TABLE B VARYING WAVELENGTH AT A LIGHT INTENSITY OF 200 LUX

Wavelength (nm)	% Maximal ATP	Number of ATP
400		
450		
500		
550		
600		
650		
700		
750		

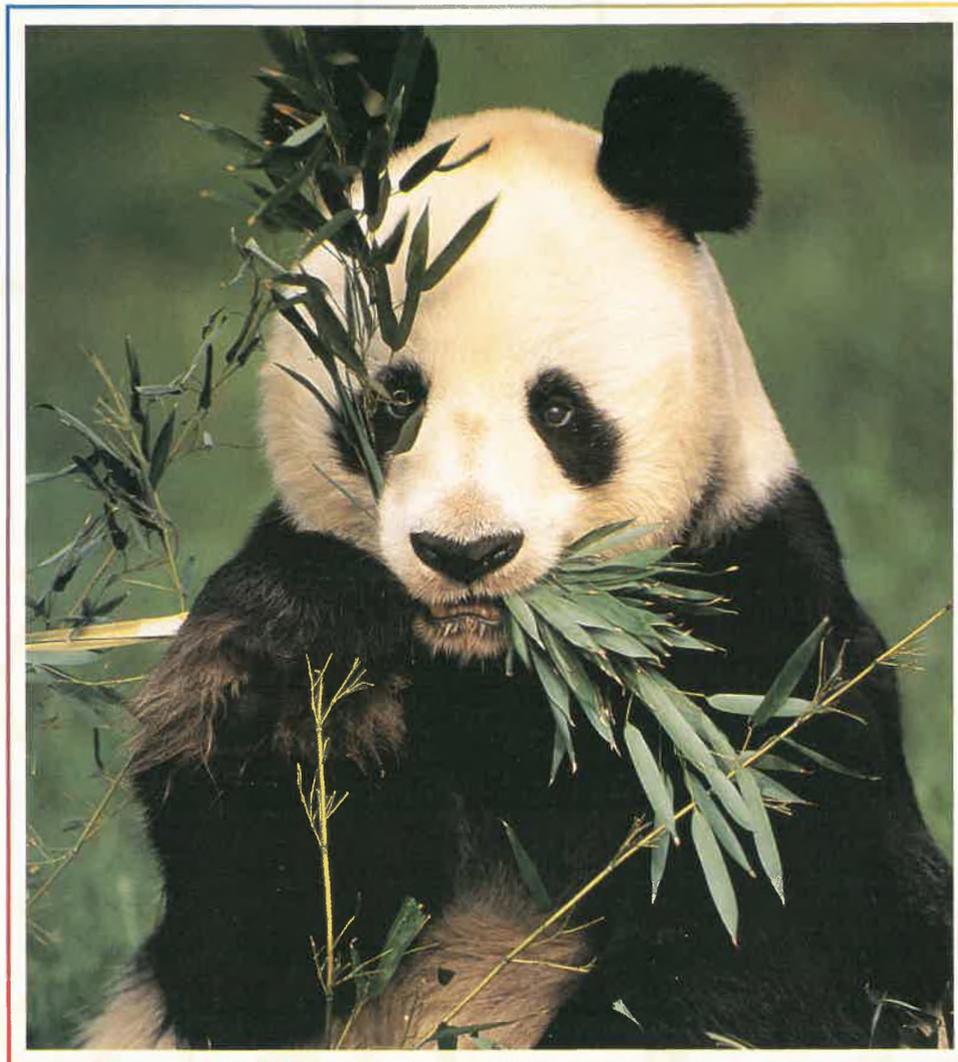
12. Click and slide the light intensity indicator to 200 lux. Click and slide the wavelength of light indicator to 400 nanometers.
13. Click the Start button and allow the simulation to run for 30 seconds, as indicated on the relative time meter.
14. Click the Stop button and record the % Maximal ATP and Number of ATP in your data table.
15. Continue testing until you have evaluated all of the wavelengths of light listed on your table.
16. Explain why you did not vary the intensity of light in this part of the investigation.

Analysis and Conclusions

1. Prepare a bar graph that shows the % Maximal ATP on the *y*-axis and the intensity of light on the *x*-axis. Above each bar, indicate the number of ATP molecules produced.
2. What can you conclude about the effect of light intensity on the rate of photosynthesis?
3. Prepare another bar graph, plotting the % Maximal ATP versus the wavelength of light.
4. Refer to your second graph. What wavelengths of light are most effective for photosynthesis?
5. Which combination of wavelength and intensity of light would produce the highest rate of photosynthesis?

CHAPTER 7

CELLULAR RESPIRATION



*Like other heterotrophs, the giant panda, *Ailuropoda melanoleuca*, obtains organic compounds by consuming other organisms. Biochemical pathways within the panda's cells transfer energy from those compounds to ATP.*

FOCUS CONCEPT: *Matter, Energy, and Organization*

As you read, compare the biochemical pathways described in this chapter with those you studied in the chapter on photosynthesis.

7-1 *Glycolysis and Fermentation*

7-2 *Aerobic Respiration*



Unit 3—*Cellular Respiration*
Topics 1–6

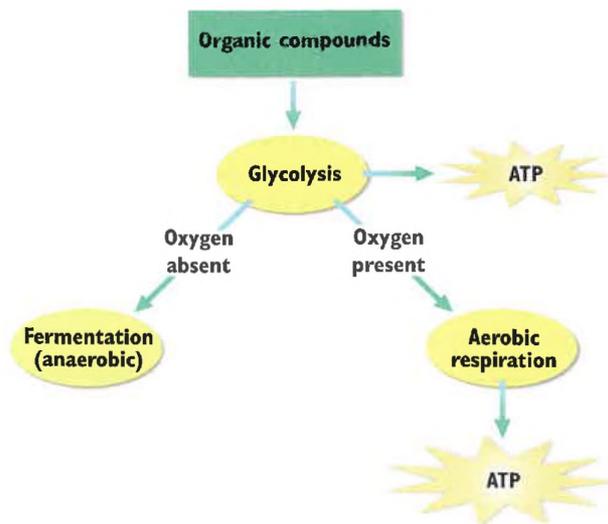
GLYCOLYSIS AND FERMENTATION

All cells break down complex organic compounds into simpler molecules. Cells use some of the energy that is released in this process to make ATP.

HARVESTING CHEMICAL ENERGY

You learned in Chapter 6 that autotrophs, such as plants, use photosynthesis to convert light energy from the sun into chemical energy, which is stored in carbohydrates and other organic compounds. Both autotrophs and heterotrophs depend on these organic compounds for the energy to power cellular activities. By breaking down these compounds into simpler molecules, cells release energy. Some of the energy is used to make ATP from ADP and phosphate. Remember from Chapter 3 that ATP is the main energy currency of cells. The complex process in which cells make ATP by breaking down organic compounds is known as **cellular respiration**.

As you can see in Figure 7-1, cellular respiration begins with a biochemical pathway called **glycolysis** (GLIE-KAHL-uh-suhs), which yields a relatively small amount of ATP. The other products of glycolysis can follow either of two main pathways, depending on whether there is oxygen in the cell. If oxygen is absent, the products of glycolysis may enter fermentation pathways that yield no



SECTION

7-1

OBJECTIVES

Define cellular respiration.

Describe the major events in glycolysis.

Compare and contrast lactic acid fermentation and alcoholic fermentation.

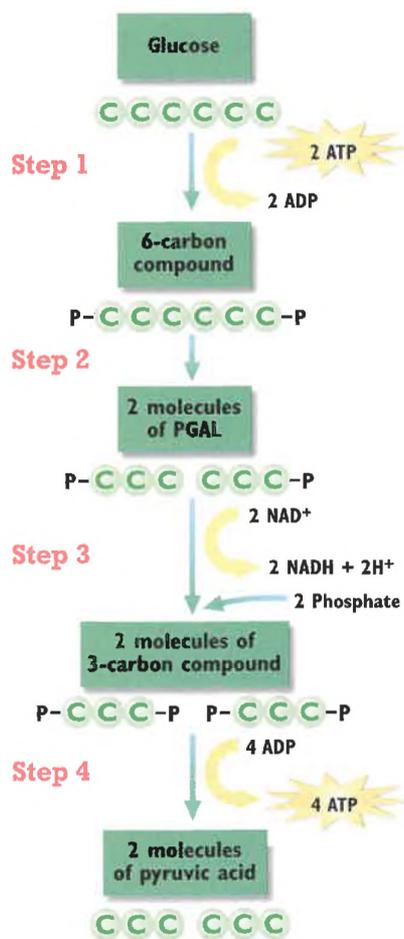
Calculate the efficiency of glycolysis.

FIGURE 7-1

Cellular respiration harnesses the energy in organic compounds to produce ATP. The initial pathway in cellular respiration, called glycolysis, produces a small amount of ATP. Glycolysis can lead to fermentation if oxygen is absent or to aerobic respiration if oxygen is present. Most of the ATP produced in cellular respiration results from aerobic respiration.

FIGURE 7-2

Glycolysis takes place in the cytosol of cells and involves four main steps. Step 1: A molecule of glucose is converted into a new six-carbon compound. Step 2: The new six-carbon compound is split into two molecules of PGAL. Step 3: The two PGAL molecules are oxidized to produce two new three-carbon compounds. Step 4: The new three-carbon compounds are converted into two molecules of pyruvic acid. Note that two ATP molecules are used in Step 1, but four more are produced in Step 4. Thus, glycolysis results in a net production of two ATP molecules.



additional ATP. Because they operate in the absence of oxygen, the fermentation pathways are said to be **anaerobic** (AN-uh-ROH-bik) **pathways**. If oxygen is present, the products of glycolysis enter the pathways of aerobic respiration. Aerobic respiration produces a much larger amount of ATP than does glycolysis alone.

Many of the reactions in cellular respiration are redox reactions. Recall from Chapter 2 that in a redox reaction, one reactant is oxidized while another is reduced. Although many kinds of organic compounds can be oxidized in cellular respiration, it is customary to focus on the simple sugar glucose, whose oxidation begins with glycolysis.

GLYCOLYSIS

Glycolysis is a pathway in which one six-carbon molecule of glucose is oxidized to produce two three-carbon molecules of **pyruvic** (pie-ROO-vik) **acid**. Like other biochemical pathways, glycolysis consists of a series of chemical reactions catalyzed by specific enzymes. All of the reactions of glycolysis take place in the cytosol of the cell. These reactions can be condensed into four main steps. Refer to Figure 7-2 as you read about each of these four steps.

Step 1. Two phosphate groups are attached to glucose, forming a new six-carbon compound. The phosphate groups are supplied by two molecules of ATP, which are converted into two molecules of ADP in the process.

Step 2. The six-carbon compound formed in Step 1 is split into two three-carbon molecules of PGAL. Recall from Chapter 6 that PGAL is also produced by the Calvin cycle in photosynthesis.

Step 3. The two PGAL molecules are oxidized, and each receives a phosphate group. The product of this step is two molecules of a new three-carbon compound. As you can see in Figure 7-2, the oxidation of PGAL is accompanied by the reduction of two molecules of **NAD⁺** to **NADH**. **NAD⁺**, or nicotinamide adenine dinucleotide, is very similar to **NADP⁺**, a compound you encountered in the light reactions of photosynthesis. Like **NADP⁺**, **NAD⁺** is an organic molecule that accepts electrons during redox reactions.

Step 4. The phosphate groups added in Step 1 and Step 3 are removed from the three-carbon compounds formed in Step 3. This reaction produces two molecules of pyruvic acid. Each phosphate group is combined with a molecule of ADP to make a molecule of ATP. Because a total of four phosphate groups were added in Step 1 and Step 3, four molecules of ATP are produced.

Notice that two ATP molecules were used in Step 1, but four were produced in Step 4. Therefore, glycolysis has a net yield of two ATP molecules for every molecule of glucose that is converted into pyruvic acid. What happens to the pyruvic acid depends on the type of cell and on whether oxygen is present.

FERMENTATION

In the absence of oxygen, some cells can convert pyruvic acid into other compounds through additional biochemical pathways that occur in the cytosol. The combination of glycolysis plus these additional pathways is known as **fermentation**. The additional fermentation pathways do not produce ATP. However, they do regenerate NAD^+ , which can be used to keep glycolysis going to make more ATP. There are many fermentation pathways, and they differ in terms of the enzymes that are used and the compounds that are made from pyruvic acid. Two common fermentation pathways result in the production of lactic acid and ethyl alcohol.

Lactic Acid Fermentation

In **lactic acid fermentation**, an enzyme converts pyruvic acid into another three-carbon compound, called lactic acid. As Figure 7-3a shows, lactic acid fermentation involves the transfer of two hydrogen atoms from $\text{NADH} + \text{H}^+$ to pyruvic acid. In the process, $\text{NADH} + \text{H}^+$ is oxidized to form NAD^+ . The resulting NAD^+ is used in glycolysis, where it is again reduced to $\text{NADH} + \text{H}^+$. Thus, the regeneration of NAD^+ in lactic acid fermentation helps to keep glycolysis operating.

Word Roots and Origins

fermentation

from the Latin *fermentum*,
meaning "yeast"

internetconnect

SCiLINKSSM
NSTA

TOPIC: Fermentation
GO TO: www.scilinks.org
KEYWORD: HM129

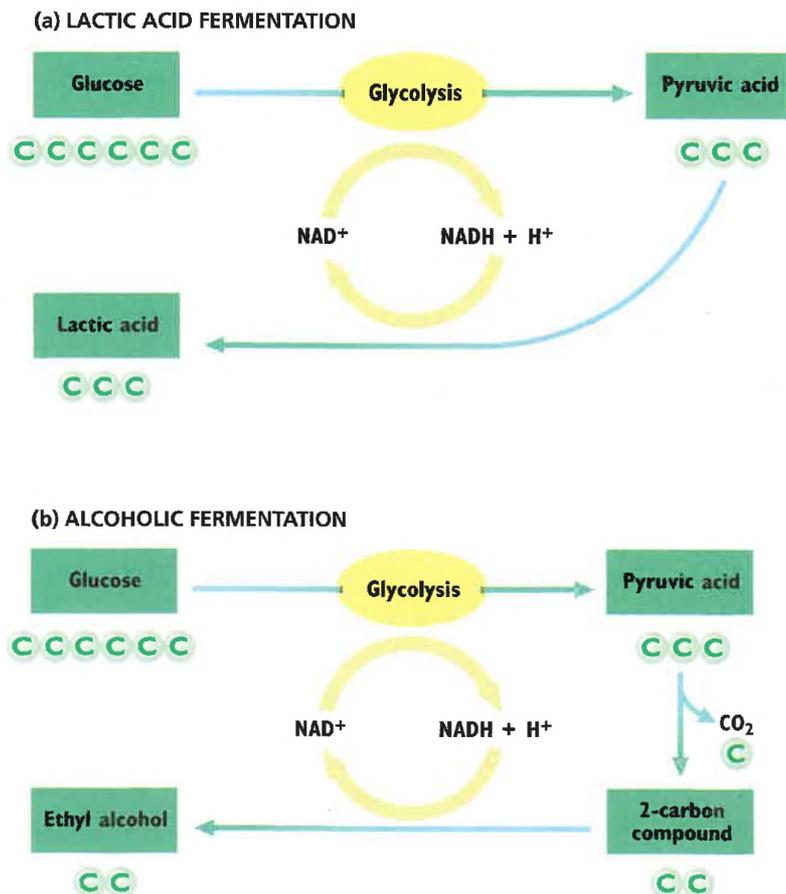


FIGURE 7-3

(a) Some cells engage in lactic acid fermentation when oxygen is absent. In this process, pyruvic acid is reduced to lactic acid and $\text{NADH} + \text{H}^+$ is oxidized to NAD^+ . (b) Other cells engage in alcoholic fermentation, converting pyruvic acid into ethyl alcohol. Again, $\text{NADH} + \text{H}^+$ is oxidized to NAD^+ .



FIGURE 7-4

In cheese making, fungi or bacteria are added to large vats of milk. The microorganisms carry out lactic acid fermentation, converting some of the sugar in the milk to lactic acid.

Lactic acid fermentation by microorganisms plays an essential role in the manufacture of food products such as yogurt and cheese, as illustrated in Figure 7-4. Lactic acid fermentation also occurs in your muscle cells during very strenuous exercise, such as sprinting at top speed. During this kind of exercise, muscle cells use up oxygen more rapidly than it can be delivered to them. As oxygen becomes depleted, the muscle cells begin to switch from aerobic respiration to lactic acid fermentation. Lactic acid accumulates in the muscle cells, making the cells' cytosol more acidic. The increased acidity may reduce the capacity of the cells to contract, resulting in muscle fatigue, pain, and even cramps. Eventually, the lactic acid diffuses into the blood and is transported to the liver, where it is converted back into pyruvic acid when oxygen becomes available.

Alcoholic Fermentation

Some plant cells and unicellular organisms, such as yeast, use a process called **alcoholic fermentation** to convert pyruvic acid into ethyl alcohol. This pathway requires two steps, which are shown in Figure 7-3b. In the first step, a CO_2 molecule is removed from pyruvic acid, leaving a two-carbon compound. In the second step, two hydrogen atoms are added to the two-carbon compound to form ethyl alcohol. As in lactic acid fermentation, these hydrogen atoms come from NADH and H^+ , regenerating NAD^+ for use in glycolysis.

Alcoholic fermentation is the basis of the wine and beer industries. Yeast cells are added to the fermentation mixture to provide the enzymes needed for alcoholic fermentation. As fermentation proceeds, ethyl alcohol accumulates in the mixture until it reaches a concentration that inhibits fermentation. For wine, that concentration is around 12 percent. To make table wines, the CO_2 that is generated in the first step of fermentation is allowed to escape from the mixture through a one-way gas valve. To make sparkling wines, such as champagne, CO_2 is retained within the mixture, "carbonating" the beverage.

Bread making also depends on alcoholic fermentation performed by yeast cells. In this case, the CO_2 that is produced by fermentation makes the bread rise by forming bubbles inside the dough, and the ethyl alcohol evaporates during baking.

ENERGY YIELD

How efficient are the anaerobic pathways at obtaining energy from glucose and using it to make ATP from ADP? To answer this question, one must compare the amount of energy available in glucose with the amount of energy contained in the ATP that is produced by the anaerobic pathways. In such comparisons, energy is often measured in units of **kilocalories** (kcal). One kilocalorie equals 1,000 calories (cal).

Word Roots and Origins

kilocalorie

from the Greek *chilioi*, meaning "thousand," and the Latin *calor*, meaning "heat"

Scientists have calculated that the complete oxidation of a standard amount of glucose releases 686 kcal. Under the conditions that exist inside most cells, the production of a standard amount of ATP from ADP absorbs about 12 kcal. Recall that two ATP molecules are produced from every glucose molecule that is broken down by glycolysis.

$$\begin{aligned}\text{Efficiency of glycolysis} &= \frac{\text{Energy required to make ATP}}{\text{Energy released by oxidation of glucose}} \\ &= \frac{2 \times 12 \text{ kcal}}{686 \text{ kcal}} \times 100\% = 3.5\%\end{aligned}$$

You can see that the two ATP molecules produced during glycolysis receive only a small percentage of the energy that could be released by the complete oxidation of each molecule of glucose. Much of the energy originally contained in glucose is still held in pyruvic acid. Even if pyruvic acid is converted into lactic acid or ethyl alcohol, no additional ATP is synthesized. It's clear that the anaerobic pathways are not very efficient in transferring energy from glucose to ATP.

The anaerobic pathways probably evolved very early in the history of life on Earth. The first organisms were bacteria, and they produced all of their ATP through glycolysis. It took more than a billion years for the first photosynthetic organisms to appear. The oxygen they released as a byproduct of photosynthesis stimulated the evolution of organisms that make most of their ATP through aerobic respiration.

By themselves, the anaerobic pathways provide enough energy for many present-day organisms. However, most of these organisms are unicellular, and those that are multicellular are very small. All of them have limited energy requirements. Larger organisms have much greater energy requirements that cannot be satisfied by the anaerobic pathways alone. These larger organisms meet their energy requirements with the more efficient pathways of aerobic respiration.

SECTION 7-1 REVIEW

1. Define *cellular respiration*.
2. What six-carbon molecule begins glycolysis, and what three-carbon molecules are produced at the end of glycolysis?
3. For each six-carbon molecule that begins glycolysis, how many ATP molecules are used and how many ATP molecules are produced?
4. What condition must exist in a cell for the cell to engage in fermentation?
5. How efficient is glycolysis?
6. **CRITICAL THINKING** A large amount of ATP in a cell inhibits the enzymes that catalyze the first few steps of glycolysis. How will this inhibition eventually affect the amount of ATP in the cell? Explain your answer.

Organelles as Organisms

This excerpt is from *The Lives of a Cell: Notes of a Biology Watcher*, by Lewis Thomas.

We seem to be living through the biologic revolution, so far anyway, without being upheaved or even much disturbed by it. . . .

It is not too early to begin looking for trouble. I can sense some, for myself anyway, in what is being learned about organelles. I was raised in the belief that these were obscure little engines inside my cells, owned and operated by me or my cellular delegates, private, sub-microscopic bits of my intelligent flesh. Now, it appears, some of them, and the most important ones at that, are total strangers.

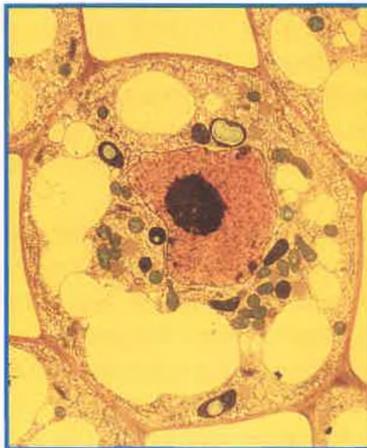
The evidence is strong, and direct. The membranes lining the inner compartment of mitochondria are unlike other animal cell membranes, and resemble most closely the membranes of bacteria. . . .

The chloroplasts in all plants are, similarly, independent and self-replicating lodgers. . . .

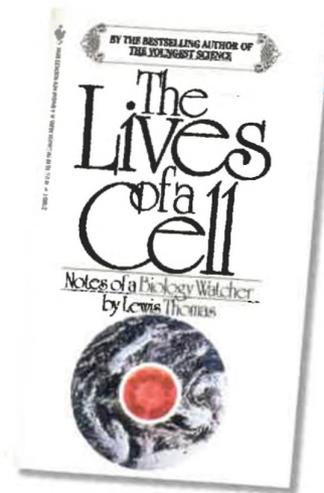
Actually, the suggestion that chloroplasts and mitochondria might be endosymbionts was made as long ago as 1885. . . . There is careful, restrained speculation on how they got there in the first place, with a consensus that they were probably engulfed by larger cells more than a billion years ago and have simply stayed there ever since.

The usual way of looking at them is as enslaved creatures, captured to supply ATP for cells

unable to respire on their own, or to provide carbohydrate and oxygen for cells unequipped for photosynthesis. This master-slave arrangement is the common view of full-grown biologists, eukaryotes all. But there is the other side. From their own standpoint, the organelles might be viewed as having learned early how to have the best of possible worlds, with least effort and risk to themselves and their



progeny. Instead of evolving as we have done, manufacturing longer and elaborately longer strands of DNA, and running ever-increasing risks of mutating into evolutionary cul-de-sacs, they elected to stay small and stick to one line of work. To accomplish this, and to assure themselves the longest possible run, they got themselves inside all the rest of us.



It is a good thing for the entire enterprise that mitochondria and chloroplasts have remained small, conservative, and stable, since these two organelles are, in a fundamental sense, the most important living things on earth. Between them they produce the oxygen and arrange for its use. In effect, they run the place.

Reading for Meaning

What do you think Thomas means when he says that the organelles "run the place"? What makes them so important?

Read Further

The Lives of a Cell: Notes of a Biology Watcher is a collection of essays by Lewis Thomas. Thomas goes on in this essay to describe things about organelles that trouble him. Some are fairly serious concerns, such as Could my organelles catch a virus? Others are more whimsical, such as Who am I really if I'm mostly organelles? What actual problems might organelles cause?

From "Organelles as Organisms, 69–74" from *The Lives of a Cell* by Lewis Thomas. Copyright © 1972 by The Massachusetts Medical Society. Reprinted by permission of Viking Penguin, a division of Penguin Putnam Inc.

SECTION

7-2

OBJECTIVES

Summarize the events of the Krebs cycle.

Summarize the events of the electron transport chain.

Relate aerobic respiration to the structure of a mitochondrion.

Calculate the efficiency of aerobic respiration.

AEROBIC RESPIRATION

*In most cells, the pyruvic acid that is produced in glycolysis does not undergo fermentation. Instead, if oxygen is available, pyruvic acid enters the pathways of **aerobic** (UHR-OH-bik) **respiration**, or cellular respiration that requires oxygen. Aerobic respiration produces nearly 20 times as much ATP as is produced by glycolysis alone.*

OVERVIEW OF AEROBIC RESPIRATION

Aerobic respiration has two major stages: the Krebs cycle and the electron transport chain. In the Krebs cycle, the oxidation of glucose that began with glycolysis is completed. As glucose is oxidized, NAD^+ is reduced to NADH. In the electron transport chain, NADH is used to make ATP. Although the Krebs cycle also produces a small amount of ATP, most of the ATP produced during aerobic respiration is made by the electron transport chain. The reactions of the Krebs cycle and the electron transport chain occur only if oxygen is present in the cell.

In prokaryotes, the reactions of the Krebs cycle and the electron transport chain take place in the cytosol of the cell. In eukaryotic cells, however, these reactions take place inside mitochondria rather than in the cytosol. The pyruvic acid that is produced in glycolysis diffuses across the double membrane of a mitochondrion and enters the **mitochondrial matrix**. The mitochondrial matrix is the space inside the inner membrane of a mitochondrion. Figure 7-5 illustrates the relationships between these mitochondrial parts. The mitochondrial matrix contains the enzymes needed to catalyze the reactions of the Krebs cycle.

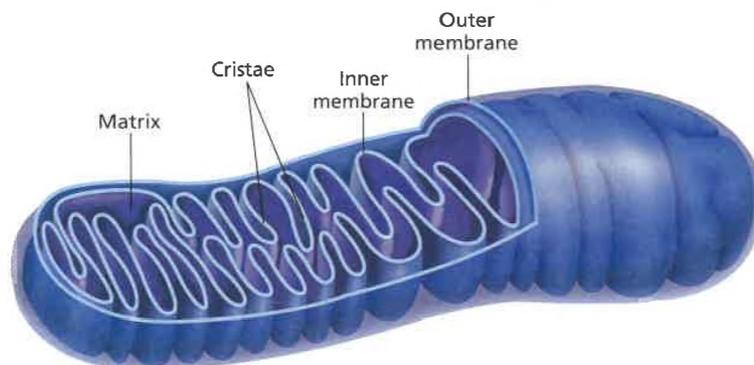


FIGURE 7-5

In eukaryotic cells, the reactions of aerobic respiration occur inside mitochondria. The Krebs cycle takes place in the mitochondrial matrix, and the electron transport chain is located in the inner membrane.

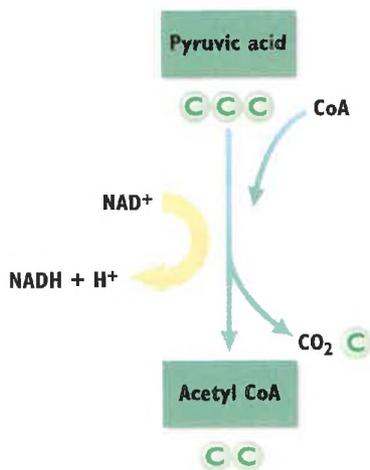


FIGURE 7-6

In aerobic respiration, pyruvic acid combines with coenzyme A to form acetyl CoA. Notice that CO₂, NADH, and H⁺ are also produced in this reaction.



Quick Lab

Comparing CO₂ Production

Materials disposable gloves, lab apron, safety goggles, 250 mL flask, 100 mL graduated cylinder, phenolphthalein solution, pipet, drinking straw, water, clock, sodium hydroxide solution

Procedure



- Put on your disposable gloves, lab apron, and safety goggles.
- Add 50 mL of water and four drops of phenolphthalein to the flask.
- Use the straw to gently blow into the solution for 1 minute. Add the sodium hydroxide one drop at a time, and gently swirl the flask.
- When the liquid turns pink, stop adding drops. Record the number of drops you used.
- Empty and rinse your flask as your teacher directs, and repeat step 2. Walk vigorously for 2 minutes, and repeat steps 3 and 4.

Analysis Which trial produced the most carbon dioxide? Which trial used the most energy?

When pyruvic acid enters the mitochondrial matrix, it reacts with a molecule called coenzyme A to form **acetyl** (uh-SEET-uhl) **coenzyme A**, abbreviated **acetyl CoA** (uh-SEET-uhl KOH-AY). This reaction is illustrated in Figure 7-6. The acetyl part of acetyl CoA contains two carbon atoms, but as you learned earlier, pyruvic acid is a three-carbon compound. The carbon atom that is lost in the conversion of pyruvic acid to acetyl CoA is released in a molecule of CO₂. Figure 7-6 also indicates that this reaction reduces a molecule of NAD⁺ to NADH.

THE KREBS CYCLE

The **Krebs cycle** is a biochemical pathway that breaks down acetyl CoA, producing CO₂, hydrogen atoms, and ATP. The reactions that make up the cycle were identified by Hans Krebs (1900–1981), a German-British biochemist. The Krebs cycle has five main steps. In eukaryotic cells, all five steps occur in the mitochondrial matrix. Examine Figure 7-7 as you read about the steps in the Krebs cycle.

Step 1. A two-carbon molecule of acetyl CoA combines with a four-carbon compound, **oxaloacetic** (AHKS-uh-loh-uh-SEET-ik) **acid**, to produce a six-carbon compound, **citric** (SI-trik) **acid**. Notice that this reaction regenerates coenzyme A.

Step 2. Citric acid releases a CO₂ molecule and a hydrogen atom to form a five-carbon compound. By losing a hydrogen atom with its electron, citric acid is oxidized. The hydrogen atom is transferred to NAD⁺, reducing it to NADH.

Step 3. The five-carbon compound formed in Step 2 also releases a CO₂ molecule and a hydrogen atom, forming a four-carbon compound. Again, NAD⁺ is reduced to NADH. Notice that in this step a molecule of ATP is also synthesized from ADP.

Step 4. The four-carbon compound formed in Step 3 releases a hydrogen atom to form another four-carbon compound. This time, the hydrogen atom is used to reduce FAD to FADH₂. **FAD**, or flavin adenine dinucleotide, is a molecule very similar to NAD⁺. Like NAD⁺, FAD accepts electrons during redox reactions.

Step 5. The four-carbon compound formed in Step 4 releases a hydrogen atom to regenerate oxaloacetic acid, which keeps the Krebs cycle operating. The hydrogen atom reduces NAD⁺ to NADH.

Recall that in glycolysis one glucose molecule produces two pyruvic acid molecules, which can then form two molecules of acetyl CoA. Thus, one glucose molecule causes two turns of the Krebs cycle. These two turns produce six NADH, two FADH₂, two ATP, and four CO₂ molecules. The CO₂ is a waste product that diffuses out of the cells and is given off by the organism. The ATP can be used for energy. But note that each glucose molecule yields only two molecules of ATP through the Krebs cycle—the same number as in glycolysis.

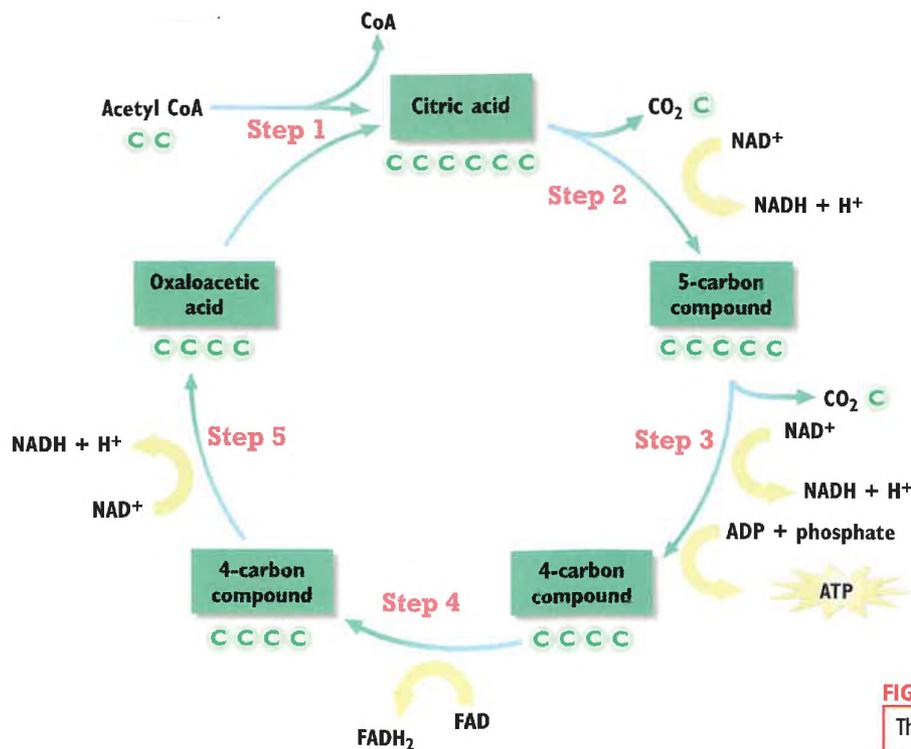


FIGURE 7-7

The Krebs cycle takes place in the mitochondrial matrix and involves five main steps. Step 1: Acetyl CoA combines with oxaloacetic acid to produce citric acid. Step 2: Citric acid releases a CO_2 molecule to form a five-carbon compound. Step 3: The five-carbon compound releases a CO_2 molecule to form a four-carbon compound. Step 4: The four-carbon compound is converted into a new four-carbon compound. Step 5: The new four-carbon compound is converted back into oxaloacetic acid. In addition to CO_2 , each turn of the Krebs cycle produces ATP, NADH, and FADH_2 .

The bulk of the energy released by the oxidation of glucose still has not been transferred to ATP. That transfer requires the NADH and FADH_2 made in the pathways you have learned about so far. Recall that glycolysis produces two NADH molecules and that the conversion of pyruvic acid to acetyl CoA produces two more. Adding the six NADH molecules from the Krebs cycle gives a total of 10 NADH molecules for every glucose molecule that is oxidized. These 10 NADH molecules and the two FADH_2 molecules from the Krebs cycle drive the next stage of aerobic respiration. That is where most of the energy transfer from glucose to ATP actually occurs.

ELECTRON TRANSPORT CHAIN

The **electron transport chain** constitutes the second stage of aerobic respiration. In eukaryotic cells, the electron transport chain lines the inner membrane of the mitochondrion. Remember from Chapter 4 that the inner membrane has many long folds called cristae. In prokaryotes, the electron transport chain lines the cell membrane. ATP is produced by the electron transport chain when NADH and FADH_2 release hydrogen atoms, regenerating NAD^+ and FAD. To understand how ATP is produced, you must follow what happens to the electrons and protons that make up these hydrogen atoms.

internetconnect	
 SCILINKS	TOPIC: Krebs cycle GO TO: www.scilinks.org KEYWORD: HM135
	NSTA

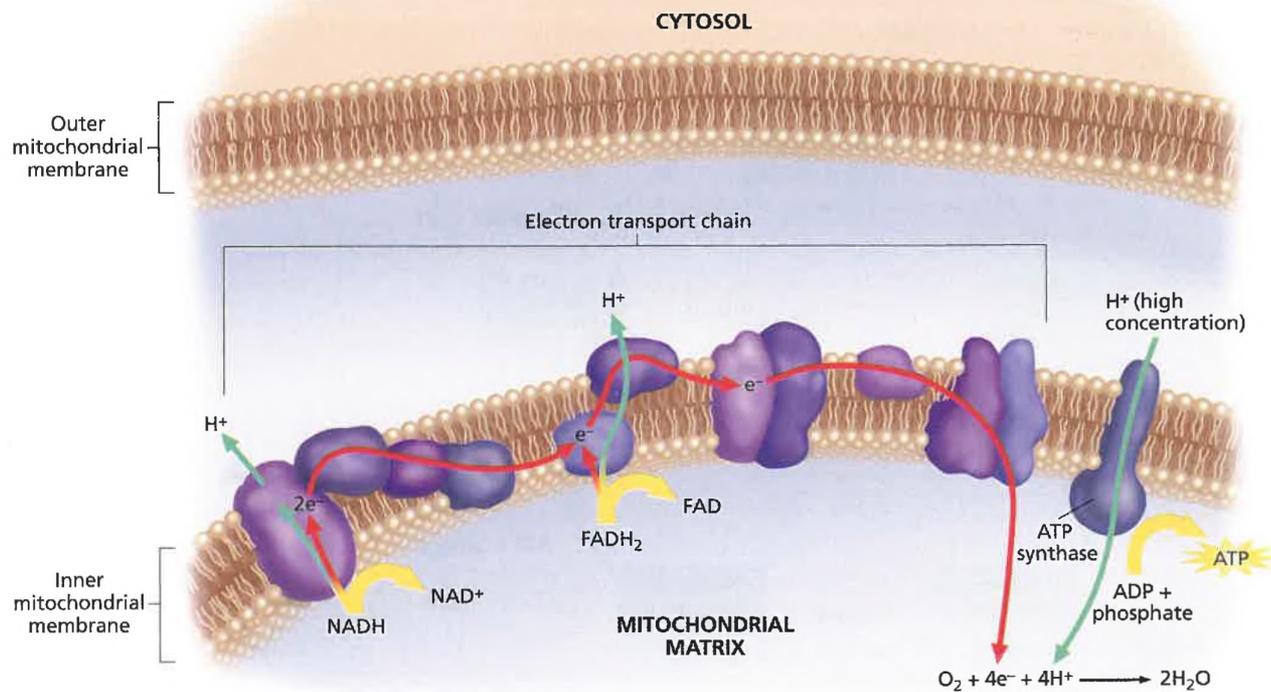


FIGURE 7-8

NADH and $FADH_2$ supply electrons and protons to the electron transport chain. The electrons are passed along the chain from molecule to molecule in a series of redox reactions. The protons are pumped out of the mitochondrial matrix. As the protons return to the mitochondrial matrix through ATP synthase, they release energy, driving the synthesis of ATP. The final acceptor of electrons is oxygen, which also accepts protons in a reaction that forms water.

The electrons in the hydrogen atoms from NADH and $FADH_2$ are at a high energy level. In the electron transport chain, these high-energy electrons are passed along a series of molecules, as shown in Figure 7-8. As they move from molecule to molecule, the electrons lose some of their energy. The energy they lose is used to pump the protons of the hydrogen atoms from the mitochondrial matrix to the other side of the inner mitochondrial membrane. This pumping builds up a high concentration of protons in the space between the inner and outer mitochondrial membranes. In other words, a concentration gradient of protons is created across the inner mitochondrial membrane.

The concentration gradient of protons drives the synthesis of ATP by chemiosmosis, the same process that generates ATP in photosynthesis. As you can see in Figure 7-8, ATP synthase molecules are located in the inner mitochondrial membrane. ATP synthase makes ATP from ADP as protons move down their concentration gradient into the mitochondrial matrix.

The Role of Oxygen

ATP can be synthesized by chemiosmosis only if electrons continue to move from molecule to molecule in the electron transport chain. Obviously, the last molecule in the electron transport chain cannot keep all of the electrons it accepts. If it did, the electron transport chain would come to a halt. Consider what would happen if cars kept entering a dead-end, one-way street. At some point, no more cars could enter the street. Similarly, if the last molecule could not “unload” the electrons it accepts, then no more electrons could enter the electron transport chain and ATP synthesis would stop.

Here is where oxygen comes into play in aerobic respiration. Figure 7-8 shows that oxygen serves as the final acceptor of electrons. By accepting electrons from the last molecule in the electron transport chain, oxygen allows additional electrons to pass along the chain. As a result, ATP can continue to be synthesized by chemiosmosis. Oxygen also accepts the protons that were once part of the hydrogen atoms supplied by NADH and FADH₂. By combining with both electrons and protons, oxygen forms water, as shown in the following equation:



ENERGY YIELD

How many ATP molecules are made in aerobic respiration? Refer to Figure 7-9 as you calculate the total. Recall that glycolysis and the Krebs cycle each produce two ATP molecules for every glucose molecule that is oxidized. Furthermore, each NADH molecule that supplies the electron transport chain can generate three ATP molecules, and each FADH₂ molecule can generate two ATP molecules. Thus, the 10 NADH and two FADH₂ molecules made through aerobic respiration can produce up to 34 ATP molecules by the electron transport chain. Adding the four ATP molecules from glycolysis and the Krebs cycle gives a maximum yield of 38 ATP molecules per molecule of glucose.

The actual number of ATP molecules generated through aerobic respiration varies from cell to cell. In most eukaryotic cells, the NADH that is made in the cytosol during glycolysis cannot diffuse through the inner membrane of the mitochondrion. Instead, it must be actively transported into the mitochondrial matrix. The active transport of NADH consumes ATP. As a result, most eukaryotic cells produce only about 36 ATP molecules per glucose molecule.

How efficient is aerobic respiration in providing a cell with energy for cellular activities? Consider the efficiency when a cell generates 38 ATP molecules:

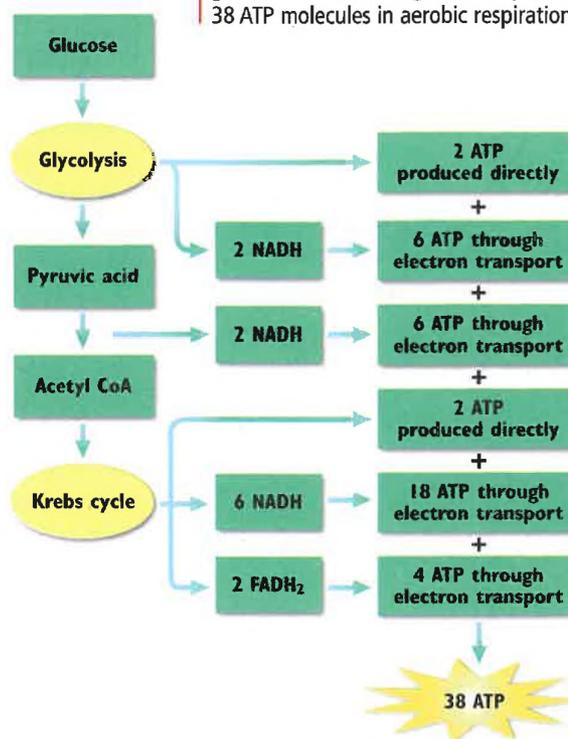
$$\text{Efficiency of aerobic respiration} = \frac{\text{Energy required to make ATP}}{\text{Energy released by oxidation of glucose}}$$

$$= \frac{38 \times 12 \text{ kcal}}{686 \text{ kcal}} \times 100\% = 66\%$$

This means that aerobic respiration is nearly 20 times more efficient than glycolysis alone. In fact, the efficiency of aerobic respiration is quite impressive compared with the efficiency of

FIGURE 7-9

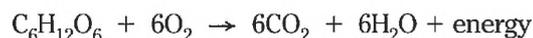
Follow each pathway to see how one glucose molecule can generate up to 38 ATP molecules in aerobic respiration.



machines that humans have designed and built. An automobile engine, for example, is only about 25 percent efficient in extracting energy from gasoline to move a car. Most of the remaining energy released from gasoline is lost as heat.

SUMMARIZING CELLULAR RESPIRATION

The complete oxidation of glucose in aerobic respiration is summarized by the following equation:



Recall the equations for photosynthesis that you learned in Chapter 6. Notice that the equation above is the opposite of the overall equation for photosynthesis, if glucose is considered to be a product of photosynthesis. That is, the products of photosynthesis are reactants in aerobic respiration, and the products of aerobic respiration are reactants in photosynthesis. However, it is important to remember that aerobic respiration is not the reverse of photosynthesis. As you have seen, these two processes involve different biochemical pathways and occur at different sites inside cells.

Cellular respiration provides the ATP that all cells need to support the activities of life. But providing cells with ATP is not the only important function of cellular respiration. Cells also need specific organic compounds from which to build the macromolecules that compose their own structure. Some of these specific compounds may not be contained in the food a heterotroph consumes. However, the molecules formed at different steps in glycolysis and the Krebs cycle are often used by cells to make the compounds that are missing in food. Thus, another important function of cellular respiration is to provide carbon skeletons that can be built up into larger molecules needed by cells.

SECTION 7-2 REVIEW

1. What four-carbon compound is regenerated at the end of the Krebs cycle? With what two-carbon compound does it combine at the start of the Krebs cycle?
2. How is the synthesis of ATP in the electron transport chain of mitochondria similar to the synthesis of ATP in chloroplasts?
3. What role does oxygen play in aerobic respiration? What molecule does oxygen become a part of as a result of aerobic respiration?
4. In what part of a mitochondrion does the Krebs cycle occur? In what part of a mitochondrion is the electron transport chain located?
5. Calculate the efficiency of aerobic respiration if a cell generates 32 ATP molecules per molecule of glucose.
6. **CRITICAL THINKING** Sometimes protons leak out of a cell or are used for other purposes besides ATP production. How would this affect the production of ATP in aerobic respiration?

CHAPTER 7 REVIEW

SUMMARY/VOCABULARY

- 7-1** ■ Cellular respiration is the process by which cells break down organic compounds to release energy and make ATP. It includes anaerobic pathways, which operate in the absence of oxygen, and aerobic respiration, which occurs when oxygen is present.
- Cellular respiration begins with glycolysis, which takes place in the cytosol of cells. During glycolysis, one glucose molecule is oxidized to form two pyruvic acid molecules. Glycolysis results in a net production of two ATP molecules and four NADH molecules.
 - Fermentation is a set of anaerobic pathways in which pyruvic acid is converted into other organic molecules in the cytosol.

Vocabulary

alcoholic fermentation (130) fermentation (129)
anaerobic pathway (128) glycolysis (127)
cellular respiration (127)

Fermentation does not produce ATP, but it does regenerate NAD^+ , which helps keep glycolysis operating.

- In lactic acid fermentation, an enzyme converts pyruvic acid into lactic acid.
- In alcoholic fermentation, other enzymes convert pyruvic acid into ethyl alcohol and CO_2 .
- Through glycolysis, only about 3.5 percent of the energy available from the oxidation of glucose is transferred to ATP.
- The anaerobic pathways probably evolved very early in the history of life on Earth. For more than a billion years, they were the only pathways available for harvesting chemical energy.

kilocalorie (130) NAD^+ (128)
lactic acid fermentation (129) pyruvic acid (128)

- 7-2** ■ In the presence of oxygen, pyruvic acid is converted into acetyl CoA. In eukaryotic cells, this reaction occurs inside the mitochondrial matrix.
- Acetyl CoA enters the Krebs cycle, a biochemical pathway that also takes place in the mitochondrial matrix. Each turn of the Krebs cycle generates three NADH, one FADH_2 , one ATP, and two CO_2 molecules.
 - NADH and FADH_2 donate electrons to the electron transport chain, which lines the inner mitochondrial membrane. Electrons are passed from molecule to molecule in the transport chain in a series of redox reactions.
 - As electrons pass along the electron transport chain, protons donated by NADH and FADH_2 are pumped into the space between the inner and outer mitochondrial membranes. This pumping creates a concentration gradient of protons across

Vocabulary

acetyl coenzyme A (134) citric acid (134)
aerobic respiration (133) electron transport chain (135)

the inner mitochondrial membrane. As protons move down their gradient and back into the mitochondrial matrix, ATP synthase uses the energy released by their movement to make ATP.

- During aerobic respiration, oxygen accepts both protons and electrons from the electron transport chain. As a result, oxygen is converted to water.
- Aerobic respiration can produce up to 38 ATP molecules from the oxidation of a single molecule of glucose. This means that up to 66 percent of the energy released by the oxidation of glucose can be transferred to ATP. However, most eukaryotic cells produce only about 36 ATP molecules per molecule of glucose.
- Besides transferring energy to ATP, cellular respiration also provides carbon skeletons that can be built up into larger molecules by cells.

FAD (134) mitochondrial matrix (133)
Krebs cycle (134) oxaloacetic acid (134)

REVIEW

Vocabulary

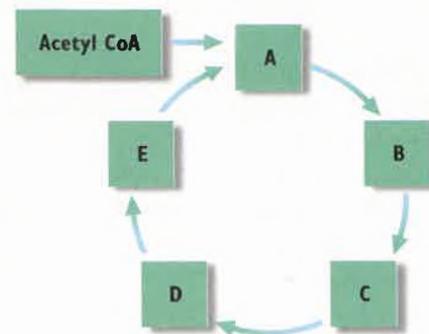
1. What molecule made during glycolysis is used in the later steps in fermentation?
2. What molecule made during the later steps in fermentation is used in glycolysis?
3. What molecules does the Krebs cycle make that the electron transport chain uses?
4. What molecule determines whether pyruvic acid will undergo fermentation or be converted for entry into the Krebs cycle?
5. What determines whether pyruvic acid will undergo lactic acid fermentation or alcoholic fermentation?

Multiple Choice

6. Before the Krebs cycle can proceed, pyruvic acid must be converted into (a) citric acid (b) glucose (c) acetyl CoA (d) NADH.
7. The net number of ATP molecules made directly by glycolysis is (a) 2 (b) 6 (c) 32 (d) 38.
8. In lactic acid fermentation, (a) NAD^+ is regenerated for use in glycolysis (b) lactic acid is converted into pyruvic acid (c) oxygen is consumed (d) electrons pass through the electron transport chain.
9. Which of the following is not a product of the Krebs cycle? (a) ATP (b) ethyl alcohol (c) CO_2 (d) FADH_2
10. Cellular respiration is similar to photosynthesis in that they both (a) produce ATP (b) involve chemiosmosis (c) make PGAL (d) all of the above.
11. ATP is synthesized in the electron transport chain when which of the following moves across the inner mitochondrial membrane? (a) NADH (b) protons (c) citric acid (d) oxygen
12. By accepting electrons and protons, the oxygen used in aerobic respiration turns into (a) CO_2 (b) H_2O (c) $\text{C}_6\text{H}_{12}\text{O}_6$ (d) ATP.
13. The Krebs cycle occurs in the (a) cytosol (b) outer mitochondrial membrane (c) mitochondrial matrix (d) space between the inner and outer mitochondrial membranes.
14. During each turn of the Krebs cycle, (a) two CO_2 molecules are produced (b) two ATP molecules are consumed (c) pyruvic acid combines with oxaloacetic acid (d) glucose combines with a four-carbon molecule.
15. Most of the ATP synthesized in aerobic respiration is made (a) during glycolysis (b) through fermentation (c) in the cytosol (d) through chemiosmosis.

Short Answer

16. Summarize the events that occur from the end of glycolysis through the first reaction of the Krebs cycle.
17. Why do most eukaryotic cells produce fewer than 38 ATP molecules for every glucose molecule that is oxidized by aerobic respiration?
18. How do the anaerobic pathways differ from the pathways of aerobic respiration, at the sites they occur in eukaryotic cells?
19. What causes your muscles to become fatigued and sometimes develop cramps when you exercise too strenuously?
20. How does aerobic respiration ultimately depend on photosynthesis?
21. What role does chemiosmosis play in aerobic respiration?
22. What role does oxygen play in aerobic respiration?
23. Refer to the diagram of the Krebs cycle shown below. How many carbon atoms are in each of the compounds represented by the letters A–E?



24. Unit 3—Cellular Respiration



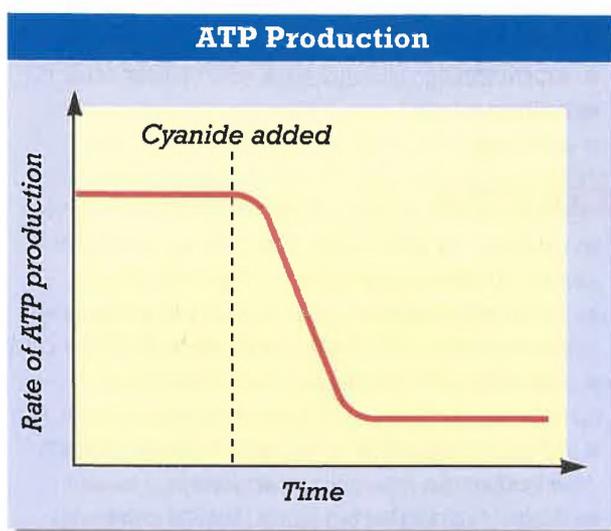
Write a report summarizing how exercise physiologists regulate the diet and training of athletes. Find out how diet varies according to the needs of each athlete. Research the relationship between exercise and metabolism.

CRITICAL THINKING

1. The enzyme that converts pyruvic acid into acetyl CoA requires vitamin B₁, also called thiamine. Like many other vitamins, thiamine cannot be made in the human body. What can you infer about the nutritional requirements of humans?
2. How does the folding of the inner mitochondrial membrane benefit aerobic respiration?
3. Yeast can produce ATP through either fermentation or aerobic respiration, depending on whether oxygen is present. If oxygen is present, yeast cells consume glucose much more slowly than if oxygen is absent. How can you explain this observation?
4. A person will breathe deeply and rapidly for some time after a period of very strenuous exercise. The longer and more intense the exercise was, the longer the deep breathing will continue after the exercise stops. Using your understanding of cellular respiration, explain why strenuous exercise stimulates deep breathing that continues after the end of exercise.
5. Some eukaryotic cells must use ATP to move NADH into the mitochondrial matrix. Knowing this, would you expect aerobic

respiration to be more efficient or less efficient in prokaryotic cells than it is in eukaryotic cells? Explain your answer.

6. The graph below shows the rate of ATP production by a culture of yeast cells over time. At the time indicated by the dashed line, cyanide was added to the culture. Cyanide blocks the flow of electrons to O₂ from the electron transport chain in mitochondria. Explain why adding cyanide has the effect on ATP production that is indicated by the graph.

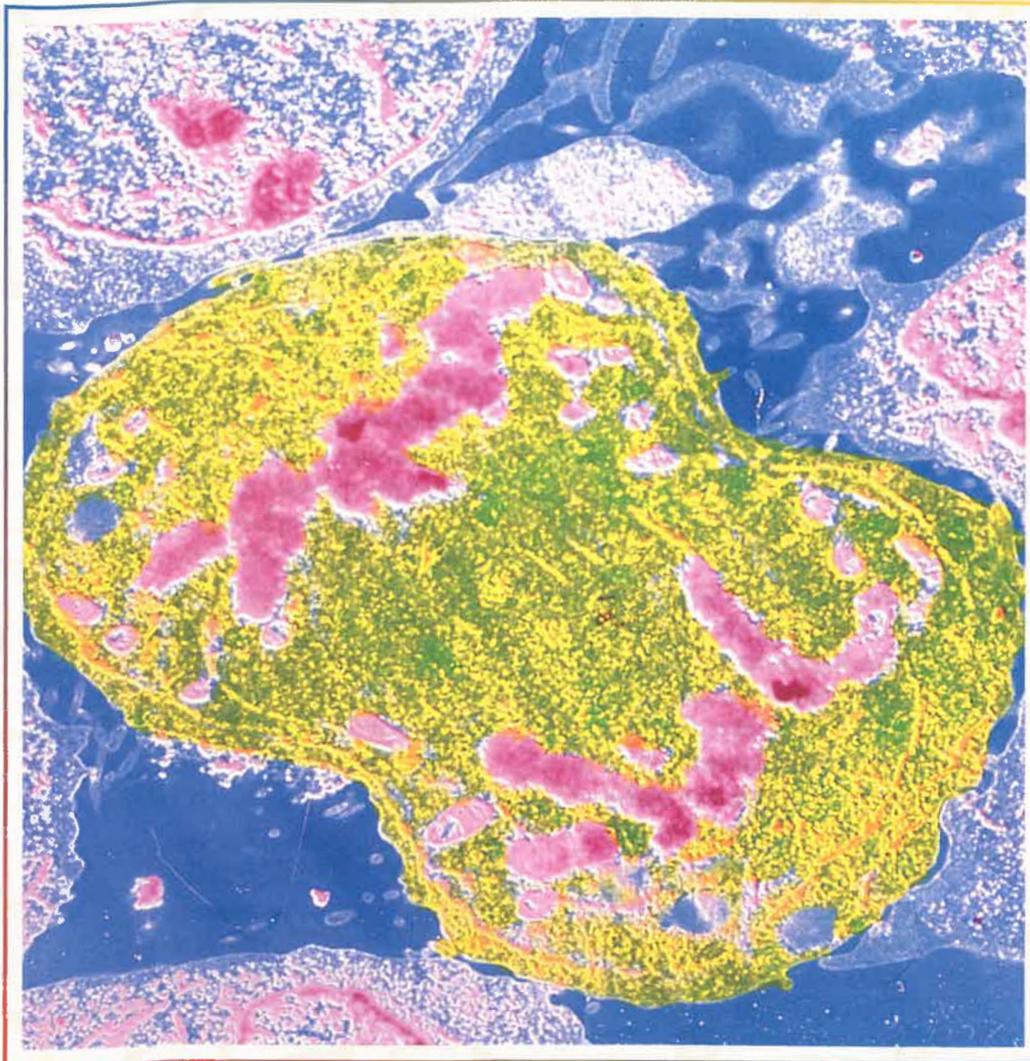


EXTENSION

1. Read "First With a Flower" in *Natural History*, March 2000, on page 12. Explain how some plants are able to obtain energy to grow and bloom under a pack of snow before they are exposed to sunlight and before photosynthesis is able to begin. What adaptation does the skunk cabbage have that enables it to extend its flowering stalk from the snow while the air temperature is still below freezing?
2. Read "Mitochondria Make a Comeback" in *Science*, March 5, 1999, on page 1475. What does the author mean when she says that mitochondria are making a comeback? Describe four more areas of research in which mitochondria play a key role.
3. As you have learned, aerobic respiration is significantly more efficient than glycolysis alone in supplying cells with ATP. Develop a hypothesis to explain why anaerobic organisms have not become extinct but instead have continued to thrive in many regions of the world. Check library and on-line references to locate information about one anaerobic species that relates to your hypothesis.
4. Find a recipe for making leavened, or raised, bread and a recipe for making unleavened bread. What ingredient that is present in the recipe for leavened bread is missing from the recipe for unleavened bread? Explain why that ingredient is omitted from the recipe.

CHAPTER 8

CELL REPRODUCTION



This human lymphocyte cell is dividing into two new cells. (17,687 \times)

FOCUS CONCEPT: *Reproduction and Inheritance*

In this chapter you will learn how cells reproduce by cell division. Pay attention to the steps of cell division in different kinds of cells.



Unit 4—Cell Reproduction
Topics 1–6

8-1 Chromosomes

8-2 Cell Division

8-3 Meiosis

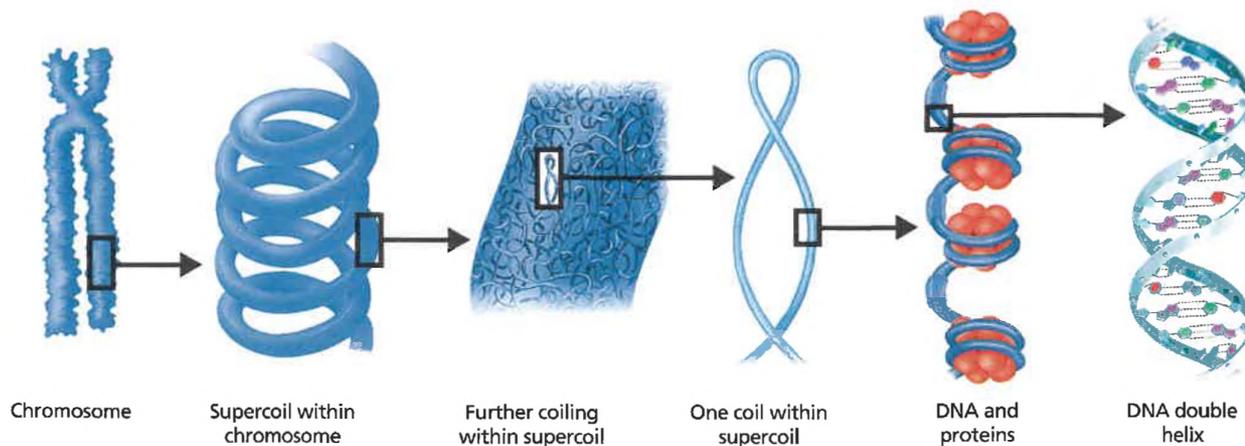
CHROMOSOMES

Recall from Chapter 3 that DNA is a long thin molecule that stores genetic information. The DNA in a human cell is estimated to consist of six billion pairs of nucleotides. To visualize the enormity of six billion pairs of nucleotides, imagine increasing a cell nucleus to the size of a basketball. Then imagine taking the DNA out of the basketball-sized nucleus and stretching it into a straight line. That line of DNA would stretch for 64 km (40 mi).

CHROMOSOME STRUCTURE

During cell division, the DNA in a eukaryotic cell's nucleus is coiled into very compact structures called chromosomes. Chromosomes are rod-shaped structures made of DNA and proteins. In Figure 8-1, you can see the many levels of DNA coiling required to form a chromosome.

The chromosomes of stained eukaryotic cells undergoing cell division are visible as darkened structures inside the nuclear membrane. Each chromosome is a single DNA molecule associated with proteins. The DNA in eukaryotic cells wraps tightly around proteins called **histones**. Histones help maintain the shape of the chromosome and aid in the tight packing of DNA. **Nonhistone** proteins are generally involved in controlling the activity of specific regions of the DNA.



SECTION

8-1

OBJECTIVES

Describe the structure of a chromosome.

Compare prokaryotic chromosomes with eukaryotic chromosomes.

Explain the differences between sex chromosomes and autosomes.

Give examples of diploid and haploid cells.

FIGURE 8-1

As a cell prepares to divide, its DNA coils around proteins and twists into rod-shaped chromosomes.

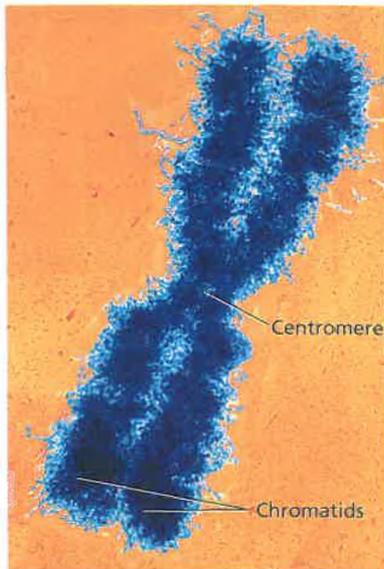


FIGURE 8-2
Chromosomes, like this one isolated from a dividing human cell, consist of two identical chromatids. (TEM 12,542 \times)

Figure 8-2 shows a chromosome that was isolated from a dividing cell. Notice that the chromosome consists of two identical halves. Each half of the chromosome is called a **chromatid**. Chromatids form as the DNA makes a copy of itself before cell division. When the cell divides, each of the two new cells will receive one chromatid from each chromosome. The constricted area of each chromatid is called a **centromere**. The centromere holds the two chromatids together until they separate during cell division. As you will learn in the next section, centromeres are especially important for the movement of chromosomes during cell division.

Between cell divisions, DNA is not so tightly coiled into chromosomes. Regions of DNA uncoil in between cell divisions so they can be read and so the information can be used to direct the activities of the cell. The less tightly coiled DNA-protein complex is called chromatin.

As you might expect, chromosomes are simpler in prokaryotes than in eukaryotes. The DNA of most prokaryotes comprises only one chromosome, which is attached to the inside of the cell membrane. Prokaryotic chromosomes consist of a circular DNA molecule and associated proteins. As with eukaryotic chromosomes, prokaryotic chromosomes must be very compact to fit into the cell.

CHROMOSOME NUMBERS

Each species has a characteristic number of chromosomes in each cell. Table 8-1 lists the number of chromosomes found in some organisms. Fruit flies, for example, have only eight chromosomes in each cell. Some species of organisms have the same number of chromosomes. For example, potatoes, plums, and chimpanzees all have 48 chromosomes in each cell.

Sex Chromosomes and Autosomes

Human and animal chromosomes are categorized as either sex chromosomes or autosomes. **Sex chromosomes** are chromosomes that determine the sex of an organism, and they may also carry genes for other characteristics. In humans, sex chromosomes are either X or Y. Normal females have two X chromosomes, and normal males have an X and a Y chromosome. All of the other chromosomes in an organism are called **autosomes**. Two of the 46 human chromosomes are sex chromosomes, while the remaining 44 chromosomes are autosomes.

Every cell of an organism produced by sexual reproduction has two copies of each autosome. The organism receives one copy of each autosome from each parent. The two copies of each autosome are called **homologous chromosomes**, or homologues. Homologous chromosomes are the same size and shape and carry genes for the same traits. For example, if one chromosome in a pair of homologous chromosomes contains a gene for eye color, so will

TABLE 8-1 Chromosome Numbers of Various Species

Organism	Number of chromosomes
Adder's tongue fern	1,262
Carrot	18
Cat	32
Chimpanzee	48
Dog	78
Orangutan	48
Earthworm	36
Fruit fly	8
Garden pea	20
Gorilla	48
Horse	64
Human	46
Lettuce	18
Sand dollar	52

the other chromosome in the homologous pair. Figure 8-3 shows a **karyotype**, which is a photomicrograph of the chromosomes in a dividing cell found in a normal human. Notice that the 46 human chromosomes exist as 22 homologous pairs of autosomes and two sex chromosomes (XY in males and XX in females). What is the sex of the person whose chromosomes are shown in Figure 8-3?

Diploid and Haploid Cells

Cells having two sets of chromosomes are said to be **diploid**. Diploid cells have both chromosomes for each homologous pair. Diploid cells also have two sex chromosomes in animals, including humans, and many other organisms that have sex chromosomes. All normal human cells, except reproductive cells (sperm cells and egg cells), are diploid cells. Diploid is commonly abbreviated as $2n$. In humans, the diploid, or $2n$, number of chromosomes is 46—22 pairs of homologous chromosomes and 2 sex chromosomes. If you count the number of chromosomes in the karyotype in Figure 8-3, you should find 46 chromosomes.

Human sperm cells and egg cells are **haploid** cells. These cells contain only one set of chromosomes. Haploid cells have half the number of chromosomes that are present in diploid cells. Thus, human haploid cells have only one chromosome of each homologous pair and only one sex chromosome. Haploid is abbreviated as $1n$. When a sperm cell ($1n$) and an egg cell ($1n$) combine to create the first cell of a new organism, the new cell will be diploid ($2n$). If the reproductive cells were diploid, the new cell would have too many chromosomes and would not be functional.

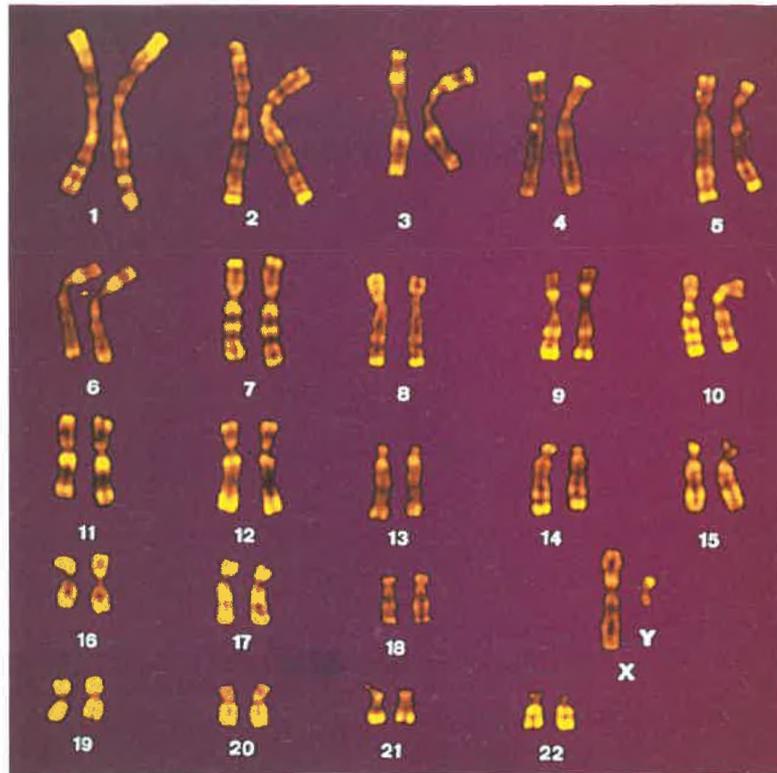


FIGURE 8-3

Karyotypes, like this one, are used to examine an individual's chromosomes. Karyotypes are made from a sample of a person's blood. White blood cells from the sample are treated chemically to stimulate mitosis and to arrest mitosis in metaphase. The chromosomes are then photographed, cut out, and arranged by size and shape into pairs.

SECTION 8-1 REVIEW

1. What are homologous chromosomes?
2. Describe the differences between a chromosome and a DNA molecule.
3. Compare the structure of prokaryotic chromosomes with that of eukaryotic chromosomes.
4. Contrast sex chromosomes with autosomes.
5. Using Table 8-1, list the haploid and diploid number of chromosomes for each organism.
6. **CRITICAL THINKING** Is there a correlation between the number of chromosomes and the complexity of an organism? Give support for your answer.

SECTION

8-2

OBJECTIVES

Describe the events of binary fission.

Describe each phase of the cell cycle.

Summarize the phases of mitosis.

Compare cytokinesis in animal cells with cytokinesis in plant cells.

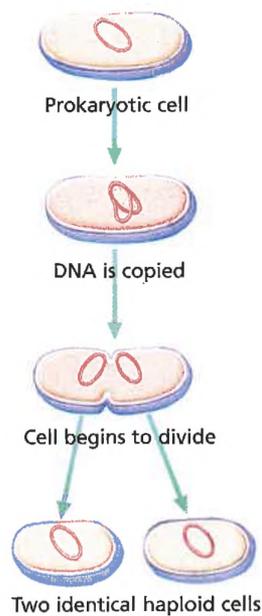


FIGURE 8-4

Most prokaryotes reproduce by binary fission, in which two identical cells are produced from one cell.

CELL DIVISION

All cells are derived from the division of preexisting cells. Cell division is the process by which cells produce offspring cells. As you will see, cell division differs in prokaryotes and eukaryotes. In eukaryotes, cell division differs in different stages of an organism's life cycle.

CELL DIVISION IN PROKARYOTES

Binary fission is the division of a prokaryotic cell into two offspring cells. Binary fission consists of three general stages, which are outlined in Figure 8-4.

First the chromosome, which is attached to the inside of the cell membrane, makes a copy of itself, resulting in two identical chromosomes attached to the inside of the prokaryote's inner cell membrane. After the chromosome is copied, the cell continues to grow until it reaches approximately twice the cell's original size. Then a cell wall forms between the two chromosomes and the cell splits into two new cells. Each new cell contains one of the identical chromosomes that resulted from the copying of the original cell's chromosome.

CELL DIVISION IN EUKARYOTES

In eukaryotic cell division, both the cytoplasm and the nucleus divide. There are two kinds of cell division in eukaryotes. The first type of cell division that you will learn about is called mitosis. **Mitosis** results in new cells with genetic material that is identical to that of the original cell. Mitosis occurs in the reproduction of unicellular organisms as well as in the addition of cells to a tissue or organ in a multicellular organism.

The type of cell division that you will learn about in Section 8-3 is called meiosis. **Meiosis** reduces the chromosome number by half in new cells. The new cells join together later in the organism's life cycle to produce cells with a complete set of chromosomes.

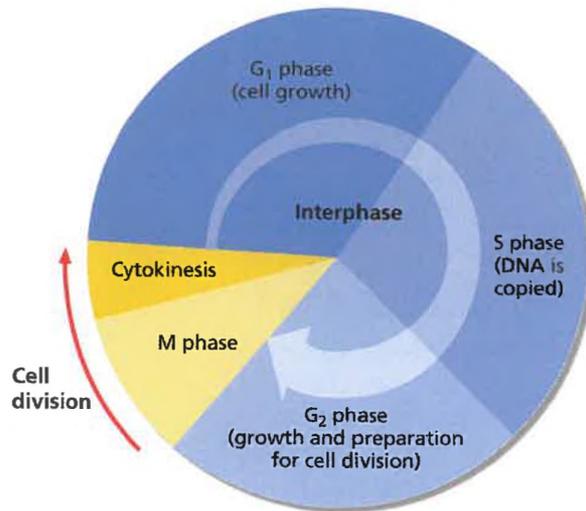


FIGURE 8-5

The life cycle of a cell—called the cell cycle—consists of interphase and cell division. Phases of growth, DNA replication, and preparation for cell division make up interphase. Cell division is divided into mitosis (division of the nucleus) and cytokinesis (division of the cytoplasm).

The Cell Cycle

The **cell cycle** is the repeating set of events that make up the life of a cell. Cell division is one phase of the cell cycle. The time between cell divisions is called **interphase**. Interphase is divided into three phases and cell division is divided into two phases, as illustrated in Figure 8-5.

During cell division, the chromosomes and cytoplasm are equally divided between two offspring cells. Cell division consists of mitosis and cytokinesis. During mitosis, or the **M phase**, the nucleus of a cell divides. **Cytokinesis** is the division of the cytoplasm of the cell.

Interphase

Notice in Figure 8-5 that cells spend most of their lifetime in interphase. Following cell division, offspring cells are approximately half the size of the original cell. During the first stage of interphase—called the **G₁ phase**—offspring cells grow to mature size. G₁ stands for the time gap following cell division and preceding DNA replication. After cells have reached a mature size, they typically proceed into the next phase of interphase, called the **S phase**. During the S phase, the cell's DNA is copied. The **G₂ phase** represents the time gap following DNA synthesis (S phase) and preceding cell division. The G₂ phase is a time during which the cell prepares for cell division.

Cells can also exit the cell cycle (usually from the G₁ phase) and enter into a state called the **G₀ phase**. During the G₀ phase, cells do not copy their DNA and do not prepare for cell division. Many cells in the human body are in the G₀ phase. For example, fully developed cells in the central nervous system stop dividing at maturity and normally never divide again.

Mitosis

Mitosis is the division of the nucleus, which occurs during cell division. Mitosis is a continuous process that is divided into four phases: prophase, metaphase, anaphase, and telophase.



Quick Lab

Identifying Prefixes and Suffixes

Materials dictionary, 3×5 in. index cards (18), pencil

Procedure

- Write each of the following prefixes and suffixes on separate cards: *pro-*, *meta-*, *ana-*, *telo-*, *cyto-*, *oo-*, *inter-*, *-kinesis*, and *-genesis*.
- Use a dictionary to find the definition of each prefix and suffix. Write the definitions on separate cards.
- Play "Memory" with a partner. Mix the cards and place each one face down on the table. Turn over two cards. If the two cards consist of a prefix or suffix and its definition, pick up the cards and take another turn. If the two cards do not match, turn them face down again and leave them in the same place.
- Repeat step 3 until no cards remain on the table. The player with the most pairs wins.

Analysis How does knowing the meaning of a prefix or suffix help you to understand the meaning of a word?

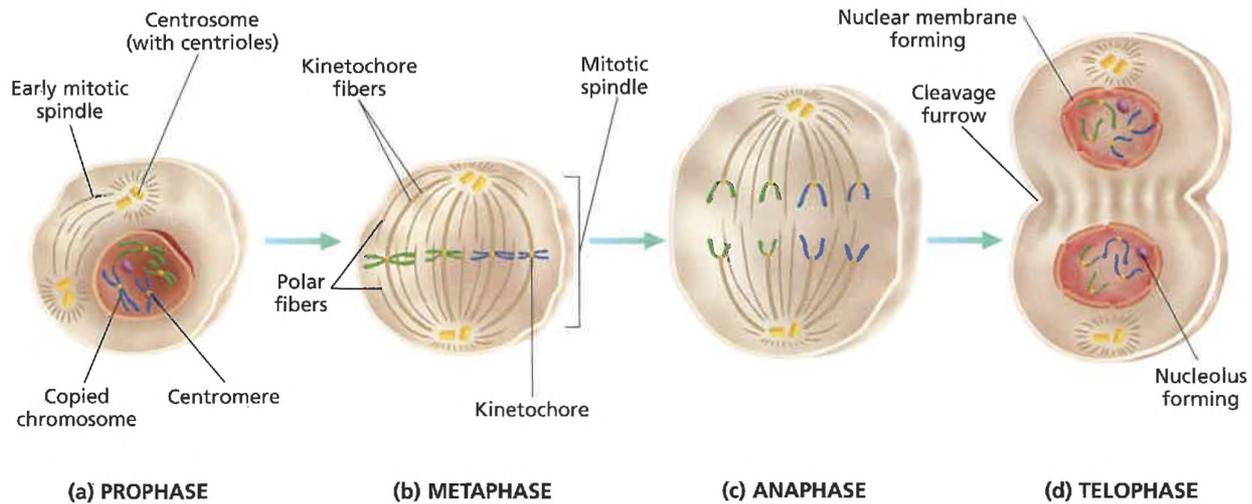


FIGURE 8-6

(a) During prophase, the copied DNA coils into chromosomes. (b) During metaphase, the chromosomes line up along the midline of the dividing cell. (c) During anaphase, the chromatids of each chromosome begin moving toward opposite poles of the cell. (d) During telophase, the chromosomes reach opposite poles of the cell, and the cytoplasm begins to divide.

Prophase is the first phase of mitosis. Prophase, shown in Figure 8-6, begins with the shortening and tight coiling of DNA into rod-shaped chromosomes that can be seen with a light microscope. Recall that during the S phase, each chromosome is copied. The two copies of each chromosome—called chromatids—stay connected to one another by the centromere. At this time, the nucleolus and the nuclear membrane break down and disappear.

Two pairs of dark spots called **centrosomes** appear next to the disappearing nucleus. In animal cells, each centrosome contains a pair of small, cylindrical bodies called **centrioles**. The centrosomes of plant cells lack centrioles. In both animal and plant cells, the centrosomes move toward opposite poles of the cell. As the centrosomes separate, **spindle fibers** made of microtubules radiate from the centrosomes in preparation for mitosis. This array of spindle fibers is called the **mitotic spindle**, which serves to equally divide the chromatids between the two offspring cells during cell division. Two types of spindle fibers make up the mitotic spindle: kinetochore fibers and polar fibers. **Kinetochore fibers** attach to a disk-shaped protein—called a **kinetochore**—that is found in the centromere region of each chromosome. Kinetochore fibers extend from the kinetochore of each chromatid to one of the centrosomes. **Polar fibers** extend across the dividing cell from centrosome to centrosome.

Metaphase is the second phase of mitosis. During metaphase, chromosomes are easier to identify using a microscope than during other phases; thus, karyotypes are typically made from photomicrographs of chromosomes in metaphase. During metaphase, the kinetochore fibers move the chromosomes to the center of the dividing cell. Once in the center of the cell, each chromosome is held in place by the kinetochore fibers.

During **anaphase**, the chromatids of each chromosome separate at the centromere and slowly move, centromere first, toward opposite poles of the dividing cell. When the chromatids separate, they are considered to be individual chromosomes.

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TOPIC: Cell cycle
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KEYWORD: HM150

Telophase is the fourth phase of mitosis. After the chromosomes reach opposite ends of the cell, the spindle fibers disassemble and the chromosomes return to a less tightly coiled chromatin state. A nuclear envelope forms around each set of chromosomes, and a nucleolus forms in each of the newly forming cells.

Cytokinesis

During telophase, the cytoplasm of the cell divides by a process called cytokinesis. In animal cells, cytokinesis begins with a pinching inward of the cell membrane midway between the dividing cell's two poles, as shown in Figure 8-7. The area of the cell membrane that pinches in and eventually separates the dividing cell into two cells is called the **cleavage furrow**. The cleavage furrow pinches the cell into two cells through the action of microfilaments.

Figure 8-8 shows cytokinesis in plant cells. In plant cells, vesicles formed by the Golgi apparatus fuse at the midline of the dividing cell, forming a membrane-bound cell wall called the **cell plate**. When complete, the cell plate separates the cell into two cells. In both animal cells and plant cells, offspring cells are approximately equal in size. Each offspring cell receives an identical copy of the original cell's chromosomes and approximately one-half of the original cell's cytoplasm and organelles.

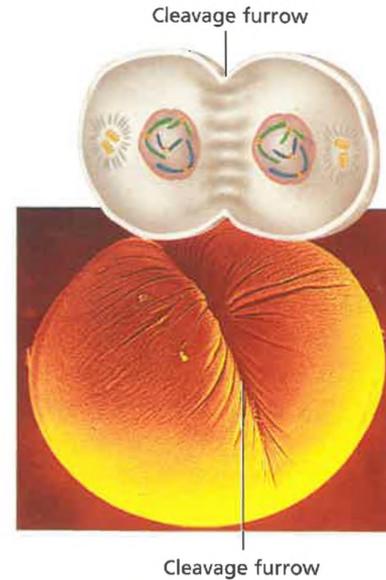


FIGURE 8-7

In animal cells, such as this frog cell, the cell membrane pinches in at the center of the dividing cell, eventually dividing the cell into two offspring cells. (SEM 78 \times)

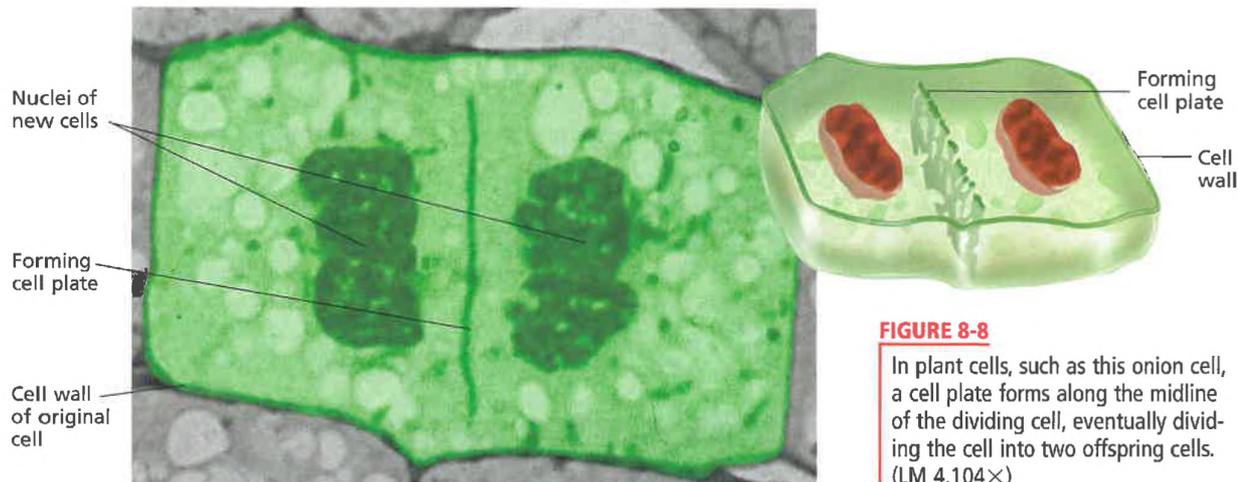


FIGURE 8-8

In plant cells, such as this onion cell, a cell plate forms along the midline of the dividing cell, eventually dividing the cell into two offspring cells. (LM 4,104 \times)

SECTION 8-2 REVIEW

1. Describe the events of binary fission.
2. During which phase of the cell cycle are chromosomes copied?
3. Which phase of the cell cycle could you identify most readily with a light microscope? Explain your answer.
4. Describe the structure and function of the mitotic spindle.
5. Explain the main differences between cytokinesis in animal cells and cytokinesis in plant cells.
6. **CRITICAL THINKING** What would happen if cytokinesis took place before mitosis?

Research Notes

To View the Invisible

What controls the movement of chromosomes when the cell nucleus divides? This basic question has been studied by biologists for over 100 years. The answer will have great significance for society. Understanding what controls cell division in normal cells will help us understand what happens in cell anomalies, such as cancer.

In 1897, a German anatomist named Walther Flemming began to stain cells with a red dye in order to observe their internal contents during cell division. Because staining kills cells, Flemming had to view mitosis as a series of still images in the various stages of cell division. For many years after Flemming's work, it was not clear whether the spindle fibers, which emerge each time a cell reproduces, were permanent cellular structures. The debate over whether these fibers actively separate the chromosomes during cell division continued among cell biologists for more than 50 years.

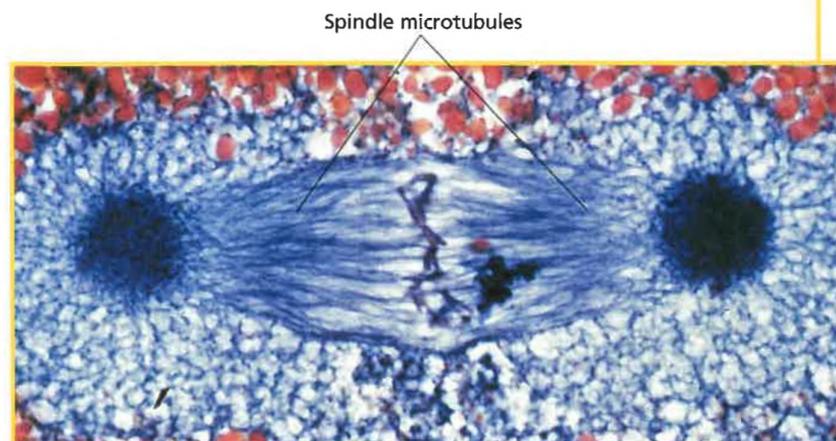
During the early 1950s, a Japanese student named Shinya Inoue helped invent the techniques necessary to observe the dynamics of living cells. Inoue worked in the marine biology lab of his professor, Katsuma Dan, who was studying cell division in sea urchins. The electron microscopes they used produced the necessary high-resolution image but required killing and slicing the specimens. Sometimes, part of a cell was altered during the preparation. At the time, there were

various light microscopes available that enabled observation of the dynamics of the living system. However, the resolution of those microscopes was not high enough to resolve fine details in the smallest areas of the cells. Dan challenged Inoue to develop a microscope that would allow biologists to study the movement of spindle fibers in dividing cells.

Inoue subsequently developed an improved microscope that enabled him to confirm the existence of spindle fibers in live sea urchin cells and to develop a model for the role the spindle fibers play in cell division. The very instability of the molecules that make up the spindle fibers suggested to Inoue a possible mechanism for chromosome movement. His experiments indicated that these fibers might move the chromosomes that are attached to them by assembling and disassembling. As the subunits of

the molecules lengthened or shortened, the chromosomes that were attached to them moved. The bundle of spindle fibers that Inoue observed has since been identified as specialized microtubules. Not until the mid-1970s, however, were these fibers isolated from living cells.

At Woods Hole Oceanographic Institute, Inoue continued to be a pioneer in microscopy techniques for more than 40 years. He developed techniques to bring out the fine structural details of cellular organization, such as showing three-dimensional views of spindle fibers. According to Inoue, this opens up new opportunities for studies of developing embryos and cells undergoing mitosis without destroying the living cells. Such technological advances have brought science one step closer to understanding the complex dynamics of cell division.



This micrograph (LM 1,080 \times) of the spindle apparatus during metaphase shows the spindle microtubules studied by Shinya Inoue. The wormlike structures in the center are the chromosomes.

SECTION

8-3

OBJECTIVES

▲
List and describe the phases of meiosis.

●
Compare the end products of mitosis with those of meiosis.

■
Explain crossing-over and how it contributes to the production of unique individuals.

◆
Summarize the major characteristics of spermatogenesis and oogenesis.

MEIOSIS

*Meiosis is a process of nuclear division that reduces the number of chromosomes in new cells to half the number in the original cell. The halving of the chromosome number counteracts a fusion of cells later in the life cycle of the organism. For example, in humans, meiosis produces haploid reproductive cells called **gametes**. Human gametes are sperm cells and egg cells, each of which contains 23 ($1n$) chromosomes. The fusion of a sperm and an egg results in a zygote that contains 46 ($2n$) chromosomes.*

STAGES OF MEIOSIS

Cells preparing to divide by meiosis undergo the G_1 , S, and G_2 phases of interphase. Recall that during interphase, the cell grows to a mature size and copies its DNA. Thus, cells begin meiosis with a duplicate set of chromosomes, just as cells beginning mitosis do. Because cells undergoing meiosis divide twice, diploid ($2n$) cells that divide meiotically result in four haploid ($1n$) cells rather than two diploid ($2n$) cells. The stages of the first cell division are called meiosis I, and the stages of the second cell division are called meiosis II.

Meiosis I

The four phases of meiosis I are illustrated in Figure 8-9 on the next page. Notice how these phases compare with the corresponding phases of mitosis.

During prophase I, DNA coils tightly into chromosomes. As in the prophase of mitosis, spindle fibers appear. Then the nucleus and nucleolus disassemble. Notice how every chromosome lines up next to its homologue. The pairing of homologous chromosomes, which does not occur in mitosis, is called **synapsis**.

Each pair of homologous chromosomes is called a **tetrad**. In each tetrad, chromatids of the homologous chromosomes are aligned lengthwise so that the genes on one chromosome are adjacent to the corresponding genes on the other chromosome. During synapsis, the chromatids within a homologous pair twist around one another, as shown in Figure 8-10. Portions of chromatids may break off and attach to adjacent chromatids on the homologous chromosome—a process called **crossing-over**. This process permits the exchange of genetic material between maternal and paternal

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Word Roots and Origins

tetrad

from the Greek *tetras*,
meaning "four"

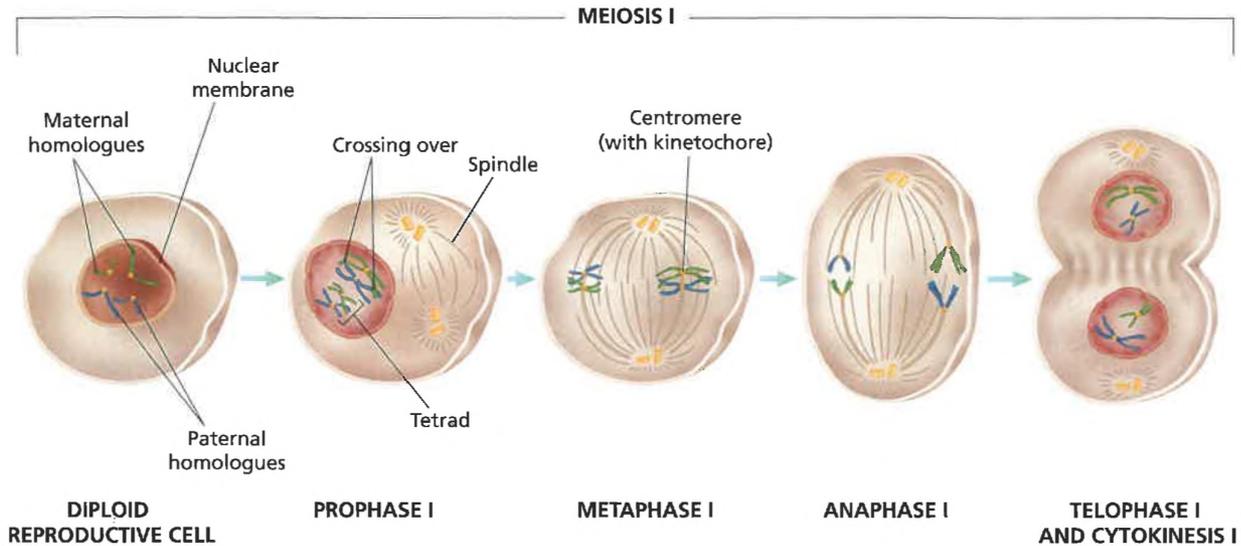


FIGURE 8-9

Meiosis occurs in diploid reproductive cells. Before meiosis begins, the DNA of the diploid reproductive cells is copied. Meiosis I results in two haploid cells.

chromosomes. Thus, crossing-over results in **genetic recombination** by producing a new mixture of genetic material.

During metaphase I, the tetrads line up randomly along the midline of the dividing cell. The orientation of the homologous pair of chromosomes is random with respect to the poles of the dividing cell. Spindle fibers from one pole attach to the centromere of one homologous chromosome. Spindle fibers from the opposite pole attach to the other homologous chromosome of the pair.

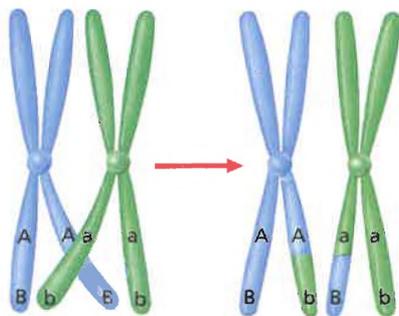
During anaphase I, each homologous chromosome (consisting of two chromatids attached by a centromere) moves to an opposite pole of the dividing cell, as shown in Figure 8-9. The random separation of the homologous chromosomes is called **independent assortment**. Independent assortment of the chromosomes results in a random separation of the maternal and paternal chromosomes, which results in genetic variation.

Telophase I is the final phase of meiosis I. During telophase I, the chromosomes reach the opposite ends of the cell, and cytokinesis begins. Notice that the new cells contain a haploid number of chromosomes.

During meiosis I, the original cell produces two new cells. Each new cell contains one chromosome from each homologous pair. The new cells contain half the number of chromosomes of the original cell. However, each new cell contains two copies of the chromosome because the original cell copied its DNA before meiosis I.

FIGURE 8-10

Crossing-over occurs when chromosomes that make up a tetrad exchange portions of their chromatids. Crossing-over results in an exchange of genes and in new combinations of genes.



Meiosis II

Meiosis II occurs in each cell formed during meiosis I and is not preceded by the copying of DNA. The events of meiosis II are shown in Figure 8-11. In some species, meiosis II begins after the nuclear membrane re-forms in the new cells. In other species, meiosis II begins immediately following meiosis I.

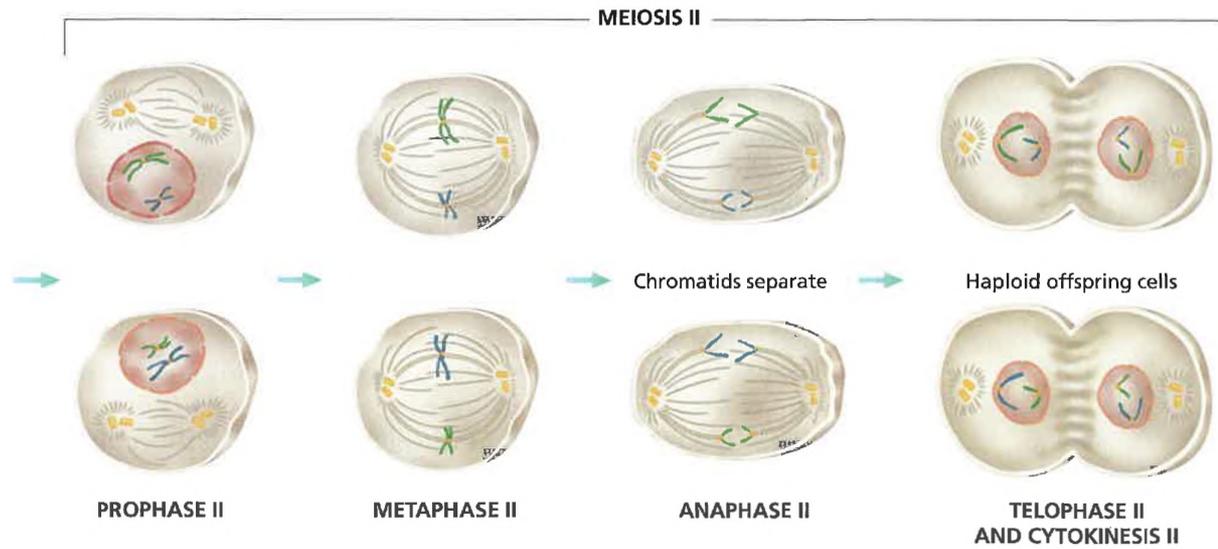


FIGURE 8-11

Meiosis II consists of prophase II, metaphase II, anaphase II, and telophase II. These events closely resemble those of mitosis. Meiosis II results in four haploid offspring cells.

During prophase II, spindle fibers form and begin to move the chromosomes toward the midline of the dividing cell. In metaphase II, the chromosomes move to the midline of the dividing cell, facing opposite poles of the dividing cell. In anaphase II, the chromatids separate and move toward opposite poles of the cell.

In telophase II, a nuclear membrane forms around the chromosomes in each of the four new cells. Cytokinesis II occurs during telophase II, resulting in four new cells, each of which contains half of the original cell's number of chromosomes.

Formation of Gametes

In animals, meiosis produces haploid reproductive cells called gametes, as shown in Figure 8-12. Because only those cells involved in the production of gametes divide by meiosis in animals, meiosis occurs only within their reproductive organs. In humans, meiosis occurs in the testes and in the ovaries.

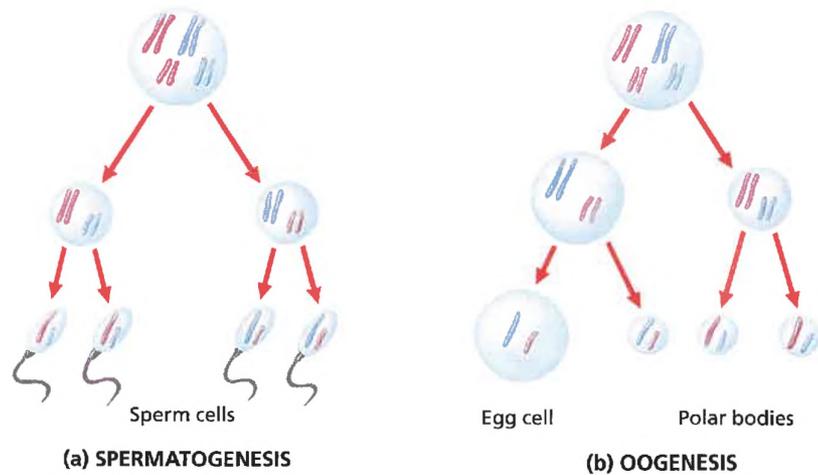


FIGURE 8-12

(a) In the formation of male gametes, the original cell produces four sperm cells by meiosis. (b) In the formation of egg cells, the original cell produces one egg and three polar bodies by meiosis. The egg cell receives most of the original cell's cytoplasm.

In the testes, meiosis is involved in the production of male gametes known as sperm cells or spermatozoa. In the development of sperm cells, a diploid reproductive cell divides meiotically to form four haploid cells called **spermatids**. Each spermatid then develops into a mature sperm cell. The production of sperm cells is called **spermatogenesis**.

Oogenesis (OH-oh-JEN-uh-sis) is the production of mature egg cells, or ova. During oogenesis, a diploid reproductive cell divides meiotically to produce one mature egg cell (ovum). During cytokinesis I and cytokinesis II of oogenesis, the cytoplasm of the original cell is divided unequally between new cells. As Figure 8-12 shows, one cell, which develops into a mature egg cell, receives most of the cytoplasm of the original cell. As a result, one egg cell is produced by meiosis. The other three products of meiosis, called **polar bodies**, degenerate.

Asexual and Sexual Reproduction

Asexual reproduction is the production of offspring from one parent. Asexual reproduction does not usually involve meiosis or the union of gametes. In unicellular organisms, such as bacteria, new organisms are created by either binary fission or mitosis. Asexual reproduction in multicellular organisms results from the budding off of portions of their bodies, as Figure 8-13 shows. The offspring from asexual reproduction are genetically identical to the parent.

Sexual reproduction is the production of offspring through meiosis and the union of a sperm and an egg. Offspring produced by sexual reproduction are genetically different from the parents because genes are combined in new ways in meiosis. In fact, except in the case of identical twins, sexually produced offspring contain unique combinations of their parents' genes. The evolutionary advantage of sexual reproduction is that it enables species to adapt rapidly to new conditions. For example, if disease strikes a crop of grain, a few plants may have genetic variations that make them resistant to the disease. While many individuals may die, these few resistant plants survive and reproduce.

FIGURE 8-13

Many plants, like this kalanchoe, produce offspring plantlets by asexual reproduction. Each plantlet, produced by mitotic cell divisions, is genetically identical to the parent plant.



SECTION 8-3 REVIEW

1. List two ways that meiosis differs from mitosis.
2. During which stage of meiosis is the diploid number of chromosomes reduced to the haploid number of chromosomes?
3. How many chromosomes do human gametes normally contain?
4. Explain the role of crossing-over in ensuring genetic variation.
5. Describe the primary differences between spermatogenesis and oogenesis.
6. **CRITICAL THINKING** Explain why the chromosomes in the haploid cells that are produced by meiosis I look different from those produced by meiosis II.

CHAPTER 8 REVIEW

SUMMARY/VOCABULARY

- 8-1**
- Chromosomes are tightly coiled DNA molecules and associated proteins.
 - In eukaryotes, histone proteins help maintain the compact structure of chromosomes.
 - In dividing cells, chromosomes are composed of two identical chromatids constricted together at a centromere.
 - Chromosomes are categorized as either sex

Vocabulary

autosome (146)
centromere (146)
chromatid (146)

diploid (147)
haploid (147)
histone (145)

- chromosomes or autosomes.
- Homologous chromosomes consist of one autosomal chromosome from each parent.
- Diploid ($2n$) is the number of chromosomes in cells that have homologous pairs of autosomes and two sex chromosomes.
- Haploid cells ($1n$) have half the number of chromosomes that are present in diploid cells.

homologous chromosome (146)
karyotype (147)

nonhistone (145)
sex chromosome (146)

- 8-2**
- Cell division is the process by which cells reproduce themselves.
 - Binary fission is the process of cell division in prokaryotes.
 - The cell cycle is the repeating of events that make up the life of a cell. The cell cycle consists of cell division and interphase.
 - Cell division in eukaryotes includes the division of the nucleus (mitosis) and the

Vocabulary

anaphase (150)
binary fission (148)
cell cycle (149)
cell plate (151)
centriole (150)
centrosome (150)

cleavage furrow (151)
cytokinesis (149)
 G_0 phase (149)
 G_1 phase (149)
 G_2 phase (149)
interphase (149)

- division of the cytoplasm (cytokinesis).
- Interphase consists of a phase of growth (G_1), a phase of DNA replication (S), and a phase of preparation for cell division (G_2).
- Mitosis is divided into prophase, metaphase, anaphase, and telophase. Mitosis results in two offspring cells that are genetically identical to the original cell.

kinetochore (150)
kinetochore fiber (150)
meiosis (148)
metaphase (150)
mitosis (148)
mitotic spindle (150)

M phase (149)
polar fiber (150)
prophase (150)
S phase (149)
spindle fiber (150)
telophase (151)

- 8-3**
- During meiosis, a cell divides twice.
 - Crossing-over during meiosis results in genetic recombination.
 - Spermatogenesis is the process by which sperm cells are produced. Oogenesis is the process that produces egg cells (ova).
 - Asexual reproduction is the formation of offspring from one parent. Offspring pro-

Vocabulary

asexual reproduction (156)
crossing-over (153)
gamete (153)
genetic recombination (154)

independent assortment (154)
oogenesis (156)

- duced by asexual reproduction are genetically identical to the parent.
- Sexual reproduction is the formation of offspring through the union of a sperm and an egg. Offspring produced by sexual reproduction are genetically different from the parents.

polar body (156)
sexual reproduction (156)
spermatid (156)

spermatogenesis (156)
synapsis (153)
tetrad (153)

REVIEW

Vocabulary

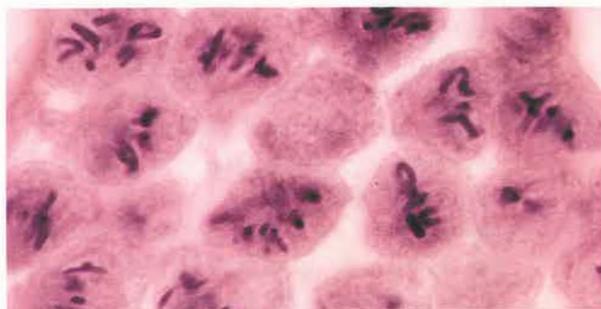
1. Differentiate between a chromosome and a homologous chromosome pair.
2. Distinguish between mitosis, meiosis, and cytokinesis.
3. Distinguish between autosomes and sex chromosomes.
4. Distinguish between kinetochore fibers and polar fibers.
5. Explain the difference in meaning of the terms *haploid* and *diploid*.

Multiple Choice

6. Prokaryotic chromosomes (a) comprise at least two chromosomes (b) are made of DNA wrapped tightly around histone proteins (c) include histone and nonhistone proteins (d) consist of a circular DNA molecule.
7. A chromatid is (a) a dark stain (b) a dense substance within the nuclear membrane of a nondividing cell (c) one of two identical parts that make up a chromosome (d) the point at which each pair of chromatids is joined.
8. Every species has (a) haploid gametes (b) a distinctive number of chromosomes per cell (c) at least eight chromosomes per cell (d) a number of chromosomes that varies with the complexity of the organism.
9. Binary fission is (a) nuclear division of cells (b) eukaryotic cell division (c) sexual reproduction of prokaryotes (d) prokaryotic cell division.
10. Mitosis (a) can increase the number of body cells without changing the information contained in the DNA of those cells (b) is a means of reproducing sexually (c) is never triggered by cell size (d) results in offspring cells that are genetically different from the original cell.
11. Interphase is (a) composed of G_1 , G_2 , and G_3 (b) the time between meiosis I and meiosis II (c) a small part of the life cycle of a cell (d) a time of cell growth and development.
12. Cytokinesis (a) differs in animal and plant cells (b) does not occur in plant cells (c) immediately precedes mitosis (d) is a process of nuclear division.
13. Spermatogenesis produces (a) four haploid cells (b) four diploid cells (c) one haploid cell and three polar bodies (d) two haploid cells.
14. Oogenesis (a) produces diploid cells (b) requires meiotic cell divisions (c) produces four egg cells (d) produces one diploid cell and three polar bodies.
15. Crossing-over occurs during (a) mitosis (b) interphase (c) meiosis II (d) meiosis I.

Short Answer

16. What does the term *binary fission* refer to? In what type of organism does this type of cell division occur?
17. Discuss the events that occur in G_0 , G_1 , and G_2 phases.
18. Discuss the role of haploid cells in sexual reproduction.
19. What is the primary functional difference between mitotic anaphase and meiotic anaphase II?
20. Do asexual organisms have homologous chromosomes? Explain your answer.
21. Is there any functional difference between meiosis II and mitosis? Explain your answer.
22. Distinguish between sexual reproduction and asexual reproduction.
23. The photograph below shows cell division in a grasshopper testis. The offspring cells are gametes. Do you think the photograph shows mitosis or meiosis? Explain your answer.



24. Unit 4—Cell Reproduction

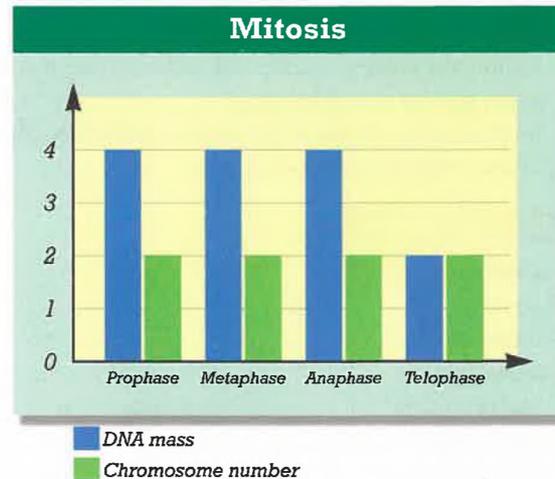


Write a report summarizing how different cancer-fighting drugs kill cancer cells by interrupting the life cycle of the cells.

CRITICAL THINKING

1. Can mitosis occur in a cell in the absence of cytokinesis? Support your answer. If your answer is yes, provide a description of how the new cell would appear in the G_1 phase of the cell cycle.
2. If you consider the mass of DNA in a sperm (a haploid cell) to be 1, what would the relative value be for the DNA mass of a cell in the G_2 phase of the cell cycle?
3. Does a cell in metaphase II have the same mass of DNA as a diploid cell in the G_1 phase of the cell cycle? Assume that both cells are from the same animal. Explain your answer.
4. Would a human cell with *any* 23 chromosomes be haploid? Explain your answer.
5. For a cell to function efficiently, the magnitude of its surface area must greatly exceed that of its volume. Explain how cell division functions to maintain this relationship between surface area and volume and in doing so maintains cell homeostasis.
6. The events of mitosis in plants and animals are very similar with the exception of the absence of centrioles in plants. How has the absence of centrioles in plant cells influenced scientists' thinking about the function of centrioles in mitosis?

7. The graph below demonstrates the mass of DNA and chromosome number in each phase of mitosis. Based on the information presented in this graph, at which phase of mitosis are chromatids considered chromosomes? Explain your answer.



8. Develop graphs to illustrate the mass of DNA and chromosome number in each phase of meiosis I and meiosis II. Your graphs should be similar in format to the one shown for mitosis. For telophase, consider the DNA in only one of the offspring cells at the end of telophase. Let the number 1 represent the mass of DNA that is found in a human ovum. Let the number 1 equal the number of chromosomes found in a human ovum.

EXTENSION

1. Read "Cell Division Gatekeepers Identified" in *Science*, January 23, 2000, on page 477. Identify the cell structures that have been found to regulate the timing of cell division during mitosis. Describe the function of these structures. What conditions in reproductive cells might occur if these structures fail to function during cell division?
2. Read "Dolly's Mixture" in *New Scientist*, September 4, 1999, on page 5. Explain how Dolly might not be the perfect clone she was once thought to be. What problems might this pose for researchers hoping to clone human tissue for transplants?
3. Do library or on-line research to find out how cancer cells differ from normal cells in relation to the cell cycle. Share the results of your research with your classmates.

CHAPTER 8 INVESTIGATION

Observing Mitosis in Plant Cells

OBJECTIVES

- Examine the dividing root-tip cells of an onion.
- Identify the phase of mitosis that different cells in an onion root tip are undergoing.
- Determine the relative length of time each phase of mitosis takes in onion root-tip cells.

PROCESS SKILLS

- observing
- classifying
- collecting
- organizing
- analyzing data
- calculating

MATERIALS

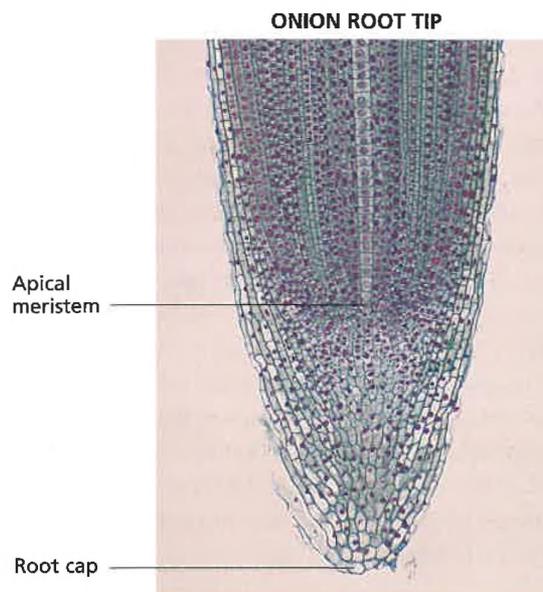
- compound light microscope
- prepared microscope slide of a longitudinal section of *Allium* (onion) root tip

Background

1. Mitosis is divided into four phases: prophase, metaphase, anaphase, and telophase.
2. Interphase is not considered a part of mitosis.
3. List the visible characteristics of each phase of mitosis.
4. In many plants, there are growth regions called meristems where mitosis is ongoing. Meristems are found in the tips of plant roots and shoots.

PART A Identifying the Phases of Mitosis

1. Look at the photograph below of a longitudinal section of an onion root tip. Find the meristem on the photograph. As you can see, the meristem is located just behind the root cap.



2. **CAUTION** Slides break easily. Use caution when handling them. Using low power on your microscope, bring the meristem region on your slide into focus.

TABLE A RELATIVE DURATION OF EACH PHASE OF MITOSIS

Phase of mitosis	Tally marks	Count	Percentage	Time (in minutes)
Prophase				
Metaphase				
Anaphase				
Telophase				

TABLE B DATA COLLECTED BY THE ENTIRE CLASS

Phase of mitosis	Count	Percentage	Time (in minutes)
Prophase			
Metaphase			
Anaphase			
Telophase			

3. Examine the meristem carefully. Choose a sample of about 50 cells. Look for a group of cells that appear to have been actively dividing at the time that the slide was made. The cells will appear in rows, so it should be easy to keep track of them. The dark-staining bodies are the nuclei.
4. In your lab report, prepare a data table like Table A.
5. For each of the cells in your sample, identify the stage of mitosis and place a mark in the "Tally marks" column beside the appropriate phase.

PART B Calculating the Relative Length of Each Phase

6. When you have classified each cell in your sample, count the tally marks for each phase and fill in the "Count" column. In which phase of mitosis were the greatest number of cells? In which phase were the fewest number of cells?
7. Calculate the percentage of cells found in each phase. Divide the number of cells in a phase by the total number of cells in your sample, and multiply by 100 percent. Enter the figures under "Percentage."
8. The percentage of cells found in each phase is a measure of how long each phase lasts. For example, if 25 percent of the cells are in prophase, then prophase takes 25 percent of the total time it takes for a cell to undergo mitosis. Mitosis in onion cells takes about 80 minutes. Calculate the actual time for each phase using this information and the percentage you have just determined.

Duration of phase (in minutes) =

$$\frac{\text{percentage}}{100} \times 80 \text{ minutes}$$

9. Record the actual time for each phase in your data table.
10. Make another data table, similar to Table B, shown above. Collect and record the count for each phase of mitosis for the entire class. Fill in the percentage and time information using the data collected by the entire class.
11.  Clean up your materials before leaving the lab.

Analysis and Conclusions

1. What color are the chromosomes stained?
2. How can you distinguish between early and late anaphase?
3. According to your data table, which phase of mitosis lasts the longest? Why might this phase require more time than other phases of mitosis?
4. According to your data table, which phase takes the least amount of time?
5. How do your results compare with those of the entire class?
6. In this investigation, you assumed that the percentage of the total time that any given phase takes is equal to the percentage of cells in that phase at any moment. Why might this not be true for very small samples of cells?

Further Inquiry

1. Given the rate of mitosis in a type of animal cells, how could you determine how long each phase of mitosis takes in those cells?
2. Cancerous tissue is composed of cells undergoing uncontrolled, rapid cell division. How could you develop a procedure to identify cancerous tissue by counting the number of cells undergoing mitosis?