

## 4.8 The Cytoskeleton

The protein components of the cytoskeleton [Gk. *kytos*, cell, and *skeleton*, dried body] interconnect and extend from the nucleus to the plasma membrane in eukaryotic cells. Prior to the 1970s, it was believed that the cytoplasm was an unorganized mixture of organic molecules. Then, high-voltage electron microscopes, which can penetrate thicker specimens, showed instead that the cytoplasm was highly organized. The technique of immunofluorescence microscopy identified the makeup of the protein components within the cytoskeletal network (Fig. 4.18).

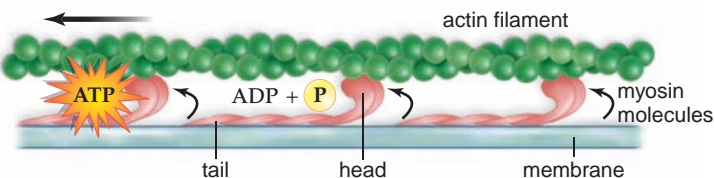
The cytoskeleton contains actin filaments, intermediate filaments, and microtubules, which maintain cell shape and allow the cell and its organelles to move. Therefore, the cytoskeleton is often compared to the bones and muscles of an animal. However, the cytoskeleton is dynamic, especially because its protein components can assemble and disassemble as appropriate. Apparently a number of different mechanisms regulate this process, including protein kinases that phosphorylate proteins. Phosphorylation leads to disassembly, and dephosphorylation causes assembly.

### Actin Filaments

**Actin filaments** (formerly called microfilaments) are long, extremely thin, flexible fibers (about 7 nm in diameter) that occur in bundles or meshlike networks. Each actin filament contains two chains of globular actin monomers twisted about one another in a helical manner.

Actin filaments play a structural role when they form a dense, complex web just under the plasma membrane, to which they are anchored by special proteins. They are also seen in the microvilli that project from intestinal cells, and their presence most likely accounts for the ability of microvilli to alternately shorten and extend into the intestine. In plant cells, actin filaments apparently form the tracks along which chloroplasts circulate in a particular direction; doing so is called cytoplasmic streaming. Also, the presence of a network of actin filaments lying beneath the plasma membrane accounts for the formation of **pseudopods** [L. *pseudo*, false, and *pod*, feet], extensions that allow certain cells to move in an amoeboid fashion.

How are actin filaments involved in the movement of the cell and its organelles? They interact with **motor molecules**, which are proteins that can attach, detach, and reattach farther along an actin filament. In the presence of ATP, the motor molecule myosin pulls actin filaments along in this way. Myosin has both a head and a tail. In muscle cells, the tails of several muscle myosin molecules are joined to form a thick filament. In nonmuscle cells, cytoplasmic myosin tails are bound to membranes, but the heads still interact with actin:



During animal cell division, the two new cells form when actin, in conjunction with myosin, pinches off the cells from one another.

### Intermediate Filaments

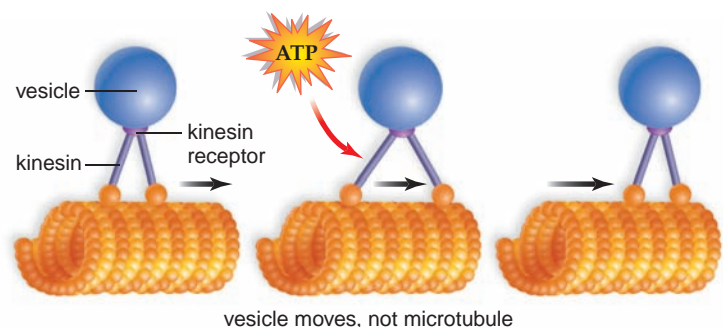
**Intermediate filaments** (8–11 nm in diameter) are intermediate in size between actin filaments and microtubules. They are a ropelike assembly of fibrous polypeptides, but the specific filament type varies according to the tissue. Some intermediate filaments support the nuclear envelope, whereas others support the plasma membrane and take part in the formation of cell-to-cell junctions. In the skin, intermediate filaments, made of the protein keratin, give great mechanical strength to skin cells. We now know that intermediate filaments are also highly dynamic and will disassemble when phosphate is added to them by a kinase.

### Microtubules

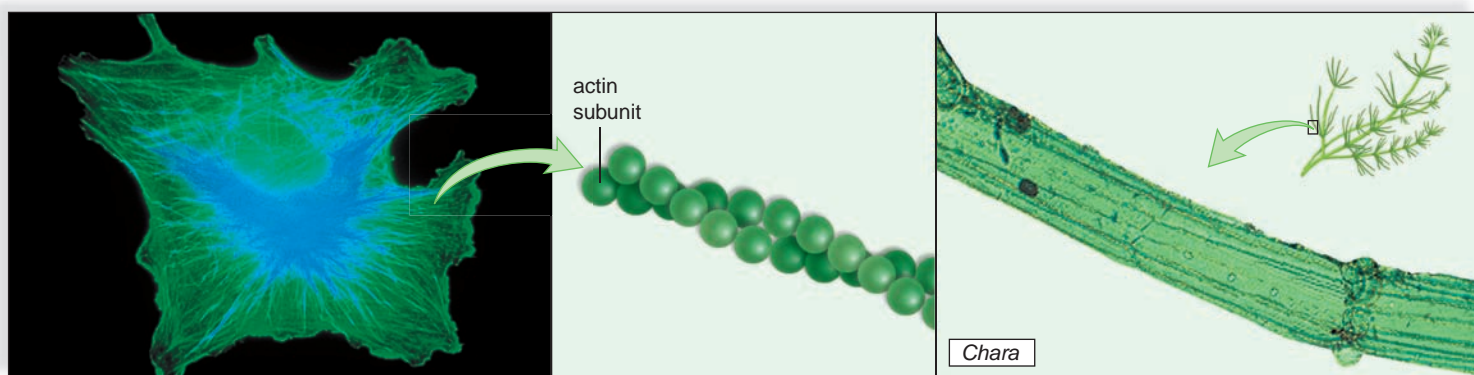
**Microtubules** [Gk. *mikros*, small, little; L. *tubus*, tube] are small, hollow cylinders about 25 nm in diameter and from 0.2–25  $\mu\text{m}$  in length.

Microtubules are made of a globular protein called tubulin, which is of two types called  $\alpha$  and  $\beta$ . There is a slightly different amino acid sequence in  $\alpha$  tubulin compared to  $\beta$  tubulin. When assembly occurs,  $\alpha$  and  $\beta$  tubulin molecules come together as dimers, and the dimers arrange themselves in rows. Microtubules have 13 rows of tubulin dimers, surrounding what appears in electron micrographs to be an empty central core.

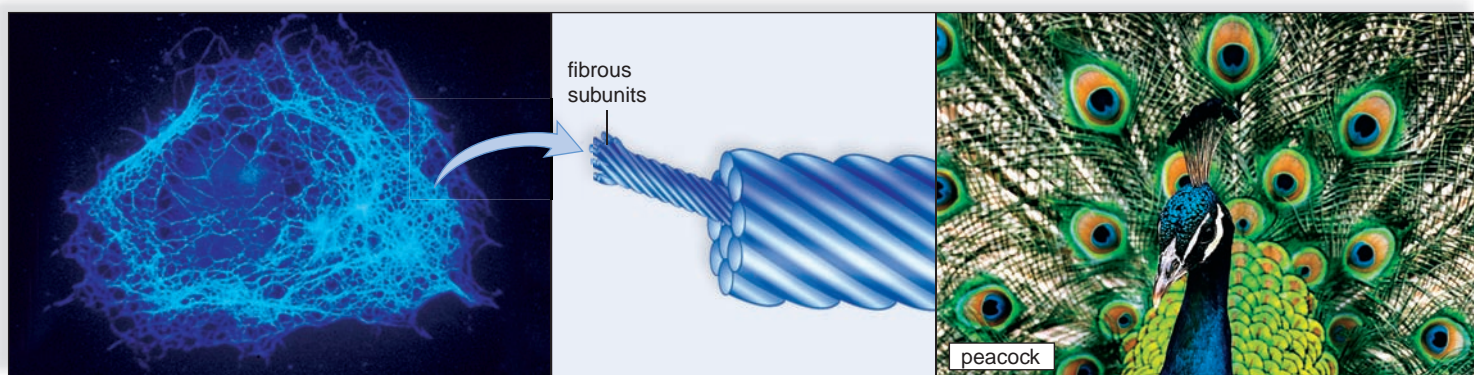
The regulation of microtubule assembly is under the control of a microtubule organizing center (MTOC). In most eukaryotic cells, the main MTOC is in the **centrosome** [Gk. *centrum*, center, and *soma*, body], which lies near the nucleus. Microtubules radiate from the centrosome, helping to maintain the shape of the cell and acting as tracks along which organelles can move. Whereas the motor molecule myosin is associated with actin filaments, the motor molecules kinesin and dynein are associated with microtubules:



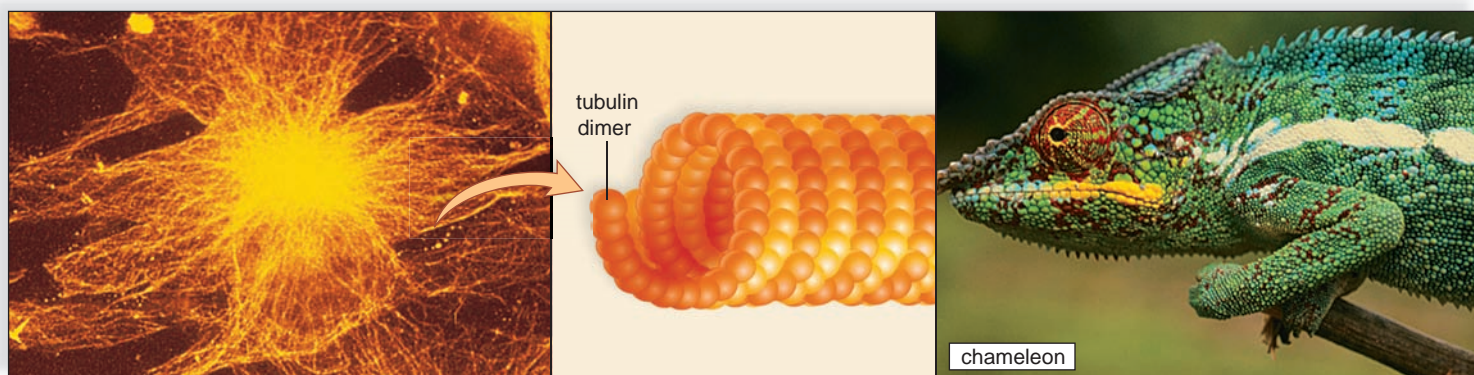
There are different types of kinesin proteins, each specialized to move one kind of vesicle or cellular organelle. Kinesin moves vesicles or organelles in an opposite direction from dynein. Cytoplasmic dynein is closely related to the molecule dynein found in flagella.



a. Actin filaments



b. Intermediate filaments



c. Microtubules

### FIGURE 4.18 The cytoskeleton.

The cytoskeleton maintains the shape of the cell and allows its parts to move. Three types of protein components make up the cytoskeleton. They can be detected in cells by using a special fluorescent technique that reveals only one type of component at a time. **a.** (left to right) Animal cells are treated so that actin filaments can be microscopically detected; the drawing shows that actin filaments are composed of a twisted double chain of actin subunits. The giant cells of the green alga *Chara* rely on actin filaments to move organelles from one end of the cell to another. **b.** (left to right) Animal cells are treated so that intermediate filaments can be microscopically detected; the drawing shows that fibrous proteins account for the ropelike structure of intermediate filaments. A peacock's colorful feathers are strengthened by the presence of intermediate filaments. **c.** (left to right) Animal cells are treated so that microtubules can be microscopically detected; the drawing shows that microtubules are hollow tubes composed of tubulin dimers. The skin cells of a chameleon rely on microtubules to move pigment granules around so that they take on the color of their environment.

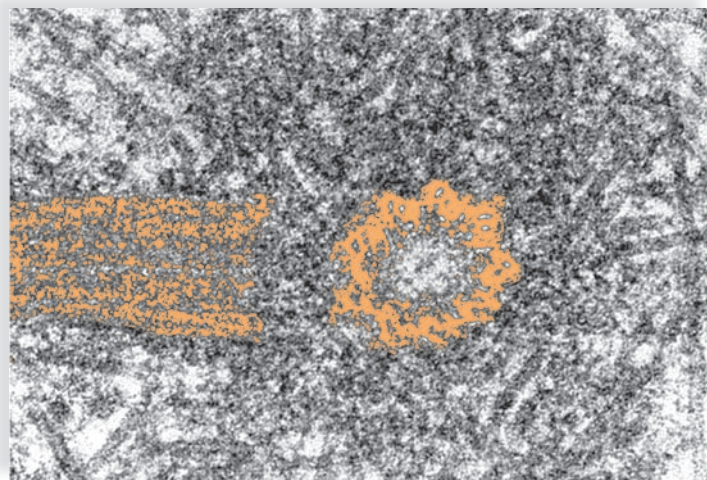
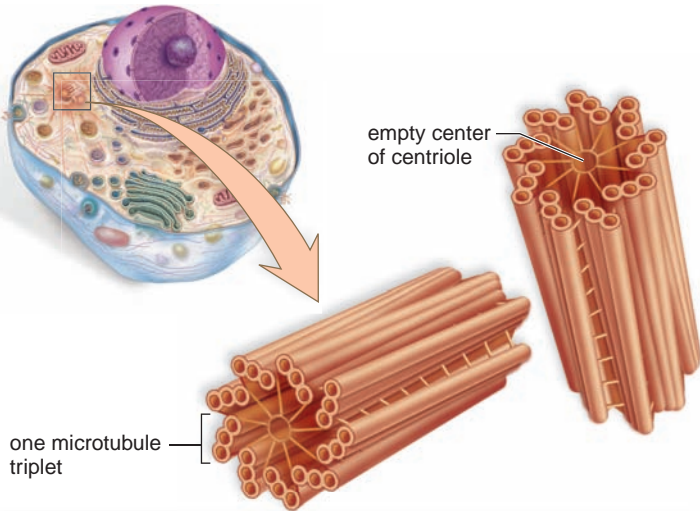
Before a cell divides, microtubules disassemble and then reassemble into a structure called a spindle that distributes chromosomes in an orderly manner. At the end of cell division, the spindle disassembles, and microtubules reassemble once again into their former

array. In the arms race between plants and herbivores, plants have evolved various types of poisons that prevent them from being eaten. Colchicine is a plant poison that binds tubulin and blocks the assembly of microtubules.

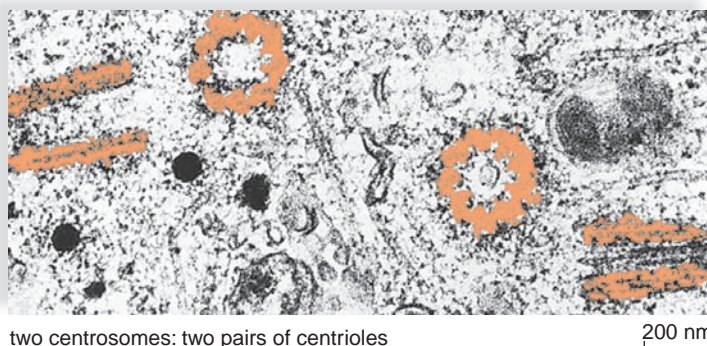


## Centrioles

**Centrioles** [Gk. *centrum*, center] are short cylinders with a  $9 + 0$  pattern of microtubule triplets—nine sets of triplets are arranged in an outer ring, but the center of a centriole does not contain a microtubule. In animal cells and most protists, a centrosome contains two centrioles lying at right angles to



one centrosome: one pair of centrioles



two centrosomes: two pairs of centrioles

**FIGURE 4.19 Centrioles.**

In a nondividing animal cell, there is a single pair of centrioles in the centrosome located just outside the nucleus. Just before a cell divides, the centrioles replicate, producing two centrosomes. During cell division, the centrosomes separate so that each new cell has one centrosome containing one pair of centrioles.

each other. A centrosome, as mentioned previously, is the major microtubule-organizing center for the cell. Therefore, it is possible that centrioles are also involved in the process by which microtubules assemble and disassemble.

Before an animal cell divides, the centrioles replicate, and the members of each pair are at right angles to one another (Fig. 4.19). Then each pair becomes part of a separate centrosome. During cell division, the centrosomes move apart and most likely function to organize the mitotic spindle. In any case, each new cell has its own centrosome and pair of centrioles. Plant and fungal cells have the equivalent of a centrosome, but this structure does not contain centrioles, suggesting that centrioles are not necessary to the assembly of cytoplasmic microtubules.

A **basal body** is an organelle that lies at the base of cilia and flagella and may direct the organization of microtubules within these structures. In other words, a basal body may do for a cilium or flagellum what the centrosome does for the cell. In cells with cilia and flagella, centrioles are believed to give rise to basal bodies.

## Cilia and Flagella

**Cilia** [L. *cilium*, eyelash, hair] and **flagella** [L. *flagello*, whip] are hairlike projections that can move either in an undulating fashion, like a whip, or stiffly, like an oar. If a cell is not attached, cilia (or flagella) move the cell through liquid. For example, unicellular paramecia are organisms that move by means of cilia, whereas sperm cells move by means of flagella. If the cell is attached, cilia (or flagella) are capable of moving liquid over the cell. The cells that line our upper respiratory tract are attached and have cilia that sweep debris trapped within mucus back up into the throat, where it can be swallowed. This action helps keep the lungs clean.

In eukaryotic cells, cilia are much shorter than flagella, but they have a similar construction. Both are membrane-bounded cylinders enclosing a matrix area. In the matrix are nine microtubule doublets arranged in a circle around two central microtubules; this is called the  $9 + 2$  pattern of microtubules (Fig. 4.20). Cilia and flagella move when the microtubule doublets slide past one another.

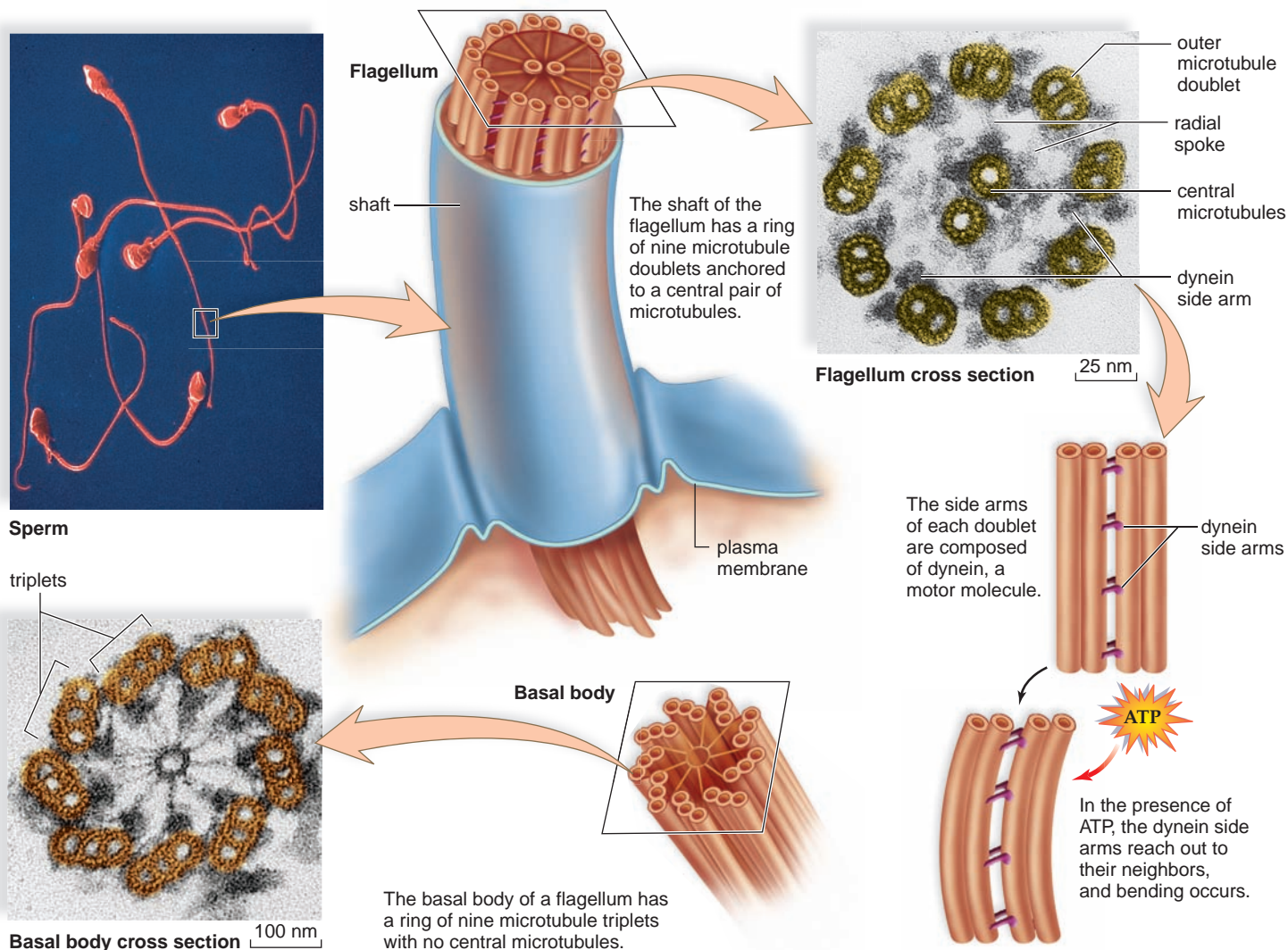
As mentioned, each cilium and flagellum has a basal body lying in the cytoplasm at its base. Basal bodies have the same circular arrangement of microtubule triplets as centrioles and are believed to be derived from them. It is possible that basal bodies organize the microtubules within cilia and flagella, but this is not supported by the observation that cilia and flagella grow by the addition of tubulin dimers to their tips.

### Check Your Progress

4.8

1. List the components of the cytoskeleton.
2. Explain the structure of cilia and flagella.
3. Give an example of a cell that has cilia and one that has flagella. Describe the functions of these cells.





**FIGURE 4.20** Structure of a flagellum.

(below, left) The basal body of a flagellum has a 9 + 0 pattern of microtubule triplets. Notice the ring of nine triplets, with no central microtubules. (above, left) In sperm, the shaft of the flagellum has a 9 + 2 pattern (a ring of nine microtubule doublets surrounds a central pair of microtubules). (middle, right) In place of the triplets seen in a basal body, a flagellum's outer doublets have side arms of dynein, a motor molecule. (below, right) In the presence of ATP, the dynein side arms reach out to their neighbors, and bending occurs. Because of the radial spokes connecting the doublets to the central microtubules, bending occurs.

## Connecting the Concepts

Our knowledge of cell anatomy has been gathered by studying micrographs of cells. This has allowed cytologists (biologists who study cells) to arrive at a picture of generalized cells, such as those depicted for the animal and plant cells in Figures 4.6 and 4.7. The Science Focus on page 67 describes the methodology for studying the function of organelles.

Eukaryotic cells, taken as a whole, contain several types of organelles, and the chapter concepts for the chapter suggest that you should know the structure and function of each one. A concept to keep in mind is that “structure suits function.” For example, ribosome subunits move from the nucleus to the cytoplasm; therefore, it seems reasonable that the nuclear envelope

has pores. Finding relationships between structure and function will give you a deeper understanding of the cell, which will boost your memory capabilities.

Not all eukaryotic cells contain every type of organelle depicted. Cells actually have many specializations of structure that are consistent with their particular functions. Because red blood cells lack a nucleus, more room is made available for molecules of hemoglobin, the molecule that transports oxygen in the blood. Muscle cells are quite large and contain many specialized contractile organelles not discussed in this chapter. They also contain many mitochondria that supply the ATP needed for muscle contraction. Therefore, it can be seen that eu-

karyotic cells are specialized according to the organelles they contain or do not contain. This leads to the specialization of tissues and organs found in complex multicellular organisms.

In Chapter 5, we continue our study of the generalized cell by considering some functions that are common to all cells. We will see that all cells exchange substances across the plasma membrane and maintain a saltwater balance within certain limits. This is an example of homeostasis, or the relative constancy of the internal environment. Another such example was mentioned in Chapter 2, when we considered that organisms contain buffers that help maintain the pH of body fluids within limits suitable to life.



## summary

### 4.1 Cellular Level of Organization

All organisms are composed of cells, the smallest units of living matter. Cells are capable of self-reproduction, and existing cells come only from preexisting cells. Cells are very small and are measured in micrometers. The plasma membrane regulates exchange of materials between the cell and the external environment. Cells must remain small in order to have an adequate amount of surface area to volume.

### 4.2 Prokaryotic Cells

There are two major groups of prokaryotic cells: the bacteria and the archaea. Prokaryotic cells lack the nucleus of eukaryotic cells. The cell envelope of bacteria includes a plasma membrane, a cell wall, and an outer glycocalyx. The cytoplasm contains ribosomes, inclusion bodies, and a nucleoid that is not bounded by a nuclear envelope. The cytoplasm of cyanobacteria also includes thylakoids. The appendages of a bacterium are the flagella, the fimbriae, and the conjugation pili.

### 4.3 Introducing Eukaryotic Cells

Eukaryotic cells are much larger than prokaryotic cells, but they are compartmentalized by the presence of organelles, each with a specific structure and function (Table 4.1). The nuclear envelope most likely evolved through invagination of the plasma membrane, but mitochondria and chloroplasts may have arisen when a eukaryotic cell took up bacteria and algae in separate events. Perhaps this accounts for why the mitochondria and chloroplasts function fairly independently. Other membranous organelles are in constant communication by way of transport vesicles.

### 4.4 The Nucleus and Ribosomes

The nucleus of eukaryotic cells is bounded by a nuclear envelope containing pores. These pores serve as passageways between the cytoplasm and the nucleoplasm. Within the nucleus, chromatin, which contains DNA, undergoes coiling into chromosomes at the time of

cell division. The nucleolus is a special region of the chromatin where rRNA is produced and ribosomal subunits are formed.

Ribosomes are organelles that function in protein synthesis. When protein synthesis occurs, mRNA leaves the nucleus with a coded message from DNA that specifies the sequence of amino acids in that protein. After mRNA attaches to a ribosome, it binds to the ER if it has a signal peptide. (Specifically, the signal peptide attaches to a signal recognition particle (SRP) that, in turn, binds to an SRP receptor on the ER.) When completed, the protein remains in the lumen of the ER.

### 4.5 The Endomembrane System

The endomembrane system includes the ER (both rough and smooth), the Golgi apparatus, the lysosomes (in animal cells), and transport vesicles. Newly produced proteins are modified in the ER before they are packaged in transport vesicles, many of which go to the Golgi apparatus. The smooth ER has various metabolic functions, depending on the cell type, but it also forms vesicles that carry lipids to different locations, particularly to the Golgi apparatus. The Golgi apparatus modifies, sorts, and repackages proteins and also processes lipids. Some proteins are packaged into lysosomes, which carry out intracellular digestion, or into vesicles that fuse with the plasma membrane. Following fusion, secretion occurs.

### 4.6 Other Vesicles and Vacuoles

Cells contain numerous vesicles and vacuoles, some of which, such as lysosomes, have already been discussed. Peroxisomes are vesicles that are involved in the metabolism of long chain fatty acids. The large central vacuole in plant cells functions in storage and also in the breakdown of molecules and cell parts.

### 4.7 The Energy-Related Organelles

Cells require a constant input of energy to maintain their structure. Chloroplasts capture the energy of the sun and carry on photosynthesis, which produces carbohydrates. Carbohydrate-derived products are broken down in mitochondria as ATP is produced. This is an oxygen-requiring process called cellular respiration.

**TABLE 4.1**

**Comparison of Prokaryotic Cells and Eukaryotic Cells**

	<i>Prokaryotic Cells</i> (1–20 $\mu\text{m}$ in diameter)	<i>Eukaryotic Cells</i> (10–100 $\mu\text{m}$ in diameter)	
		<i>Animal</i>	<i>Plant</i>
Cell wall	Usually (peptidoglycan)	No	Yes (cellulose)
Plasma membrane	Yes	Yes	Yes
Nucleus	No	Yes	Yes
Nucleolus	No	Yes	Yes
Ribosomes	Yes (smaller)	Yes	Yes
Endoplasmic reticulum	No	Yes	Yes
Golgi apparatus	No	Yes	Yes
Lysosomes	No	Yes	No
Mitochondria	No	Yes	Yes
Chloroplasts	No	No	Yes
Peroxisomes	No	Usually	Usually
Cytoskeleton	No	Yes	Yes
Centrioles	No	Yes	No
9 + 2 cilia or flagella	No	Often	No (in flowering plants) Yes (sperm of bryophytes, ferns, and cycads)

### 4.8 The Cytoskeleton

The cytoskeleton contains actin filaments, intermediate filaments, and microtubules. These maintain cell shape and allow it and the organelles to move. Actin filaments, the thinnest filaments, interact with the motor molecule myosin in muscle cells to bring about contraction; in other cells, they pinch off daughter cells and have other dynamic functions. Intermediate filaments support the nuclear envelope and the plasma membrane and probably participate in cell-to-cell junctions. Microtubules radiate out from the centrosome and are present in centrioles, cilia, and flagella. They serve as tracks along which vesicles and other organelles move, due to the action of specific motor molecules.

### understanding the terms

actin filament 78	intermediate filament 78
bacillus 64	leucoplast 76
basal body 80	lysosome 73
capsule 64	magnification 62
cell 60	matrix 77
cell envelope	mesosome 64
(of prokaryotes) 64	microtubule 78
cell theory 60	mitochondrion 76
cell wall 64	motor molecule 78
central vacuole	nuclear envelope 70
(of plant cell) 75	nuclear pore 70
centriole 80	nucleoid 64
centrosome 78	nucleolus 70
chloroplast 76	nucleoplasm 70
chromatin 70	organelle 66
chromoplast 76	peroxisome 75
chromosome 70	plasma membrane 64
cilium 80	plasmid 64
coccus 64	plastid 76
conjugation pili 65	polyribosome 71
contrast 63	prokaryotic cell 64
cristae 77	pseudopod 78
cyanobacteria 65	resolution 63
cytoplasm 64	ribosome 64, 71
cytoskeleton 67	rough ER 72
endomembrane system 72	secretion 72
endoplasmic reticulum (ER) 72	signal peptide 71
endosymbiotic theory 66	smooth ER 72
eukaryotic cell 64	spirillum 64
fimbriae 65	spirochete 64
flagellum (pl., flagella) 65, 80	stroma 76
gene 70	surface-area-to-volume ratio 61
glycocalyx 64	thylakoid 65, 76
Golgi apparatus 72	vacuole 75
granum 76	vesicle 66
inclusion body 65	

Match the terms to these definitions:

- \_\_\_\_\_ Organelle, consisting of saccules and vesicles, that processes, packages, and distributes molecules about or from the cell.
- \_\_\_\_\_ Especially active in lipid metabolism; always produces  $H_2O_2$ .
- \_\_\_\_\_ Dark-staining, spherical body in the cell nucleus that produces ribosomal subunits.
- \_\_\_\_\_ Internal framework of the cell, consisting of microtubules, actin filaments, and intermediate filaments.
- \_\_\_\_\_ Allows prokaryotic cells to attach to other cells.

### reviewing this chapter

- What are the three basic principles of the cell theory? 60
- Why is it advantageous for cells to be small? 61
- Roughly sketch a bacterial (prokaryotic) cell, label its parts, and state a function for each of these. 65
- How do eukaryotic and prokaryotic cells differ? 66
- Describe how the nucleus, the chloroplast, and the mitochondrion may have become a part of the eukaryotic cell. 66
- What does it mean to say that the eukaryotic cell is compartmentalized? 66–67
- Describe the structure and the function of the nuclear envelope and the nuclear pores. 70–71
- Distinguish between the nucleolus, rRNA, and ribosomes. 70–71
- Name organelles that are a part of the endomembrane system and explain the term. 72
- Trace the path of a protein from rough ER to the plasma membrane. 74
- Give the overall equations for photosynthesis and cellular respiration, contrast the two, and tell how they are related. 76
- Describe the structure and function of chloroplasts and mitochondria. How are these two organelles related to one another? 76–77
- What are the three components of the cytoskeleton? What are their structures and functions? 78–79
- Relate the structure of flagella (and cilia) to centrioles, and discuss the function of both. 80

### testing yourself

Choose the best answer for each question.

- The small size of cells best correlates with
  - the fact that they are self-reproducing.
  - their prokaryotic versus eukaryotic nature.
  - an adequate surface area for exchange of materials.
  - the fact that they come in multiple sizes.
  - All of these are correct.
- Which of these is not a true comparison of the compound light microscope and the transmission electron microscope?

#### LIGHT

- Uses light to “view” object
- Uses glass lenses for focusing
- Specimen must be killed and stained
- Magnification is not as great
- Resolution is not as great

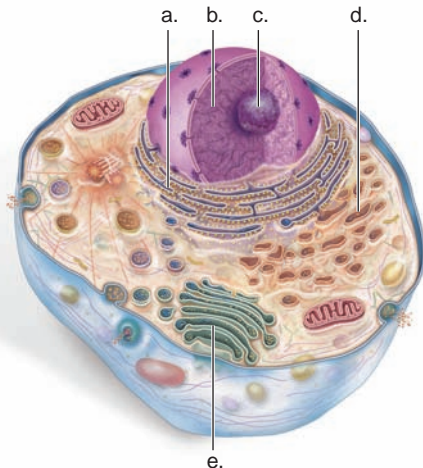
#### ELECTRON

- Uses electrons to “view” object  
 Uses magnetic lenses for focusing  
 Specimen may be alive and nonstained  
 Magnification is greater  
 Resolution is greater

- Which of these best distinguishes a prokaryotic cell from a eukaryotic cell?
  - Prokaryotic cells have a cell wall, but eukaryotic cells never do.
  - Prokaryotic cells are much larger than eukaryotic cells.
  - Prokaryotic cells have flagella, but eukaryotic cells do not.
  - Prokaryotic cells do not have a membrane-bounded nucleus, but eukaryotic cells do have such a nucleus.
  - Prokaryotic cells have ribosomes, but eukaryotic cells do not have ribosomes.
- Which of these is not found in the nucleus?
  - functioning ribosomes
  - chromatin that condenses to chromosomes
  - nucleolus that produces rRNA
  - nucleoplasm instead of cytoplasm
  - all forms of RNA



5. Vesicles from the ER most likely are on their way to
  - a. the rough ER.
  - b. the lysosomes.
  - c. the Golgi apparatus.
  - d. the plant cell vacuole only.
  - e. the location suitable to their size.
6. Lysosomes function in
  - a. protein synthesis.
  - b. processing and packaging.
  - c. intracellular digestion.
  - d. lipid synthesis.
  - e. production of hydrogen peroxide.
7. Mitochondria
  - a. are involved in cellular respiration.
  - b. break down ATP to release energy for cells.
  - c. contain grana and cristae.
  - d. are present in animal cells but not plant cells.
  - e. All of these are correct.
8. Which organelle releases oxygen?
  - a. ribosome
  - b. Golgi apparatus
  - c. chloroplast
  - d. smooth ER
9. Label only the parts of the cell that are involved in protein synthesis and modification. Give a function for each structure.



10. Which of these is not true?
  - a. Actin filaments are found in muscle cells.
  - b. Microtubules radiate out from the ER.
  - c. Intermediate filaments sometimes contain keratin.
  - d. Motor molecules use microtubules as tracks.
11. Cilia and flagella
  - a. have a 9 + 0 pattern of microtubules, same as basal bodies.
  - b. contain myosin that pulls on actin filaments.
  - c. are organized by basal bodies derived from centrioles.
  - d. are constructed similarly in prokaryotes and eukaryotes.
  - e. Both a and c are correct.
12. Which of the following organelles contains its (their) own DNA, suggesting they were once independent prokaryotes?
  - a. Golgi apparatus
  - b. mitochondria
  - c. chloroplasts
  - d. ribosomes
  - e. Both b and c are correct.
13. Which organelle most likely originated by invagination of the plasma membrane?
  - a. mitochondria
  - b. flagella
  - c. nucleus
  - d. chloroplasts
  - e. All of these are correct.

14. Which structures are found in a prokaryotic cell?
  - a. cell wall, ribosomes, thylakoids, chromosome
  - b. cell wall, plasma membrane, nucleus, flagellum
  - c. nucleoid, ribosomes, chloroplasts, capsule
  - d. plasmid, ribosomes, enzymes, DNA, mitochondria
  - e. chlorophyll, enzymes, Golgi apparatus, plasmids
15. Study the example given in (a) below. Then for each other organelle listed, state another that is structurally and functionally related. Tell why you paired these two organelles.
  - a. The nucleus can be paired with nucleoli because nucleoli are found in the nucleus. Nucleoli occur where chromatin is producing rRNA.
  - b. mitochondria
  - c. centrioles
  - d. ER

## thinking scientifically

1. The protists that cause malaria contribute to infections associated with AIDS. Scientists have discovered that an antibiotic that inhibits prokaryotic enzymes will kill the parasite because it is effective against the plastids in the protist. What can you conclude about the origin of the plastids?
2. For your cytology study, you have decided to label and, thereby, detect the presence of the base uracil in an animal cell. In what parts of the cell do you expect to find your radioactive tracer?

## bioethical issue

### Stem Cells

A stem cell is an immature cell that is capable of producing cells that will differentiate into mature cells. Stem cells exist in the various organs of the human body; however, they are difficult to obtain, except for those that reside in red bone marrow and produce all types of blood cells. One method of obtaining stem cells is to take a 2n adult nucleus from, say, skin, manipulate it genetically, and put it in an enucleated egg cell. If all goes well, development will begin, and the cells that result can be pried apart and used to make neurological tissues that could possibly cure Alzheimer or Parkinson disease or any other type of neurological disorder. However, if development were to continue, a clone of the human that donated the 2n nucleus could possibly result.

Is it bioethical to continue investigating such research?

Especially when you consider that the “embryo” that provided the stem cells was not produced by the normal method of having a sperm fertilize an egg? Or, is it wrong to produce an embryo only to serve as a source of stem cells?

## Biology website

The companion website for *Biology* provides a wealth of information organized and integrated by chapter. You will find practice tests, animations, videos, and much more that will complement your learning and understanding of general biology.

<http://www.mhhe.com/maderbiology10>



## 5

# Membrane Structure and Function

**a**n African pygmy, an overweight diabetic, and a young child with cystic fibrosis suffer from a defect in their cells' plasma membrane. Growth hormone does not bind to the pygmy's plasma membrane, the diabetic's does not respond properly to insulin, and the membrane does not transport chloride from the cells of a child who has cystic fibrosis.

A plasma membrane encloses every cell, whether the cell is a unicellular amoeba or one of many from the body of a squid, carnation, mushroom, or human. Universally, a plasma membrane protects a cell by acting as a barrier between its living contents and the surrounding environment. It regulates what goes into and out of the cell and serves as a means of communication between cells. Inside eukaryotic cells, membrane compartmentalizes the cell so that specific enzymes for particular functions are isolated from one another. This chapter describes the plasma membrane and its numerous functions. It also discusses various ways cells communicate so that the activities of tissues and organs are coordinated.

A eukaryotic cell is surrounded by a plasma membrane, and membrane also compartmentalizes the cell into various organelles.

## 5.1 PLASMA MEMBRANE STRUCTURE AND FUNCTION

- The plasma membrane is a phospholipid bilayer that contains proteins. The plasma membrane has numerous functions, including regulating the passage of molecules into and out of the cell. 86–88
- Cell-to-cell communication is an important function of the plasma membrane to achieve coordination between cells of the same tissue and between different tissues of the body. 89
- The plasma membrane allows small, noncharged molecules to passively cross the membrane. Other molecules are assisted across the membrane by carriers or by vesicle formation. 90

## 5.2 PASSIVE TRANSPORT ACROSS A MEMBRANE

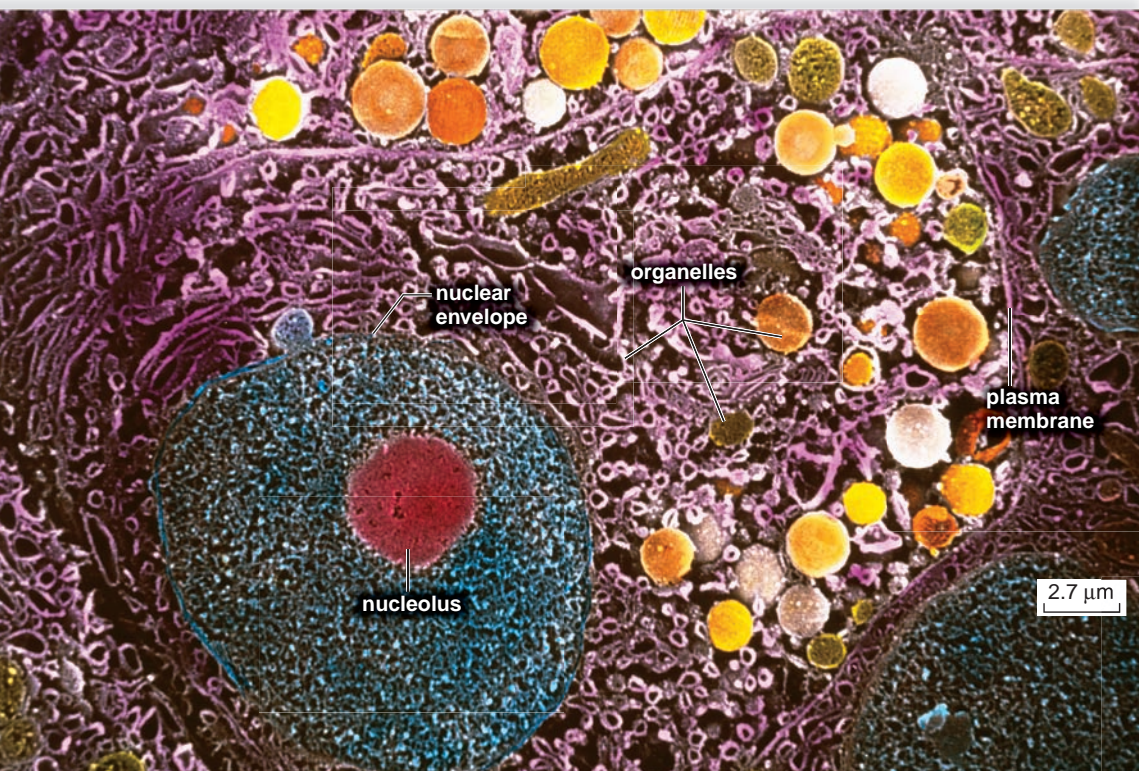
- A few types of molecules simply diffuse down their concentration gradient to cross the membrane. Some molecules move at a faster rate because they are transported by carriers. 91–94

## 5.3 ACTIVE TRANSPORT ACROSS A MEMBRANE

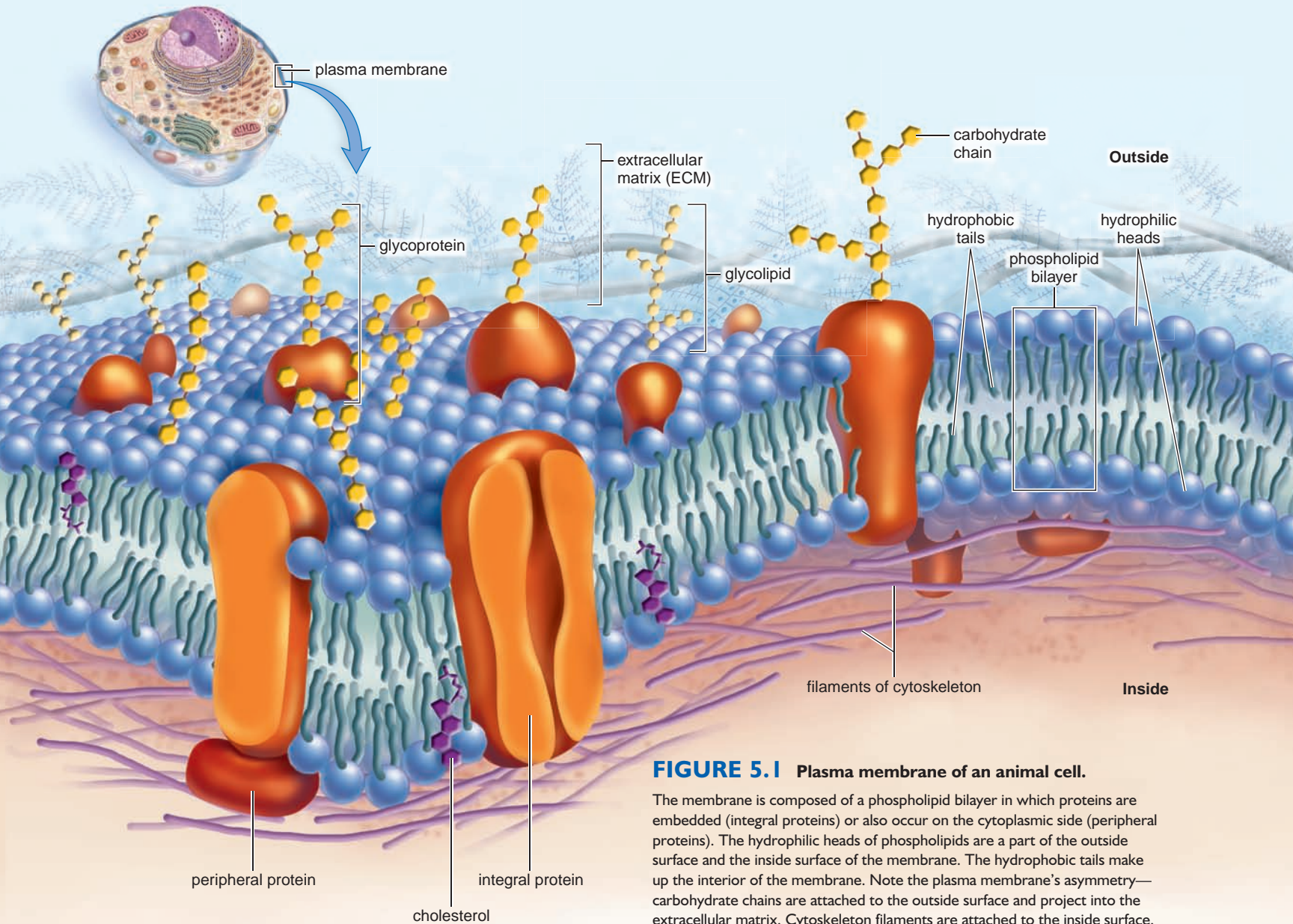
- The expenditure of energy, plus the use of a carrier, is required when molecules are transported across the membrane against their concentration gradient. 94–95
- Bulk transport is possible when vesicles fuse with the plasma membrane to secrete macromolecules, or vesicles form to bring macromolecules into the cell. 96–97

## 5.4 MODIFICATION OF CELL SURFACES

- In animals, the extracellular matrix of cells influences the shape, movement, and function of cells. 98
- In certain animal tissues, communication between cells is assisted by the presence of various types of cell junctions. 98–99
- In plants, cells have a permeable cell wall that supports the cell. Plasmodesmata often permit a flow of water and some solutes between plant cells. 99







**FIGURE 5.1** Plasma membrane of an animal cell.

The membrane is composed of a phospholipid bilayer in which proteins are embedded (integral proteins) or also occur on the cytoplasmic side (peripheral proteins). The hydrophilic heads of phospholipids are a part of the outside surface and the inside surface of the membrane. The hydrophobic tails make up the interior of the membrane. Note the plasma membrane's asymmetry—carbohydrate chains are attached to the outside surface and project into the extracellular matrix. Cytoskeleton filaments are attached to the inside surface.

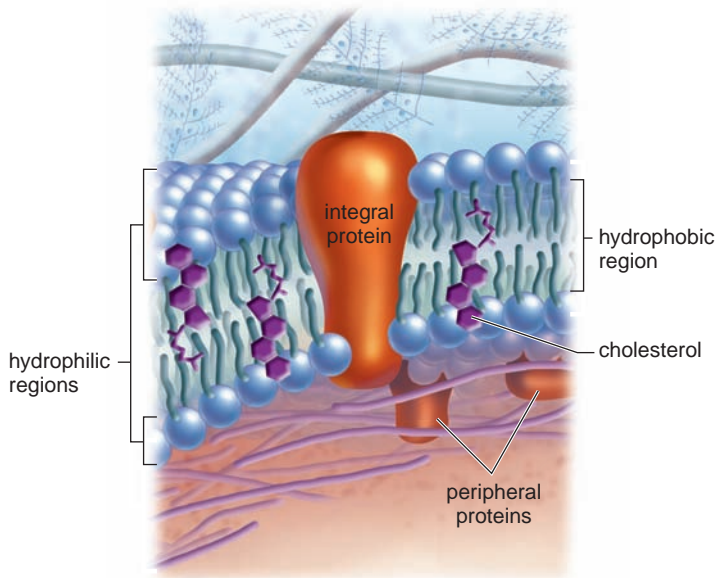
## 5.1 Plasma Membrane Structure and Function

The structure of an animal cell's plasma membrane is depicted in Figure 5.1. The drawing shows that the membrane is a phospholipid bilayer in which protein molecules are either partially or wholly embedded. A phospholipid is an *amphipathic molecule*, meaning that it has both a hydrophilic (water-loving) region and a hydrophobic (water-fearing) region. The amphipathic nature of phospholipids largely explains why the membrane is a bilayer—has two layers of phospholipids. The hydrophilic polar heads of the phospholipid molecules naturally face the outside and inside of the cell, where water is found. The hydrophobic nonpolar tails face each other. **Cholesterol** is another lipid found in the animal plasma membrane; related steroids are found in the

plasma membrane of plants. Cholesterol helps modify the fluidity of the membrane, as discussed later.

As shown in Figure 5.1, the proteins are scattered throughout the membrane in an irregular pattern, and this pattern can vary from membrane to membrane. Electron micrographs verify that many of the proteins are embedded within the membrane. During freeze-fracture, the membrane is first frozen and then split so that the upper layer is separated from the lower layer. The proteins remain intact and go with one layer or the other. The embedded proteins are termed *integral proteins*, and other proteins that occur only on the cytoplasmic side of the membrane are termed *peripheral proteins*. Some integral proteins protrude from only one surface of the bilayer but most span the membrane, with a hydrophobic region within the membrane, while their hydrophilic heads protrude from both surfaces of the bilayer. These

proteins can be held in place by attachments to protein fibers of the cytoskeleton (inside) and fibers of the extracellular matrix (outside). Only animal cells have an **extracellular matrix (ECM)**, which contains various protein fibers and also very large and complex carbohydrate molecules. The ECM, which is discussed in greater detail at the end of the chapter, has various functions, from lending support to the plasma membrane to assisting communication between cells.



## Fluid-Mosaic Model

The model currently in use to describe the plasma membrane is called the **fluid-mosaic model**. The fluidity of the membrane is due to its lipid component. At body temperature, the phospholipid bilayer of the plasma membrane has the consistency of olive oil. The greater the concentration of unsaturated fatty acid residues, the more fluid is the bilayer. In each monolayer, the hydrocarbon tails wiggle, and the entire phospholipid molecule can move sideways at a rate averaging about  $2\ \mu\text{m}$ —the length of a prokaryotic cell—per second. (Phospholipid molecules rarely flip-flop from one layer to the other, because this would require the hydrophilic head to move through the hydrophobic center of the membrane.) The fluidity of a phospholipid bilayer means that cells are pliable. Imagine if they were not—the long nerve fibers in your neck would crack whenever you nodded your head! The fluidity of the membrane also prevents it from solidifying as external temperatures drop.

The presence of cholesterol molecules in the plasma membrane affects its fluidity. At higher temperatures, cholesterol stiffens the membrane and makes it less fluid than it would otherwise be. At lower temperatures, cholesterol helps prevent the membrane from freezing by not allowing contact between certain phospholipid tails.

The mosaic nature of the plasma membrane is due to its protein content. The number and kinds of proteins can vary in the plasma membrane and in the membrane of the various organelles. The presence of various proteins that seem to have no set positions is consistent with the idea that they form a mosaic pattern. Further, it was once thought that the proteins could

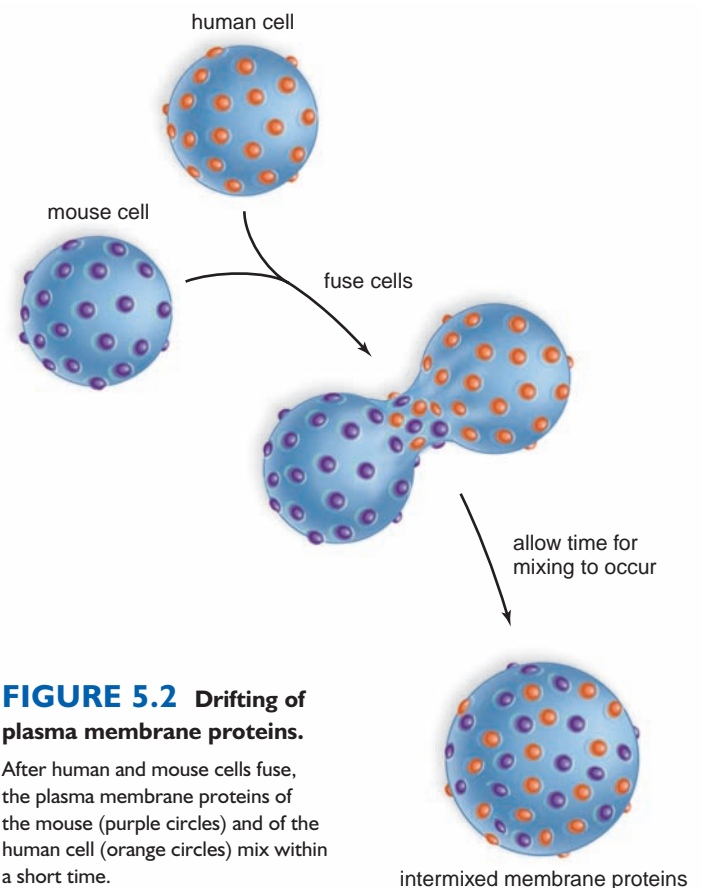
freely move sideways within the fluid bilayer. Figure 5.2 describes an experiment in which the proteins were tagged prior to allowing mouse and human cells to fuse. An hour after fusion, the proteins were completely mixed. Such an experiment suggests that at least some proteins are able to move sideways in the membrane. Today, however, we know that proteins are often bond to either or both the ECM and the cytoskeleton. These connections hold a protein in place and prevent it from moving in the fluid phospholipid bilayer.

## Carbohydrate Chains

Both phospholipids and proteins can have attached carbohydrate (sugar) chains. If so, these molecules are called **glycolipids** and **glycoproteins**, respectively. Since the carbohydrate chains occur only on the outside surface and peripheral proteins occur asymmetrically on one surface or the other, the two sides of the membrane are not identical.

In animal cells, the carbohydrate chains of proteins give the cell a “sugar coat,” more properly called the glycocalyx. The glycocalyx protects the cell and has various other functions. For example, it facilitates adhesion between cells, reception of signaling molecules, and cell-to-cell recognition.

The possible diversity of the carbohydrate (sugar) chains is enormous. The chains can vary by the number (15 is usual, but there can be several hundred) and sequence of sugars and by whether the chain is branched. Each cell within the individual has its own particular “fingerprint” because of these chains. As you probably know, transplanted tissues are often rejected by the recipient. This is because the



**FIGURE 5.2** Drifting of plasma membrane proteins.

After human and mouse cells fuse, the plasma membrane proteins of the mouse (purple circles) and of the human cell (orange circles) mix within a short time.



immune system is able to recognize that the foreign tissue's cells do not have the appropriate carbohydrate chains. In humans, carbohydrate chains are also the basis for the A, B, and O blood groups.

## The Functions of the Proteins

While the plasma membranes of various cells and the membranes of various organelles can contain various proteins at different times, these types of proteins are apt to be present:

**Channel proteins** Channel proteins are involved in the passage of molecules through the membrane. They have a channel that allows a substance to simply move across the membrane (Fig. 5.3a). For example, a channel protein allows hydrogen ions to flow across the inner mitochondrial membrane. Without this movement of hydrogen ions, ATP would never be produced.

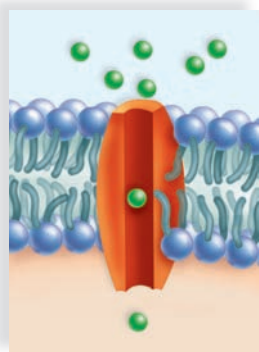
**Carrier proteins** Carrier proteins are also involved in the passage of molecules through the membrane. They combine with a substance and help it move across the membrane (Fig. 5.3b). A carrier protein transports sodium and potassium ions across the plasma membrane of a nerve cell. Without this carrier protein, nerve conduction would be impossible.

**Cell recognition proteins** Cell recognition proteins are glycoproteins (Fig. 5.3c). Among other functions, these proteins help the body recognize when it is being invaded by pathogens so that an immune response can occur. Without this recognition, pathogens would be able to freely invade the body.

**Receptor proteins** Receptor proteins have a shape that allows a specific molecule to bind to it (Fig. 5.3d). The binding of this molecule causes the protein to change its shape and thereby bring about a cellular response. The coordination of the body's organs is totally dependent on such signaling molecules. For example, the liver stores glucose after it is signaled to do so by insulin.

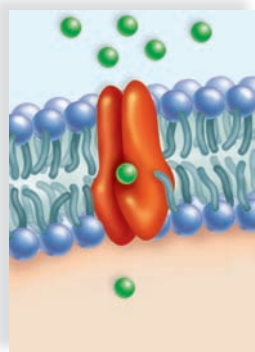
**Enzymatic proteins** Some plasma membrane proteins are enzymatic proteins that carry out metabolic reactions directly (Fig. 5.3e). Without the presence of enzymes, some of which are attached to the various membranes of the cell, a cell would never be able to perform the metabolic reactions necessary to its proper function.

**Junction proteins** As discussed on page 98, proteins are involved in forming various types of junctions between animal cells (Fig. 5.3f). Signaling molecules that pass through gap junctions allow the cilia of cells that line your respiratory tract to beat in unison.



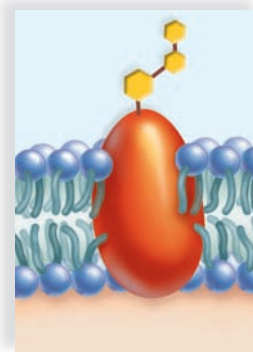
a.

**Channel Protein:** Allows a particular molecule or ion to cross the plasma membrane freely. Cystic fibrosis, an inherited disorder, is caused by a faulty chloride ( $\text{Cl}^-$ ) channel; a thick mucus collects in airways and in pancreatic and liver ducts.



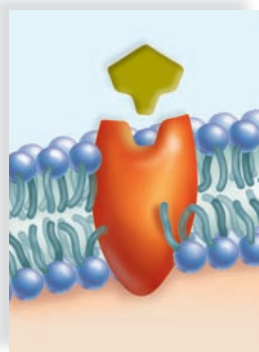
b.

**Carrier Protein:** Selectively interacts with a specific molecule or ion so that it can cross the plasma membrane. The inability of some persons to use energy for sodium-potassium ( $\text{Na}^+/\text{K}^+$ ) transport has been suggested as the cause of their obesity.



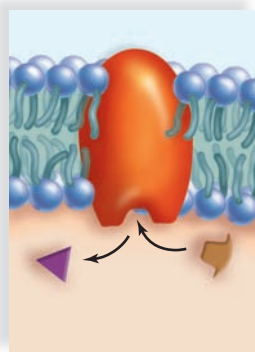
c.

**Cell Recognition Protein:** The MHC (major histocompatibility complex) glycoproteins are different for each person, so organ transplants are difficult to achieve. Cells with foreign MHC glycoproteins are attacked by white blood cells responsible for immunity.



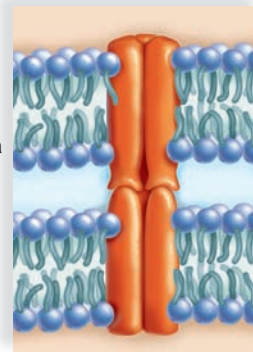
d.

**Receptor Protein:** Is shaped in such a way that a specific molecule can bind to it. Pygmies are short, not because they do not produce enough growth hormone, but because their plasma membrane growth hormone receptors are faulty and cannot interact with growth hormone.



e.

**Enzymatic Protein:** Catalyzes a specific reaction. The membrane protein, adenylate cyclase, is involved in ATP metabolism. Cholera bacteria release a toxin that interferes with the proper functioning of adenylate cyclase; sodium ( $\text{Na}^+$ ) and water leave intestinal cells, and the individual may die from severe diarrhea.



f.

**Junction Proteins:** Tight junctions join cells so that a tissue can fulfill a function, as when a tissue pinches off the neural tube during development. Without this cooperation between cells, an animal embryo would have no nervous system.

**FIGURE 5.3** Membrane protein diversity.

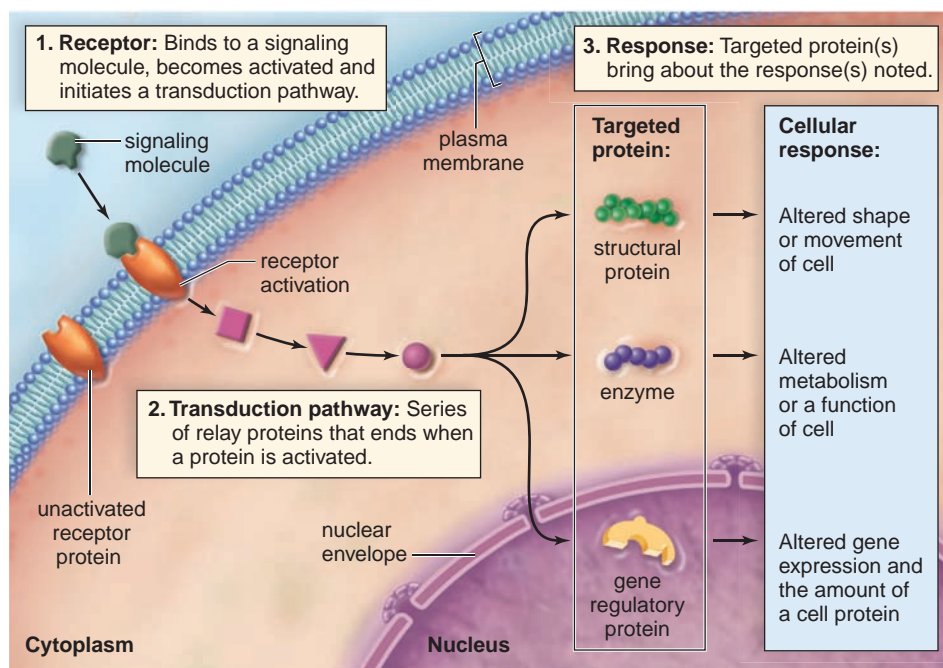
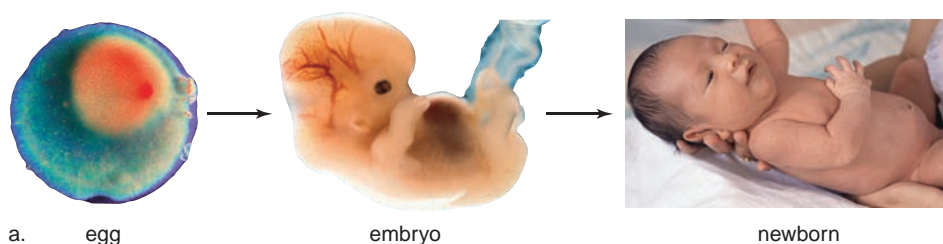
These are some of the functions performed by proteins found in the plasma membrane.

## science focus

### How Cells Talk to One Another

**A**ll organisms are able to sense and respond to specific signals in their environment. A bacterium that has taken up residence in your body is responding to signaling molecules when it finds food and escapes immune cells in order to stay alive. Signaling helps bread mold on stale bread in your refrigerator detect the presence of an opposite mating strain and begin its sexual life cycle. Similarly, the cells of an embryo are responding to signaling molecules when they move to specific locations and assume the

shape and perform the functions of specific tissues (Fig. 5Aa). In the newborn, signaling is still required because the functions of a specific tissue may be necessary only on occasion, or one tissue may need to perform one of its various functions only at particular times. In plants, external signals, such as a change in the amount of light, tells them when it is time to resume growth or flower. Internal signaling molecules enable plants to coordinate the activities of roots, stems, and leaves.



b.

**FIGURE 5A Cell signaling.**

**a.** The process of signaling helps account for the transformation of an egg into an embryo and then an embryo into a newborn. **b.** The process of signaling involves three steps: binding of the signaling molecule, transduction of the signal, and response of the cell depending on what type protein is targeted.

### Cell Signaling

The cells of a multicellular organism “talk” to one another by using signaling molecules, sometimes called chemical messengers. Some messengers are produced at a distance from a target tissue and, in animals, are carried by the circulatory system to various sites around the body. For example, the pancreas releases a hormone called insulin, which is transported in blood vessels to the liver, and thereafter, the liver stores glucose as glycogen. Failure of the liver to respond appropriately results in a medical condition called diabetes. In Chapter 9, we are particularly interested in growth factors, which act locally as signaling molecules and cause cells to divide. Overreacting to growth factors can result in a tumor characterized by unlimited cell division. The importance of cell signaling causes much research to be directed toward understanding the intricacies of the process.

We have learned that cells respond to only certain signaling molecules. Why? Because they must bind to a receptor protein, and cells have receptors for only certain signaling molecules. Each cell has receptors for numerous signaling molecules and often the final response is due to a summing up of all the various signals received. These molecules tell a cell what it should be doing at the moment, and without any signals, the cell dies.

Signaling not only involves a receptor protein, it also involves a pathway called a transduction pathway and a response. To understand the process, consider an analogy. When a TV camera (the receptor) is shooting a scene, the picture is converted to electrical signals (transduction pathway) that are understood by the TV in your house and are converted to a picture on your screen (the response). The process in cells is more complicated because each member of the pathway can turn on the activity of a number of other proteins. As shown in Figure 5Ab, the cell response to a transduction pathway can be a change in the shape or movement of a cell, the activation of a particular enzyme, or the activation of a specific gene. We will be mentioning and giving examples of cell signaling between cells throughout the text.



**TABLE 5.1****Passage of Molecules into and out of the Cell**

	Name	Direction	Requirement	Examples
Energy Not Required	Diffusion	Toward lower concentration	Concentration gradient	Lipid-soluble molecules, and gases
	Facilitated transport	Toward lower concentration	Channels or carrier and concentration gradient	Some sugars, and amino acids
Energy Required	Active transport	Toward higher concentration	Carrier plus energy	Sugars, amino acids, and ions
	Bulk transport	Toward outside or inside	Vesicle utilization	Macromolecules

## Permeability of the Plasma Membrane

The plasma membrane regulates the passage of molecules into and out of the cell. This function is critical because the life of the cell depends on maintenance of its normal composition. The plasma membrane can carry out this function because it is **differentially** (selectively) **permeable**, meaning that certain substances can move across the membrane while others cannot.

Table 5.1 lists, and Figure 5.4 illustrates, which types of molecules can passively (no energy required) cross a membrane and which may require transport by a carrier protein and/or an expenditure of energy. In general, small, noncharged molecules, such as carbon dioxide, oxygen, glycerol,

and alcohol, can freely cross the membrane. They are able to slip between the hydrophilic heads of the phospholipids and pass through the hydrophobic tails of the membrane. These molecules are said to follow their **concentration gradient** as they move from an area where their concentration is high to an area where their concentration is low. Consider that a cell is always using oxygen when it carries on cellular respiration. Therefore, the concentration of oxygen is always lower inside a cell than outside a cell, and so oxygen has a tendency to enter a cell. Carbon dioxide, on the other hand, is produced when a cell carries on cellular respiration. Therefore, carbon dioxide is also following a concentration gradient when it moves from inside the cell to outside the cell.

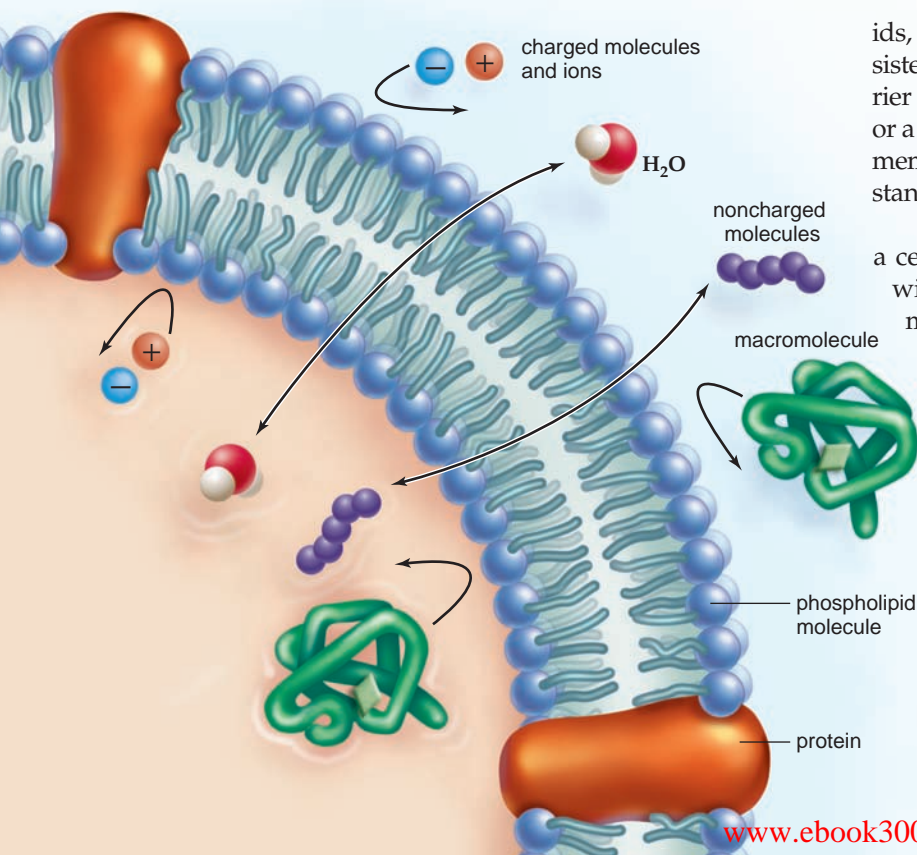
A new finding has been that at least in some cells, and perhaps all cells, water passively moves through a membrane channel protein now called an **aquaporin**. The presence of aquaporins accounts for why water can cross a membrane more quickly than expected.

Ions and polar molecules, such as glucose and amino acids, can slowly cross a membrane. Therefore, they are often assisted across the plasma membrane by carrier proteins. The carrier protein must combine with an ion, such as sodium ( $\text{Na}^+$ ), or a molecule, such as glucose, before transporting it across the membrane. Therefore, carrier proteins are specific for the substances they transport across the plasma membrane.

**Bulk transport** is a way that large particles can exit a cell or enter a cell. During exocytosis, fusion of a vesicle with the plasma membrane moves a particle to outside the membrane. During endocytosis, vesicle formation moves a particle to inside the plasma membrane. Vesicle formation is reserved for movement of macromolecules or even for something larger, such as a virus. You might think that endocytosis is not specific, but we will see that a cell does have a means to be selective about what enters by endocytosis.

**FIGURE 5.4** How molecules cross the plasma membrane.

The curved arrows indicate that these substances cannot passively cross the plasma membrane, and the long back-and-forth arrows indicate that these substances can diffuse across the plasma membrane.



### Check Your Progress

### 5.1

1. Briefly describe the structure of the plasma membrane.
2. List six types of proteins found in the plasma membrane.

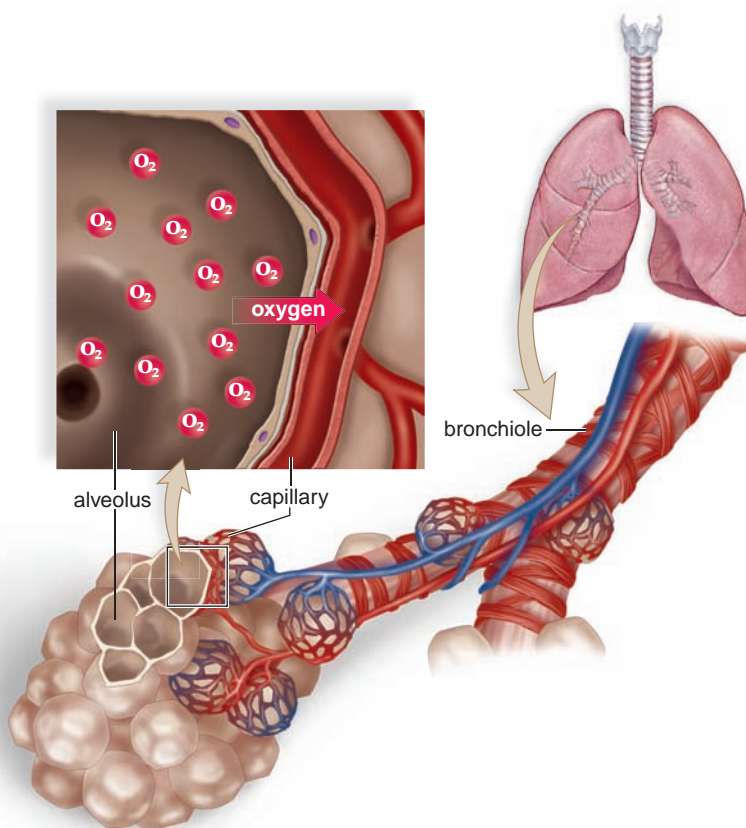
## 5.2 Passive Transport Across a Membrane

**Diffusion** is the movement of molecules from a higher to a lower concentration—that is, down their concentration gradient—until equilibrium is achieved and they are distributed equally. Diffusion is a physical process due to random molecular motion that can be observed with any type of molecule. For example, when a crystal of dye is placed in water (Fig. 5.5), the dye and water molecules move in various directions, but their net movement, which is the sum of their motion, is toward the region of lower concentration. Eventually, the dye is dissolved in the water, resulting in equilibrium and a colored solution.

A **solution** contains both a solute, usually a solid, and a solvent, usually a liquid. In this case, the **solute** is the dye and the **solvent** is the water molecules. Once the solute and solvent are evenly distributed, they continue to move about, but there is no net movement of either one in any direction.

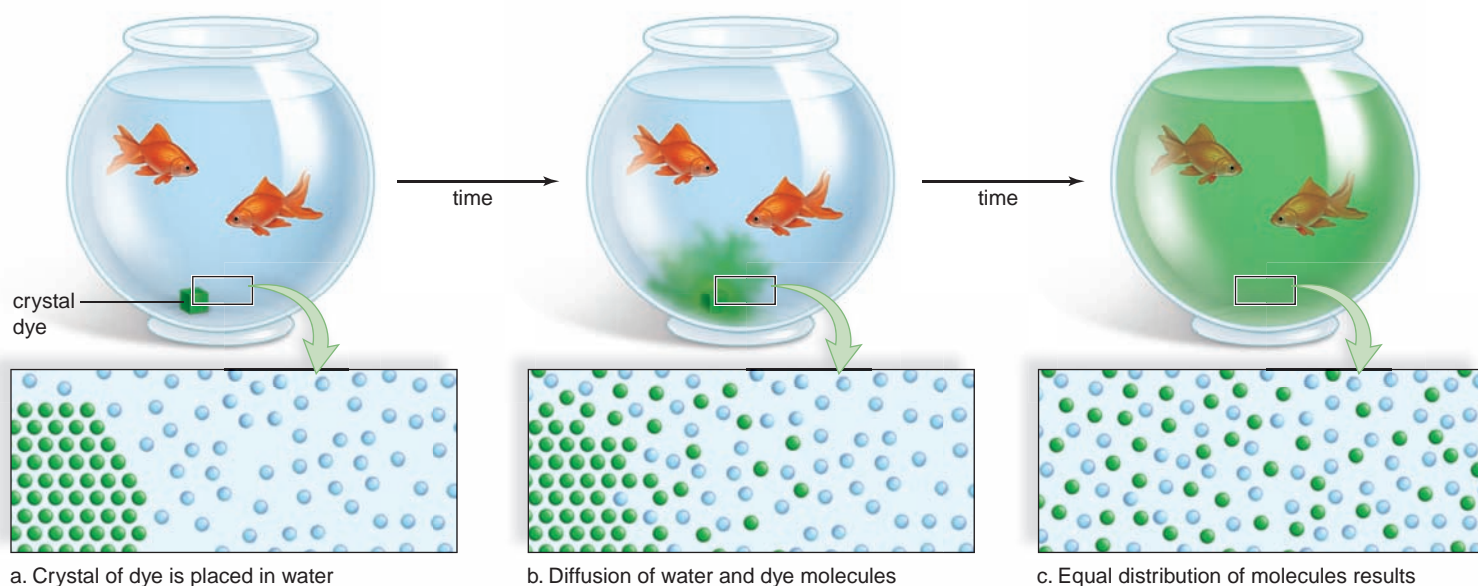
The chemical and physical properties of the plasma membrane allow only a few types of molecules to enter and exit a cell simply by diffusion. Gases can diffuse through the lipid bilayer; this is the mechanism by which oxygen enters cells and carbon dioxide exits cells. Also, consider the movement of oxygen from the alveoli (air sacs) of the lungs to the blood in the lung capillaries (Fig. 5.6). After inhalation (breathing in), the concentration of oxygen in the alveoli is higher than that in the blood; therefore, oxygen diffuses into the blood.

Several factors influence the rate of diffusion. Among these factors are temperature, pressure, electrical currents, and molecular size. For example, as temperature increases, the rate of diffusion increases. The movement of fishes in the tank would certainly speed the rate of diffusion (Fig. 5.5).



**FIGURE 5.6** Gas exchange in lungs.

Oxygen ( $O_2$ ) diffuses into the capillaries of the lungs because there is a higher concentration of oxygen in the alveoli (air sacs) than in the capillaries.



**FIGURE 5.5** Process of diffusion.

Diffusion is spontaneous, and no chemical energy is required to bring it about. **a.** When a dye crystal is placed in water, it is concentrated in one area. **b.** The dye dissolves in the water, and there is a net movement of dye molecules from a higher to a lower concentration. There is also a net movement of water molecules from a higher to a lower concentration. **c.** Eventually, the water and the dye molecules are equally distributed throughout the container.



## Osmosis

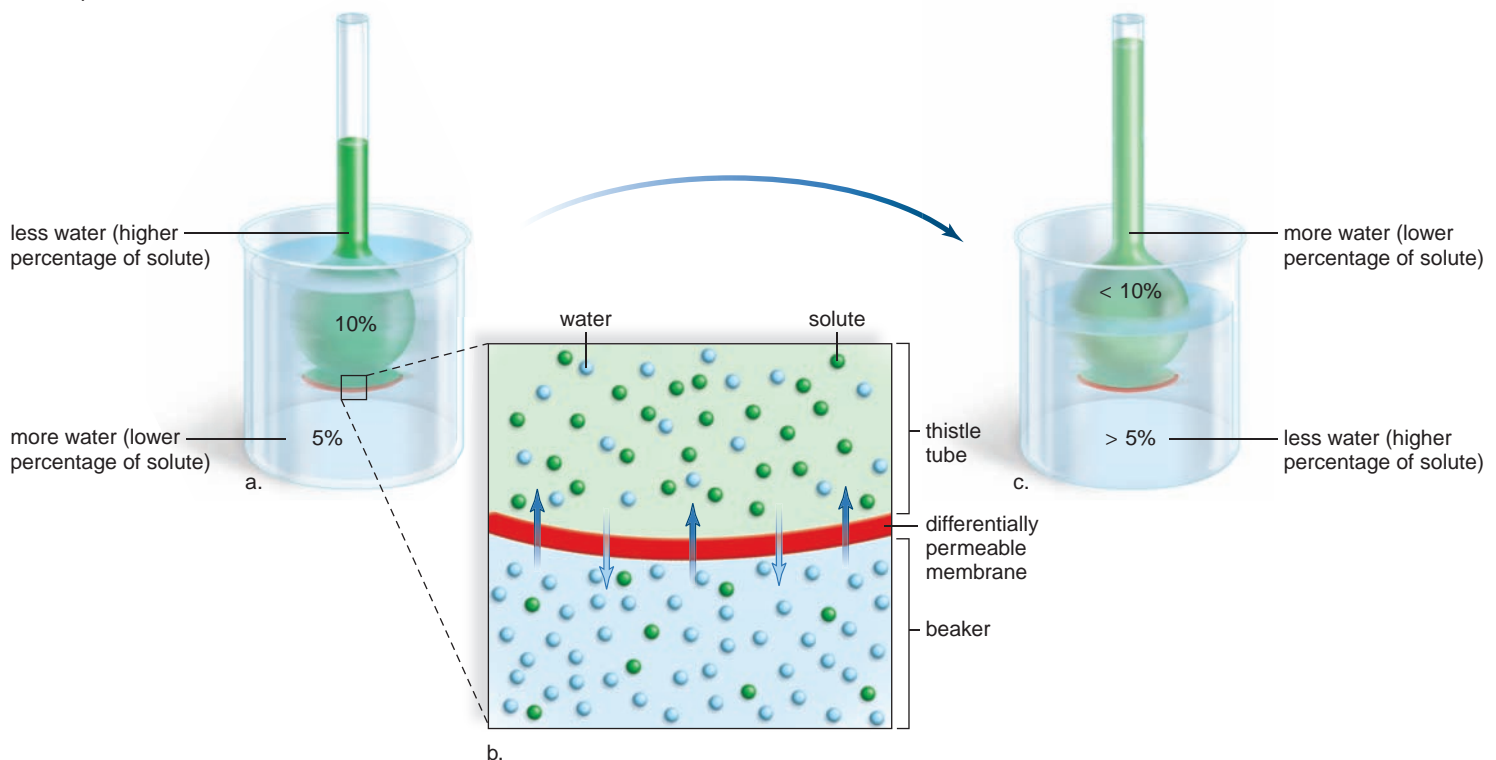
The diffusion of water across a differentially (selectively) permeable membrane due to concentration differences is called **osmosis**. To illustrate osmosis, a thistle tube containing a 10% solute solution<sup>1</sup> is covered at one end by a differentially permeable membrane and then placed in a beaker containing a 5% solute solution (Fig. 5.7a). The beaker has a higher concentration of water molecules (lower percentage of solute), and the thistle tube has a lower concentration of water molecules (higher percentage of solute). Diffusion always occurs from higher to lower concentration. Therefore, a net movement of water takes place across the membrane from the beaker to the inside of the thistle tube (Fig. 5.7b).

The solute does not diffuse out of the thistle tube. Why not? Because the membrane is not permeable to the solute. As water enters and the solute does not exit, the level of the solution within the thistle tube rises (Fig. 5.7c). In the end, the concentration of solute in the thistle tube is less than 10%. Why? Because there is now less solute per unit volume. And the concentration of solute in the beaker is greater than 5%. Why? Because there is now more solute per unit volume.

Water enters the thistle tube due to the osmotic pressure of the solution within the thistle tube. **Osmotic pressure** is the pressure that develops in a system due to osmosis.<sup>2</sup> In

<sup>1</sup> Percent solutions are grams of solute per 100 mL of solvent. Therefore, a 10% solution is 10 g of sugar with water added to make 100 mL of solution.

<sup>2</sup> Osmotic pressure is measured by placing a solution in an osmometer and then immersing the osmometer in pure water. The pressure that develops is the osmotic pressure of a solution.



**FIGURE 5.7** Osmosis demonstration.

**a.** A thistle tube, covered at the broad end by a differentially permeable membrane, contains a 10% solute solution. The beaker contains a 5% solute solution. **b.** The solute (green circles) is unable to pass through the membrane, but the water (blue circles) passes through in both directions. There is a net movement of water toward the inside of the thistle tube, where there is a lower percentage of water molecules. **c.** Due to the incoming water molecules, the level of the solution rises in the thistle tube.

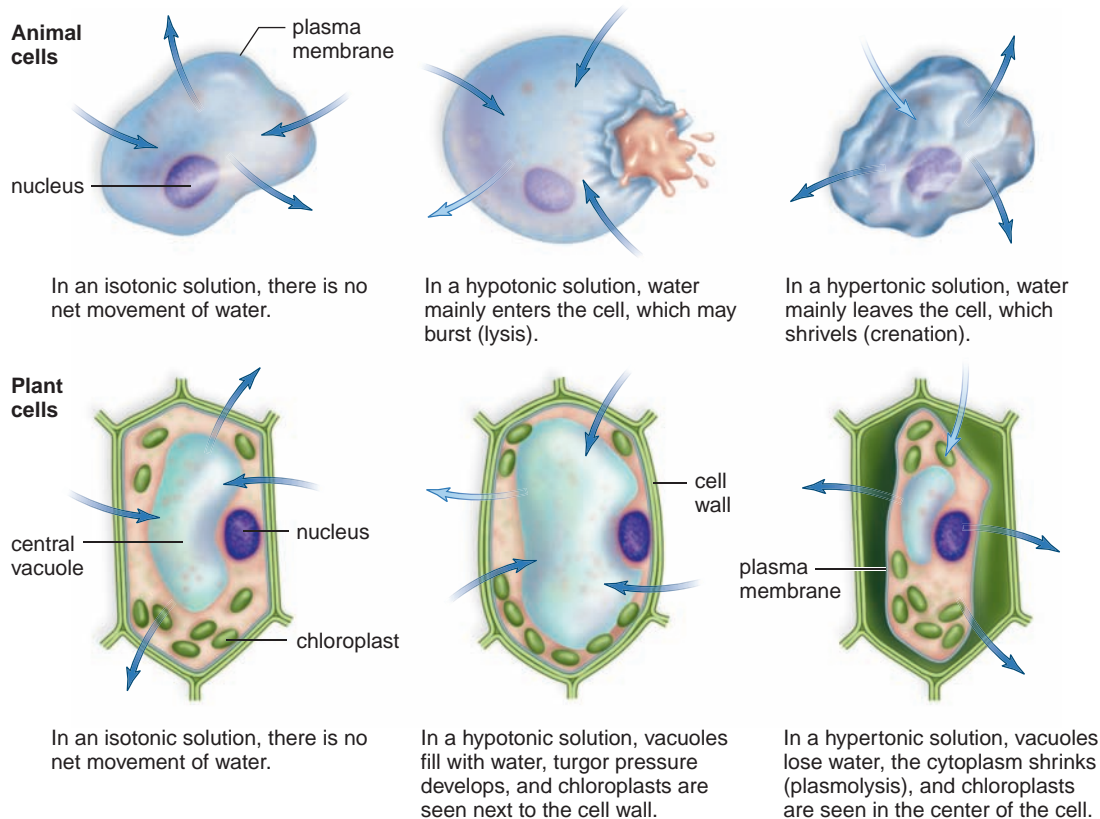
other words, the greater the possible osmotic pressure, the more likely it is that water will diffuse in that direction. Due to osmotic pressure, water is absorbed by the kidneys and taken up by capillaries in the tissues. Osmosis also occurs across the plasma membrane, as we shall now see (Fig. 5.8).

## Isotonic Solution

In the laboratory, cells are normally placed in **isotonic solutions**—that is, the solute concentration and the water concentration both inside and outside the cell are equal, and therefore there is no net gain or loss of water. The prefix *iso* means “the same as,” and the term **tonicity** refers to the strength of the solution. A 0.9% solution of the salt sodium chloride (NaCl) is known to be isotonic to red blood cells. Therefore, intravenous solutions medically administered usually have this tonicity. Terrestrial animals can usually take in either water or salt as needed to maintain the tonicity of their internal environment. Many animals living in an estuary, such as oysters, blue crabs, and some fishes, are able to cope with changes in the salinity (salt concentrations) of their environment. Their kidneys, gills, and other structures help them do this.

## Hypotonic Solution

Solutions that cause cells to swell, or even to burst, due to an intake of water are said to be **hypotonic solutions**. The prefix *hypo* means “less than” and refers to a solution with a lower concentration of solute (higher concentration of water) than inside the cell. If a cell is placed in a hypotonic solution, water enters the cell; the net movement of water is from the outside to the inside of the cell.



**FIGURE 5.8** Osmosis in animal and plant cells.

The arrows indicate the movement of water molecules. To determine the net movement of water, compare the number of dark blue arrows that are taking water molecules into the cell versus the number of light blue arrows that are taking water out of the cell. In an isotonic solution, a cell neither gains nor loses water; in a hypotonic solution, a cell gains water; and in a hypertonic solution, a cell loses water.

Any concentration of a salt solution lower than 0.9% is hypotonic to red blood cells. Animal cells placed in such a solution expand and sometimes burst due to the buildup of pressure. The term *cytolysis* is used to refer to disrupted cells; hemolysis, then, is disrupted red blood cells.

The swelling of a plant cell in a hypotonic solution creates **turgor pressure**. When a plant cell is placed in a hypotonic solution, we observe expansion of the cytoplasm because the large central vacuole gains water and the plasma membrane pushes against the rigid cell wall. The plant cell does not burst because the cell wall does not give way. Turgor pressure in plant cells is extremely important to the maintenance of the plant's erect position. If you forget to water your plants, they wilt due to decreased turgor pressure.

Organisms that live in fresh water have to prevent the uptake of too much water. Many protozoans, such as paramecia, have contractile vacuoles that rid the body of excess water. Freshwater fishes have well-developed kidneys that excrete a large volume of dilute urine. Even so, they have to take in salts at their gills. Even though freshwater fishes are good osmoregulators, they would not be able to survive in either distilled water or a marine environment.

### Hypertonic Solution

Solutions that cause cells to shrink or shrivel due to loss of water are said to be **hypertonic solutions**. The prefix *hyper* means "more than" and refers to a solution with a higher

percentage of solute (lower concentration of water) than the cell. If a cell is placed in a hypertonic solution, water leaves the cell; the net movement of water is from the inside to the outside of the cell.

Any concentration of a salt solution higher than 0.9% is hypertonic to red blood cells. If animal cells are placed in this solution, they shrink. The term **crenation** refers to red blood cells in this condition. Meats are sometimes preserved by salting them. The bacteria are not killed by the salt but by the lack of water in the meat.

When a plant cell is placed in a hypertonic solution, the plasma membrane pulls away from the cell wall as the large central vacuole loses water. This is an example of **plasmolysis**, a shrinking of the cytoplasm due to osmosis. The dead plants you may see along a salted roadside died because they were exposed to a hypertonic solution during the winter. Also, when salt water invades coastal marshes due to storms and human activities, coastal plants die. Without roots to hold the soil, it washes into the sea, doing away with many acres of valuable wetlands.

Marine animals cope with their hypertonic environment in various ways that prevent them from losing water to the environment. Sharks increase or decrease urea in their blood until their blood is isotonic with the environment and in this way do not lose excessive water. Marine fishes and other types of animals drink no water but excrete salts across their gills. Have you ever seen a marine turtle cry? It is ridding its body of salt by means of glands near the eye.



## Facilitated Transport

The plasma membrane impedes the passage of all but a few substances. Yet, biologically useful molecules are able to enter and exit the cell at a rapid rate either by way of a channel protein or because of carrier proteins in the membrane. These transport proteins are specific; each can transport with only a certain type of molecule or ion, which is then transported through the membrane. It is not completely understood how carrier proteins function, but after a carrier combines with a molecule, the carrier is believed to undergo a change in shape that moves the molecule across the membrane. Carrier proteins are utilized for both facilitated transport and active transport (see Table 5.1).

**Facilitated transport** explains the rapid passage of water and also such molecules as glucose and amino acids across the plasma membrane. Whereas water moves through a channel protein, the passage of glucose and amino acids is facilitated by their reversible combination with carrier proteins, which transport them through the plasma membrane. These carrier proteins are specific. For example, various sugar molecules of identical size might be present inside or outside the cell, but glucose can cross the membrane hundreds of times faster than the other sugars. As stated earlier, this is the reason the membrane can be called differentially permeable.

A model for facilitated transport (Fig. 5.9) shows that after a carrier has assisted the movement of a molecule to the other side of the membrane, it is free to assist the passage of other similar molecules. Neither diffusion nor facilitated transport requires an expenditure of energy because the molecules are moving down their concentration gradient in the same direction they tend to move anyway.

## Check Your Progress

## 5.2

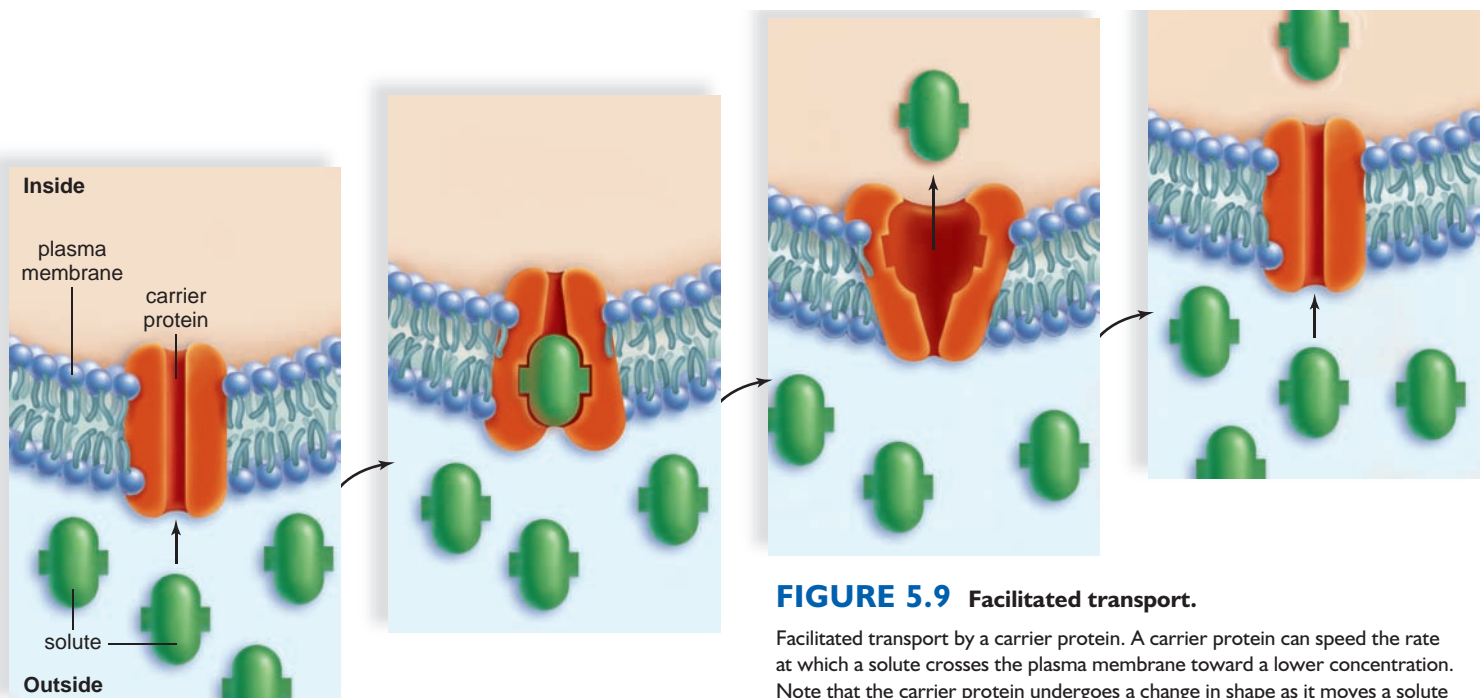
1. Use the terms solute and solvent to describe a hypotonic and hypertonic solution.
2. Compare and contrast diffusion with facilitated transport.

## 5.3 Active Transport Across a Membrane

During **active transport**, molecules or ions move through the plasma membrane, accumulating either inside or outside the cell. For example, iodine collects in the cells of the thyroid gland; glucose is completely absorbed from the gut by the cells lining the digestive tract; and sodium can be almost completely withdrawn from urine by cells lining the kidney tubules. In these instances, molecules have moved to the region of higher concentration, exactly opposite to the process of diffusion.

Both carrier proteins and an expenditure of energy are needed to transport molecules against their concentration gradient. In this case, chemical energy (ATP molecules usually) is required for the carrier to combine with the substance to be transported. Therefore, it is not surprising that cells involved primarily in active transport, such as kidney cells, have a large number of mitochondria near membranes where active transport is occurring.

Proteins involved in active transport often are called pumps because, just as a water pump uses energy to move water against the force of gravity, proteins use energy to move a substance against its concentration gradient. One



**FIGURE 5.9** Facilitated transport.

Facilitated transport by a carrier protein. A carrier protein can speed the rate at which a solute crosses the plasma membrane toward a lower concentration. Note that the carrier protein undergoes a change in shape as it moves a solute across the membrane.

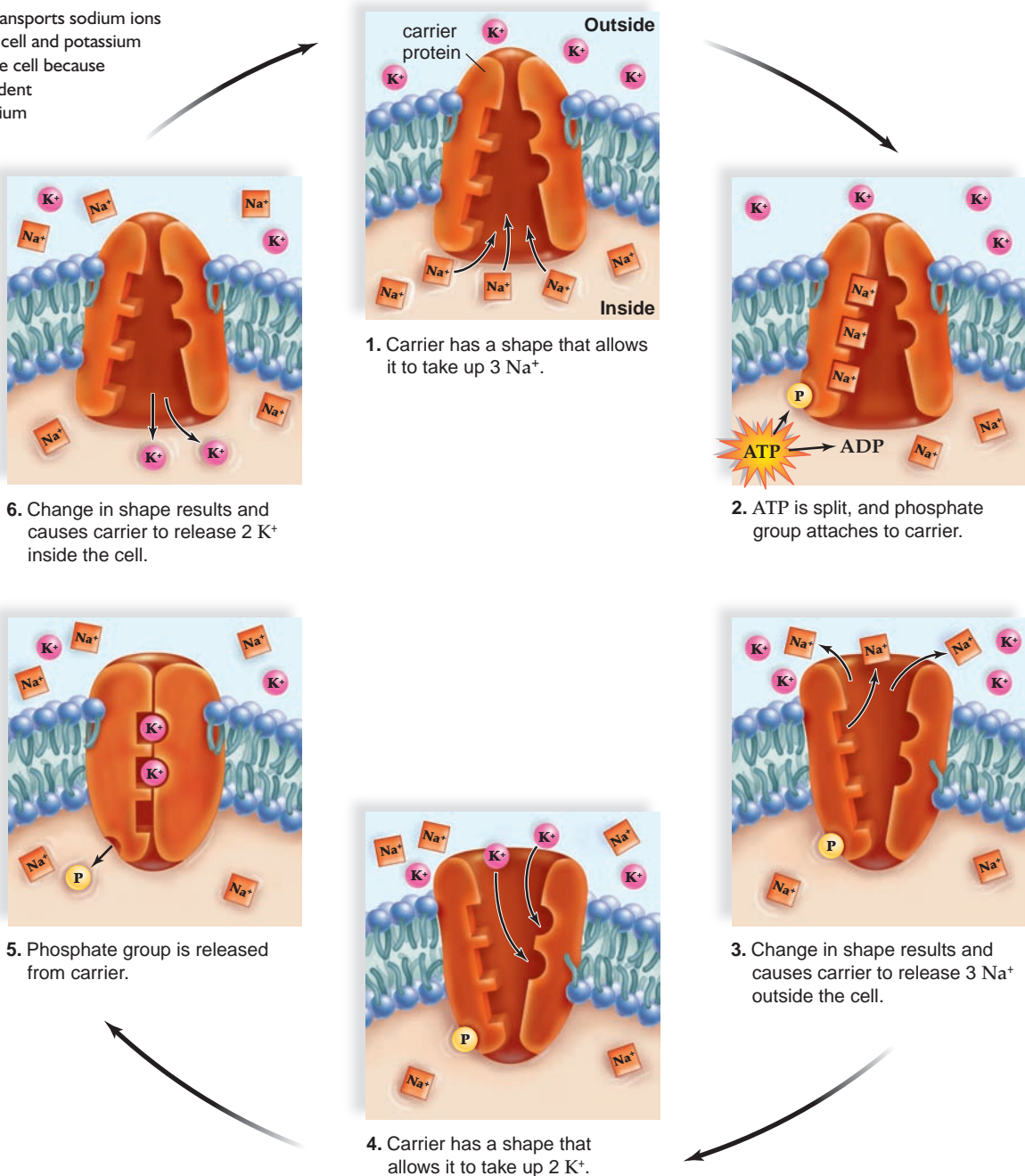
type of pump that is active in all animal cells, but is especially associated with nerve and muscle cells, moves sodium ions ( $\text{Na}^+$ ) to the outside of the cell and potassium ions ( $\text{K}^+$ ) to the inside of the cell. These two events are linked, and the carrier protein is called a **sodium-potassium pump**. A change in carrier shape after the attachment and again after the detachment of a phosphate group allows it to combine alternately with sodium ions and potassium ions (Fig. 5.10). The phosphate group is donated by ATP when it is broken down enzymatically by the carrier. The sodium-potassium pump results in both a solute concentration gradient and an electrical gradient for these ions across the plasma membrane.

The passage of salt ( $\text{NaCl}$ ) across a plasma membrane is of primary importance to most cells. The chloride ion ( $\text{Cl}^-$ ) usually crosses the plasma membrane because it is attracted by positively charged sodium ions ( $\text{Na}^+$ ). First sodium ions are pumped across a membrane, and then chloride ions simply diffuse through channels that allow their passage.

As noted in Figure 5.3a, the genetic disorder cystic fibrosis results from a faulty chloride channel. When chloride is unable to exit a cell, water stays behind. The lack of water causes abnormally thick mucus in the bronchial tubes and pancreatic ducts, thus interfering with the function of the lungs and pancreas.

**FIGURE 5.10** The sodium-potassium pump.

The same carrier protein transports sodium ions ( $\text{Na}^+$ ) to the outside of the cell and potassium ions ( $\text{K}^+$ ) to the inside of the cell because it undergoes an ATP-dependent change in shape. Three sodium ions are carried outward for every two potassium ions carried inward; therefore, the inside of the cell is negatively charged compared to the outside.



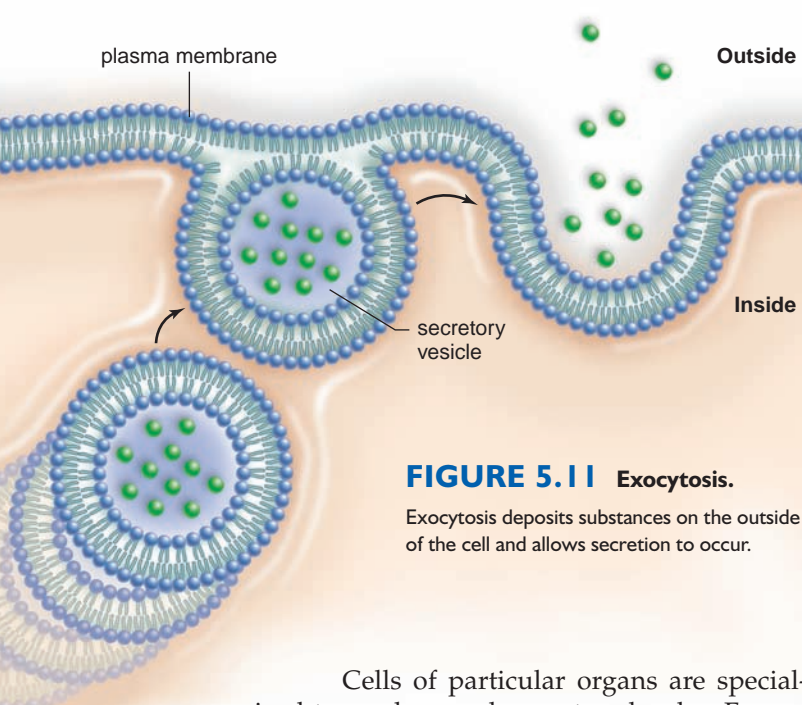


## Bulk Transport

How do macromolecules such as polypeptides, polysaccharides, or polynucleotides enter and exit a cell? Because they are too large to be transported by carrier proteins, macromolecules are transported into and out of the cell by vesicle formation. Vesicle formation is membrane-assisted transport because membrane is needed to form the vesicle. Vesicle formation requires an expenditure of cellular energy, but vesicle formation has the added benefit that the vesicle membrane keeps the contained macromolecules from mixing with molecules within the cytoplasm. Exocytosis is a way substances can exit a cell, and endocytosis is a way substances can enter a cell.

### Exocytosis

During **exocytosis**, a vesicle fuses with the plasma membrane as secretion occurs (Fig. 5.11). Hormones, neurotransmitters, and digestive enzymes are secreted from cells in this manner. The Golgi body often produces the vesicles that carry these cell products to the membrane. During exocytosis, the membrane of the vesicle becomes a part of the plasma membrane, which is thereby enlarged. For this reason, exocytosis can be a normal part of cell growth. The proteins released from the vesicle adhere to the cell surface or become incorporated in an extracellular matrix.



**FIGURE 5.11 Exocytosis.**

Exocytosis deposits substances on the outside of the cell and allows secretion to occur.

Cells of particular organs are specialized to produce and export molecules. For example, pancreatic cells produce digestive enzymes or insulin, and anterior pituitary cells produce growth hormone, among other hormones. In these cells, secretory vesicles accumulate near the plasma membrane, and the vesicles release their contents only when the cell is stimulated by a signal received at the plasma membrane. A rise in blood sugar, for example, signals pancreatic cells to release

the hormone insulin. This is called regulated secretion, because vesicles fuse with the plasma membrane only when it is appropriate to the needs of the body.

### Endocytosis

During **endocytosis**, cells take in substances by vesicle formation. A portion of the plasma membrane invaginates to envelop the substance, and then the membrane pinches off to form an intracellular vesicle. Endocytosis occurs in one of three ways, as illustrated in Figure 5.12. Phagocytosis transports large substances, such as a virus, and pinocytosis transports small substances, such as a macromolecule, into a cell. Receptor-mediated endocytosis is a special form of pinocytosis.

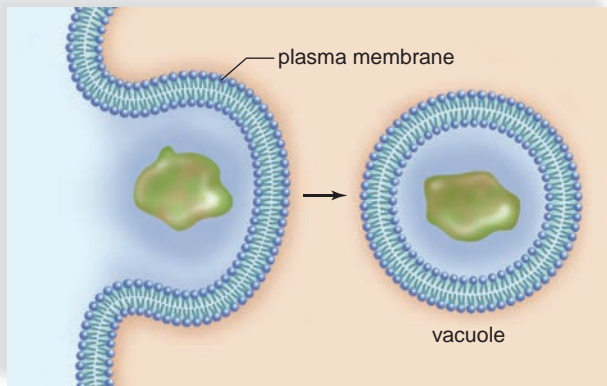
**Phagocytosis.** When the material taken in by endocytosis is large, such as a food particle or another cell, the process is called **phagocytosis** [Gk. *phagein*, to eat]. Phagocytosis is common in unicellular organisms such as amoebas (Fig. 5.12a). It also occurs in humans. Certain types of human white blood cells are amoeboid—that is, they are mobile like an amoeba, and they are able to engulf debris such as worn-out red blood cells or viruses. When an endocytic vesicle fuses with a lysosome, digestion occurs. We will see that this process is a necessary and preliminary step toward the development of immunity to bacterial diseases.

**Pinocytosis.** **Pinocytosis** [Gk. *pinein*, to drink] occurs when vesicles form around a liquid or around very small particles (Fig. 5.12b). Blood cells, cells that line the kidney tubules or the intestinal wall, and plant root cells all use pinocytosis to ingest substances.

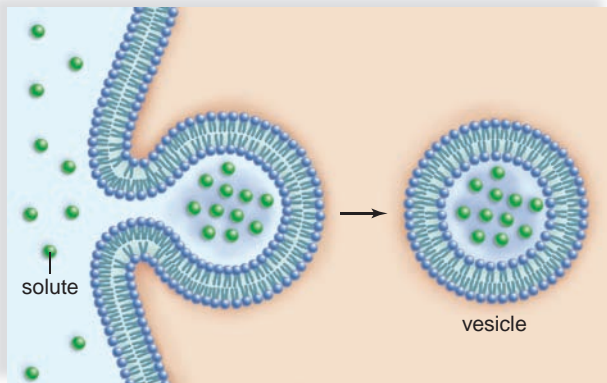
Whereas phagocytosis can be seen with the light microscope, the electron microscope must be used to observe pinocytic vesicles, which are no larger than 0.1–0.2  $\mu\text{m}$ . Still, pinocytosis involves a significant amount of the plasma membrane because it occurs continuously. The loss of plasma membrane due to pinocytosis is balanced by the occurrence of exocytosis, however.

**Receptor-Mediated Endocytosis.** **Receptor-mediated endocytosis** is a form of pinocytosis that is quite specific because it uses a receptor protein shaped in such a way that a specific molecule such as a vitamin, peptide hormone, or lipoprotein can bind to it (Fig. 5.12c). The receptors for these substances are found at one location in the plasma membrane. This location is called a coated pit because there is a layer of protein on the cytoplasmic side of the pit. Once formed, the vesicle is uncoated and may fuse with a lysosome. When an empty, used vesicle fuses with the plasma membrane, the receptors return to their former location.

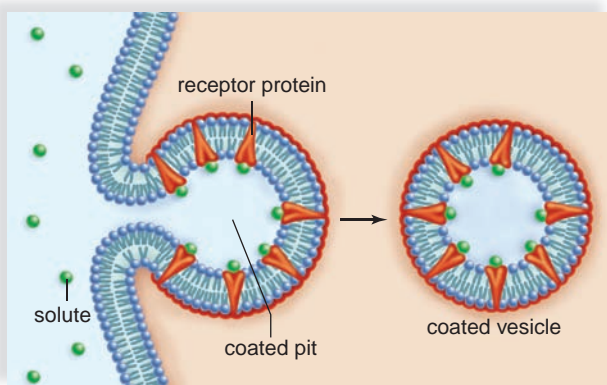
Receptor-mediated endocytosis is selective and much more efficient than ordinary pinocytosis. It is involved in uptake and also in the transfer and exchange of substances between cells. Such exchanges take place when substances move from maternal blood into fetal blood at the placenta, for example.



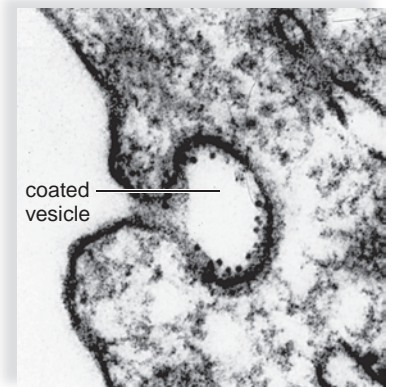
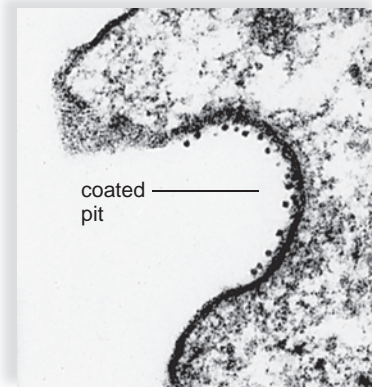
a. Phagocytosis



b. Pinocytosis



c. Receptor-mediated endocytosis



### FIGURE 5.12 Three methods of endocytosis.

**a.** Phagocytosis occurs when the substance to be transported into the cell is large; amoebas ingest by phagocytosis. Digestion occurs when the resulting vacuole fuses with a lysosome. **b.** Pinocytosis occurs when a macromolecule such as a polypeptide is transported into the cell. The result is a vesicle (small vacuole). **c.** Receptor-mediated endocytosis is a form of pinocytosis. Molecules first bind to specific receptor proteins, which migrate to or are already in a coated pit. The vesicle that forms contains the molecules and their receptors.

The importance of receptor-mediated endocytosis is demonstrated by a genetic disorder called familial hypercholesterolemia. Cholesterol is transported in blood by a complex of lipids and proteins called low-density lipoprotein (LDL). Ordinarily, body cells take up LDL when LDL receptors gather in a coated pit. But in some individuals, the LDL receptor is unable to properly bind to the coated pit, and the cells are unable to take up cholesterol. Instead, cholesterol accumulates in the walls of arterial blood vessels,

leading to high blood pressure, occluded (blocked) arteries, and heart attacks.

### Check Your Progress

### 5.3

1. Compare facilitated transport with active transport.
2. Compare and contrast exocytosis and endocytosis.



## 5.4 Modification of Cell Surfaces

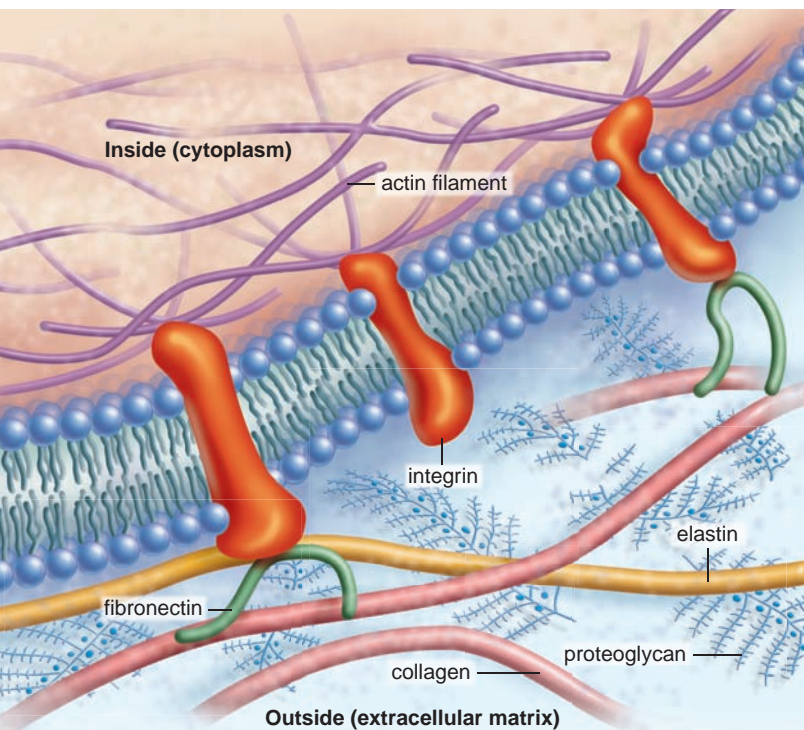
Extracellular structures take shape from materials the cell produces and secretes across its plasma membrane. In plants, prokaryotes, fungi, and most algae, the extracellular component of the cell is a fairly rigid cell wall. A cell wall occurs in organisms that have a rather inactive lifestyle. Animals that have an active way of life have a more varied extracellular anatomy appropriate to the particular tissue type.

### Cell Surfaces in Animals

We will consider two different types of animal cell surface features: (1) the extracellular matrix (ECM) that is observed outside cells and (2) junctions that occur between some types of cells. Both of these can connect to the cytoskeleton and contribute to communication between cells and, therefore, tissue formation.

#### Extracellular Matrix

A protective extracellular matrix is a meshwork of proteins and polysaccharides in close association with the cell that produced them (Fig. 5.13). Collagen and elastin fibers are two well-known structural proteins in the ECM; collagen resists stretching and elastin gives the ECM resilience. Fibronectin is an adhesive protein, colored green in Figure 5.13, that binds to a protein in the plasma membrane called integrin. Notice that integrin also makes contact with the cytoskeleton inside the cell. Through its connections with both the ECM and the cytoskeleton, integrin plays a role in cell signaling, permitting the ECM to influence the activities of the cytoskeleton and, therefore, the shape and activities of the cell.



**FIGURE 5.13** Animal cell extracellular matrix.

In the extracellular matrix, collagen and elastin have a support function, while fibronectins bind to integrin, and in this way, assist communication between ECM and the cytoskeleton.

Amino sugars in the ECM form multiple polysaccharides that attach to a protein and are, therefore, called proteoglycans. Proteoglycans, in turn, attach to a very long, centrally placed polysaccharide. The entire structure, which looks like an enormous bottle brush, resists compression of the extracellular matrix. Proteoglycans assist cell signaling when they regulate the passage of molecules through the ECM to the plasma membrane, where receptors are located. During development, they help bring about differentiation by guiding cell migration along collagen fibers to specific locations. In short, the ECM has a dynamic role in all aspects of a cell's behavior.

When we study tissues, we will see that the extracellular matrix varies in quantity and in consistency from being quite flexible, as in loose connective tissue, semiflexible as in cartilage, and being rock solid, as in bone. The extracellular matrix of bone is hard because, in addition to the components mentioned, mineral salts, notably calcium salts, are deposited outside the cell.

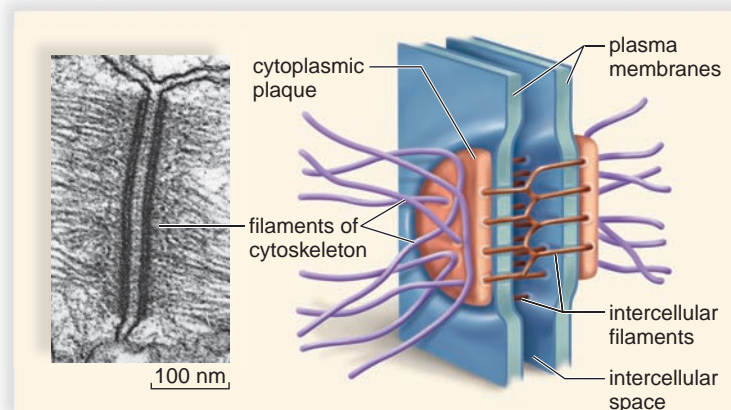
#### Junctions Between Cells

Certain tissues of vertebrate animals are well known to have junctions between their cells that allow them to behave in a coordinated manner. These junctions are of the three types shown in Figure 5.14.

**Adhesion junctions** serve to mechanically attach adjacent cells. Two types of adhesion junctions are described here. In **desmosomes**, internal cytoplasmic plaques, firmly attached to the cytoskeleton within each cell, are joined by intercellular filaments. The result is a sturdy but flexible sheet of cells. In some organs—such as the heart, stomach, and bladder, where tissues get stretched—desmosomes hold the cells together. At a **hemidesmosome**, a single point of attachment between adjacent cells connects the cytoskeletons of adjacent cells. Adhesion junctions are the most common type of intercellular junction between skin cells.

**FIGURE 5.14** Junctions between cells of the intestinal wall.

**a.** In adhesion junctions such as a desmosome, intercellular filaments run between two cells. **b.** Tight junctions between cells form an impermeable barrier because their adjacent plasma membranes are joined. **c.** Gap junctions allow communication between two cells because adjacent plasma membrane channels are joined.



**a.** Adhesion junction

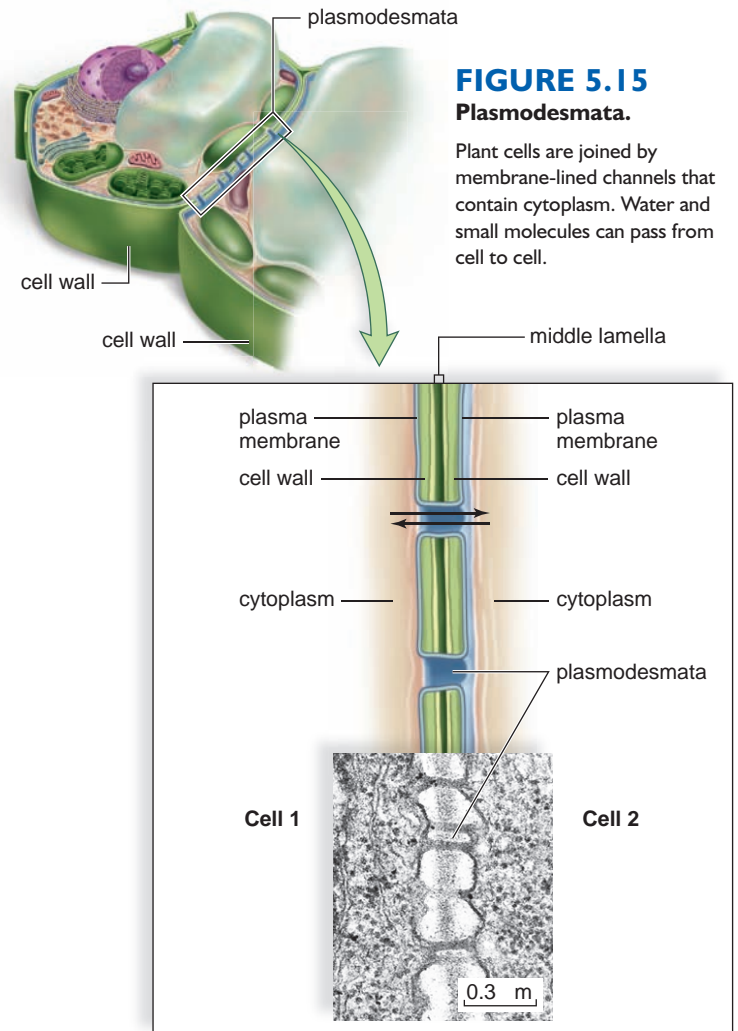
Adjacent cells are even more closely joined by **tight junctions**, in which plasma membrane proteins actually attach to each other, producing a zipperlike fastening. The cells of tissues that serve as barriers are held together by tight junctions; in the intestine, the digestive juices stay out of the body, and in the kidneys the urine stays within kidney tubules, because the cells are joined by tight junctions.

A **gap junction** allows cells to communicate. A gap junction is formed when two identical plasma membrane channels join. The channel of each cell is lined by six plasma membrane proteins. A gap junction lends strength to the cells, but it also allows small molecules and ions to pass between them. Gap junctions are important in heart muscle and smooth muscle because they permit a flow of ions that is required for the cells to contract as a unit.

## Plant Cell Walls

In addition to a plasma membrane, plant cells are surrounded by a porous **cell wall** that varies in thickness, depending on the function of the cell. All plant cells have a primary cell wall. The primary cell wall contains cellulose fibrils in which microfibrils are held together by noncellulose substances. Pectins allow the wall to stretch when the cell is growing, and noncellulose polysaccharides harden the wall when the cell is mature. Pectins are especially abundant in the middle lamella, which is a layer of adhesive substances that holds the cells together. Some cells in woody plants have a secondary wall that forms inside the primary cell wall. The secondary wall has a greater quantity of cellulose fibrils than the primary wall, and layers of cellulose fibrils are laid down at right angles to one another. Lignin, a substance that adds strength, is a common ingredient of secondary cell walls in woody plants.

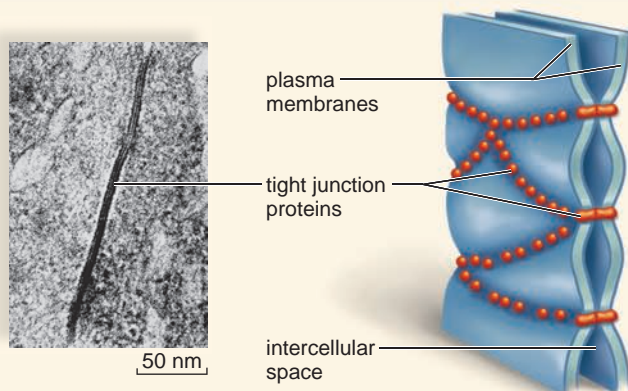
In a plant, the cytoplasm of living cells is connected by **plasmodesmata** (sing., plasmodesma), numerous narrow, membrane-lined channels that pass through the cell wall (Fig. 5.15). Cytoplasmic strands within these channels allow direct exchange of some materials between adjacent plant cells and eventually all the cells of a plant. The plasmodesmata are large enough to allow only water and small solutes to pass freely from cell to cell. This limitation means that plant cells can maintain their own concentrations of larger substances and differentiate into particular cell types.



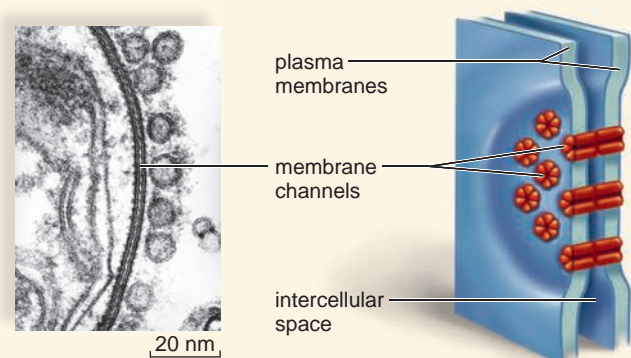
## Check Your Progress

5.4

1. Describe the chemical composition of the extracellular matrix of an animal cell.
2. Give a function for an adhesion junction, tight junction, and gap junction.
3. Contrast a plant's primary cell wall with its secondary cell wall.



b. Tight junction



c. Gap junction



## Connecting the Concepts

The plasma membrane is quite appropriately called the gatekeeper of the cell because it maintains the integrity of the cell and stands guard over what enters and leaves. But we have seen that the plasma membrane also does much more than this. Its glycoproteins and glycolipids mark the cell as belonging to the organism. Its numerous proteins allow communication between cells and, thereby, enable tissues to function as a whole. A new endeavor is to understand how the extracel-

lular matrix in animal cells assists the plasma membrane in its varied functions.

The progression in our knowledge about the plasma membrane illustrates how science works. The concepts and techniques of science evolve and change, and the knowledge we have today will be amended and expanded by new investigative work. Also, basic science has applications that promote the health of human beings. To know that the plasma membrane is malfunctioning in a person who has

diabetes or cystic fibrosis or in someone who has a high cholesterol count is a first step toward curing these conditions. Even cancer is sometimes due to receptor proteins that signal the cell to divide even when no growth factor is present.

Our ability to understand the functioning of the plasma membrane is dependent on a working knowledge of the molecules that make up the cell. We continue this theme as we discuss metabolism in the next three chapters.

### summary

#### 5.1 Plasma Membrane Structure and Function

Two components of the plasma membrane are lipids and proteins. In the lipid bilayer, phospholipids are arranged with their hydrophilic (polar) heads at the surfaces and their hydrophobic (nonpolar) tails in the interior. The lipid bilayer has the consistency of oil but acts as a barrier to the entrance and exit of most biological molecules. Membrane glycolipids and glycoproteins are involved in marking the cell as belonging to a particular individual and tissue.

The hydrophobic portion of an integral protein lies in the lipid bilayer of the plasma membrane, and the hydrophilic portion lies at the surfaces. Proteins act as receptors, carry on enzymatic reactions, join cells together, form channels, or act as carriers to move substances across the membrane. Some of these proteins make contact with the extracellular matrix (ECM) outside and with the cytoskeleton inside. Thus, the ECM can influence the happenings inside the cell.

#### 5.2 Passive Transport Across a Membrane

The plasma membrane is differentially permeable. Some molecules (lipid-soluble compounds, water, and gases) simply diffuse across the membrane from the area of higher concentration to the area of lower concentration. No metabolic energy is required for diffusion to occur.

The diffusion of water across a differentially permeable membrane is called osmosis. Water moves across the membrane into the area of higher solute (less water) content per volume. When cells are in an isotonic solution, they neither gain nor lose water. When cells are in a hypotonic solution, they gain water, and when they are in a hypertonic solution, they lose water (Table 5.2).

Other molecules are transported across the membrane either by a channel protein or by carrier proteins that span the membrane. During facilitated transport, a substance moves down its concentration gradient. No energy is required.

#### 5.3 Active Transport Across a Membrane

During active transport, a carrier protein acts as a pump that causes a substance to move against its concentration gradient. The sodium-potassium pump carries  $\text{Na}^+$  to the outside of the cell and  $\text{K}^+$  to the inside of the cell. Energy in the form of ATP molecules is required for active transport to occur.

Larger substances can enter and exit a membrane by exocytosis and endocytosis. Exocytosis involves secretion. Endocytosis includes phagocytosis, pinocytosis, and receptor-mediated endocytosis. Receptor-mediated endocytosis makes use of receptor proteins in the plasma membrane. Once a specific solute binds to receptors, a coated pit becomes a coated vesicle. After losing the coat, the vesicle can join with the lysosome, or after discharging the substance, the receptor-containing vesicle can fuse with the plasma membrane.

#### 5.4 Modification of Cell Surfaces

Animal cells have an extracellular matrix (ECM) that influences their shape and behavior. Tissues vary as to the amount and character of the ECM. Some animal cells have junction proteins that join them to other cells of the same tissue. Adhesion junctions and tight junctions help hold cells together; gap junctions allow passage of small molecules between cells.

Plant cells have a freely permeable cell wall, with cellulose as its main component. Also, plant cells are joined by narrow, membrane-lined channels called plasmodesmata that span the cell wall and contain strands of cytoplasm that allow materials to pass from one cell to another.

**TABLE 5.2**

**Effect of Osmosis on a Cell**

Tonicity of Solution	Concentrations			Effect on Cell
	Solute	Water	Net Movement of Water	
Isotonic	Same as cell	Same as cell	None	None
Hypotonic	Less than cell	More than cell	Cell gains water	Swells, turgor pressure
Hypertonic	More than cell	Less than cell	Cell loses water	Shrinks, plasmolysis

## understanding the terms

active transport 94	glycoprotein 87
adhesion junction 98	hypertonic solution 93
aquaporin 90	hypotonic solution 92
bulk transport 90	isotonic solution 92
carrier protein 88	junction protein 88
cell recognition protein 88	osmosis 92
cell wall 99	osmotic pressure 92
channel protein 88	phagocytosis 96
cholesterol 86	pinocytosis 96
concentration gradient 90	plasmodesmata 99
crenation 93	plasmolysis 93
desmosome 98	receptor-mediated endocytosis 96
differentially permeable 90	receptor protein 88
diffusion 91	sodium-potassium pump 94
endocytosis 96	solute 91
enzymatic protein 88	solution 91
exocytosis 96	solvent 91
extracellular matrix (ECM) 87	tight junction 99
facilitated transport 94	tonicity 92
fluid-mosaic model 87	turgor pressure 93
gap junction 99	
glycolipid 87	

Match the terms to these definitions:

- \_\_\_\_\_ Characteristic of the plasma membrane due to its ability to allow certain molecules but not others to pass through.
- \_\_\_\_\_ Diffusion of water through the plasma membrane of cells.
- \_\_\_\_\_ Higher solute concentration (less water) than the cytoplasm of a cell; causes cell to lose water by osmosis.
- \_\_\_\_\_ Protein in plasma membrane that bears a carbohydrate chain.
- \_\_\_\_\_ Process by which a cell engulfs a substance, forming an intracellular vacuole.

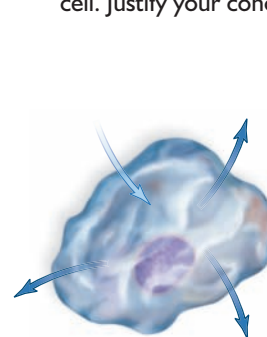
## reviewing this chapter

- Describe the fluid-mosaic model of membrane structure. 86–87
- Tell how the phospholipids are arranged in the plasma membrane. What other lipid is present in the membrane, and what functions does it serve? 87–88
- Describe the possible functions of proteins in the plasma membrane. 88
- What is cell signaling and how does it occur? 89
- Define diffusion. What factors can influence the rate of diffusion? What substances can diffuse through a differentially permeable membrane? 90–91
- Define osmosis. Describe verbally and with drawings what happens to an animal cell and a plant cell when placed in isotonic, hypotonic, and hypertonic solutions. 92–93
- Why do most substances have to be assisted through the plasma membrane? Contrast movement by facilitated transport with movement by active transport. 94–95
- Draw and explain a diagram that shows how the sodium-potassium pump works. 94–95
- Describe and contrast three methods of endocytosis. 96–97
- Describe the structure and function of animal and plant cell modifications. 98–99

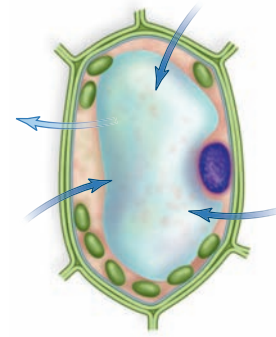
## testing yourself

Choose the best answer for each question.

- Write hypotonic solution or hypertonic solution beneath each cell. Justify your conclusions.



a. \_\_\_\_\_

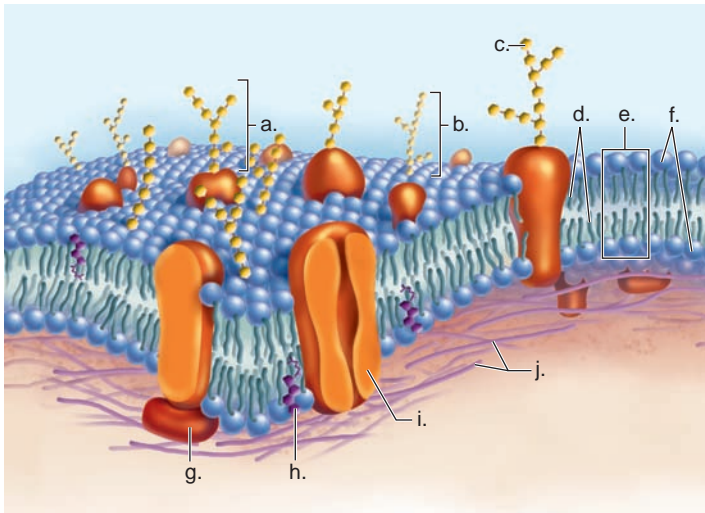


b. \_\_\_\_\_

- Electron micrographs following freeze-fracture of the plasma membrane indicate that
  - the membrane is a phospholipid bilayer.
  - some proteins span the membrane.
  - protein is found only on the surfaces of the membrane.
  - glycolipids and glycoproteins are antigenic.
  - there are receptors in the membrane.
- A phospholipid molecule has a head and two tails. The tails are found
  - at the surfaces of the membrane.
  - in the interior of the membrane.
  - spanning the membrane.
  - where the environment is hydrophilic.
  - Both a and b are correct.
- During diffusion,
  - solvents move from the area of higher to lower concentration, but solutes do not.
  - there is a net movement of molecules from the area of higher to lower concentration.
  - a cell must be present for any movement of molecules to occur.
  - molecules move against their concentration gradient if they are small and charged.
  - All of these are correct.
- When a cell is placed in a hypotonic solution,
  - solute exits the cell to equalize the concentration on both sides of the membrane.
  - water exits the cell toward the area of lower solute concentration.
  - water enters the cell toward the area of higher solute concentration.
  - solute exits and water enters the cell.
  - Both c and d are correct.
- When a cell is placed in a hypertonic solution,
  - solute exits the cell to equalize the concentration on both sides of the membrane.
  - water exits the cell toward the area of lower solute concentration.
  - water exits the cell toward the area of higher solute concentration.
  - solute exits and water enters the cell.
  - Both a and c are correct.



7. Active transport
  - a. requires a carrier protein.
  - b. moves a molecule against its concentration gradient.
  - c. requires a supply of chemical energy.
  - d. does not occur during facilitated transport.
  - e. All of these are correct.
8. The sodium-potassium pump
  - a. helps establish an electrochemical gradient across the membrane.
  - b. concentrates sodium on the outside of the membrane.
  - c. uses a carrier protein and chemical energy.
  - d. is present in the plasma membrane.
  - e. All of these are correct.
9. Receptor-mediated endocytosis
  - a. is no different from phagocytosis.
  - b. brings specific solutes into the cell.
  - c. helps concentrate proteins in vesicles.
  - d. results in high osmotic pressure.
  - e. All of these are correct.
10. Plant cells
  - a. always have a secondary cell wall, even though the primary one may disappear.
  - b. have channels between cells that allow strands of cytoplasm to pass from cell to cell.
  - c. develop turgor pressure when water enters the nucleus.
  - d. do not have cell-to-cell junctions like animal cells.
  - e. All of these are correct.
11. Label this diagram of the plasma membrane.



12. The fluid-mosaic model of membrane structure refers to
  - a. the fluidity of proteins and the pattern of phospholipids in the membrane.
  - b. the fluidity of phospholipids and the pattern of proteins in the membrane.
  - c. the fluidity of cholesterol and the pattern of carbohydrate chains outside the membrane.
  - d. the lack of fluidity of internal membranes compared to the plasma membrane, and the ability of the proteins to move laterally in the membrane.
  - e. the fluidity of hydrophobic regions, proteins, and the mosaic pattern of hydrophilic regions.

13. Which of the following is not a function of proteins present in the plasma membrane? Proteins
  - a. assist the passage of materials into the cell.
  - b. interact and recognize other cells.
  - c. bind with specific hormones.
  - d. carry out specific metabolic reactions.
  - e. produce lipid molecules.
14. The carbohydrate chains projecting from the plasma membrane are involved in
  - a. adhesion between cells.
  - b. reception of molecules.
  - c. cell-to-cell recognition.
  - d. All of these are correct.
15. Plants wilt on a hot summer day because of a decrease in
  - a. turgor pressure.
  - b. evaporation.
  - c. condensation.
  - d. diffusion.
16. The extracellular matrix
  - a. assists in the movement of substances across the plasma membrane.
  - b. prevents the loss of water when cells are placed in a hypertonic solution.
  - c. has numerous functions that affect the shape and activities of the cell that produced it.
  - d. contains the junctions that sometimes occur between cells.
  - e. All of these are correct.

## thinking scientifically

1. The mucus in bronchial tubes must be thin enough for cilia to move bacteria and viruses up into the throat away from the lungs. Which way would  $\text{Cl}^-$  normally cross the plasma membrane of bronchial tube cells in order for mucus to be thin (see Fig. 5.3a)? Use the concept of osmosis to explain your answer.
2. Winter wheat is planted in the early fall, grows over the winter when the weather is colder, and is harvested in the spring. As the temperature drops, the makeup of the plasma membrane of winter wheat changes. Unsaturated fatty acids replace saturated fatty acids in the phospholipids of the membrane. Why is this a suitable adaptation?

## Biology website

The companion website for *Biology* provides a wealth of information organized and integrated by chapter. You will find practice tests, animations, videos, and much more that will complement your learning and understanding of general biology.

<http://www.mhhe.com/maderbiology10>

# 6

## Metabolism: Energy and Enzymes

**P**hotosynthesizing grasses on an African plain provide impalas with building blocks and the energy they need to evade being caught by a cheetah. Eating impalas provides cheetahs with food and the energy they need to be quick enough to catch impalas!

All life on Earth is dependent on the flow of energy coming from the sun. You, like the cheetah, are dependent on energy from the sun. Even as you digest your food, be it veggies or meat, energy escapes into the environment as heat. This heat is no longer usable by photosynthesizers; it is too diffuse. Solar energy is concentrated enough to allow plants to keep on photosynthesizing and, in that way, provide a continual supply of food for you and the biosphere.

Energy, so important to metabolism and enzymatic reactions, is the first topic we consider in this chapter. Without enzymes, you and the cheetah would not be able to make use of energy to maintain your bodies, nor to carry on any type of activity.

The cheetah, and more directly the impala, is dependent on solar energy captured by photosynthesizers.



### 6.1 CELLS AND THE FLOW OF ENERGY

- Energy cannot be created or destroyed; energy can be changed from one form to another, but there is always a loss of usable energy. 104–5

### 6.2 METABOLIC REACTIONS AND ENERGY TRANSFORMATIONS

- The breakdown of ATP, which releases energy, can be coupled to reactions that require an input of energy. 106
- ATP goes through a cycle: Energy from glucose breakdown drives ATP buildup, and then ATP breakdown provides energy for cellular work. 106–7

### 6.3 METABOLIC PATHWAYS AND ENZYMES

- Cells have metabolic pathways in which every reaction has a specific enzyme. Enzymes speed reactions because they have an active site where a specific reaction occurs. 108–9
- The speed of a reaction is affected by the concentration of reactants and the enzyme. Environmental factors, such as temperature and pH, also affect the activity of enzymes. 109–11

### 6.4 ORGANELLES AND THE FLOW OF ENERGY

- Photosynthesis and cellular respiration are metabolic pathways that include oxidation-reduction reactions. Thereby, energy becomes available to living things. 112–13



## 6.1 Cells and the Flow of Energy

In order to maintain their organization and carry out metabolic activities, cells—as well as organisms—need a constant supply of energy. **Energy**, defined as the ability to do work or bring about a change, allows living things to carry on the processes of life, including growth, development, metabolism, and reproduction.

Organic nutrients, produced by photosynthesizers (algae, plants, and some bacteria), directly provide organisms with energy. But, consider that photosynthesizers use solar energy to produce organic nutrients; therefore, life on Earth is ultimately dependent on solar energy.

### Forms of Energy

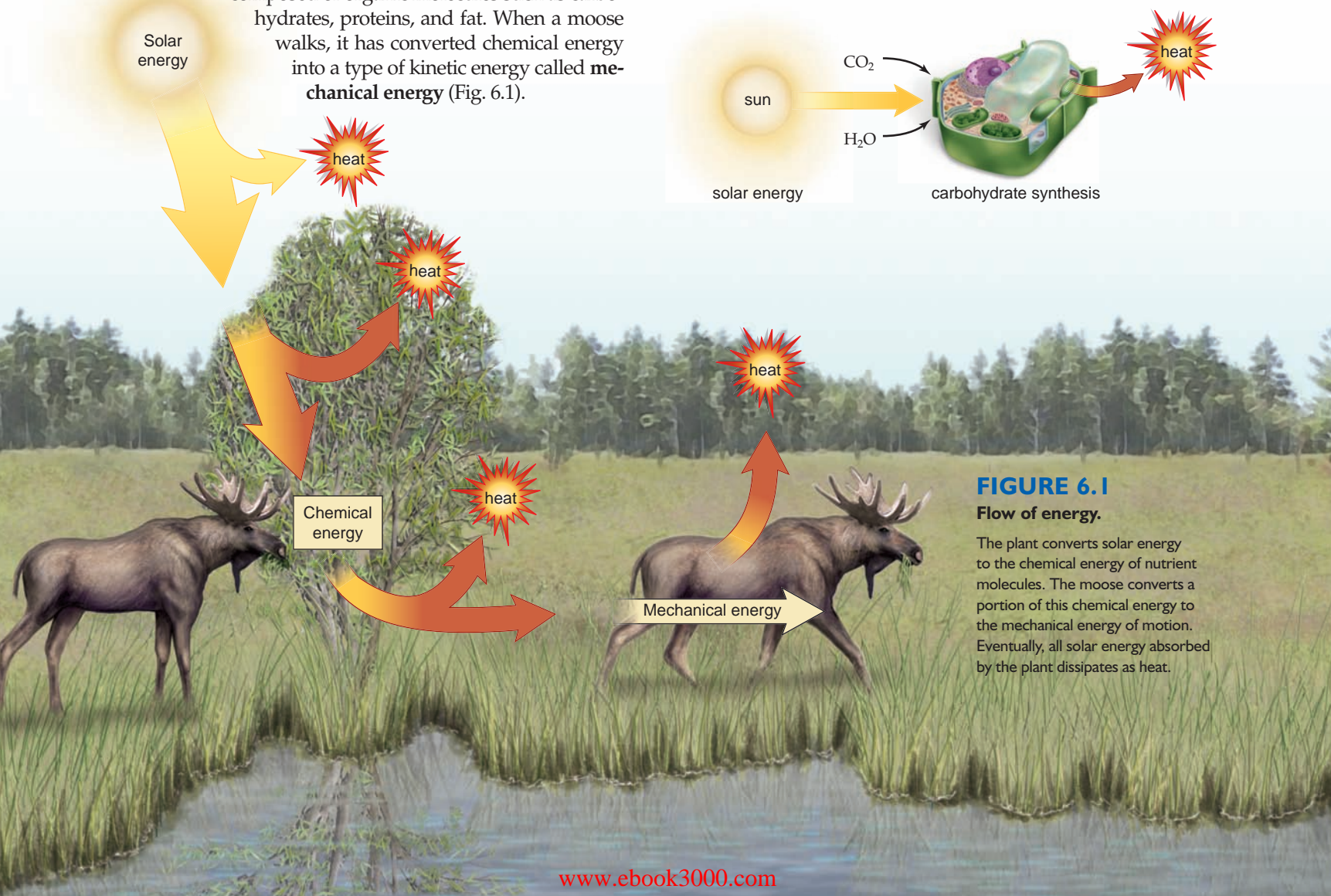
Energy occurs in two forms: kinetic and potential energy. **Kinetic energy** is the energy of motion, as when a ball rolls down a hill or a moose walks through grass. **Potential energy** is stored energy—its capacity to accomplish work is not being used at the moment. The food we eat has potential energy because it can be converted into various types of kinetic energy. Food is specifically called **chemical energy** because it is composed of organic molecules such as carbohydrates, proteins, and fat. When a moose walks, it has converted chemical energy into a type of kinetic energy called **mechanical energy** (Fig. 6.1).

### Two Laws of Thermodynamics

Figure 6.1 illustrates the flow of energy in a terrestrial ecosystem. Plants capture only a small portion of solar energy, and much of it dissipates as **heat**. When plants photosynthesize and then make use of the food they produce, more heat results. Still, there is enough remaining to sustain a moose and the other organisms in an ecosystem. As they metabolize nutrient molecules, all the captured solar energy eventually dissipates as heat. Therefore, energy flows and does not cycle. Two **laws of thermodynamics** explain why energy flows through ecosystems and through cells. These laws were formulated by early researchers who studied energy relationships and exchanges:

The first law of thermodynamics—the law of conservation of energy—states energy cannot be created or destroyed, but it can be changed from one form to another.

When leaf cells photosynthesize, they use solar energy to form carbohydrate molecules from carbon dioxide and water. (Carbohydrates are energy-rich molecules, while carbon dioxide and water are energy-poor molecules.) Not all of the captured solar energy becomes carbohydrates; some becomes heat:



**FIGURE 6.1**

#### Flow of energy.

The plant converts solar energy to the chemical energy of nutrient molecules. The moose converts a portion of this chemical energy to the mechanical energy of motion. Eventually, all solar energy absorbed by the plant dissipates as heat.

Obviously, plant cells do not create the energy they use to produce carbohydrate molecules; that energy comes from the sun. Is any energy destroyed? No, because the heat they give off is also a form of energy. Similarly, a moose uses the energy derived from carbohydrates to power its muscles. And as its cells use this energy, none is destroyed, but some becomes heat, which dissipates into the environment:



The second law of thermodynamics therefore applies to living systems:

The second law of thermodynamics states energy cannot be changed from one form to another without a loss of usable energy.

In our example, this law is upheld because some of the solar energy taken in by the plant and some of the chemical energy within the nutrient molecules taken in by the moose become heat. When heat dissipates into the environment, it is no longer usable—that is, it is not available to do work. With transformation upon transformation, eventually all usable forms of energy become heat that is lost to the environment. Heat that dissipates into the environment cannot be captured and converted to one of the other forms of energy.

As a result of the second law of thermodynamics, no process requiring a conversion of energy is ever 100% efficient. Much of the energy is lost in the form of heat. In automobiles, the gasoline engine is between 20% and 30% efficient in converting chemical energy into mechanical energy. The majority of energy is obviously lost as heat. Cells are capable of about 40% efficiency, with the remaining energy being given off to the surroundings as heat.

## Cells and Entropy

The second law of thermodynamics can be stated another way: Every energy transformation makes the universe less organized and more disordered. The term **entropy** [Gk. *entropē*, a turning inward] is used to indicate the relative amount of disorganization. Since the processes that occur in cells are energy transformations, the second law means that every process that occurs in cells always does so in a way that increases the total entropy of the universe. Then, too, any one of these processes makes less energy available to do useful work in the future.

Figure 6.2 shows two processes that occur in cells. The second law of thermodynamics tells us that glucose tends to break apart into carbon dioxide and water. Why? Because glucose is more organized, and therefore less stable, than its breakdown products. Also, hydrogen ions on one side of a membrane tend to move to the other side unless they are prevented from doing so. Why? Because when they are distributed randomly, entropy has increased. As an analogy,

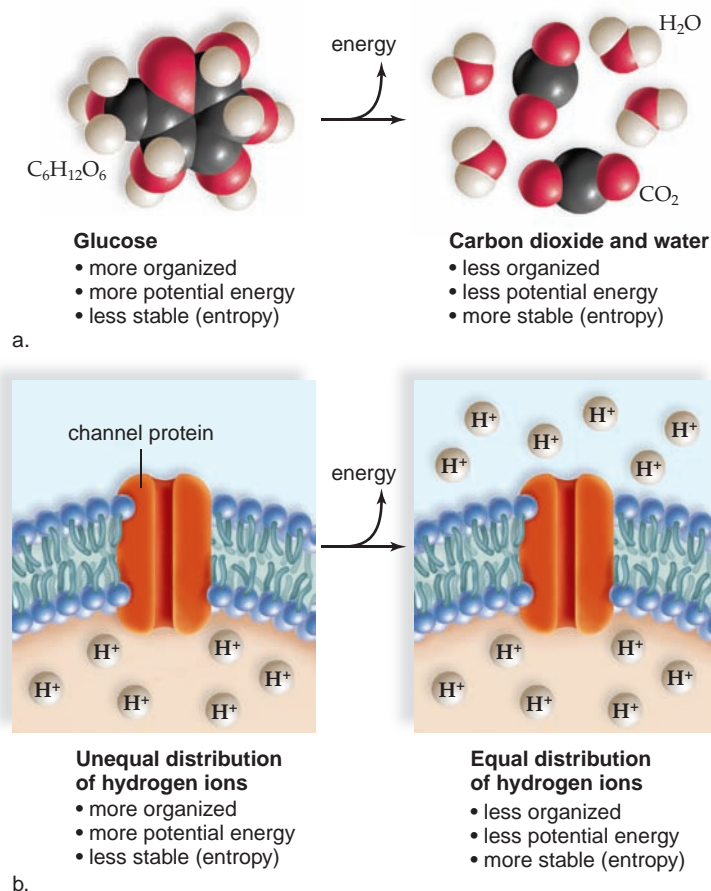
you know from experience that a neat room is more organized but less stable than a messy room, which is disorganized but more stable. How do you know a neat room is less stable than a messy room? Consider that a neat room always tends to become more messy.

On the other hand, you know that some cells can make glucose out of carbon dioxide and water, and all cells can actively move ions to one side of the membrane. How do they do it? These cellular processes obviously require an input of energy from an outside source. This energy ultimately comes from the sun. Living things depend on a constant supply of energy from the sun because the ultimate fate of all solar energy in the biosphere is to become randomized in the universe as heat. A living cell is a temporary repository of order purchased at the cost of a constant flow of energy.

## Check Your Progress

**6.1**

1. Contrast potential energy with kinetic energy.
2. Explain how the second energy law is related to entropy.



**FIGURE 6.2** Cells and entropy.

The second law of thermodynamics tells us that (a) glucose, which is more organized, tends to break down to carbon dioxide and water, which are less organized. (b) Similarly, hydrogen ions ( $H^+$ ) on one side of a membrane tend to move to the other side so that the ions are randomly distributed. Both processes result in an increase in entropy.



## 6.2 Metabolic Reactions and Energy Transformations

**Metabolism** is the sum of all the chemical reactions that occur in a cell. **Reactants** are substances that participate in a reaction, while **products** are substances that form as a result of a reaction. In the reaction  $A + B \rightarrow C + D$ , A and B are the reactants while C and D are the products. How would you know that this reaction will occur spontaneously—that is, without an input of energy? Using the concept of entropy, it is possible to state that a reaction will occur spontaneously if it increases the entropy of the universe. But in cell biology, we do not usually wish to consider the entire universe. We simply want to consider this reaction. In such instances, cell biologists use the concept of free energy instead of entropy. **Free energy** is the amount of energy available—that is, energy that is still “free” to do work—after a chemical reaction has occurred. The change in free energy after a reaction occurs is calculated by subtracting the free energy content of the reactants from that of the products. A negative result means that the products have less free energy than the reactants, and the reaction will occur spontaneously. In our reaction, if C and D have less free energy than A and B, then the reaction will “go.”

**Exergonic reactions** are spontaneous and release energy, while **endergonic reactions** require an input of energy to occur. In the body, many reactions, such as protein synthesis, nerve conduction, or muscle contraction, are endergonic,

and they occur because exergonic reactions, which release energy, can be used to drive endergonic reactions, which require energy. ATP is a carrier of energy between exergonic and endergonic reactions.

### ATP: Energy for Cells

**ATP (adenosine triphosphate)** is the common energy currency of cells; when cells require energy, they “spend” ATP. A sedentary oak tree as well as a flying bat requires vast amounts of ATP. The more active the organism, the greater the demand for ATP. However, the amount on hand at any one moment is minimal because ATP is constantly being generated from **ADP (adenosine diphosphate)** and a molecule of inorganic phosphate  $\text{P}$  (Fig. 6.3). A cell is assured of a supply of ATP, because glucose breakdown during cellular respiration provides the energy for the buildup of ATP in mitochondria. Only 39% of the free energy of glucose is transformed to ATP; the rest is lost as heat.

There are many biological advantages to the use of ATP as an energy carrier in living systems. ATP provides a common and universal energy currency because it can be used in many different types of reactions. Also, when ATP is converted to energy, ADP, and  $\text{P}$ , the amount of energy released is sufficient for a particular biological function, and there is little waste of energy. In addition, ATP breakdown can be coupled to endergonic reactions in such a way that it minimizes energy loss.

### Structure of ATP

ATP is a nucleotide composed of the nitrogen-containing base adenine and the 5-carbon sugar ribose (together called adenosine) and three phosphate groups. ATP is called a “high-energy” compound because a phosphate group can be easily removed. Under cellular conditions, the amount of energy released when ATP is hydrolyzed to ADP +  $\text{P}$  is about 7.3 kcal per mole.<sup>1</sup>

<sup>1</sup> A mole is the number of molecules present in the molecular weight of a substance (in grams).

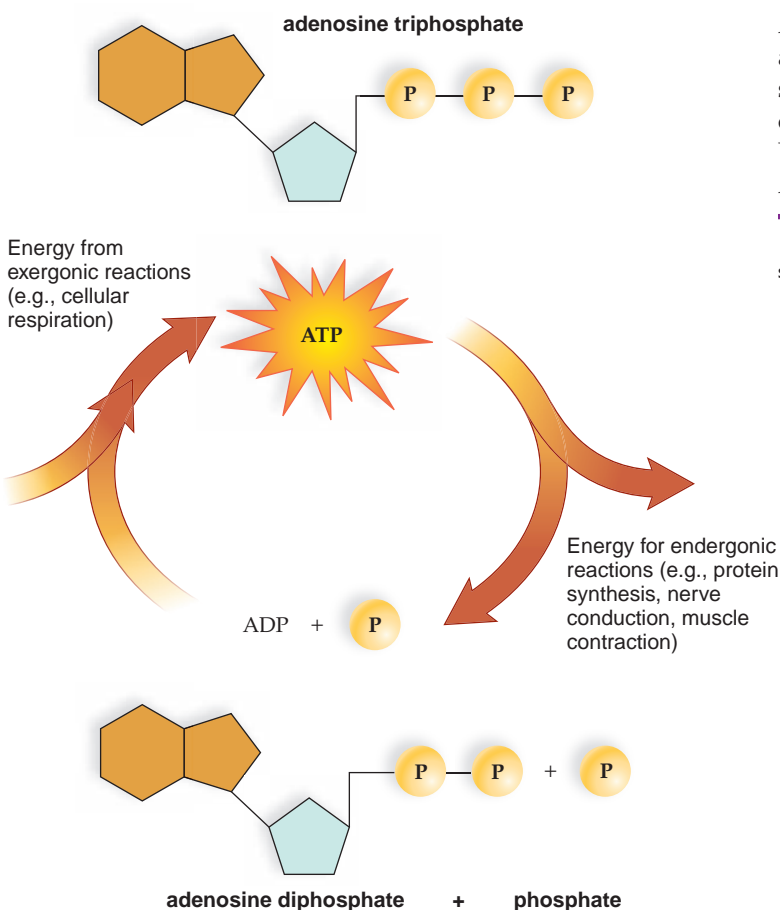
**FIGURE 6.3** The ATP cycle.

**a.** In cells, ATP carries energy between exergonic reactions and endergonic reactions. When a phosphate group is removed by hydrolysis, ATP releases the appropriate amount of energy for most metabolic reactions. **b.** In order to produce light, a firefly breaks down ATP.



**b.**

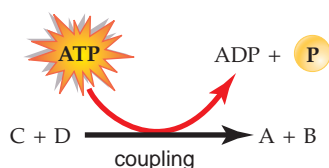
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**a.**

## Coupled Reactions

How can the energy released by ATP hydrolysis be transferred to a reaction that requires energy, and therefore would not ordinarily occur? In other words, how does ATP act as a carrier of chemical energy? The answer is that ATP breakdown is coupled to the energy-requiring reaction. **Coupled reactions** are reactions that occur in the same place, at the same time, and in such a way that an energy-releasing (exergonic) reaction drives an energy requiring (endergonic) reaction. Usually the energy-releasing reaction is the hydrolysis of ATP. Because the cleavage of ATP's phosphate groups releases more energy than the amount consumed by the energy-requiring reaction, entropy will increase, and both reactions will proceed. The simplest way to represent a coupled reaction is like this:



This reaction tells you that coupling occurs, but it does not show how coupling is achieved. A cell has two main ways to couple ATP hydrolysis to an energy-requiring reaction: ATP is used to energize a reactant, or ATP is used to change the shape of a reactant. Both can be achieved by transferring a phosphate group to the reactant so that the product is *phosphorylated*.

For example, when an ion moves across the plasma membrane of a cell, ATP is hydrolyzed and, instead of the last phosphate group floating away, an enzyme attaches it to a carrier protein. This causes the protein to undergo a change in shape that allows it to move the ion into or out of the cell. As

a contrasting example, when a polypeptide is synthesized at a ribosome, an enzyme transfers a phosphate group from ATP to each amino acid in turn, and this transfer supplies the energy that allows an amino acid to bond with another amino acid.

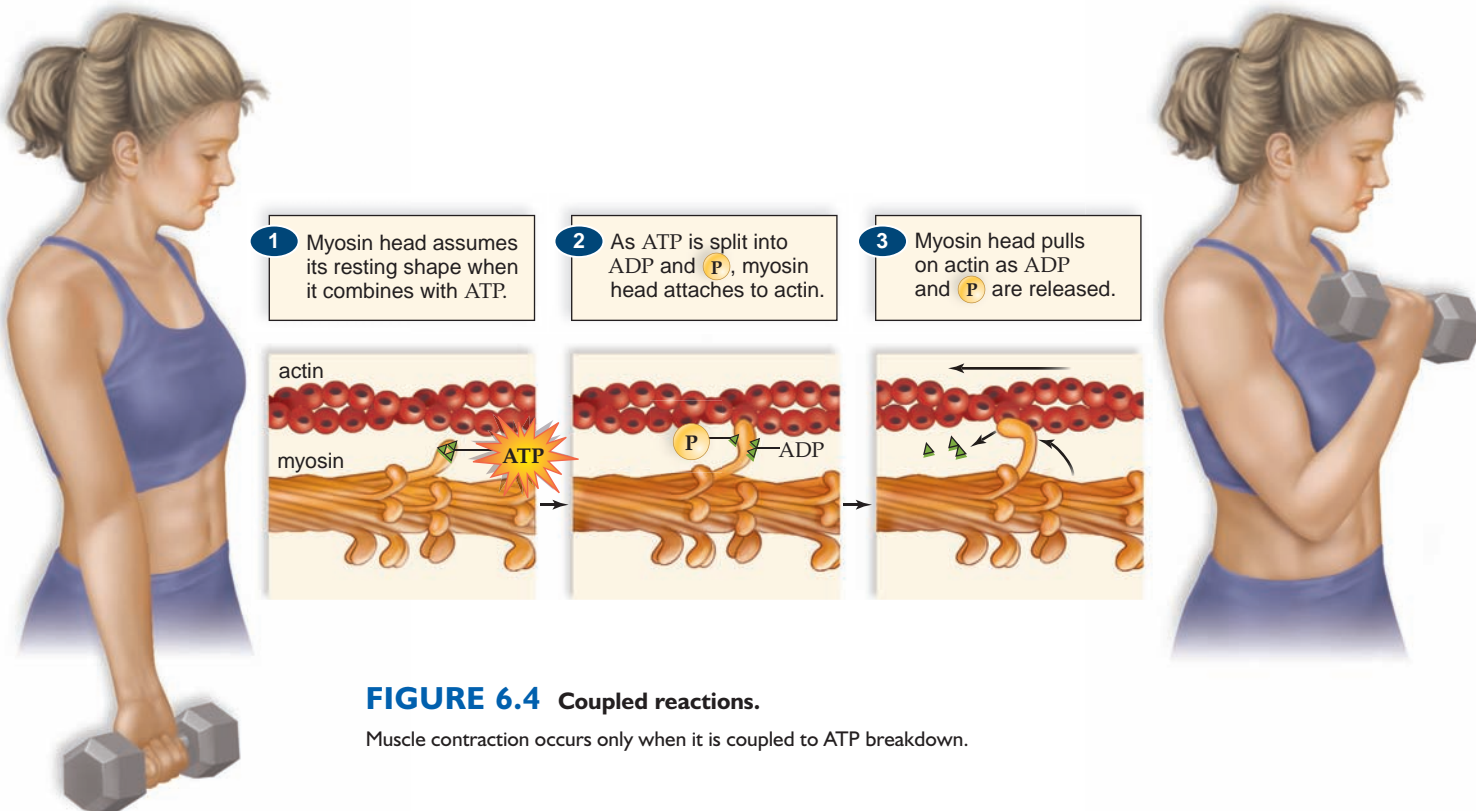
Figure 6.4 shows how ATP hydrolysis provides the necessary energy for muscle contraction. During muscle contraction, myosin filaments pull actin filaments to the center of the cell, and the muscle shortens. **1** Myosin head combines with ATP (three connected green triangles) and takes on its resting shape. **2** ATP breaks down to ADP (two connected green triangles) plus **P** (one green triangle). Now a change in shape allows myosin to attach to actin. **3** The release of ADP and **P** from myosin head causes it to change its shape again and pull on the actin filament. The cycle begins again at **1**, when myosin head combines with ATP and takes on its resting shape. During this cycle, chemical energy has been transformed to mechanical energy, and entropy has increased.

Through coupled reactions, ATP drives forward energetically unfavorable processes that must occur to create the high degree of order essential for life. Macromolecules must be made and organized to form cells and tissues; the internal composition of the cell and the organism must be maintained; and movement of cellular organelles and the organism must occur if life is to continue.

## Check Your Progress

## 6.2

1. Explain why ATP is a good short-term energy storage molecule.
2. Briefly explain the function of ATP in coupled reactions.



**FIGURE 6.4** Coupled reactions.

Muscle contraction occurs only when it is coupled to ATP breakdown.



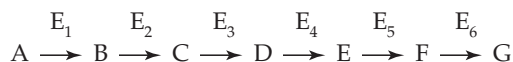
## 6.3 Metabolic Pathways and Enzymes

An **enzyme** is a protein molecule that functions as an organic catalyst to speed a chemical reaction without itself being affected by the reaction. In this part of the chapter, we will also see that enzymes allow reactions to occur under mild conditions, and that they regulate metabolism, including the elimination of side reactions.

First, we will mention that not all enzymes are proteins. **Ribozymes**, which are made of RNA instead of proteins, can also serve as biological catalysts. Ribozymes are involved in the synthesis of RNA and the synthesis of proteins at the ribosomes.

Let's also recognize that reactions do not occur haphazardly in cells; they are usually part of a **metabolic pathway**, a series of linked reactions. Metabolic pathways begin with a particular reactant and terminate with an end product. While it is possible to write an overall equation for a pathway as if the beginning reactant went to the end product in one step, actually many specific steps occur in between. In the pathway, one reaction leads to the next reaction, which leads to the next reaction, and so forth, in an organized, highly structured manner. This arrangement makes it possible for one pathway to lead to several others, because various pathways have several molecules in common. Also, metabolic energy is captured and used more easily if it is released in small increments rather than all at once.

A metabolic pathway can be represented by the following diagram:



In this diagram, the letters A–F are reactants and the letters B–G are products in the various reactions. In other words, the products from the previous reaction become the reactants of the next reaction. The letters  $E_1$ – $E_6$  are enzymes. Any one of the molecules (A–G) in this linear pathway could also be a reactant in another pathway. A diagram showing all the possibilities would be highly branched.

### Energy of Activation

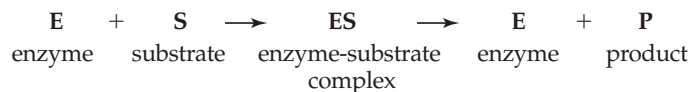
Molecules frequently do not react with one another unless they are activated in some way. In the lab, for example, in the absence of an enzyme, activation is very often achieved by heating a reaction flask to increase the number of effective collisions between molecules. The energy that must be added to cause molecules to react with one another is called the **energy of activation** ( $E_a$ ). Figure 6.5 compares  $E_a$  when an enzyme is not present to when an enzyme is present, illustrating that enzymes lower the amount of energy required for activation to occur. The energy content of the product remains the same, however.

Enzymes allow reactions to occur under mild conditions by bringing reactants into contact with one another and even by participating in the reaction at times.

### Enzyme-Substrate Complex

The reactants in an enzymatic reaction are called the **substrates** for that enzyme. Considering the metabolic pathway shown previously, A is the substrate for  $E_1$ , and B is the product. Now B becomes the substrate for  $E_2$ , and C is the product. This process continues until the final product G forms.

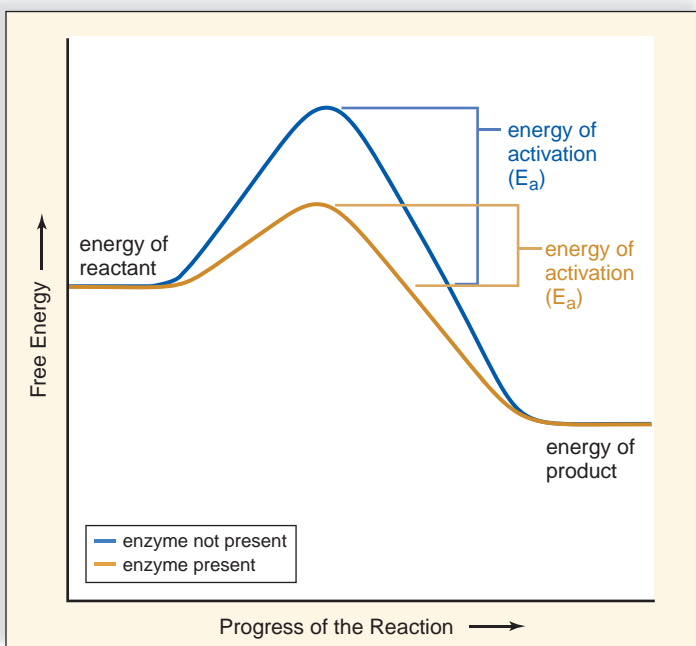
The following equation, which is pictorially shown in Figure 6.6, is often used to indicate that an enzyme forms a complex with its substrate:



In most instances, only one small part of the enzyme, called the **active site**, binds with the substrate(s). It is here that the enzyme and substrate fit together, seemingly like a key fits a lock; however, it is now known that the active site undergoes a slight change in shape to accommodate the substrate(s). This is called the **induced fit model** because the enzyme is induced to undergo a slight alteration to achieve optimum fit.

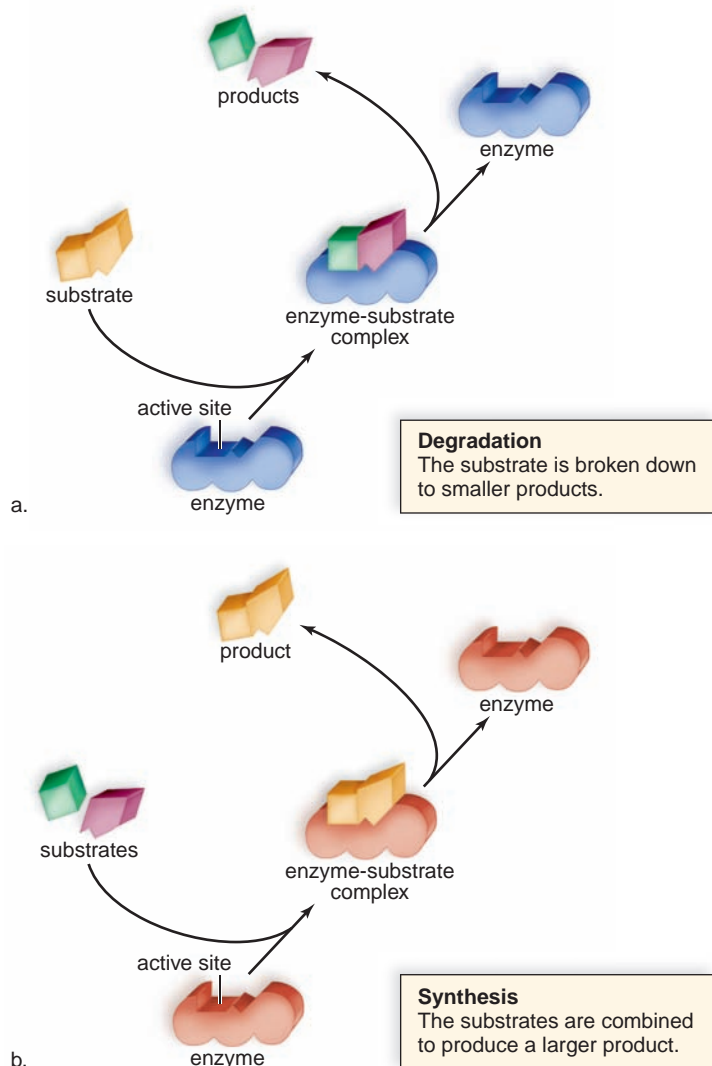
The change in shape of the active site facilitates the reaction that now occurs. After the reaction has been completed, the product(s) is released, and the active site returns to its original state, ready to bind to another substrate molecule. Only a small amount of enzyme is actually needed in a cell because enzymes are not used up by the reaction.

Some enzymes do more than simply complex with their substrate(s); they participate in the reaction. Trypsin digests protein by breaking peptide bonds. The active site of trypsin contains three amino acids with R groups that



**FIGURE 6.5** Energy of activation ( $E_a$ ).

Enzymes speed the rate of reactions because they lower the amount of energy required for the reactants to react. Even reactions like this one, in which the energy of the product is less than the energy of the reactant, speed up when an enzyme is present.



**FIGURE 6.6** Enzymatic actions.

Enzymes have an active site where the substrate(s) and the enzyme fit together so the reaction will occur. Following the reaction, the product(s) is released, and the enzyme is free to act again. Certain enzymes carry out (a) degradation and others carry out (b) synthesis.

actually interact with members of the peptide bond—first to break the bond and then to introduce the components of water. This illustrates that the formation of the enzyme-substrate complex is very important in speeding the reaction. Because enzymes only complex with their substrates, they are sometimes named for their substrates, and usually end in *ase*. For example, lipase is involved in hydrolyzing lipids.

### Regulation of Metabolism

Because enzymes are specific, they participate in regulating metabolism. First, which metabolic pathways are being utilized is dependent on which enzymes are present. Since metabolic pathways can intersect, the presence of particular enzymes can determine the direction of metabolism. Then, too, some particular reactants can produce more than one type of product. Therefore, which enzyme is present determines which product is produced and the direction of metabolism without several side pathways being activated.

## Factors Affecting Enzymatic Speed

Generally, enzymes work quickly, and in some instances they can increase the reaction rate more than 10 million times. The rate of a reaction is the amount of product produced per unit time. The amount of product per unit time depends on how much substrate is at the active sites of enzymes. Therefore, increasing the amount of substrate and also the amount of enzyme can increase the rate of the reaction. Any factor that alters the shape of the active site, such as pH or temperature or an inhibitor, can decrease the rate of a reaction. Finally, some enzymes require cofactors that help speed the rate of the reaction because they help bind the substrate to the active site or they participate in the reaction at the active site.

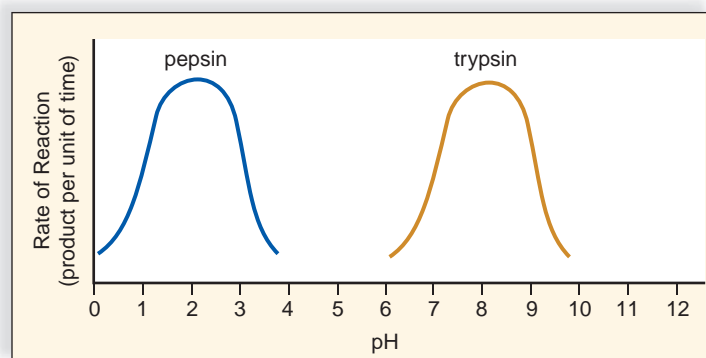
### Substrate Concentration

Molecules must collide to react. Generally, enzyme activity increases as substrate concentration increases because there are more collisions between substrate molecules and the enzyme. As more substrate molecules fill active sites, more product results per unit time. But when the active sites are filled almost continuously with substrate, the rate of the reaction cannot increase any more. Maximum rate has been reached.

Just as the amount of substrate can increase or limit the rate of an enzymatic reaction, so the amount of active enzyme can also increase or limit the rate of an enzymatic reaction.

### Optimal pH

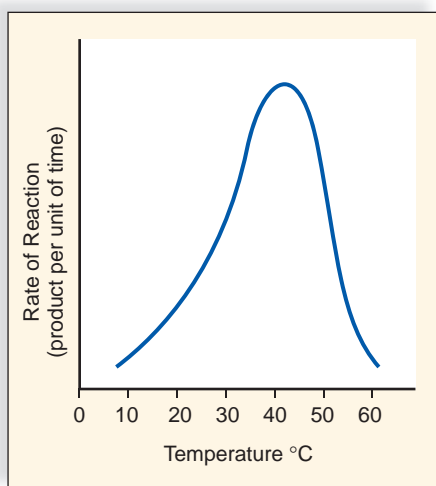
Each enzyme also has an optimal pH at which the rate of the reaction is highest. Figure 6.7 shows the optimal pH for the enzymes pepsin and trypsin. At this pH value, these enzymes have their normal configurations. The globular structure of an enzyme is dependent on interactions, such as hydrogen bonding, between *R* groups. A change in pH can alter the ionization of these side chains and disrupt normal interactions, and under extreme conditions of pH, the enzyme becomes inactive. Inactivity occurs because the enzyme has an altered shape and is then unable to combine efficiently with its substrate.



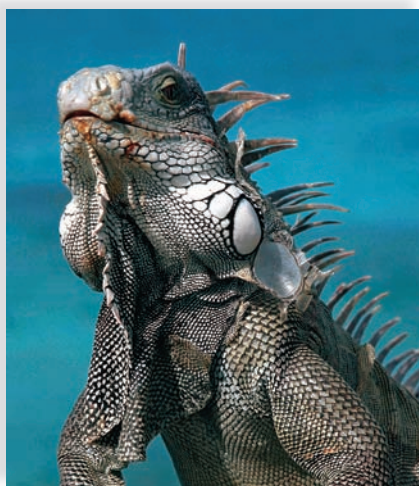
**FIGURE 6.7** The effect of pH on rate of reaction.

The optimal pH for pepsin, an enzyme that acts in the stomach, is about 2, while the optimal pH for trypsin, an enzyme that acts in the small intestine, is about 8. The optimal pH of an enzyme maintains its shape so that it can bind with its substrates.





a. Rate of reaction as a function of temperature



b. Body temperature of ectothermic animals often limits rates of reactions.



c. Body temperature of endothermic animals promotes rates of reactions.

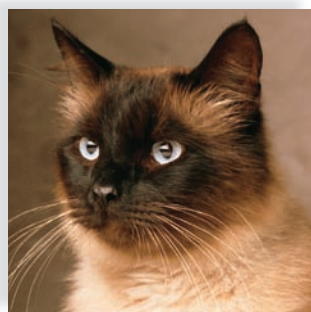
### FIGURE 6.8 The effect of temperature on rate of reaction.

a. Usually, the rate of an enzymatic reaction doubles with every 10°C rise in temperature. This enzymatic reaction is maximum at about 40°C; then it decreases until the reaction stops altogether, because the enzyme has become denatured. b. The body temperature of ectothermic animals, such as an iguana, which take on the temperature of their environment, often limits rates of reactions. c. The body temperature of endothermic animals, such as a polar bear, promotes rates of reaction.

### Temperature

Typically, as temperature rises, enzyme activity increases (Fig. 6.8a). This occurs because warmer temperatures cause more effective collisions between enzyme and substrate. The body temperature of an animal seems to affect whether it is normally active or inactive (Fig. 6.8b, c). It has been suggested that mammals are more prevalent today than reptiles because they maintain a warm internal temperature that allows their enzymes to work at a rapid rate.

In the laboratory, if the temperature rises beyond a certain point, enzyme activity eventually levels out and then declines rapidly because the enzyme is **denatured**. An enzyme's shape changes during denaturation, and then it can no longer bind its substrate(s) efficiently. Exceptions to this generalization do occur. For example, some prokaryotes can live in hot springs because their enzymes do not denature. These organisms are responsible for the brilliant colors of the hot springs. Another exception involves the coat color of animals. Siamese cats have inherited a mutation that causes an enzyme to be active only at cooler body temperatures! Their activity causes the cooler regions of the body—the face, ears, legs, and tail—to be dark in color (Fig. 6.9). The coat color pattern in several other animals can be explained similarly.



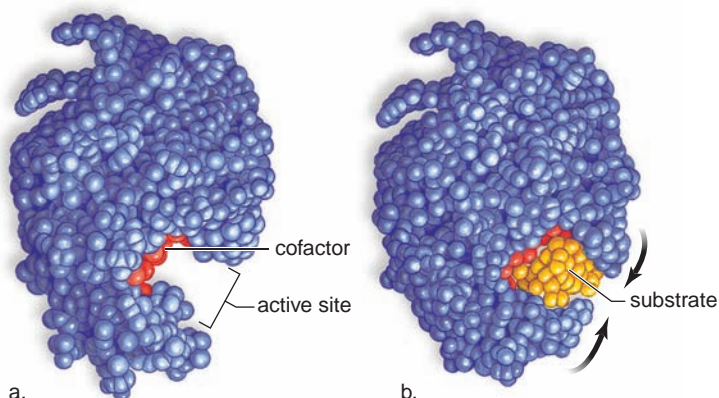
**FIGURE 6.9** The effect of temperature on enzymes.

Siamese cats have inherited a mutation that causes an enzyme to be active only at cooler body temperatures. Therefore, only certain regions of the body are dark in color.

### Enzyme Cofactors

Many enzymes require the presence of an inorganic ion or nonprotein organic molecule at the active site in order to be active; these necessary ions or molecules are called **cofactors** (Fig. 6.10). The inorganic ions are metals such as copper, zinc, or iron. The nonprotein organic molecules are called **coenzymes**. These cofactors participate in the reaction and may even accept or contribute atoms to the reactions. In the next section, we will discuss two coenzymes that play significant roles in photosynthesis and cellular respiration, respectively.

**Vitamins** are relatively small organic molecules that are required in trace amounts in our diet and in the diets of other animals for synthesis of coenzymes. The vitamin becomes part of a coenzyme's molecular structure. If a vitamin is not available, enzymatic activity will decrease, and the result will be a vitamin-deficiency disorder: Niacin deficiency results in a skin disease called pellagra, and riboflavin deficiency results in cracks at the corners of the mouth.



**FIGURE 6.10** Cofactors at active site.

a. Cofactors, including inorganic ions and organic coenzymes, may participate in the reaction at the active site (b).

## Enzyme Inhibition

**Enzyme inhibition** occurs when a molecule (the inhibitor) binds to an enzyme and decreases its activity. **1** In Figure 6.11, F is the end product of a metabolic pathway that can act as an inhibitor. This is beneficial because once sufficient end product of a metabolic pathway is present, it is best to inhibit further production to conserve raw materials and energy.

**2** Figure 6.11 also illustrates **noncompetitive inhibition** because the inhibitor (F, the end product) binds to the enzyme  $E_1$  at a location other than the active site. The site is called an **allosteric site**. When an inhibitor is at the allosteric site, the active site of the enzyme changes shape.

**3** The enzyme  $E_1$  is inhibited because it is unable to bind to A, its substrate. The inhibition of  $E_1$  means that the metabolic pathway is inhibited and no more end product will be produced.

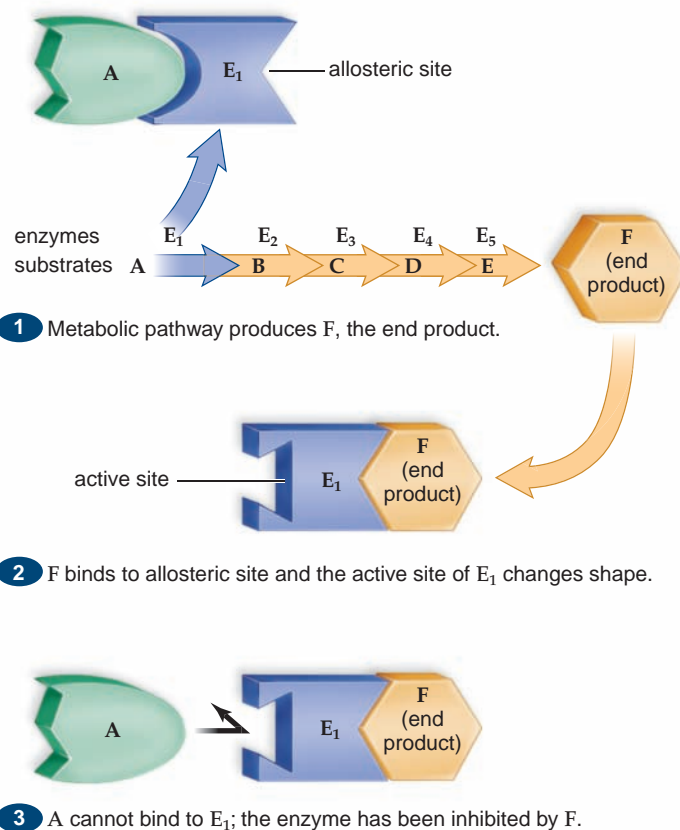
In contrast to noncompetitive inhibition, **competitive inhibition** occurs when an inhibitor and the substrate compete for the active site of an enzyme. Product will form only when the substrate, not the inhibitor, is at the active site. In this way, the amount of product is regulated.

Normally, enzyme inhibition is reversible, and the enzyme is not damaged by being inhibited. When enzyme inhibition is irreversible, the inhibitor permanently inactivates or destroys an enzyme.

### Check Your Progress

6.3

1. How do enzymes lower the energy of activation?
2. What factors can affect the speed of an enzymatic reaction?



**FIGURE 6.11** Noncompetitive inhibition of an enzyme.

In the pathway, A–E are substrates,  $E_1$ – $E_5$  are enzymes, and F is the end product of the pathway that inhibits the enzyme  $E_1$ .

## health focus

### Enzyme Inhibitors Can Spell Death

**C**yanide gas was formerly used to execute people. How did it work? Cyanide can be fatal because it binds to a mitochondrial enzyme necessary for the production of ATP. MPTP (1-methyl-4-phenyl-1,2,3,6-tetrahydropyridine) is another enzyme inhibitor that stops mitochondria from producing ATP. The toxic nature of MPTP was discovered in the early 1980s, when a group of intravenous drug users in California suddenly developed symptoms of Parkinson disease, including uncontrollable tremors and rigidity. All of the drug users had injected a synthetic form of heroin that was contaminated with MPTP. Parkinson disease is characterized by the death of brain cells, the very ones that are also destroyed by MPTP.

Sarin is a chemical that inhibits an enzyme at neuromuscular junctions, where nerves stimulate muscles. When the enzyme is inhibited,

the signal for muscle contraction cannot be turned off, so the muscles are unable to relax and become paralyzed. Sarin can be fatal if the muscles needed for breathing become paralyzed. In 1995, terrorists released sarin gas on a subway in Japan (Fig. 6A). Although many people developed symptoms, only 17 died.

A fungus that contaminates and causes spoilage of sweet clover produces a chemical called warfarin. Cattle that eat the spoiled feed die from internal bleeding because warfarin inhibits a crucial enzyme for blood clotting. Today, warfarin is widely used as a rat poison. Unfortunately, it is not uncommon for warfarin to be mistakenly eaten by pets and even very small children, with tragic results.

Many people are prescribed a medicine called Coumadin to prevent inappropriate blood clotting. For example, those who have received an artificial heart valve need such a

medication. Coumadin contains a nonlethal dose of warfarin.



**Figure 6A** Sarin gas. The aftermath when sarin, a nerve gas that results in the inability to breathe, was released by terrorists in a Japanese subway in 1995.

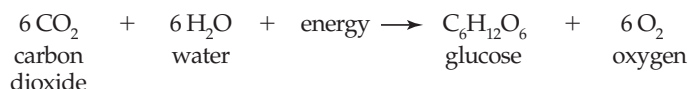


## 6.4 Organelles and the Flow of Energy

Two organelles are particularly involved in the flow of energy from the sun through all living things. Photosynthesis, a process that captures solar energy to produce carbohydrates, takes place in chloroplasts. Cellular respiration, which breaks down carbohydrates, takes place in mitochondria.

### Photosynthesis

The overall reaction for photosynthesis can be written like this:



This equation shows that hydrogen atoms ( $\text{H}^+ + \text{e}^-$ ) are transferred from water to carbon dioxide, when glucose is formed. **Oxidation** is defined as the loss of electrons and **reduction** is the gain of electrons. Therefore, water has been oxidized and carbon dioxide has been reduced.

Since glucose is a high-energy molecule, an input of energy is needed to make the reaction go. Chloroplasts are able to capture solar energy and convert it by way of an electron transport chain (discussed next) to the chemical energy of ATP molecules. ATP is then used along with hydrogen atoms to reduce carbon dioxide to glucose.

A coenzyme of oxidation-reduction called **NADP<sup>+</sup> (nicotinamide adenine dinucleotide phosphate)** is active during photosynthesis. This molecule carries a positive charge, and therefore is written as  $\text{NADP}^+$ . During photosynthesis,  $\text{NADP}^+$  accepts electrons and a hydrogen ion derived from water and later passes them by way of a metabolic pathway to carbon dioxide, forming glucose. The reaction that reduces  $\text{NADP}^+$  is:



### Cellular Respiration

The overall equation for cellular respiration is opposite to that for photosynthesis:



In this reaction, glucose has lost hydrogen atoms (been oxidized), and oxygen has gained hydrogen atoms (been reduced). The hydrogen atoms that were formerly bonded to carbon are now bonded to oxygen. Glucose is a high-energy molecule, while its breakdown products, carbon dioxide and water, are low-energy molecules; therefore, energy is released. Mitochondria use the energy released from glucose breakdown to build ATP molecules by way of an electron transport chain, as depicted in Figure 6.12.

In metabolic pathways, most oxidations such as those that occur during cellular respiration involve a coenzyme called **NAD<sup>+</sup> (nicotinamide adenine dinucleotide)**. This molecule carries a positive charge, and therefore it is represented as  $\text{NAD}^+$ .

During oxidation reactions,  $\text{NAD}^+$  accepts two electrons but only one hydrogen ion. The reaction that reduces  $\text{NAD}^+$  is:



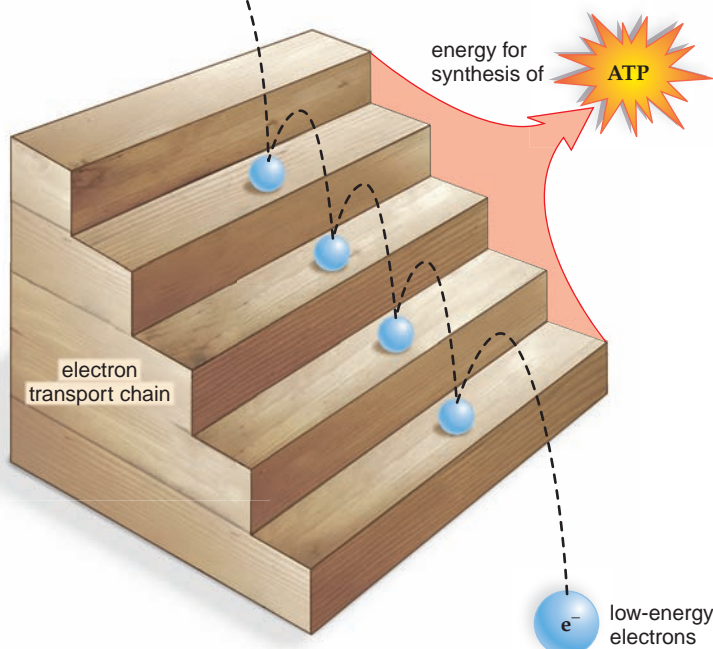
### Electron Transport Chain

As previously mentioned, chloroplasts use solar energy to generate ATP, and mitochondria use glucose energy to generate ATP by way of an electron transport chain. An **electron transport chain (ETC)** is a series of membrane-bound carriers that pass electrons from one carrier to another. High-energy electrons are delivered to the chain, and low-energy electrons leave it. If a hot potato were passed from one person to another, it would lose heat with each transfer. In the same manner, every time electrons are transferred to a new carrier, energy is released. However, unlike the hot potato transfer example, the cell is able to capture the released energy and use it to produce ATP molecules (Fig. 6.12).

In certain redox reactions, the result is release of energy, and in others, energy is required. In an ETC, each carrier is reduced and then oxidized in turn. The overall effect of oxidation-reduction as electrons are passed from carrier to carrier of the electron transport chain is the release of energy for ATP production.

### ATP Production

For many years, it was known that ATP synthesis was somehow coupled to the ETC, but the exact mechanism could not be determined. Peter Mitchell, a British biochemist, received a Nobel Prize in 1978 for his theory of ATP production in both mitochondria and chloroplasts.



**FIGURE 6.12** Electron transport chain.

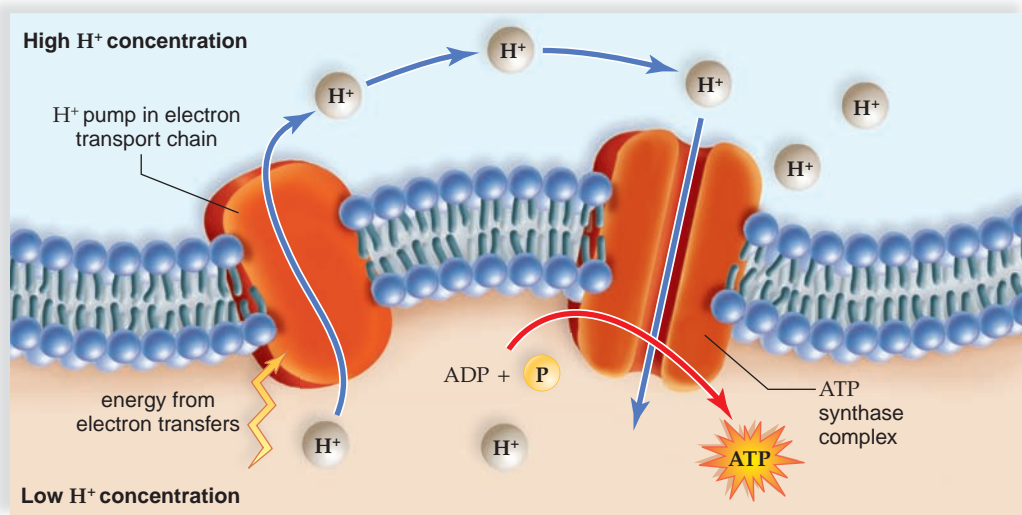
High-energy electrons are delivered to the chain and, with each step as they pass from carrier to carrier, energy is released and used for ATP production.

**FIGURE 6.13 Chemiosmosis.**

Carriers in the electron transport chain pump hydrogen ions ( $H^+$ ) across a membrane. When the hydrogen ions flow back across the membrane through an ATP synthase complex, ATP is synthesized by an enzyme called ATP synthase. Chemiosmosis occurs in chloroplasts and mitochondria.

In chloroplasts and mitochondria, the carriers of the ETC are located within a membrane: thylakoid membranes in chloroplasts and cristae in mitochondria. Hydrogen ions ( $H^+$ ), which are often referred to as protons in this context, tend to collect on one side of the membrane because they are pumped there by certain carriers of the electron transport chain. This establishes an electrochemical gradient across the membrane that can be used to provide energy for ATP production. Enzymes and their carrier proteins, called **ATP synthase complexes**, span the membrane. Each complex contains a channel that allows hydrogen ions to flow down their electrochemical gradient. The flow of hydrogen ions through the channel provides the energy for the ATP synthase enzyme to produce ATP from  $ADP + P$  (Fig. 6.13). The production of ATP due to a hydrogen ion gradient across a membrane is called **chemiosmosis** [Gk. *osmos*, push].

Consider this analogy to understand chemiosmosis. The sun's rays evaporate water from the seas and help create the winds that blow clouds to the mountains, where water falls in the form of rain and snow. The water in a mountain reservoir has a higher potential energy than water in the ocean. The potential energy is converted to electrical energy when water is released and used to turn turbines in an electrochemical dam before it makes its way to the ocean. The continual release of water results in a continual production of electricity.



Similarly, during photosynthesis, solar energy collected by chloroplasts continually leads to ATP production. Energized electrons lead to the pumping of hydrogen ions across a thylakoid membrane, which acts like a dam to retain them. The hydrogen ions flow through the channel of an ATP synthase complex. This complex couples the flow of hydrogen ions to the formation of ATP, just as the turbines in a hydroelectric dam system couple the flow of water to the formation of electricity.

Similarly, during cellular respiration, glucose breakdown provides the energy to establish a hydrogen ion gradient across the cristae of mitochondria. And again, hydrogen ions flow through the channel within an ATP synthase complex that couples the flow of hydrogen ions to the formation of ATP.

**Check Your Progress****6.4**

1. **a.** In particular, what molecule does the grass make available to the impala as a source of energy? **b.** What happens to this molecule during cellular respiration?
2. Carbon dioxide is **(a)** \_\_\_\_\_ to produce glucose during photosynthesis and glucose is **(b)** \_\_\_\_\_ to produce ATP molecules during cellular respiration.

**Connecting the Concepts**

All cells use energy. Energy is the ability to do work, to bring about change, and to make things happen, whether it's a leaf growing or a human running. The metabolic pathways inside cells use the chemical energy of ATP to synthesize molecules, cause muscle contraction, and even allow you to read these words.

A metabolic pathway consists of a series of individual chemical reactions, each with its own enzyme. The cell can regulate the activity of the many hundreds of different enzymes taking part in cellular metabolism. Enzymes are proteins, and as such they are sensitive to environmental

conditions, including pH, temperature, and even certain pollutants, as will be discussed in later chapters.

ATP is called the universal energy "currency" of life. This is an apt analogy—before we can spend currency (e.g., money), we must first make some money. Similarly, before the cell can spend ATP molecules, it must make them. Cellular respiration in mitochondria transforms the chemical energy of carbohydrates into that of ATP molecules. ATP is spent when it is hydrolyzed, and the resulting energy is coupled to an endergonic reaction. All cells are continually making and

breaking down ATP. If ATP is lacking, the organism dies.

What is the ultimate source of energy for ATP production? In Chapter 7, we will see that, except for a few deep ocean vents and certain cave communities, the answer is the sun. Photosynthesis inside chloroplasts transforms solar energy into the chemical energy of carbohydrates. And then in Chapter 8 we will discuss how carbohydrate products are broken down in mitochondria as ATP is built up. Chloroplasts and mitochondria are the cellular organelles that permit a flow of energy from the sun through all living things.



## summary

### 6.1 Cells and the Flow of Energy

Two energy laws are basic to understanding energy-use patterns at all levels of biological organization. The first law of thermodynamics states that energy cannot be created or destroyed, but can only be transferred or transformed. The second law of thermodynamics states that one usable form of energy cannot be completely converted into another usable form. As a result of these laws, we know that the entropy of the universe is increasing and that only a flow of energy from the sun maintains the organization of living things.

### 6.2 Metabolic Reactions and Energy Transformations

The term *metabolism* encompasses all the chemical reactions occurring in a cell. Considering individual reactions, only those that result in a negative free-energy difference—that is, the products have less usable energy than the reactants—occur spontaneously. Such reactions, called exergonic reactions, release energy. Endergonic reactions, which require an input of energy, occur only in cells because it is possible to couple an exergonic process with an endergonic process. For example, glucose breakdown is an exergonic metabolic pathway that drives the buildup of many ATP molecules. ATP goes through a cycle in which it is constantly being built up from, and then broken down to, ADP +  $\text{P}_i$ . When ATP breaks down, energy is released that can drive forward energy requiring metabolic reactions, if the two reactions are coupled. In general, ATP is used to energize a reactant or change the shape of a reactant so the reaction occurs.

### 6.3 Metabolic Pathways and Enzymes

A metabolic pathway is a series of reactions that proceed in an orderly, step-by-step manner. Enzymes speed reactions by lowering the energy of activation when they form a complex with their substrates. Enzymes regulate metabolism because, in general, no reaction occurs unless its enzyme is present. Which enzymes are present determine which metabolic pathways will be utilized.

Generally, enzyme activity increases as substrate concentration increases; once all active sites are filled, maximum rate has been achieved. Any environmental factor, such as temperature or pH, affects the shape of a protein and, therefore, also affects the ability of an enzyme to do its job. Many enzymes need cofactors or coenzymes to carry out their reactions. The activity of most metabolic pathways is regulated by feedback inhibition.

### 6.4 Organelles and the Flow of Energy

A flow of energy occurs through organisms because (1) photosynthesis in chloroplasts captures solar energy and produces carbohydrates, and (2) cellular respiration in mitochondria breaks down this carbohydrate to produce ATP molecules, which (3) are used to provide energy for metabolic reactions. The overall equation for photosynthesis is the opposite of that for cellular respiration. During photosynthesis, the coenzyme NADPH reduces substrates, while during cellular respiration, the coenzyme  $\text{NAD}^+$  oxidizes substrates.

Both processes make use of an electron transport chain in which electrons are transferred from one carrier to the next with the release of energy that is ultimately used to produce ATP molecules. Chemiosmosis explains how the electron transport chain produces ATP. The carriers of this system deposit hydrogen ions ( $\text{H}^+$ ) on one side of a membrane. When hydrogen ions flow down an electrochemical gradient through an ATP synthase complex, an enzyme uses the release of energy to make ATP from ADP and  $\text{P}_i$ .

## understanding the terms

active site	108	free energy	106
ADP (adenosine diphosphate)	106	heat	104
allosteric site	111	induced fit model	108
ATP (adenosine triphosphate)	106	kinetic energy	104
ATP synthase complex	113	laws of thermodynamics	104
chemical energy	104	mechanical energy	104
chemiosmosis	113	metabolic pathway	108
coenzyme	110	metabolism	106
cofactor	110	$\text{NAD}^+$ (nicotinamide adenine dinucleotide)	112
competitive inhibition	111	$\text{NADP}^+$ (nicotinamide adenine dinucleotide phosphate)	112
coupled reactions	107	noncompetitive inhibition	111
denatured	110	oxidation	112
electron transport chain (ETC)	112	potential energy	104
endergonic reaction	106	product	106
energy	104	reactant	106
energy of activation	108	reduction	112
entropy	105	ribozyme	108
enzyme	108	substrate	108
enzyme inhibition	111	vitamin	110
exergonic reaction	106		

Match the terms to these definitions:

- \_\_\_\_\_ All of the chemical reactions that occur in a cell during growth and repair.
- \_\_\_\_\_ Stored energy as a result of location or spatial arrangement.
- \_\_\_\_\_ Essential requirement in the diet, needed in small amounts. They are often part of coenzymes.
- \_\_\_\_\_ Measure of disorder or randomness.
- \_\_\_\_\_ Nonprotein organic molecule that aids the action of the enzyme to which it is loosely bound.
- \_\_\_\_\_ Loss of one or more electrons from an atom or molecule; in biological systems, generally the loss of hydrogen atoms.

## reviewing this chapter

- State the first law of thermodynamics, and give an example. 104
- State the second law of thermodynamics, and give an example. 104–5
- Explain why the entropy of the universe is always increasing and why an organized system such as an organism requires a constant input of useful energy. 105
- What is the difference between exergonic reactions and endergonic reactions? Why can exergonic but not endergonic reactions occur spontaneously? 106
- Why is ATP called the energy currency of cells? What is the ATP cycle? 106
- Define coupling, and write an equation that shows an endergonic reaction being coupled to ATP breakdown. 107
- Diagram a metabolic pathway. Label the reactants, products, and enzymes. Explain how enzymes regulate metabolism. 108–9
- Why is less energy needed for a reaction to occur when an enzyme is present? 108
- Why are enzymes specific, and why can't each one speed many different reactions? 108–9
- Name and explain the manner in which at least three environmental factors can influence the speed of an enzymatic reaction. How do cells regulate the activity of enzymes? 109–11

11. What are cofactors and coenzymes? 110
12. Compare and contrast competitive and noncompetitive inhibition. 111
13. How do chloroplasts and mitochondria permit a flow of energy through all organisms. What role is played by oxidation and reduction? 112
14. Describe an electron transport chain. 112
15. Tell how cells form ATP during chemiosmosis. 112–13

## testing yourself

Choose the best answer for each question.

1. A form of potential energy is
  - a. a boulder at the top of a hill.
  - b. the bonds of a glucose molecule.
  - c. a starch molecule.
  - d. stored fat tissue.
  - e. All of these are correct.
2. A lit lightbulb can be used to explain the
  - a. creation of heat energy.
  - b. second law of thermodynamics.
  - c. conversion of electrical energy into heat energy.
  - d. first law of thermodynamics.
  - e. All of the above except a are correct.
3. Consider this reaction:  $A + B \rightarrow C + D + \text{energy}$ .
  - a. This reaction is exergonic.
  - b. An enzyme could still speed the reaction.
  - c. ATP is not needed to make the reaction go.
  - d. A and B are reactants; C and D are products.
  - e. All of these are correct.
4. The active site of an enzyme
  - a. is similar to that of any other enzyme.
  - b. is the part of the enzyme where its substrate can fit.
  - c. can be used over and over again.
  - d. is not affected by environmental factors, such as pH and temperature.
  - e. Both b and c are correct.
5. If you want to increase the amount of product per unit time of an enzymatic reaction, do not increase the
  - a. amount of substrate.
  - b. amount of enzyme.
  - c. temperature somewhat.
  - d. pH.
  - e. All of these are correct.
6. An allosteric site on an enzyme is
  - a. the same as the active site.
  - b. nonprotein in nature.
  - c. where ATP attaches and gives up its energy.
  - d. often involved in feedback inhibition.
  - e. All of these are correct.
7. During photosynthesis, carbon dioxide
  - a. is oxidized to oxygen.
  - b. is reduced to glucose.
  - c. gives up water to the environment.
  - d. is a coenzyme of oxidation-reduction.
  - e. All of these are correct.
8. Use these terms to label the following diagram: substrates, enzyme (used twice), active site, product, and enzyme-substrate complex. Explain the importance of an enzyme's shape to its activity.
9. Coenzymes
  - a. have specific functions in reactions.
  - b. have an active site just as enzymes do.
  - c. can be carriers for proteins.
  - d. always have a phosphate group.
  - e. are used in photosynthesis, but not in cellular respiration.

For questions 10–16, match each description to a process in the key.

### KEY:

- a. photosynthesis
- b. cellular respiration
- c. Both
- d. Neither
10. captures solar energy
11. requires enzymes and coenzymes
12. releases  $\text{CO}_2$  and  $\text{H}_2\text{O}$
13. utilizes an electron transport chain
14. performed by plants
15. transforms one form of energy into another form with the release of heat
16. creates energy for the living world

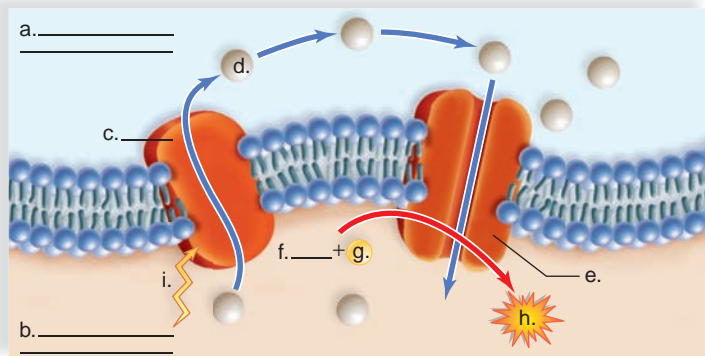
For questions 17–22, match each pair to a description in the key. Choose more than one answer if correct.

### KEY:

- a. first includes the other
- b. first breaks down to the other
- c. have nothing to do with each other
- d. work together
17. metabolic pathway, enzyme
18. allosteric site, reduction
19. kinetic energy, mechanical energy
20. ATP,  $\text{ADP} + \text{P}$
21. enzyme, coenzyme
22. chemiosmosis, electron transport chain



23. Oxidation
- is the opposite of reduction.
  - sometimes uses  $\text{NAD}^+$ .
  - is involved in cellular respiration.
  - occurs when ATP goes to  $\text{ADP} + \text{P}$ .
  - All of these but d are correct.
24.  $\text{NAD}^+$  is the \_\_\_\_\_ form, and when it later becomes NADH, it is said to be \_\_\_\_\_.
- reduced, oxidized
  - neutral, a coenzyme
  - oxidized, reduced
  - active, denatured
25. Electron transport chains
- are found in both mitochondria and chloroplasts.
  - release energy as electrons are transferred.
  - are involved in the production of ATP.
  - are located in a membrane.
  - All of these are correct.
26. Chemiosmosis is dependent on
- the diffusion of water across a differentially permeable membrane.
  - an outside supply of phosphate and other chemicals.
  - the establishment of an electrochemical hydrogen ion ( $\text{H}^+$ ) gradient.
  - the ability of ADP to join with  $\text{P}$  even in the absence of a supply of energy.
  - All of these are correct.
27. The difference between  $\text{NAD}^+$  and  $\text{NADP}^+$  is that
- only  $\text{NAD}^+$  production requires niacin in the diet.
  - one is an organic molecule, and the other is inorganic because it contains phosphate.
  - one carries electrons to the electron transport chain, and the other carries them to synthetic reactions.
  - one is involved in cellular respiration, and the other is involved in photosynthesis.
  - Both c and d are correct.
28. Label this diagram describing chemiosmosis.



## thinking scientifically

- A flower generates heat in order to attract pollinating insects. Why might the flower break down a sugar and not ATP to produce heat?
- You decide to calculate how much energy is released when sucrose is broken down by a flower and run into complications because you have to first heat the sucrose before it breaks down. Explain why this complication is not a problem for the flower.

## bioethical issue

### Global Warming and Emerging Diseases

In this chapter, we learned that a rise in temperature fosters enzymatic reactions. Could a rise in environmental temperatures due to global warming cause an increase in the number of pathogens? For example, a 2006 outbreak of diarrhea in Washington state was due to eating raw or partly cooked shellfish infected with *Vibrio* bacteria. Warmer-than-usual ocean waters may have caused the extensive growth of *Vibrio* bacteria that infected the shellfish and led to the outbreak. The connection between global warming and emerging diseases can be more subtle. In 1993, the hantavirus strain emerged from the common deer mouse and killed about 60 young people in the Southwest. In this instance, we know that climate was involved. An unusually mild winter and wet spring caused piñon trees to bloom well and provide pine nuts to the mice. The increasing deer mouse population came into contact with humans, and the hantavirus leaped easily from mice to humans.

Evidence suggests that global warming, caused in part by the burning of fossil fuels, as explained on page 125, contributes to outbreaks of hantavirus as well as malaria, dengue and yellow fevers, filariasis, encephalitis, schistosomiasis, and cholera. Clearly, any connection between global warming and emerging diseases offers another reason why fossil fuel consumption should be curtailed. Would you as a homeowner or a CEO of a company be willing to switch to renewable energy supplies because a warming of the environment may increase the incidence of human illnesses? Instead, would you approve of giving companies monetary incentives to use renewable energy supplies that do not contribute to global warming? Or, do you think we should wait for more confirmation that global warming is due to human activities and leads to an increase in diseases that could affect us and our families? What type of confirmation would you be looking for?

## Biology website

The companion website for *Biology* provides a wealth of information organized and integrated by chapter. You will find practice tests, animations, videos, and much more that will complement your learning and understanding of general biology.

<http://www.mhhe.com/maderbiology10>

# 7

## Photosynthesis

**W**hite light, the kind that shines down on us everyday, contains different colors of light, from violet to green, yellow, orange, and red. Plants use all the colors of light, except green, when they photosynthesize—and that's why we see them as green! Does this mean that if plants weren't so wasteful and used green light, in addition to other colors, they would appear black to us? Yes, natural areas like the one pictured below would be black, as shown on the right.

How did it happen that plants do not use green light for photosynthesis? When the ancestors of plants arose in the ocean, green light was already being absorbed by other photosynthesizers, so natural selection favored the evolution of a pigment such as chlorophyll, which does not absorb green light. On land, there is plentiful sunlight, and a more efficient pigment has no advantage. As discussed in this chapter, two interconnected pathways allow chloroplasts to produce carbohydrate while releasing oxygen. Such a remarkable process deserves our close attention.

Plants appear green because chlorophyll reflects green light (*left*). Otherwise, plants would be black (*right*).



### 7.1 PHOTOSYNTHETIC ORGANISMS

- Photosynthesis provides food for the biosphere, oxygen for cellular respiration, and various significant products. 118
- In flowering plants, photosynthesis takes place within membrane-bounded chloroplasts, organelles that contain membranous thylakoids surrounded by a fluid called stroma. 118–19

### 7.2 THE PROCESS OF PHOTOSYNTHESIS

- Photosynthesis has two sets of reactions: During the light reactions, solar energy is captured by the pigments in thylakoid membranes, and during the Calvin cycle reactions, carbon dioxide is reduced by enzymes to a carbohydrate in the stroma. 120–21

### 7.3 PLANTS AS SOLAR ENERGY CONVERTERS

- Plants use solar energy in the visible light range when they carry on photosynthesis. 122
- The light reactions, which occur in thylakoid membranes, produce ATP and NADH. 122–24

### 7.4 CALVIN CYCLE REACTIONS

- The Calvin cycle reactions, which occur in the stroma, use ATP and NADH from the light reactions to reduce carbon dioxide to a carbohydrate. 126–27

### 7.5 OTHER TYPES OF PHOTOSYNTHESIS

- Plants use  $C_3$  or  $C_4$  or CAM photosynthesis, which are distinguishable by the manner in which  $CO_2$  is fixed. 128–29



## 7.1 Photosynthetic Organisms

**Photosynthesis** converts solar energy into the chemical energy of a carbohydrate. Photosynthetic organisms, including land plants, algae, and cyanobacteria, are called **autotrophs** because they produce their own food (Fig. 7.1). Photosynthesis produces an enormous amount of carbohydrate. So much that, if it were instantly converted to coal and the coal were loaded into standard railroad cars (each car holding about 50 tons), the photosynthesizers of the biosphere would fill more than 100 cars per second with coal.

No wonder photosynthetic organisms are able to sustain themselves and all other living things on Earth. With few exceptions, it is possible to trace any food chain back to plants and algae. In other words, producers, which have the ability to synthesize carbohydrates, feed not only themselves but also consumers, which must take in preformed organic molecules. Collectively, consumers are called **heterotrophs**. Both autotrophs and heterotrophs use organic molecules produced by photosynthesis as a source of building blocks for growth and repair and as a source of chemical energy for cellular work.

Photosynthesizers also produce copious amounts of oxygen as a by-product. Oxygen, which is required by organisms when they carry on cellular respiration, rises high into the atmosphere, where it forms an ozone shield that filters out ultraviolet radiation and makes terrestrial life possible.

Our analogy about photosynthetic products becoming coal is apt because the bodies of many ancient plants did become the coal we burn today, usually to produce electricity. Coal formation happened several hundred million years ago, and that is why coal is called a fossil fuel. Today's trees are also commonly used as fuel. Then, too, the fermentation of plant materials produces ethanol, which can be used directly to fuel automobiles or as a gasoline additive.

The products of photosynthesis are critical to humankind in a number of other ways. They serve as a source of building materials, fabrics, paper, and pharmaceuticals. And while we are thanking green plants for their services, let's not forget the simple beauty of a magnolia blossom or the majesty of the Earth's forests.

### FIGURE 7.1 Photosynthetic organisms.

Photosynthetic organisms include plants, such as trees, garden plants, and mosses, which typically live on land; photosynthetic protists, such as *Euglena*, diatoms, and kelp, which typically live in water; and cyanobacteria, a type of bacterium that lives in water, damp soil, and rocks.

