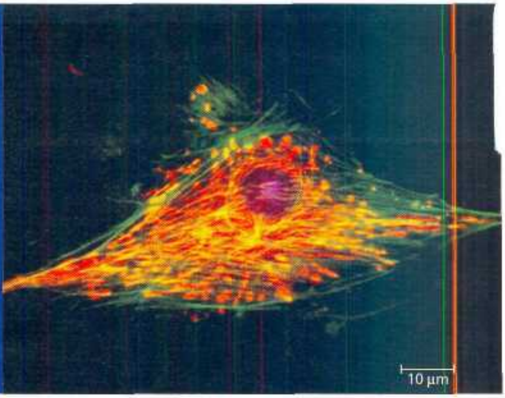
6

A Tour of the Cell



4 Figure 6.1 A cell and its skeleton viewed by fluorescence microscopy.

Key Concepts

8.1 To study cells, biologists use microscopes and the tools of biochemistry
6.2 Eukaryotic cells have internal membranes that compartmentalize their functions
6.3 The eukaryotic cell's genetic instructions are housed in the nucleus and carried out by the ribosomes
6.4 The endomembrane system regulates protein traffic and performs metabolic functions in the cell
6.5 Mitochondria and chloroplasts change energy from one form to another
6.6 The cytoskeleton is a network of fibers that organizes structures and activities in the cell
6.7 Extracellular components and connections between cells help coordinate cellular activities

Overview

The Importance of Cells

The cell is as fundamental to biology as the atom is to chemistry: All organisms are made of cells. In the hierarchy of biological organization, the cell is the simplest collection of matter that can live. Indeed, there are diverse forms of life existing as single-celled organisms. More complex organisms, including plants and animals, are multicellular; their bodies are cooperatives of many kinds of specialized cells that could not survive for long on their own. However, even when they are arranged into higher levels of organization, such as tissues and organs, cells can be singled out as the organisms basic units of structure and function. The contraction of muscle cells moves your eyes as you read this sentence; when you decide to turn the next page, nerve cells will transmit that decision from your brain to the muscle cells of your hand. Everything an organism does occurs fundamentally at the cellular level.

The cell is a microcosm that demonstrates most of the themes introduced in Chapter 1. Life at the ceilular level arises from structural order, reinforcing the themes of emergent properties and the correlation between structure and function. For example, the movement oi an animal cell depends on an intricate interplay of the structures that make up a cellular skeleton (green and red in the micrograph in **Figure 6.1).** Another recurring theme in biology is the interaction of organisms with their environment. Cells sense and respond to environmental fluctuations. And keep in mind the one biological theme that unifies all others: evolution. All cells are related by their descent from earlier cells. However, they have been modified in many different ways during the long evolutionary history of life on Earth.

Although cells can differ substantially from each other, they share certain common characteristics. In this chapter, we'll first learn about the tools and experimental approaches that have allowed us to understand subcellular details; then we'll tour the cell and become acquainted with its components.

Concept 1#«

To study cells, biologists use microscopes and the tools of biochemistry

Tt can be difficult to understand how a cell, usually too small to be seen by the unaided eye, can be so complex. How can cell biologists possibly investigate the inner workings of such tiny entities? Before we actually tour the cell, it will be helpful to learn how cells are studied.

Concept 6.2

Eukaryotic cells have internal membranes that compartmentalize their functions

The basic structural and functional unit of every organism is one of two types of cells—prokaryotic or eukaryotic. Only organisms of the domains Bacteria and Archaea consist of prokaryotic cells. Protists, fungi, animals, and plants all consist of eukaryotic cells. This chapter focuses on generalized animal and plant cells, after first comparing them with prokaryotic cells.

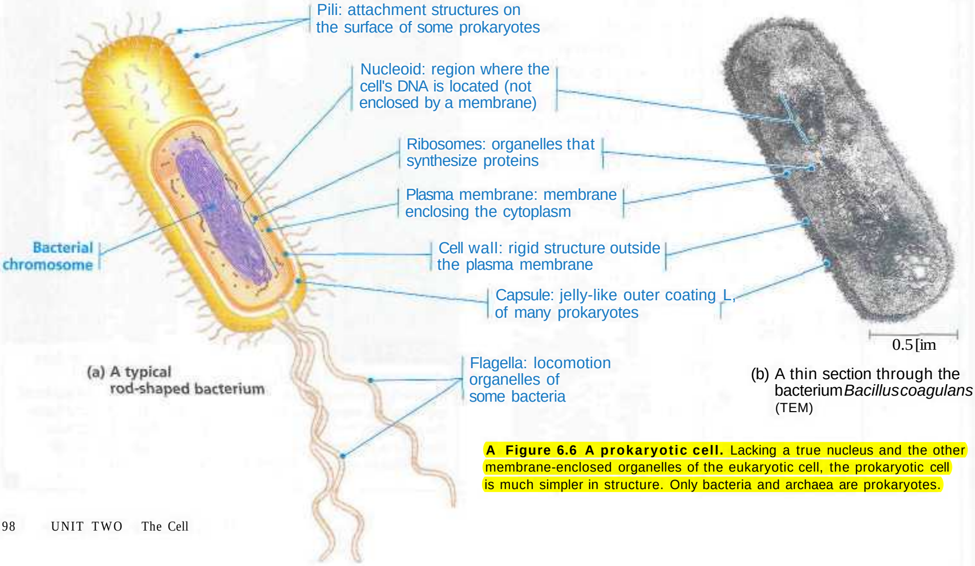
Comparing Prokaryotic and Eukaryotic Cells

All cells have several basic features in common: They are all bounded by a membrane, called a *plasma membrane*. Within the membrane is a semifluid substance, **cytosol,** in which organelles are found. All cells contain *chromosomes*, carrying genes in the form of DNA. And all cells have *ribosomes*, tiny organelles that make proteins according to instructions from the genes.

A major difference between prokaryotic and eukaryotic cells, indicated by their names, is that the chromosomes of a eukaryotic cell are located in a membrane-enclosed organelle called the *nucleus.* The word *prokaryotic* is from the Greek *pro,* meaning "before," and *karyon,* meaning "kernel," referring here to the nucleus. In a **prokaryotic cell (Figure 6.6),** the DNA is concentrated in a region called the **nucleoid,** but no membrane separates this region from the rest of the cell. In contrast, the **eukaryotic cell** (Greek *eu*, true, and *karyon)* has a **true** nucleus, bounded by a membranous nuclear envelope (see Figure 6.9, pp. 100-101). The entire region between the nucleus and the plasma membrane is called the **cytoplasm,** a term also used for the interior of a prokaryotic cell. Within the cytoplasm of a eukaryotic cell, suspended in cytosol, are a variety of membrane-bounded organelles of specialized form and function. These are absent in prokaryotic cells. Thus, the presence or absence of a true nucleus is just one example of the disparity in structural complexity between the two types of cells.

Eukaryotic cells are generally quite a bit bigger than prokaryotic cells (see Figure 6.2). Size is a general aspect of cell structure that relates to function. The logistics of carrying out cellular metabolism sets limits on cell size. At the lower limit, the smallest cells known are bacteria called mycoplasmas. which have diameters between 0.1 and 1.0 µm. These are perhaps the smallest packages with enough DNA to program metabolism and enough enzymes and other cellular equipment to carry out the activities necessary for a cell to sustain itself and reproduce. Most bacteria are 1-10 µm in diameter, a dimension about ten times greater than that of mycoplasmas. Eukaryotic cells are typically 10-100 µm in diameter.

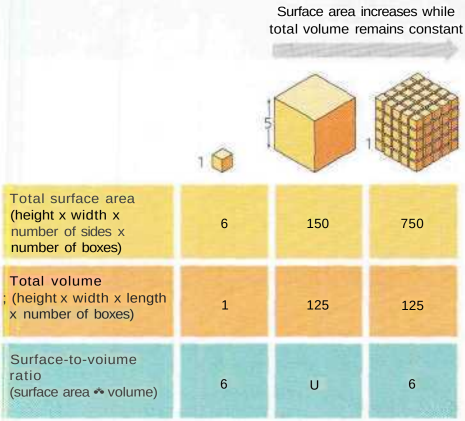
Metabolic requirements also impose theoretical upper limits on the size that is practical for a single cell. As an object of a particular shape increases in size, its volume grows proportionately more than its surface area. (Area is proportional to a linear dimension squared, whereas volume is proportional to the linear dimension cubed.) Thus, the smaller the object, the greater its ratio of surface area to volume **(Figure 6.7).**



(a) A typical rod-shaped bacterium

(b) A thin section through the bacterium *Bacillus coagulans* (TEM)

▲ **Figure 6.6 A prokaryotic cell.** Lacking a true nucleus and the other membrane-enclosed organelles of the eukaryotic cell, the prokaryotic cell is much simpler in structure. Only bacteria and archaea are prokaryotes.



Total surface area (height x width x number of sides x number of boxes)	6	150	750
Total volume ; (height x width x length x number of boxes)	1	125	125
Surface-to-voiume ratio (surface area ✤ volume)	6	U	6

A **Figure 6.7 Geometric relationships between surface area and volume.** In this diagram, cells are represented as boxes. Using arbitrary units of length, we can calculate the cell's surface area (in square units), volume (in cubic units), and ratio of surface area to volume. The smaller the cell, the higher the surface-to-volume ratio. A high surface-to-volume ratio facilitates the exchange of materials between a cell and its environment.

At the boundary of every cell, the **plasma membrane** functions as a selective barrier that allows sufficient passage of oxygen, nutrients, and wastes to service the entire volume of the cell **(Figure 6.8).** For each square micrometer of membrane, only so much of a particular substance can cross per second. Rates of chemical exchange with the extracellular environment might be inadequate to maintain a cell with a very large cytoplasm. The need for a surface area sufficiently large to accommodate the volume helps explain the microscopic size of most cells. Larger organisms do not generally have *larger* cells than smaller organisms—simply *more* cells. A sufficiently high ratio of surface area to volume is especially important in cells that exchange a lot of material with their surroundings, such as intestinal cells. Such cells may have many long, thin projections from their surface called microvilli, which increase surface area without an appreciable increase in volume.

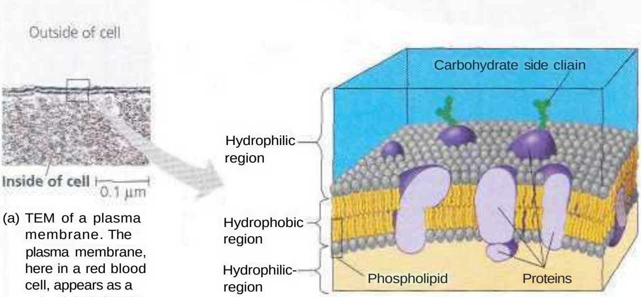
Prokaryotic cells will be described in detail in Chapters 18 and 27 (see Table 27.2 for a comparison of prokaryotes and eukaryotes), and the possible evolutionary relationships between prokaryotic and eukaryotic cells will be discussed in Chapter 28. Most of the discussion of cell structure that follows in this chapter applies to eukaryotic cells.

A Panoramic View of the Eukaryotic Cell

In addition to the plasma membrane at its outer surface, a eukaryotic cell has extensive and elaborately arranged internal membranes, which partition the cell into compartments—the membranous organelles mentioned earlier. These membranes also participate directly in the cell's metabolism, because many enzymes are built right into the membranes. Furthermore, the cell's compartments provide different local environments that facilitate specific metabolic functions, so incompatible processes can go on simultaneously inside the same cell.

Membranes of various kinds are fundamental to the organization of the cell. In general, biological membranes consist of a double layer of pbospholipids and other lipids. Embedded in this lipid bilayer or attached to its surfaces are diverse proteins (see Figure 6.8). However, each type of membrane has a unique composition of lipids and proteins suited to that membrane's speciftc functions. For example, enzymes embedded in the membranes of the organelles called mitochondria function in cellular respiration,

Before continuing with this chapter, examine the overviews of eukaryotic cells in **Figure 6.9** on the next two pages. These generalized cell diagrams introduce the various organelles and provide a map of the cell for the detailed tour upon which we will now embark. Figure 6.9 also contrasts animal and plant cells. As eukaryotic cells, they have much more in common than either has with any prokaiyotic cell. As you will see, however, there are important differences between animal and plant cells.



(a) TEM of a plasma membrane. The plasma membrane, here in a red blood cell, appears as a pair of dark bands separated by a light band.

(b) Structure of the plasma membrane

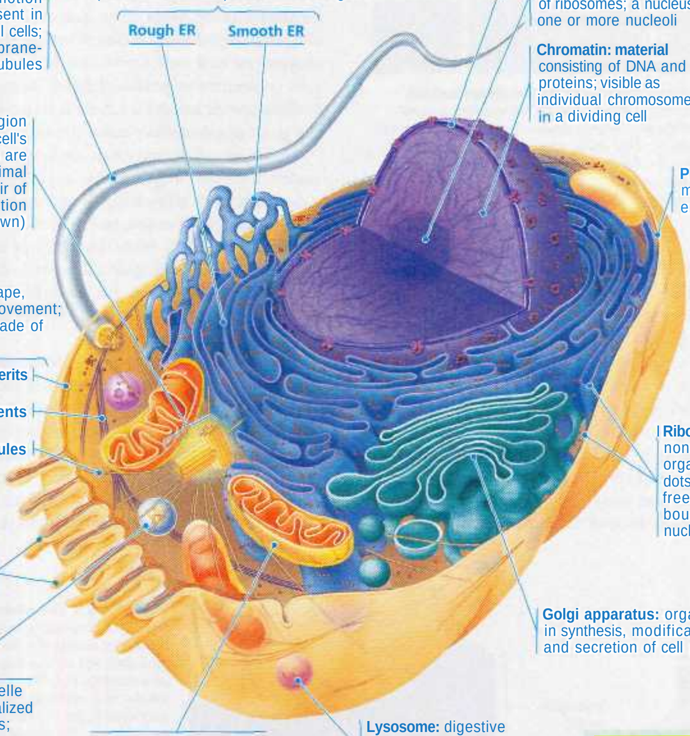
•*4* **Figure 6.8 The plasma membrane.** The plasma membrane and the membranes of organelles consist of a double layer (bilayer) of phospholipids with various proteins attached to or embedded in it. The phospholipid tails in the interior of a membrane are hydrophobic; the interior portions of membrane proteins are also hydrophobic. The phospholipid heads, exterior proteins, exterior parts of proteins, and carbohydrate side chains are hydrophilic and in contact with the aqueous solution on either side of the membrane. Carbohydrate side chains are found only on the outer surface of the plasma membrane. The specific functions of a membrane depend on the kinds of phospholipids and proteins present.

Figure 6.9

Exploring Animal and Plant Cells

ANIMAL CELL

This drawing of a generalized animal cell incorporates the most common structures of animal cells (no cell actually looks just like this). As shown by this cutaway view, the cell has a variety of organelles ("little organs"), many of which are bounded by membranes. The most prominent organelle in an animal cell is usually the nucleus. Most of the cells metabolic activities occur in the cytoplasm, the entire region between the nucleus and the plasma membrane. The cytoplasm contains many organelles suspended in a semifluid medium, the cytosol. Pervading much of the cytoplasm is a labyrinth of membranes called the endoplasmic reticulum (ER).



ENDOPLASMIC RETICULUM (ER): network of membranous sacs and tubes; active in membrane synthesis and other synthetic and metabolic processes; has rough (ribosome-studded) and smooth regions

Flagellum: locomotion organelle present in some animal cells; composed of membrane-enclosed microtubules

Centrosome: region where the cell's microtubules are initiated; in an animal cell, contains a pair of centrioles (function unknown)

CYTOSKELETON: reinforces cell's shape, functions in cell movement; components are made of protein

Microfilamerits

Intermediate filaments

Microtubules

Microvilli: projections that increase the cell's surface area

Peroxisome: organelle with various specialized metabolic functions; produces hydrogen peroxide

Mitochondrion: organelle where cellular respiration occurs and most ATP is generated

Lysosome: digestive organelle where macromolecules are hydrolyzed

Nuclear envelope: double membrane enclosing the nucleus; perforated by pores, contiguous with ER

Nucleolus: nonmembranous organelle involved in production of ribosomes; a nucleus has one or more nucleoli

Chromatin: material consisting of DNA and proteins; visible as individual chromosomes in a dividing cell

> **NUCLEUS**

Plasma membrane: membrane enclosing the cell

Ribosomes: nonmembranous organelles (small brown dots) that make proteins; free in cytoplasm or bound to rough ER or nuclear envelope

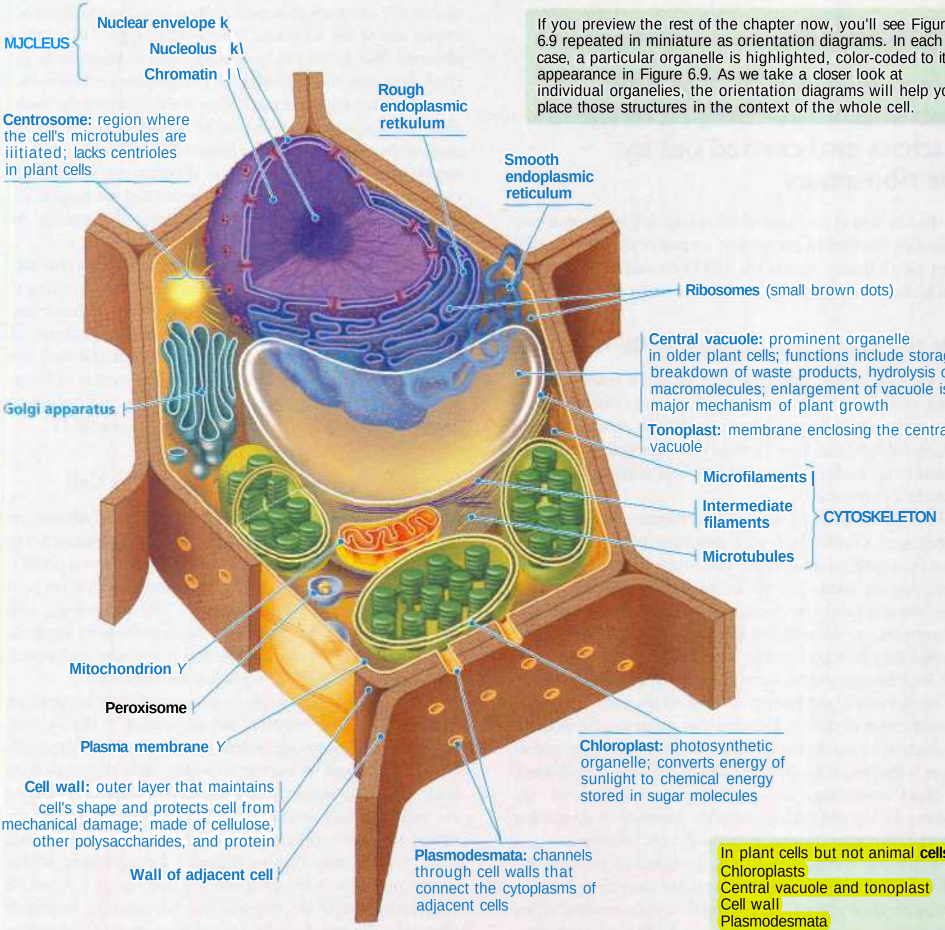
Golgi apparatus: organelle active in synthesis, modification, sorting, and secretion of cell products

In animal cells but not plant **cells:**
Lysosomes
Centrioles
Flagella (in some plant sperm)

PLANT CELL

This drawing of a generalized plant cell reveals the similarities and differences between an animal cell and a plant cell. In addition to most of the features seen in an animal cell, a plant cell has membrane-enclosed organelles called plastids. The most important type of plastid is the chloroplast. which carries out photosynthesis. Many plant cells have a large central vacuole; some may have one or more smaller vacuoles. Outside a plant cell's plasma membrane is a thick cell wall, perforated by channels called plasmodesmata.

If you preview the rest of the chapter now, you'll see Figure 6.9 repeated in miniature as orientation diagrams. In each case, a particular organelle is highlighted, color-coded to its appearance in Figure 6.9. As we take a closer look at individual organelles, the orientation diagrams will help you place those structures in the context of the whole cell.



Centrosome: region where the cell's microtubules are initiated; lacks centrioles in plant cells

Ribosomes (small brown dots)

Central vacuole: prominent organelle in older plant cells; functions include storage, breakdown of waste products, hydrolysis of macromolecules; enlargement of vacuole is a major mechanism of plant growth

Tonoplast: membrane enclosing the central vacuole

Cell wall: outer layer that maintains cell's shape and protects cell from mechanical damage; made of cellulose, other polysaccharides, and protein

Chloroplast: photosynthetic organelle; converts energy of sunlight to chemical energy stored in sugar molecules

Plasmodesmata: channels through cell walls that connect the cytoplasms of adjacent cells

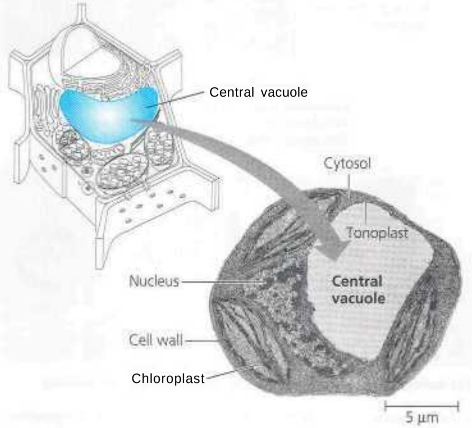
In plant cells but not animal **cells:**
Chloroplasts
Central vacuole and tonoplast
Cell wall
Plasmodesmata

becomes surrounded by a membrane, and a lysosome fuses with this vesicle **(Figure 6.14b).** The lysosomal enzymes dismantle the enclosed material, and the organic monomers are returned to the cytosol for reuse. With the help of lysosomes, the cell continually renews itself. A human liver cell, for example, recycles half of its macromolecules each week.

The cells of people with inherited lysosomal storage diseases lack a functioning hydrolytic enzyme normally present in lysosomes. The lysosomes become engorged with indigestible substrates, which begin to interfere with other cellular activities. In Tay-Sachs disease, for example, a lipid-digesting enzyme is missing or inactive, and the brain becomes impaired by an accumulation of lipids in the cells. Fortunately lysosomal storage diseases are rare in the general population.

Vacuoles: Diverse Maintenance Compartments

A plant or fungal cell may have one or several vacuoles. While vacuoles carry out hydrolysis and are thus similar to lysosomes, they carry out other functions as well. Food vacuoles, formed by phagocytosis, have already been mentioned (see Figure 6.14a). Many freshwater protists have contractile vacuoles that pump excess water out of the cell, thereby maintaining the appropriate concentration of salts and other molecules (see Figure 7.14). Mature plant cells generally contain a large central vacuole **(Figure 6.15)** enclosed by a membrane called the tonoplast. The central vacuole develops by the coalescence of smaller vacuoles, themselves derived from the endoplasmic reticulum and Golgi apparatus. The vacuole is in this way an integral part of a plant cells endomembrane system. Like all cellular membranes, the tonoplast is selective in transporting solutes; as a result, the solution inside the vacuole, called cell sap, differs in composition from the cytosol.



A **Figure 6.15 The plant cell vacuole.** The central vacuole is usually the largest compartment in a plant cell; the rest of the cytoplasm is generally confined to a narrow zone between the vacuolar membrane (tonoplast) and the plasma membrane (TEM).

The plant cell's central vacuole is a versatile compartment. It can hold reserves of important organic compounds, such as the proteins stockpiled in the vacuoles of storage cells in seeds. It is also the plant cells main repository of inorganic ions, such as potassium and chloride. Many plant cells use their vacuoles as disposal sites for metabolic by-products that would endanger the cell if they accumulated in the cytosol. Some vacuoles contain pigments that color the cells, such as the red and blue pigments of petals that help attract pollinating insects to flowers. Vacuoles may also help protect the plant against predators by containing compounds that are poisonous or unpalatable to animals. The vacuole has a major role in the growth of plant cells, which enlarge as their vacuoles absorb water, enabling the cell to become larger with a minimal investment in new cytoplasm. And because of the large vacuole, the cytosol often occupies only a thin layer between the plasma membrane and the tonoplast, so the ratio of membrane surface to cytosolic volume is great, even for a large plant cell.

The Endomembrane System: *A* Review

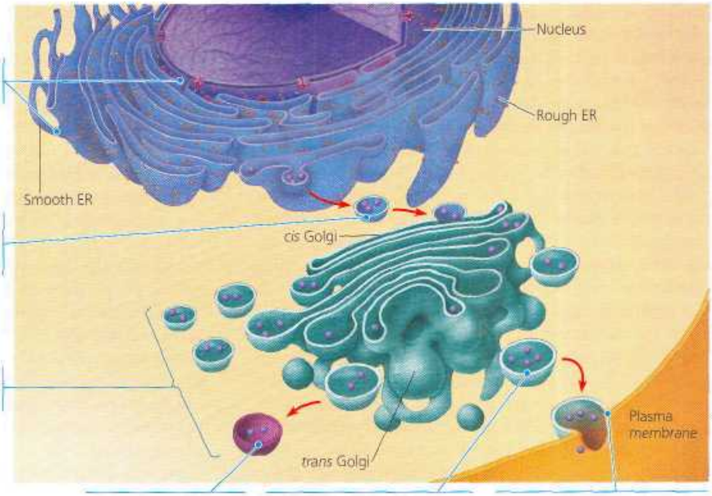
Figure 6.16 reviews the endomembrane system, showing the flow of membrane lipids and proteins through the various organelles. As the membrane moves from the ER to the Golgi and then elsewhere, its molecular composition and metabolic functions are modified, along with those of its contents. The endomembrane system is a complex and dynamic player in the cells compartmental organization.

We'll continue our tour of the cell with some membranous organelles that are *not* closely related to the endomembrane system, but play crucial roles in the energy transformations carried out by cells.

Concept Check 6.4

1. Describe the structural and functional distinctions between rough and smooth ER.
2. Imagine a protein that functions in the ER, but requires modification in the Golgi apparatus before it can achieve that function. Describe the protein's path through the cell, starting with the mRNA molecule that specifies the protein.
3. How do transport vesicles serve to integrate the endomembrcrne systi^{1}:"?

For suggested answers, see Appendix A.



① Nuclear envelope is connected to rough ER, which is also continuous with smooth ER

② Membranes and proteins produced by the ER flow in the form of transport vesicles to the Golgi

③ Golgi pinches off transport vesicles and other vesicles that give rise to lysosomes and vacuoles

④ Lysosome available for fusion with another vesicle for digestion

⑤ Transport vesicle carries proteins to plasma membrane for secretion

⑥ Plasma membrane expands by fusion of vesicles; proteins are secreted from cell

▲ **Figure 6.16 Review: relationships among organelles of the endomembrane system.** The red arrows show some of the migration pathways for membranes and the materials they enclose.

Concept 6.5

Mitochondria and chloroplasts change energy from one form to another

Organisms transform energy they acquire from their surroundings. In eukaryotic cells, mitochondria and chloroplasts are the organelles that convert energy to forms that cells can use for work. Mitochondria (singular, *mitochondrion)* are the sites of cellular respiration, the metabolic process that generates ATP by extracting energy from sugars, fats, and other fuels with the help of oxygen. **Chloroplasts,** found only in plants and algae, are the sites of photosynthesis. They convert solar energy to chemical energy by absorbing sunlight and using it to drive the synthesis of organic compounds such as sugars from carbon dioxide and water.

Although mitochondria and chloroplasts are enclosed by membranes, they are not part of the endomembrane system. In contrast to organelles of the endomembrane system, each of these organelles has at least two membranes separating the innermost space from the cytosol. Their membrane proteins are made not by the ER, but by free ribosomes in the cytosol and by **ribosomes** contained within these organelles themselves. Not only do these organelles have ribosomes, but they also contain a small amount of DNA. It is this DNA that programs the synthesis of the proteins made on the organelle's own ribosomes. (Proteins imported from the cytosol—constituting most of the organelle's proteins—are programmed by nuclear DNA.) Mitochondria and chloroplasts are semiautonomous organelles that grow and reproduce within the cell. In Chapters 9 and 10, we will focus on how mitochondria and chloroplasts function. We will consider the evolution of these organelles in Chapter 28. Here we are concerned mainly with the structure of these energy transformers.

In this section, we will also consider the **peroxisome,** an oxidative organelle that is not part of the endomembrane system. Like mitochondria and chloroplasts, the peroxisome imports its proteins primarily from the cytosol.

Mitochondria: Chemical Energy Conversion

Mitochondria are found in nearly all eukaryotic cells, including those of plants, animals, fungi, and protists. Some cells have a single large mitochondrion, but more often a cell has hundreds or even thousands of mitochondria; the number is correlated with the cell's level of metabolic activity. For example, motile or contractile cells have proportionally more mitochondria per volume than less active cells. Mitochondria are about 1—10 urn long. Time-lapse films of living cells reveal mitochondria moving around, changing their shapes, and dividing in two, unlike the static cylinders seen in electron micrographs of dead cells.

The mitochondrion is enclosed by two membranes, each a phospholipid bilayer with a unique collection of embedded proteins **(Figure 6.17).** The outer membrane is smooth, but the inner membrane is convoluted, with infoldings called cristae. The inner membrane divides the mitochondrion into two internal compartments. The first is the intermembrane space, the narrow region between the inner and outer membranes. The second compartment, the mitochondrial matrix, is enclosed by the inner membrane. The matrix contains many different enzymes as well as the mitochondrial DNA and ribosomes. Some of the metabolic steps of cellular respiration are catalyzed by enzymes in the matrix. Other proteins that function in respiration, including the enzyme that makes ATT^ are built into the inner membrane. As highly folded surfaces, the cristae give the inner mitochondrial membrane a large surface area for these proteins, thus enhancing the productivity of cellular respiration. This is another example of structure fitting function.

Chloroplasts: Capture of Light Energy

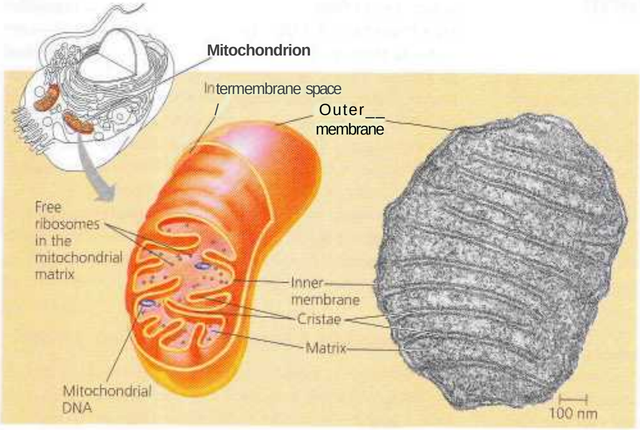
The chloroplast is a specialized member of a family of closely related plant organelles called plastids. *Amyloplasts* are colorless plastids that store starch (amylose), particularly in roots and tubers. *Oiromoplasts* have pigments that give fruits and flowers their orange and yellow hues. *Chloroplasts* contain the green pigment chlorophyll, along with enzymes and other molecules that function in the photosynthetic production of sugar. These lens-shaped organelles, measuring about 2 urn by 5 jim, are found in leaves and other green organs of plants and in algae **(Figure 6.18).**

The contents of a chloroplast are partitioned from the cytosol by an envelope consisting of two membranes separated by a very narrow intermembrane space. Inside the chloroplast is another membranous system in the form of flattened, interconnected sacs called thylakoids. In some regions, thylakoids are stacked like poker chips; each stack is called a granum (plural, *grand).* The fluid outside the thylakoids is the stroma, which contains the chloroplast DNA and ribosomes as well as many enzymes. The membranes of the chloroplast divide the chloroplast space into three compartments: the intermembrane space, the stroma, and the thylakoid space. In Chapter 10, you will learn how this compartmental organization enables the chloroplast to convert light energy to chemical energy during photosynthesis.

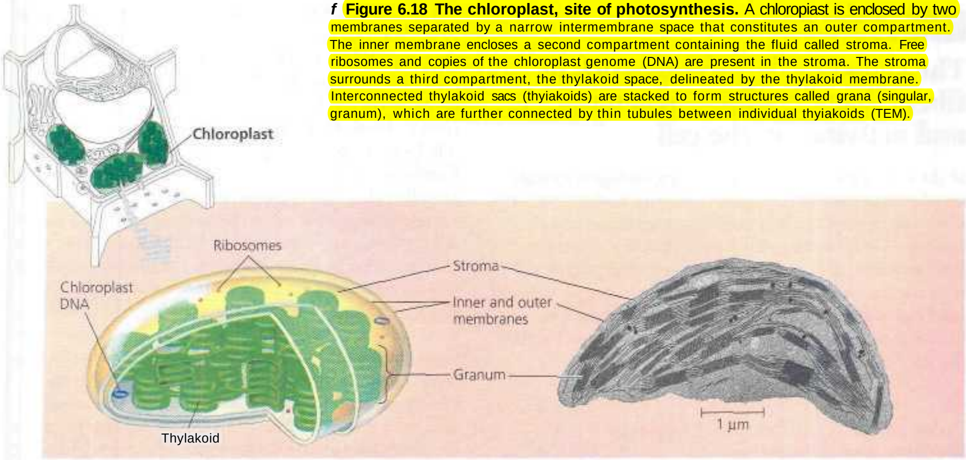
As with mitochondria, the static and rigid appearance of chloroplasts in micrographs or schematic diagrams is not true to their dynamic behavior in the living cell. Their shapes are changeable, and they grow and occasionally pinch in two, reproducing themselves. They are mobile and move around the cell with mitochondria and other organelles along tracks of the cytoskeleton, a structural network we will consider later in this chapter.

Peroxisomes: Oxidation

The peroxisome is a specialized metabolic compartment bounded by a single membrane **(Figure 6.19).** Peroxisomes



^ **Figure 6.17 The mitochondrion, site of cellular respiration.** The inner and outer membranes of the mitochondrion are evident in the drawing and micrograph (TEM). The cristae are infoldings of the inner membrane. The cutaway drawing shows the two compartments bounded by the membranes: the intermembrane space and the mitochondrial matrix. Free ribosomes are seen in the matrix, along with one to several copies of the mitochondrial genome (DNA). The DNA molecules are usually circular and are attached to the inner mitochondrial membrane.

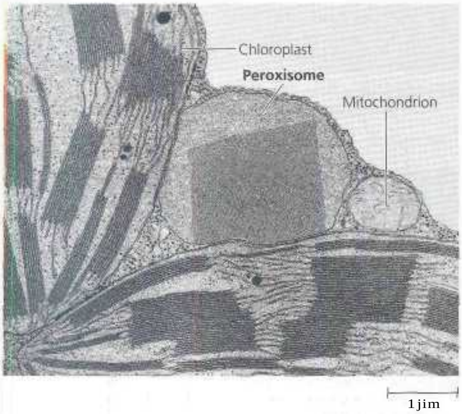


f **Figure 6.18 The chloroplast, site of photosynthesis.** A chloropiast is enclosed by two membranes separated by a narrow intermembrane space that constitutes an outer compartment. The inner membrane encloses a second compartment containing the fluid called stroma. Free ribosomes and copies of the chloroplast genome (DNA) are present in the stroma. The stroma surrounds a third compartment, the thylakoid space, delineated by the thylakoid membrane. Interconnected thylakoid sacs (thyiakoids) are stacked to form structures called grana (singular, granum), which are further connected by thin tubules between individual thyiakoids (TEM).

contain enzymes that transfer hydrogen from various substrates to oxygen, producing hydrogen peroxide (H_2O_2) as a by-product, from which the organelle derives its name. These reactions may have many different functions. Some peroxisomes use oxygen to break fatty acids down into smaller molecules that can then be transported to mitochondria, where they are used as fuel for cellular respiration. Peroxisomes in the liver detoxify alcohol and other harmful compounds by transferring hydrogen from the poisons to oxygen. The H_2O_2 formed by peroxisome metabolism is itself toxic, but the organelle contains an enzyme that converts the H_2O_2 to water. Enclosing in the same space both the enzymes that produce hydrogen peroxide and those that dispose of this toxic compound is another example of how the cell's compartmental structure is crucial to its functions.

Specialized peroxisomes called glyoxysom.es are found in the fat-storing tissues of plant seeds. These organelles contain enzymes that initiate the conversion of fatty acids to sugar, which the emerging seedling can use as a source of energy and carbon until it is able to produce its own sugar by photosynthesis.

Unlike lysosomes, peroxisomes do not bud from the endomembrane system. They grow larger by incorporating proteins made primarily in the cytosol, lipids made in the ER, and lipids synthesized within the peroxisome itself. Peroxisomes may increase in number by splitting in two when they reach a certain size.



At> **Figure 6.19 Peroxisomes.** Peroxisomes are roughly spherical and often have a granular or crystalline core that is thought to be a dense collection of enzyme molecules. This peroxisome is in a leaf cell. Notice its proximity to two chloroplasts and a mitochondrion. These organelles cooperate with peroxisomes in certain metabolic functions (TEM).

Concept Check 6.5

1. Describe at least two common characteristics of chloroplasts and mitochondria.
2. Explain the characteristics of mitochondria and chloroplasts that place them in a separate category from organelles in the endomembrane system.

For suggested answers, see *Appendix A.*

the actin reassembles into a network. Amoebas are not the only cells that move by crawling; so do many cells in the animal body, including some white blood cells.

In plant cells, both actin-myosin interactions and sol-gel transformations brought about by actin may be involved in cytoplasmic streaming, a circular flow of cytoplasm within cells **(Figure 6.27c).** This movement, which is especially common in large plant cells, speeds the distribution of materials within the cell.

Intermediate Filaments

Intermediate filaments are named for their diameter, which, at 8-12 nm, is larger than the diameter of microfilaments but smaller than that of microtubules (see Table 6.1, p. 113). Specialized for bearing tension (like microfilaments), intermediate filaments are a diverse class of cytoskeletal elements. Each type is constructed from a different molecular subunit belonging to a family of proteins whose members include the keratins. Microtubules and microfilaments, in contrast, are consistent in diameter and composition in all eukaryotic cells.

Intermediate filaments are more permanent fixtures of cells than are microfilaments and microtubules, which are often disassembled and reassembled in various parts of a cell. Even after cells die, intermediate filament networks often persist; for example, the outer layer of our skin consists of dead skin cells full of keratin proteins. Chemical treatments that remove microfilaments and microtubules from the cytoplasm of living cells leave a web of intermediate filaments that retains its original shape. Such experiments suggest that intermediate filaments are especially important in reinforcing the shape of a cell and fixing the position of certain organelles. For example, the nucleus commonly sits within a cage made of intermediate filaments, fixed in location by branches of the filaments that extend into the cytoplasm. Other intermediate filaments make up the nuclear lamina that lines the interior of the nuclear envelope (see Figure 6.10). In cases where the shape of the entire cell is correlated with function, intermediate filaments support that shape. For instance, the long extensions (axons) of nerve cells that transmit impulses are strengthened by one class of intermediate filament. Thus, the various kinds of intermediate filaments may function as the framework of the entire cytoskeleton.

Concept Check 6.6

1. Describe how the properties of microtubules, microfilaments, and intermediate filaments allow them to determine cell shape.
2. How do cilia and flagella bend?

For suggested answers, see Appendix A.

Concept 6.7

Extracellular components and connections between cells help coordinate cellular activities

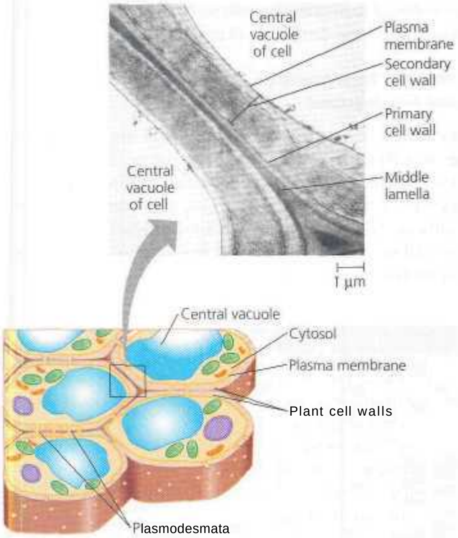
Having crisscrossed the interior of the cell to explore various organelles, we complete our tour of the cell by returning to the surface of this microscopic world, where there are additional structures with important functions. The plasma membrane is usually regarded as the boundary of the living cell, but most cells synthesize and secrete materials of one kind or another that are external to the plasma membrane. Although they are outside the cell, the study of these extracellular structures is central to cell biology because they are involved in so many cellular functions.

Cell Walls of Plants

The cell wall is an extracellular structure of plant cells that distinguishes them from animal cells. The wall protects the plant cell, maintains its shape, and prevents excessive uptake of water. On the level of the whole plant, the strong walls of specialized cells hold the plant up against the force of gravity. Prokaryotes, fungi, and some protists also have cell walls, but we will postpone discussion of them until Unit Five.

Plant cell walls are much thicker than the plasma membrane, ranging from 0.1 μm to several micrometers. The exact chemical composition of the wall varies from species to species and even from one cell type to another in the same plant, but the basic design of the wall is consistent. Microfibrils made of the polysaccharide cellulose (see Figure 5.8) are embedded in a matrix of other polysaccharides and protein. This combination of materials, strong fibers in a "ground substance" (matrix), is the same basic architectural design found in steel-reinforced concrete and in fiberglass.

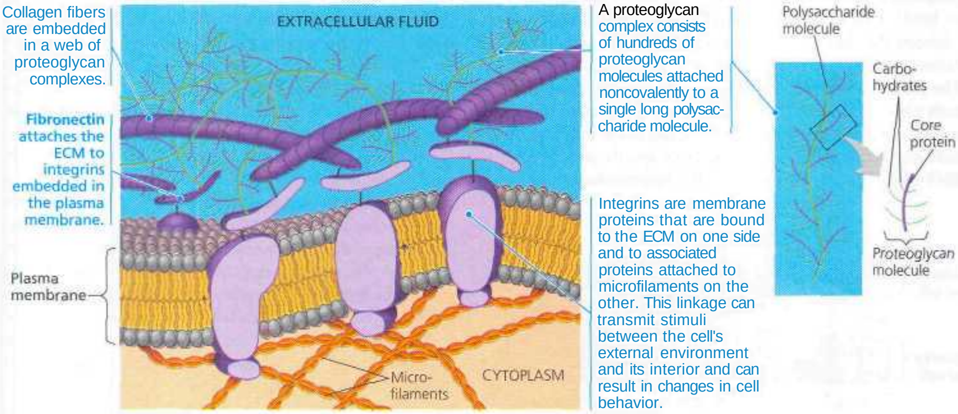
A young plant cell first secretes a relatively thin and flexible wall called the primary cell wall **(Figure 6.28).** Between primary walls of adjacent cells is the middle lamella, a thin layer rich in sticky polysaccharides called pectins. The middle lamella glues adjacent cells together (pectin is used as a thickening agent in jams and jellies). When the cell matures and stops growing, it strengthens its wall. Some plant cells do this simply by secreting hardening substances into the primary wall. Other cells add a secondary cell wall between the plasma membrane and the primary wall. The secondary wall, often deposited in several laminated layers, has a strong and durable matrix that affords the cell protection and support. Wood, for example, consists mainly of secondary walls. Plant cell walls are commonly perforated by channels between adjacent cells called plasmodesmata (see Figure 6.28), which will be discussed shortly.



iii **Figure 6.28 Plant cell walls.** The orientation drawing shows several cells, each with a large vacuole, a nucleus, and several chloroplasts and mitochondria. The transmission electron micrograph (TEM) shows the cell walls where two cells come together. The multilayered partition between plant cells consists of adjoining walls individually secreted by the cells.

The Extracellular Matrix (ECM) of Animal Cells

Although animal cells lack walls akin to those of plant cells, they do have an elaborate **extracellular matrix (ECM)** **(Figure 6.29).** The main ingredients of the ECM are glycoproteins secreted by the cells. (Recall that glycoproteins are proteins with covalently bonded carbohydrate, usually short chains of sugars.) The most abundant glycoprotein in the ECM of most animal cells is **collagen,** which forms strong fibers outside the cells. In fact, collagen accounts for about half of the total protein in the human body. The collagen fibers are embedded in a network woven from proteoglycans, which are glycoproteins of another class. A proteoglycan molecule consists of a small core protein with many carbohydrate chains covalently attached, so that it may be up to 95% carbohydrate. Large proteoglycan complexes can form when hundreds of proteoglycans become noncovalently attached to a single long polysaccharide molecule, as shown in Figure 6.29. Some cells are attached to the ECM by still other ECM glycoproteins, including **fibronectin.** Fibronectin and other ECM proteins bind to cell surface receptor proteins called integrins that are built into the plasma membrane. Integrins span the membrane and bind on their cytoplasmic side to associated proteins attached to microfilaments of the cytoskeleton. The name integrin is based on the word *integrate:* Integrins are in a position to transmit changes between the ECM and the cytoskeleton and thus to integrate changes occurring outside and inside the cell.



Collagen fibers are embedded in a web of proteoglycan complexes.

Fibronectin attaches the ECM to integrins embedded in the plasma membrane.

A proteoglycan complex consists of hundreds of proteoglycan molecules attached noncovalently to a single long polysaccharide molecule.

Integrins are membrane proteins that are bound to the ECM on one side and to associated proteins attached to microfilaments on the other. This linkage can transmit stimuli between the cell's external environment and its interior and can result in changes in cell behavior.

A. **Figure 6.29 Extracellular matrix (ECM) of an animal cell.** The molecular composition and structure of the ECM varies from one cell type to another. In this example, three different types of glycoproteins are present: proteoglycans, collagen, and fibronectin.

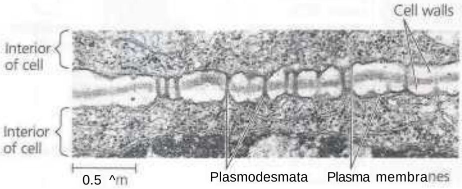
Current research on fibronectin, other ECM molecules, and integrins is revealing the influential role of the extracellular matrix in the lives of cells. By communicating with a cell through integrins, the ECM can regulate a cell's behavior. For example, some cells in a developing **embryo** migrate along specific pathways by matching ihe orientation of their microfilaments to the "grain" of fibers in the extracellular matrix. Researchers are also learning that the extracellular matrix around a cell can influence the activity of genes in the nucleus. Information about the ECM probably reaches the nucleus by a combination of mechanical and chemical signaling pathways. Mechanical signaling involves fibronectin, integrins, and microfilaments of the cytoskeleton. Changes in the cytoskeleton may in turn trigger chemical signaling pathways inside the cell, leading to changes in the set of proteins being made by the cell and therefore changes in the cell's function. In this way, the extracellular matrix of a particular tissue may help coordinate the behavior of all the cells within that tissue. Direct connections between cells also function in this coordination, as we discuss next.

Intercellular Junctions

The many cells of an animal or plant are organized into tissues, organs, and organ systems. Neighboring cells often adhere, interact, and communicate through special patches of direct physical contact.

Plants: *Plasmodesmata*

It might seem that the nonliving cell walls of plants would isolate cells from one another. But in fact, as shown in **Figure 6.30,** plant cell walls are perforated with channels called plasmodesmata (singular, *plasmodesma;* from the Greek *desmos,* to bind). Cytosol passes through the plasmodesmata and connects the chemical environments of adjacent cells. These connections unify most of the plant into one living continuum. The plasma membranes of adjacent cells line the channel of each plasmodesma and thus are continuous. Water and small solutes can pass freely from cell to cell, and recent experiments have shown that in certain circumstances, specific proteins and RNA molecules can also do this. The macromolecules to be transported to neighboring cells seem to reach the plasmodesmata by moving along fibers of the cytoskeleton.



A **Figure 6.30 Plasmodesmata between plant cells.** The cytoplasm of one plant cell is continuous with the cytoplasm of its neighbors via plasmodesmata, channels through the cell walls (T£M).

Animals.'*Tight]unctions,Desmosomes,* ***and Gap Junctions***

In animals, there are three main types of intercellular junctions: *tight junctions, desmosomes,* and *gap junctions* (which are most like the plasmodesmata of plants). All three types are especially common in epithelial tissue, which lines the internal surfaces of the body. **Figure 6.31** uses epithelial cells of the intestinal lining to illustrate these junctions: please study this figure before moving on.

Concept Check 5 6.7

1. In what ways are the cells of multicellular plants and animals structurally different from single-celled plants or animals?
2. What characteristics of the plant cell wall and animal cell extracellular matrix allow the cells to fulfill their need to exchange matter and information with their external environment?

For *suggested answers, see Appendix A.*

The Cell: A Living Unit Greater Than the Sum of Its Parts

From our panoramic **view** of the cell's overall compartmental organization to our close-up inspection of each organelle's architecture, this tour of the cell has provided many opportunities to correlate structure with function. (This would be a good time to review cell structure by returning to Figure 6.9, pp. 100 and 101.) But even as we dissect the cell, remember that none of its organelles works alone. As an example of cellular integration, consider the microscopic scene in **Figure 6.32.** The large cell is a macrophage (see Figure 6.14a). It helps defend the body against infections by ingesting bacteria (the smaller cells) into phagocytic vesicles. The macrophage crawls along a surface and reaches out to the bacteria with thin pseudopodia (called filopodia). Actin filaments interact with other elements of the cytoskeleton in these movements. After the macrophage engulfs the bacteria, they are destroyed by lysosomes. The elaborate endomembrane system produces the lysosomes. The digestive enzymes of the lysosomes and the proteins of the cytoskeleton are all made on ribosomes. And the synthesis of these proteins is programmed by genetic messages dispatched from the DNA in the nucleus. All these processes require energy, which mitochondria supply in the form of ATP. Cellular functions arise from cellular order: The cell is a living unit greater than the sum of its parts.