

*Biology of the Cell***How Do the Cells of a Growing Plant Know in Which Direction to Elongate?**

Sometimes questions that seem simple can be devilishly difficult to answer. Imagine, for example, that you are holding a green blade of grass in your hand. The grass blade has been actively growing, its cells dividing and then stretching and elongating as the blade lengthens. Did you ever wonder how the individual cells within the blade of grass know in what direction to grow?

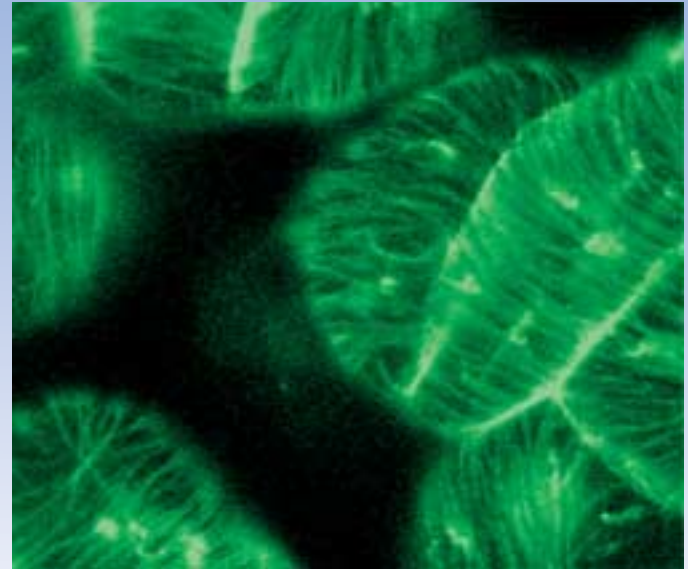
To answer this deceptively simple question, we will first need to provide answers to several others. Like Sherlock Holmes following a trail of clues, we must approach the answer we seek in stages.

**Question One.** First, we need to ask how a blade of grass is able to grow at all. Plant cells are very different from animal cells in one key respect: every plant cell is encased within a tough cell wall made of cellulose and other tough building materials. This wall provides structural strength and protection to the plant cell, just as armor plate does for a battle tank. But battle tanks can't stretch into longer shapes! How is a plant cell able to elongate?

It works like this. A growing cell first performs a little chemistry to make its wall slightly acidic. The acidity activates enzymes that attack the cell wall from the inside, rearranging cellulose cross-links until the wall loses its rigidity. The cell wall is now able to stretch. The cell then sucks in water, creating pressure. Like blowing up a long balloon, the now-stretchable cell elongates.

**Question Two.** In a growing plant organ, like the blade of grass, each growing cell balloons out lengthwise. Stating this more formally, a botanist would say the cell elongates parallel to the axis along which the blade of grass is extending. This observation leads to the second question we must answer: How does an individual plant cell control the direction in which it elongates?

It works like this. Before the stretchable cell balloons out, tiny microfibrils of cellulose are laid down along its inside surface. On a per weight basis, these tiny fibrils have the tensile strength of steel! Arrays of these cellulose microfibrils are



**Seeing cortical microtubules.** Cortical microtubules in epidermal cells of a fava bean are tagged with a fluorescent protein so that their ordered array can be seen.

organized in bands perpendicular to the axis of elongation, like steel belts. These tough bands reinforce the plant cell wall laterally, so that when the cell sucks in water, there is only one way for the cell to expand—lengthwise, along the axis.

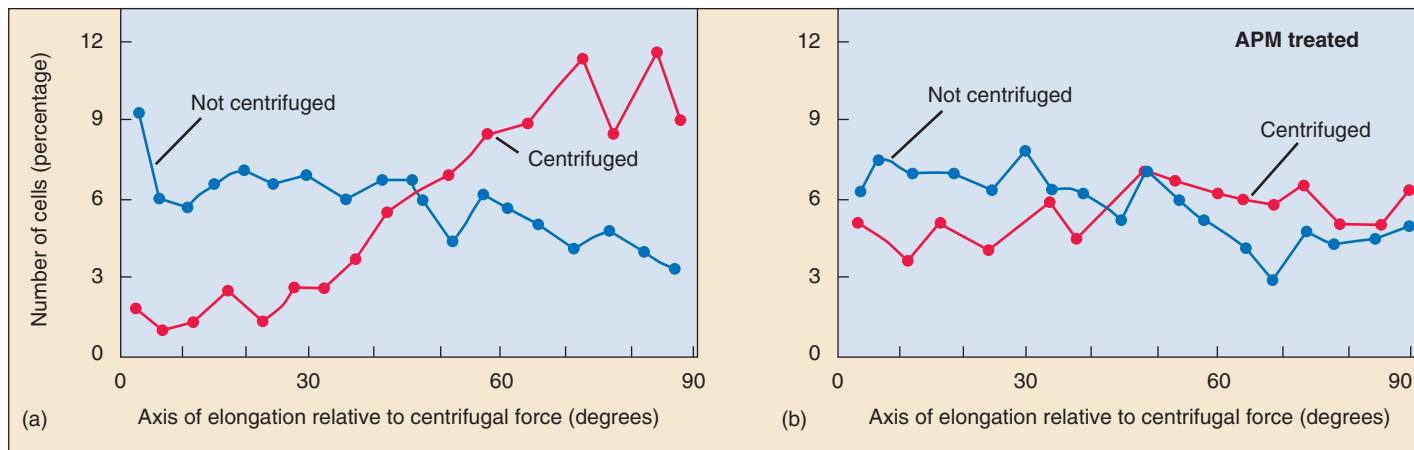
**Question Three.** Now we're getting somewhere. How are the newly made cellulose microfibrils laid down so that they are oriented correctly, perpendicular to the axis of elongation?

It works like this. The complicated enzymic machine that makes the cellulose microfibrils is guided by special guiderails that run like railroad tracks along the interior surface. The enzyme complex travels along these guiderails, laying down microfibrils as it goes. The guiderails are constructed of chainlike protein molecules called microtubules, assembled into overlapping arrays. Botanists call these arrays of microtubules associated with the interior of the cell surface "cortical microtubules."

**Question Four.** But we have only traded one puzzle for another. How are the cortical microtubules positioned correctly, perpendicular to the axis of elongation?

It works like this. In newly made cells, the microtubule assemblies are already present, but are not organized. They simply lie about in random disarray. As the cell prepares to elongate by lessening the rigidity of its cell wall, the microtubule assemblies become organized into the orderly transverse arrays we call cortical microtubules.

**Question Five.** Finally, we arrive at the question we had initially set out to answer. How are microtubule assemblies aligned properly? What sort of signal directs them to orient perpendicular to the axis of elongation? THAT is the question we need to answer.



**Effects of centrifugation on cell elongation.** (a) Protoplasts (plant cells without cell walls) that were centrifuged showed preferential elongation in a direction approximately perpendicular to the direction of the force. (b) Protoplasts exposed to APM, a microtubule disrupting chemical, exhibited random cell elongation with or without centrifugation.

## The Experiment

This question has been addressed experimentally in a simple and direct way in the laboratory of Richard Cyr at Pennsylvania State University. Rigid plant cells conduct mechanical force well from one cell to another, and Carol Wymer (then a graduate student in the Cyr lab) suspected some sort of mechanical force is the signal guiding cortical microtubule alignment.

Wymer set out to test this hypothesis using centrifugation. If cortical microtubules are obtaining their positional information from an applied force, then their alignment should be affected by centrifugal force, and should be impossible if the integrity of the cell wall (which is supposedly transmitting the mechanical force) is perturbed with chemicals that prevent cell wall formation.

Wymer, along with others in the Cyr lab, started out with cells that were not elongated. She isolated protoplasts (cells without walls) from the tobacco plant, *Nicotiana tabacum*, by exposing the plant cells to enzymes that break down the cell wall, creating a spherical plant cell. If allowed to grow in culture, these protoplasts will eventually re-form their cell walls.

In order to examine the effects of directional force on the elongation patterns of plant cells, Wymer and co-workers exposed the tobacco protoplasts to a directional force generated by a centrifuge. Prior experiments had determined that centrifugation at the low speeds used in these experiments does not disrupt the integrity or shape of the protoplasts. The protoplasts were immobilized for centrifugation by embedding them in an agar medium supported in a mold. The embedded protoplasts were spun in a centrifuge at 450 rpm for 15 minutes. Following centrifugation, the embedded cells were cultured for 72 hours, allowing for cell elongation to occur.

Following centrifugation, fluorescently tagged microtubule antibody was applied to the protoplasts, which were then examined with immunofluorescence microscopy for microtubule orientation.

To confirm the involvement of microtubules as sensors of directional force in cell elongation, some protoplasts were incubated prior to centrifugation with a chemical herbicide, APM, which disrupts microtubules.

## The Results

The biophysical force of centrifugation had significant effects on the pattern of elongation in the protoplasts following the 72-hour culturing period. The microtubules were randomly arranged in protoplasts that were not centrifuged but were more ordered in protoplasts that had been centrifuged. The microtubules in these cells were oriented parallel to the direction of the force, in a direction approximately perpendicular to the axis of elongation (graph *a* above). These results support the hypothesis that plant cell growth responds to an external biophysical force.

It is true that plant cells are not usually exposed to the type of mechanical force generated by centrifugation but this manipulation demonstrates how a physical force can affect cell growth, assumably by influencing the orientation of cortical microtubules. These could be small, transient biophysical forces acting at the subcellular level.

In preparations exposed to the microtubule disrupting chemical amiprophos-methyl (APM), directed elongation was blocked (graph *b* above). This suggests that reorientation of microtubules is indeed necessary to direct the elongation axis of the plant.

Taken together, these experiments support the hypothesis that the microtubule reorientation that directs cell elongation may be oriented by a mechanical force. Just what the natural force might be is an open question, providing an opportunity for lots of interesting future experiments that are being pursued in the Cyr lab.



To explore this experiment further, go to the Virtual Lab at [www.mhhe.com/raven6/vlab2.mhtml](http://www.mhhe.com/raven6/vlab2.mhtml)

# 5

## Cell Structure

### Concept Outline

#### 5.1 All organisms are composed of cells.

**Cells.** A cell is a membrane-bounded unit that contains DNA and cytoplasm. All organisms are cells or aggregates of cells, descendants of the first cells.

**Cells Are Small.** The greater relative surface area of small cells enables more rapid communication between the cell interior and the environment.

#### 5.2 Eukaryotic cells are far more complex than bacterial cells.

**Bacteria Are Simple Cells.** Bacterial cells are small and lack membrane-bounded organelles.

**Eukaryotic Cells Have Complex Interiors.** Eukaryotic cells are compartmentalized by membranes.

#### 5.3 Take a tour of a eukaryotic cell.

**The Nucleus: Information Center for the Cell.** The nucleus of a eukaryotic cell isolates the cell's DNA.

**The Endoplasmic Reticulum: Compartmentalizing the Cell.** An extensive system of membranes subdivides the cell interior.

**The Golgi Apparatus: Delivery System of the Cell.** A system of membrane channels collects, modifies, packages, and distributes molecules within the cell.

**Vesicles: Enzyme Storehouses.** Sacs that contain enzymes digest or modify particles in the cell, while other vesicles transport substances in and out of cells.

**Ribosomes: Sites of Protein Synthesis.** An RNA-protein complex directs the production of proteins.

**Organelles That Contain DNA.** Some organelles with very different functions contain their own DNA.

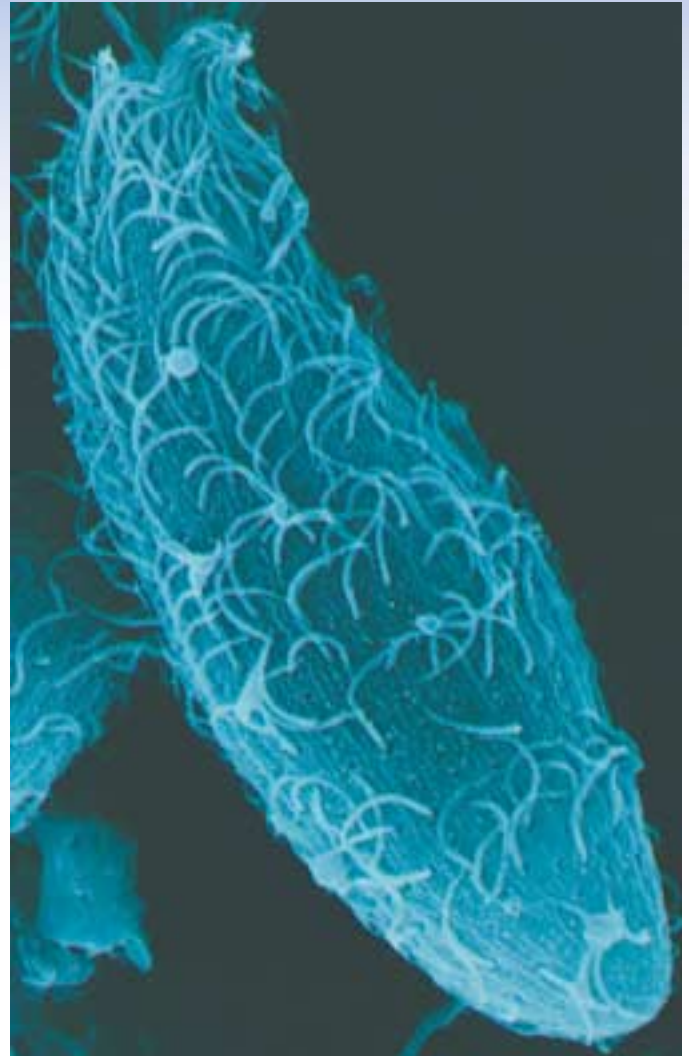
**The Cytoskeleton: Interior Framework of the Cell.** A network of protein fibers supports the shape of the cell and anchors organelles.

**Cell Movement.** Eukaryotic cell movement utilizes cytoskeletal elements.

**Special Things about Plant Cells.** Plant cells have a large central vacuole and strong, multilayered cell walls.

#### 5.4 Symbiosis played a key role in the origin of some eukaryotic organelles.

**Endosymbiosis.** Mitochondria and chloroplasts may have arisen from prokaryotes engulfed by other prokaryotes.



**FIGURE. 5.1**  
**The single-celled organism *Dileptus*.** The hairlike projections that cover its surface are cilia, which it undulates to propel itself through the water (1000 $\times$ ).

All organisms are composed of cells. The gossamer wing of a butterfly is a thin sheet of cells, and so is the glistening outer layer of your eyes. The hamburger or tomato you eat is composed of cells, and its contents soon become part of your cells. Some organisms consist of a single cell too small to see with the unaided eye (figure 5.1), while others, like us, are composed of many cells. Cells are so much a part of life as we know it that we cannot imagine an organism that is not cellular in nature. In this chapter we will take a close look at the internal structure of cells. In the following chapters, we will focus on cells in action—on how they communicate with their environment, grow, and reproduce.

## 5.1 All organisms are composed of cells.

### Cells

What is a typical cell like, and what would we find inside it? The general plan of cellular organization varies in the cells of different organisms, but despite these modifications, all cells resemble each other in certain fundamental ways. Before we begin our detailed examination of cell structure, let's first summarize three major features all cells have in common: a plasma membrane, a nucleoid or nucleus, and cytoplasm.

#### The Plasma Membrane Surrounds the Cell

The **plasma membrane** encloses a cell and separates its contents from its surroundings. The plasma membrane is a phospholipid bilayer about 5 to 10 nanometers (5 to 10 billionths of a meter) thick with proteins embedded in it. Viewed in cross-section with the electron microscope, such membranes appear as two dark lines separated by a lighter area. This distinctive appearance arises from the tail-to-tail packing of the phospholipid molecules that make up the membrane (see figure 3.18). The proteins of a membrane may have large hydrophobic domains, which associate with and become embedded in the phospholipid bilayer.

The proteins of the plasma membrane are in large part responsible for a cell's ability to interact with its environment. *Transport proteins* help molecules and ions move across the plasma membrane, either from the environment to the interior of the cell or vice versa. *Receptor proteins* induce changes within the cell when they come in contact with specific molecules in the environment, such as hormones. *Markers* identify the cell as a particular type. This is especially important in multicellular

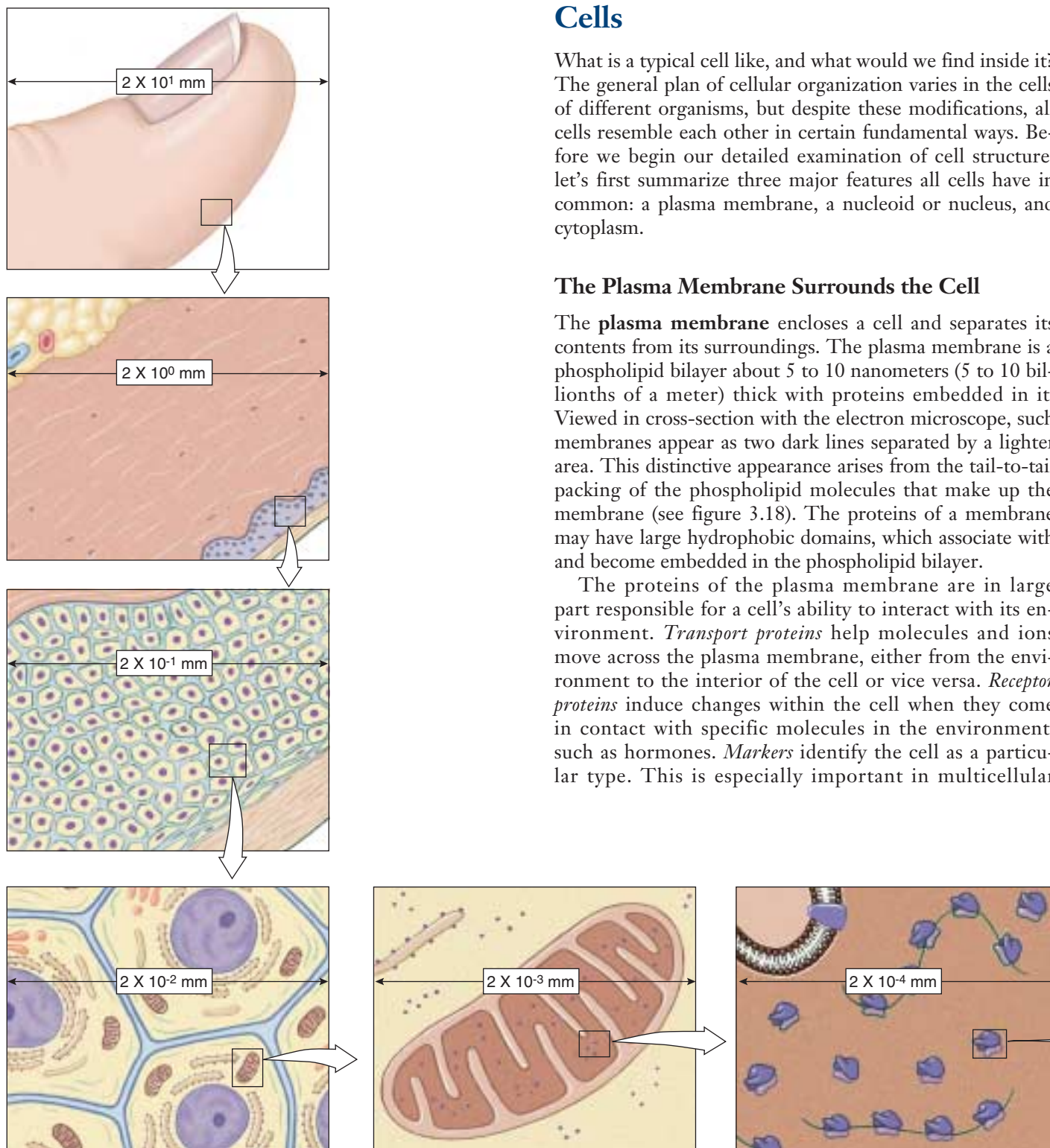


FIGURE 5.2

**The size of cells and their contents.** This diagram shows the size of human skin cells, organelles, and molecules. In general, the diameter of a human skin cell is 20 micrometers ( $\mu\text{m}$ ) or  $2 \times 10^{-2}$  mm, of a mitochondrion is 2  $\mu\text{m}$  or  $2 \times 10^{-3}$  mm, of a ribosome is 20 nanometers (nm) or  $2 \times 10^{-5}$  mm, of a protein molecule is 2 nm or  $2 \times 10^{-6}$  mm, and of an atom is 0.2 nm or  $2 \times 10^{-7}$  mm.

organisms, whose cells must be able to recognize each other as they form tissues.

We'll examine the structure and function of cell membranes more thoroughly in chapter 6.

### The Central Portion of the Cell Contains the Genetic Material

Every cell contains DNA, the hereditary molecule. In **prokaryotes** (bacteria), most of the genetic material lies in a single circular molecule of DNA. It typically resides near the center of the cell in an area called the **nucleoid**, but this area is not segregated from the rest of the cell's interior by membranes. By contrast, the DNA of **eukaryotes** is contained in the **nucleus**, which is surrounded by two membranes. In both types of organisms, the DNA contains the genes that code for the proteins synthesized by the cell.

### The Cytoplasm Comprises the Rest of the Cell's Interior

A semifluid matrix called the **cytoplasm** fills the interior of the cell, exclusive of the nucleus (nucleoid in prokaryotes) lying within it. The cytoplasm contains the chemical wealth of the cell: the sugars, amino acids, and proteins the cell uses to carry out its everyday activities. In eukaryotic cells, the cytoplasm also contains specialized membrane-bounded compartments called **organelles**.

### The Cell Theory

A general characteristic of cells is their microscopic size. While there are a few exceptions—the marine alga *Acetabularia* can be up to 5 centimeters long—a typical eukaryotic cell is 10 to 100 micrometers (10 to 100 millionths of a meter) in diameter (figure 5.2); most bacterial cells are only 1 to 10 micrometers in diameter.

Because cells are so small, no one observed them until microscopes were invented in the mid-seventeenth century. Robert Hooke first described cells in 1665, when he used a microscope he had built to examine a thin slice of cork, a nonliving tissue found in the bark of certain trees. Hooke observed a honeycomb of tiny, empty (because the cells were dead) compartments. He called the compartments in the cork *cellulae* (Latin, “small rooms”), and the term has come down to us as *cells*. The first living cells were observed a few years later by the Dutch naturalist Antonie van Leeuwenhoek, who called the tiny organisms that he observed “animalcules,” meaning little animals. For another century and a half, however, biologists failed to recognize the importance of cells. In 1838, botanist Matthias Schleiden made a careful study of plant tissues and developed the first statement of the cell theory. He stated that all plants “are aggregates of fully individualized, independent, separate beings, namely the cells themselves.” In 1839, Theodor Schwann reported that all animal tissues also consist of individual cells.

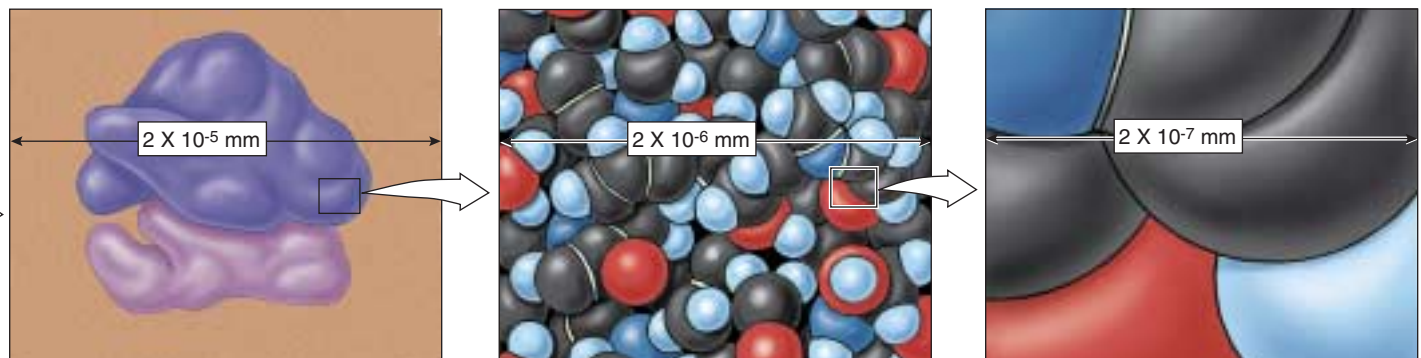
The **cell theory**, in its modern form, includes the following three principles:

1. All organisms are composed of one or more cells, and the life processes of metabolism and heredity occur within these cells.
2. Cells are the smallest living things, the basic units of organization of all organisms.
3. Cells arise only by division of a previously existing cell. Although life likely evolved spontaneously in the environment of the early earth, biologists have concluded that no additional cells are originating spontaneously at present. Rather, life on earth represents a continuous line of descent from those early cells.

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**A cell is a membrane-bounded unit that contains the DNA hereditary machinery and cytoplasm. All organisms are cells or aggregates of cells.**

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## Cells Are Small

How many cells are big enough to see with the unaided eye? Other than egg cells, not many. Most are less than 50 micrometers in diameter, far smaller than the period at the end of this sentence.

### The Resolution Problem

How do we study cells if they are too small to see? The key is to understand *why* we can't see them. The reason we can't see such small objects is the limited resolution of the human eye. **Resolution** is defined as the minimum distance two points can be apart and still be distinguished as two separated points. When two objects are closer together than about 100 micrometers, the light reflected from each strikes the same "detector" cell at the rear of the eye. Only when the objects are farther than 100 micrometers apart will the light from each strike different cells, allowing your eye to resolve them as two objects rather than one.

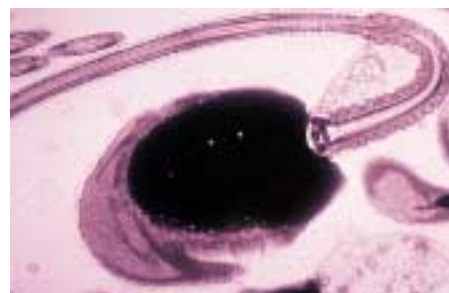
### Microscopes

One way to increase resolution is to increase magnification, so that small objects appear larger. Robert Hooke and Antonie van Leeuwenhoek were able to see small cells by magnifying their size, so that the cells appeared larger than the 100-micrometer limit imposed by the human eye. Hooke and van Leeuwenhoek accomplished this feat with **microscopes** that magnified images of cells by bending light through a glass lens. The size of the image that falls on the sheet of detector cells lining the back of your eye depends on how close the object is to your eye—the closer the object, the bigger the image. Your eye, however, is incapable of focusing comfortably on an object closer than about 25 centimeters, because the eye is limited by the size and thickness of its lens. Hooke and van Leeuwenhoek assisted the eye by interposing a glass lens between object and eye. The glass lens adds additional focusing power. Because the glass lens makes the object appear closer, the image on the back of the eye is bigger than it would be without the lens.

Modern light microscopes use two magnifying lenses (and a variety of correcting lenses) that act like back-to-back eyes. The first lens focuses the image of the object on the second lens, which magnifies it again and focuses it on the back of the eye. Microscopes that magnify in stages using several lenses are called **compound microscopes**. They can resolve structures that are separated by more than 200 nm. An image from a compound microscope is shown in figure 5.3*a*.



(a)



(b)



(c)

**FIGURE 5.3**

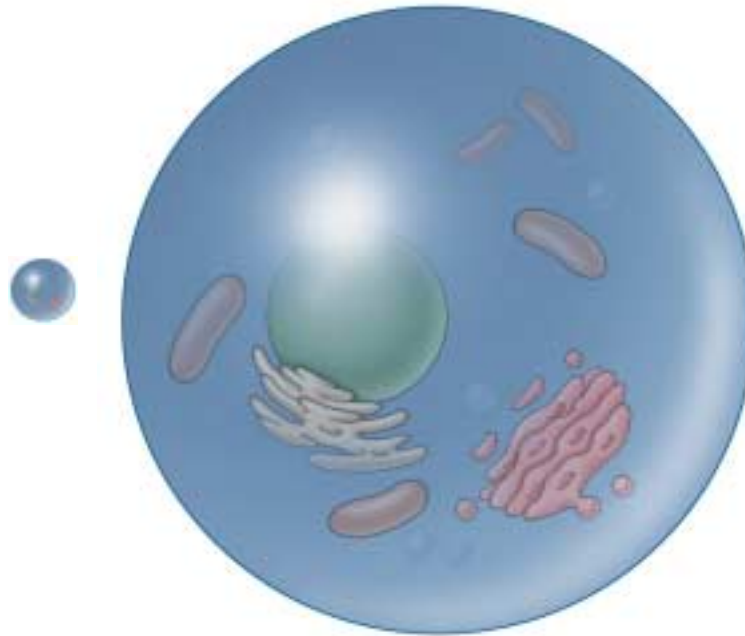
**Human sperm cells viewed with three different microscopes.** (a) Image of sperm taken with a light microscope. (b) Transmission electron micrograph of a sperm cell. (c) Scanning electron micrograph of sperm cells.

### Increasing Resolution

Light microscopes, even compound ones, are not powerful enough to resolve many structures within cells. For example, a membrane is only 5 nanometers thick. Why not just add another magnifying stage to the microscope and so increase its resolving power? Because when two objects are closer than a few hundred nanometers, the light beams reflecting from the two images start to overlap. The only way two light beams can get closer together and still be resolved is if their "wavelengths" are shorter.

One way to avoid overlap is by using a beam of electrons rather than a beam of light. Electrons have a much shorter wavelength, and a microscope employing electron beams has 1000 times the resolving power of a light microscope. **Transmission electron microscopes**, so called because the electrons used to visualize the specimens are transmitted through the material, are capable of resolving objects only 0.2 nanometer apart—just twice the diameter of a hydrogen atom! Figure 5.3*b* shows a transmission electron micrograph.

A second kind of electron microscope, the **scanning electron microscope**, beams the electrons onto the surface of the specimen from a fine probe that passes rapidly back and forth. The electrons reflected back from the surface of the specimen, together with other electrons that the specimen itself emits as a result of the bombardment, are amplified and transmitted to a television screen, where the image can be viewed and photographed. Scanning electron microscopy yields striking three-dimensional images and has improved our understanding of many biological and physical phenomena (figure 5.3*c*).



Cell radius ( $r$ )	1 cm	10 cm
Surface area ( $4\pi r^2$ )	12.57 cm <sup>2</sup>	1257 cm <sup>2</sup>
Volume ( $\frac{4}{3}\pi r^3$ )	4.189 cm <sup>3</sup>	4189 cm <sup>3</sup>

**FIGURE 5.4**

**Surface area-to-volume ratio.** As a cell gets larger, its volume increases at a faster rate than its surface area. If the cell radius increases by 10 times, the surface area increases by 100 times, but the volume increases by 1000 times. A cell's surface area must be large enough to meet the needs of its volume.

### Why Aren't Cells Larger?

Most cells are not large for practical reasons. The most important of these is communication. The different regions of a cell need to communicate with one another in order for the cell as a whole to function effectively. Proteins and organelles are being synthesized, and materials are continually entering and leaving the cell. All of these processes involve the diffusion of substances at some point, and the larger a cell is, the longer it takes for substances to diffuse from the plasma membrane to the center of the cell. For this reason, an organism made up of many relatively small cells has an advantage over one composed of fewer, larger cells.

The advantage of small cell size is readily visualized in terms of the **surface area-to-volume ratio**. As a cell's size increases, its volume increases much more rapidly than its surface area. For a spherical cell, the increase in surface area is equal to the square of the increase in diameter, while the increase in volume is equal to the cube of the increase in diameter. Thus, if two cells differ by a factor of 10 cm in diameter, the larger cell will have 10<sup>2</sup>, or 100 times, the surface area, but 10<sup>3</sup>, or 1000 times, the volume, of the smaller cell (figure 5.4). A cell's surface provides its only opportunity for interaction with

the environment, as all substances enter and exit a cell via the plasma membrane. This membrane plays a key role in controlling cell function, and because small cells have more surface area per unit of volume than large ones, the control is more effective when cells are relatively small.

Although most cells are small, some cells are nonetheless quite large and have apparently overcome the surface area-to-volume problem by one or more adaptive mechanisms. For example, some cells have more than one nucleus, allowing genetic information to be spread around a large cell. Also, some large cells actively move material around their cytoplasm so that diffusion is not a limiting factor. Lastly, some large cells, like your own neurons, are long and skinny so that any given point in the cytoplasm is close to the plasma membrane, and thus diffusion between the inside and outside of the cell can still be rapid.

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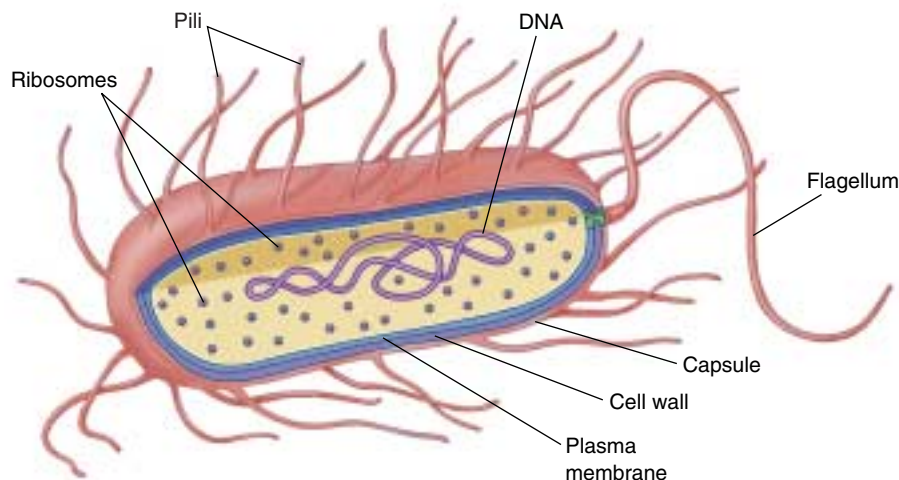
**Multicellular organisms usually consist of many small cells rather than a few large ones because small cells function more efficiently. They have a greater relative surface area, enabling more rapid communication between the center of the cell and the environment.**

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## 5.2 Eukaryotic cells are far more complex than bacterial cells.

### Bacteria Are Simple Cells

Prokaryotes, the bacteria, are the simplest organisms. Prokaryotic cells are small, consisting of cytoplasm surrounded by a plasma membrane and encased within a rigid cell wall, with no distinct interior compartments (figure 5.5). A prokaryotic cell is like a one-room cabin in which eating, sleeping, and watching TV all occur in the same room. Bacteria are very important in the economy of living organisms. They harvest light in photosynthesis, break down dead organisms and recycle their components, cause disease, and are involved in many important industrial processes. Bacteria are the subject of chapter 34.



**FIGURE 5.5** Structure of a bacterial cell. Generalized cell organization of a bacterium. Some bacteria have hairlike growths on the outside of the cell called pili.

### Strong Cell Walls

Most bacteria are encased by a strong **cell wall** composed of *peptidoglycan*, which consists of a carbohydrate matrix (polymers of sugars) that is cross-linked by short polypeptide units. No eukaryotes possess cell walls with this type of chemical composition. With a few exceptions like TB and leprosy-causing bacteria, all bacteria may be classified into two types based on differences in their cell walls detected by the Gram staining procedure. The name refers to the Danish microbiologist Hans Christian Gram, who developed the procedure to detect the presence of certain disease-causing bacteria. **Gram-positive** bacteria have a thick, single-layered cell wall that retains a violet dye from the Gram stain procedure, causing the stained cells to appear purple under a microscope. More complex cell walls have evolved in other groups of bacteria. In them, the wall is multilayered and does not retain the purple dye after Gram staining; such bacteria exhibit the background red dye and are characterized as **gram-negative**.

The susceptibility of bacteria to antibiotics often depends on the structure of their cell walls. Penicillin and vancomycin, for example, interfere with the ability of bacteria to cross-link the peptide units that hold the carbohydrate chains of the wall together. Like removing all the nails from a wooden house, this destroys the integrity of the matrix, which can no longer prevent water from rushing in, swelling the cell to bursting.

Cell walls protect the cell, maintain its shape, and prevent excessive uptake of water. Plants, fungi, and most protists also have cell walls of a different chemical structure, which we will discuss in later chapters.

Long chains of sugars called polysaccharides cover the cell walls of many bacteria. They enable a bacterium to adhere to teeth, skin, food—practically any surface that will support their growth. Many disease-causing bacteria secrete a jellylike protective capsule of polysaccharide around the cell.

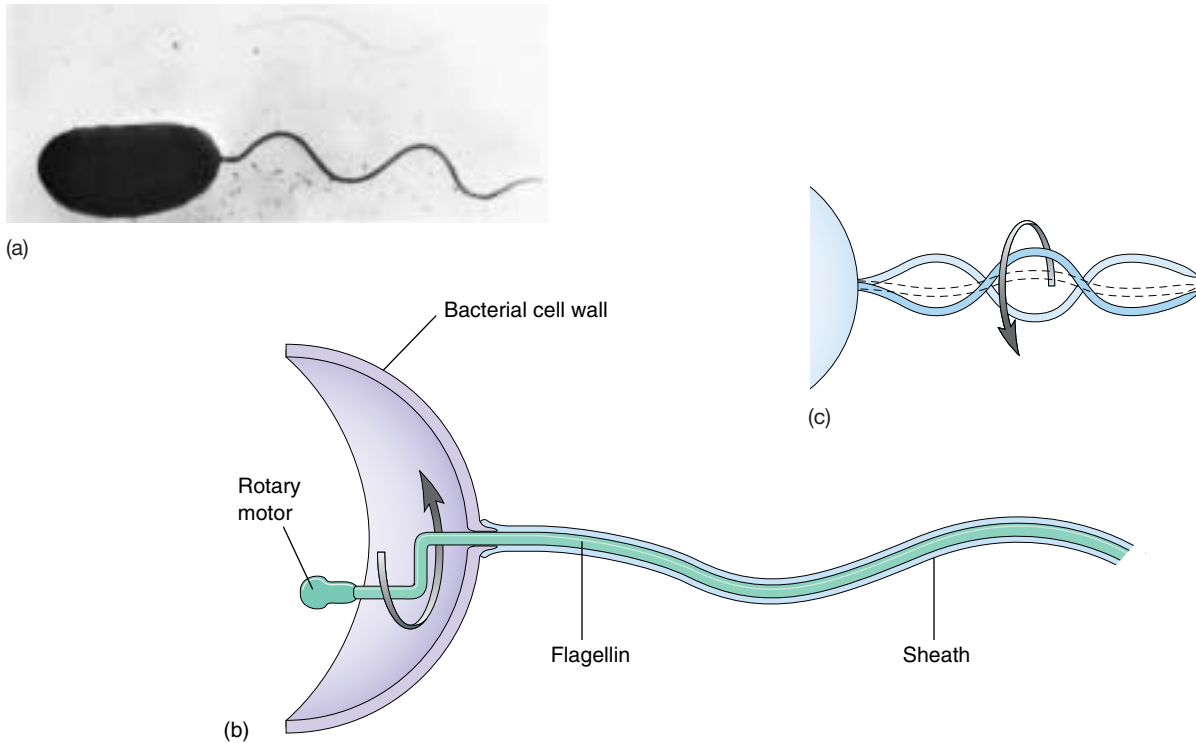
### Rotating Flagella

Some bacteria use a flagellum (plural, flagella) to move. **Flagella** are long, threadlike structures protruding from the surface of a cell that are used in locomotion and feeding. Bacterial flagella are protein fibers that extend out from a bacterial cell. There may be one or more per cell, or none, depending on the species. Bacteria can swim at speeds up to 20 cell diameters per second by rotating their flagella like screws (figure 5.6). A “motor” unique to bacteria that is embedded within their cell walls and membranes powers the rotation. Only a few eukaryotic cells have structures that truly rotate.

### Simple Interior Organization

If you were to look at an electron micrograph of a bacterial cell, you would be struck by the cell’s simple organization. There are few, if any, internal compartments, and while they contain simple structures like ribosomes, most have no membrane-bounded organelles, the kinds so characteristic of eukaryotic cells. Nor do bacteria have a true nucleus. The entire cytoplasm of a bacterial cell is one unit with no internal support structure. Consequently,





**FIGURE 5.6**

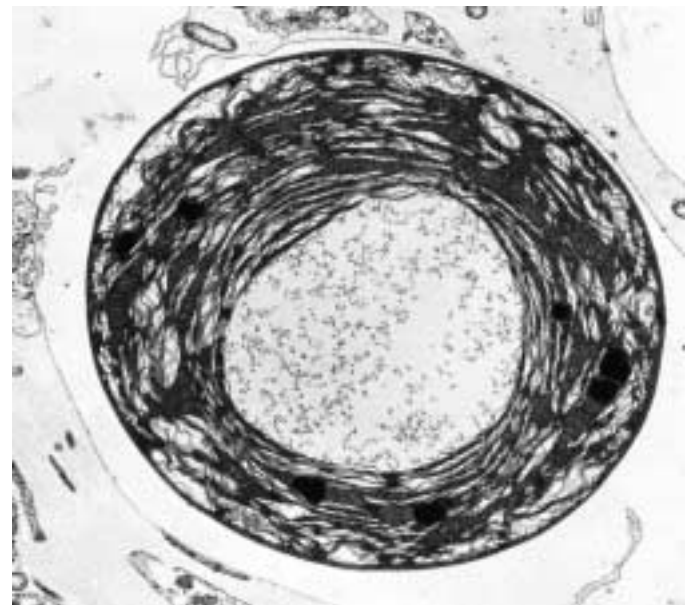
**Bacteria swim by rotating their flagella.** (a) The photograph is of *Vibrio cholerae*, the microbe that causes the serious disease cholera. The unsheathed core visible at the top of the photograph is composed of a single crystal of the protein flagellin. (b) In intact flagella, the core is surrounded by a flexible sheath. Imagine that you are standing inside the *Vibrio* cell, turning the flagellum like a crank. (c) You would create a spiral wave that travels down the flagellum, just as if you were turning a wire within a flexible tube. The bacterium creates this kind of rotary motion when it swims.

the strength of the cell comes primarily from its rigid wall (see figure 5.5).

The plasma membrane of a bacterial cell carries out some of the functions organelles perform in eukaryotic cells. When a bacterial cell divides, for example, the bacterial chromosome, a simple circle of DNA, replicates before the cell divides. The two DNA molecules that result from the replication attach to the plasma membrane at different points, ensuring that each daughter cell will contain one of the identical units of DNA. Moreover, some photosynthetic bacteria, such as cyanobacteria and *Prochloron* (figure 5.7), have an extensively folded plasma membrane, with the folds extending into the cell's interior. These membrane folds contain the bacterial pigments connected with photosynthesis.

Because a bacterial cell contains no membrane-bounded organelles, the DNA, enzymes, and other cytoplasmic constituents have access to all parts of the cell. Reactions are not compartmentalized as they are in eukaryotic cells, and the whole bacterium operates as a single unit.

**Bacteria are small cells that lack interior organization. They are encased by an exterior wall composed of carbohydrates cross-linked by short polypeptides, and some are propelled by rotating flagella.**

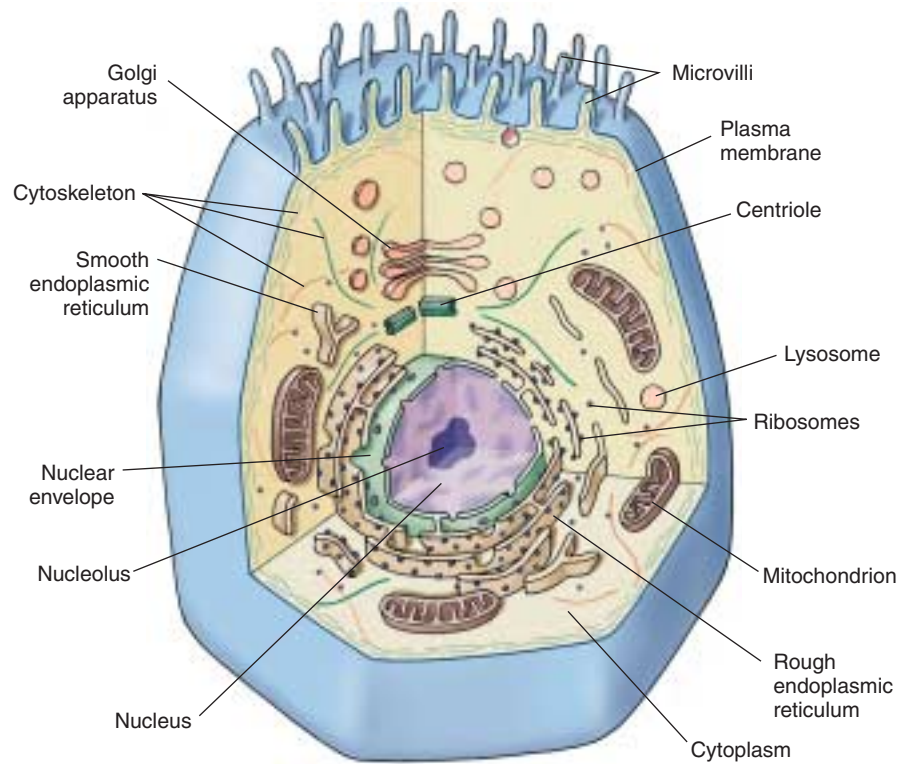


**FIGURE 5.7**

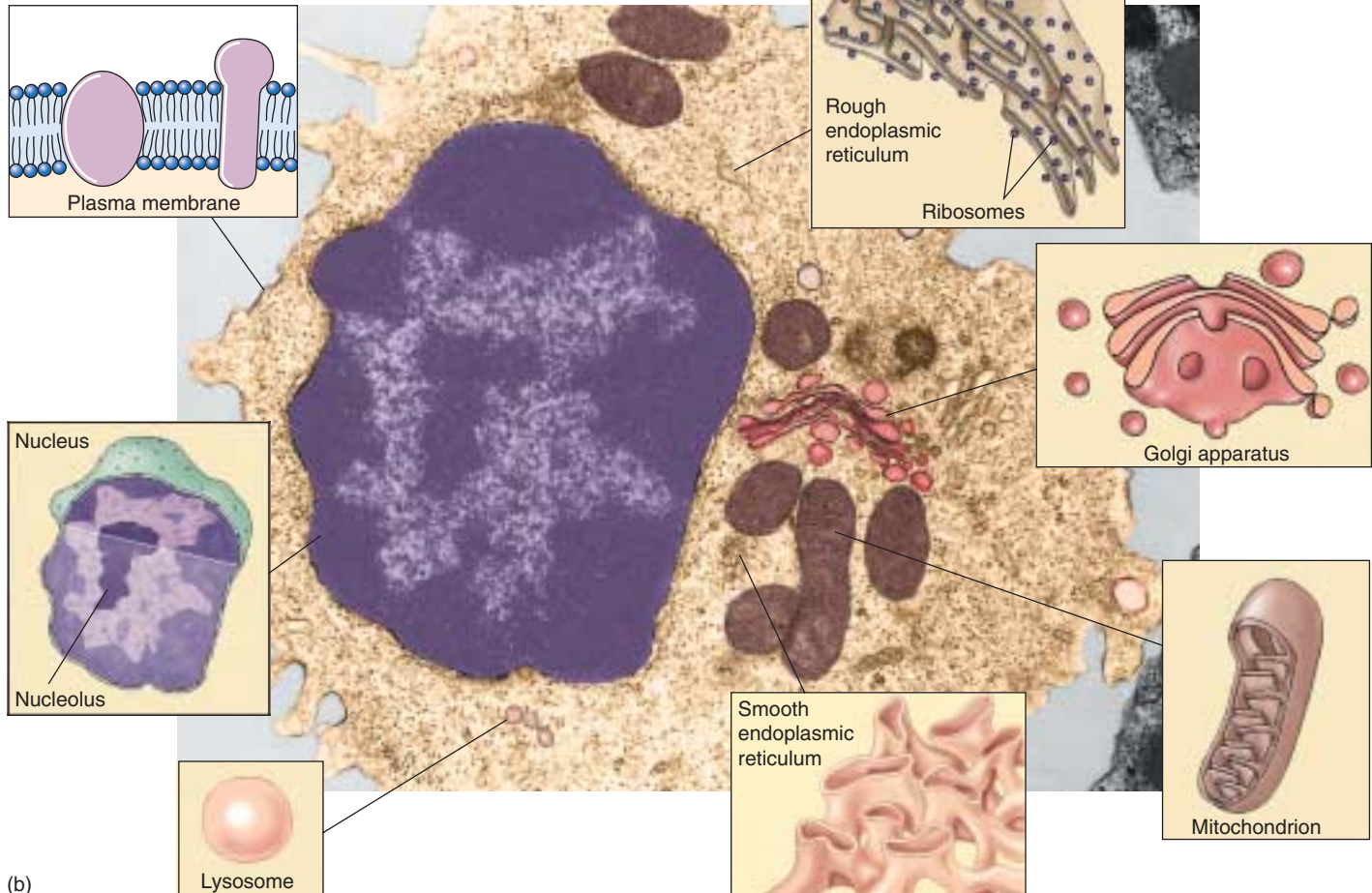
**Electron micrograph of a photosynthetic bacterial cell.** Extensive folded photosynthetic membranes are visible in this *Prochloron* cell (14,500 $\times$ ). The single, circular DNA molecule is located in the clear area in the central region of the cell.

## Eukaryotic Cells Have Complex Interiors

Eukaryotic cells (figures 5.8 and 5.9) are far more complex than prokaryotic cells. The hallmark of the eukaryotic cell is compartmentalization. The interiors of eukaryotic cells contain numerous **organelles**, membrane-bounded structures that close off compartments within which multiple biochemical processes can proceed simultaneously and independently. Plant cells often have a large membrane-bounded sac called a **central vacuole**, which stores proteins, pigments, and waste materials. Both plant and animal cells contain **vesicles**, smaller sacs that store and transport a variety of materials. Inside the nucleus, the DNA is

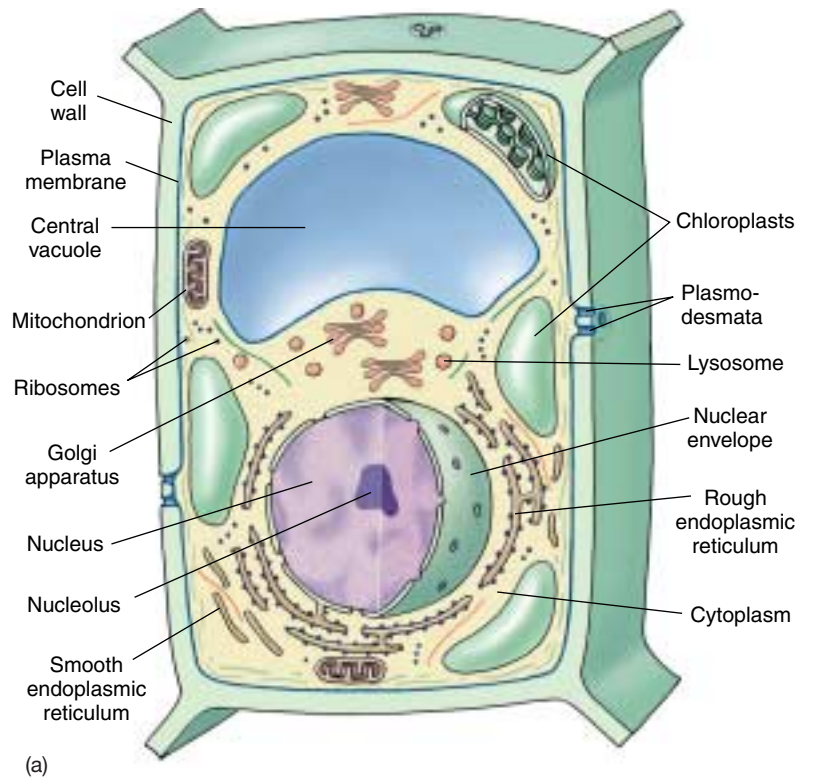


**FIGURE 5.8**  
**Structure of an animal cell.** (a) A generalized diagram of an animal cell. (b) Micrograph of a human white blood cell (40,500 $\times$ ) with drawings detailing organelles.

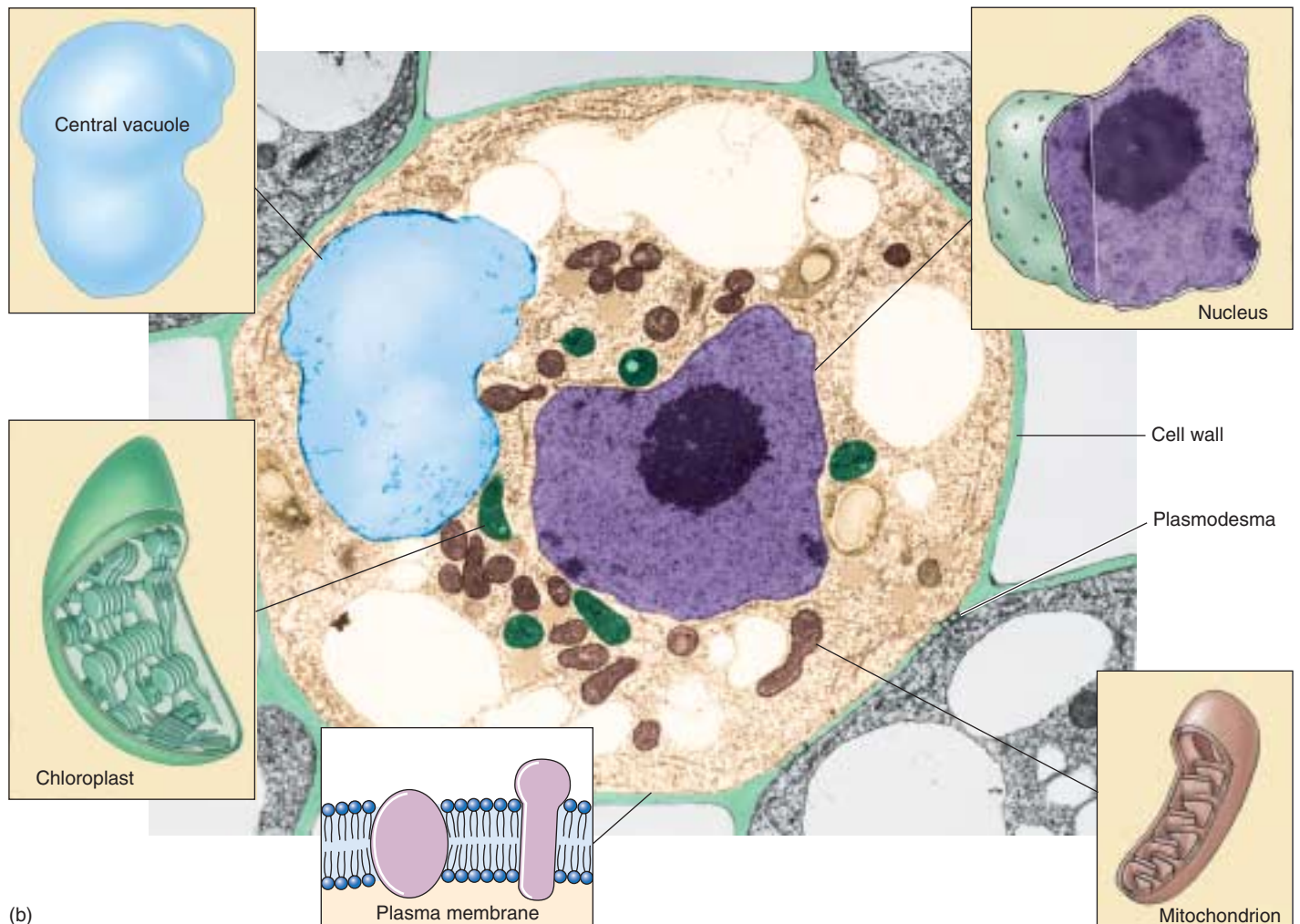


wound tightly around proteins and packaged into compact units called **chromosomes**. All eukaryotic cells are supported by an internal protein scaffold, the **cytoskeleton**. While the cells of animals and some protists lack cell walls, the cells of fungi, plants, and many protists have strong **cell walls** composed of cellulose or chitin fibers embedded in a matrix of other polysaccharides and proteins. This composition is very different from the peptidoglycan that makes up bacterial cell walls. Let's now examine the structure and function of the internal components of eukaryotic cells in more detail.

**Eukaryotic cells contain membrane-bounded organelles that carry out specialized functions.**



**FIGURE 5.9**  
**Structure of a plant cell.** A generalized illustration (a) and micrograph (b) of a plant cell. Most mature plant cells contain large central vacuoles which occupy a major portion of the internal volume of the cell (14,000 $\times$ ).

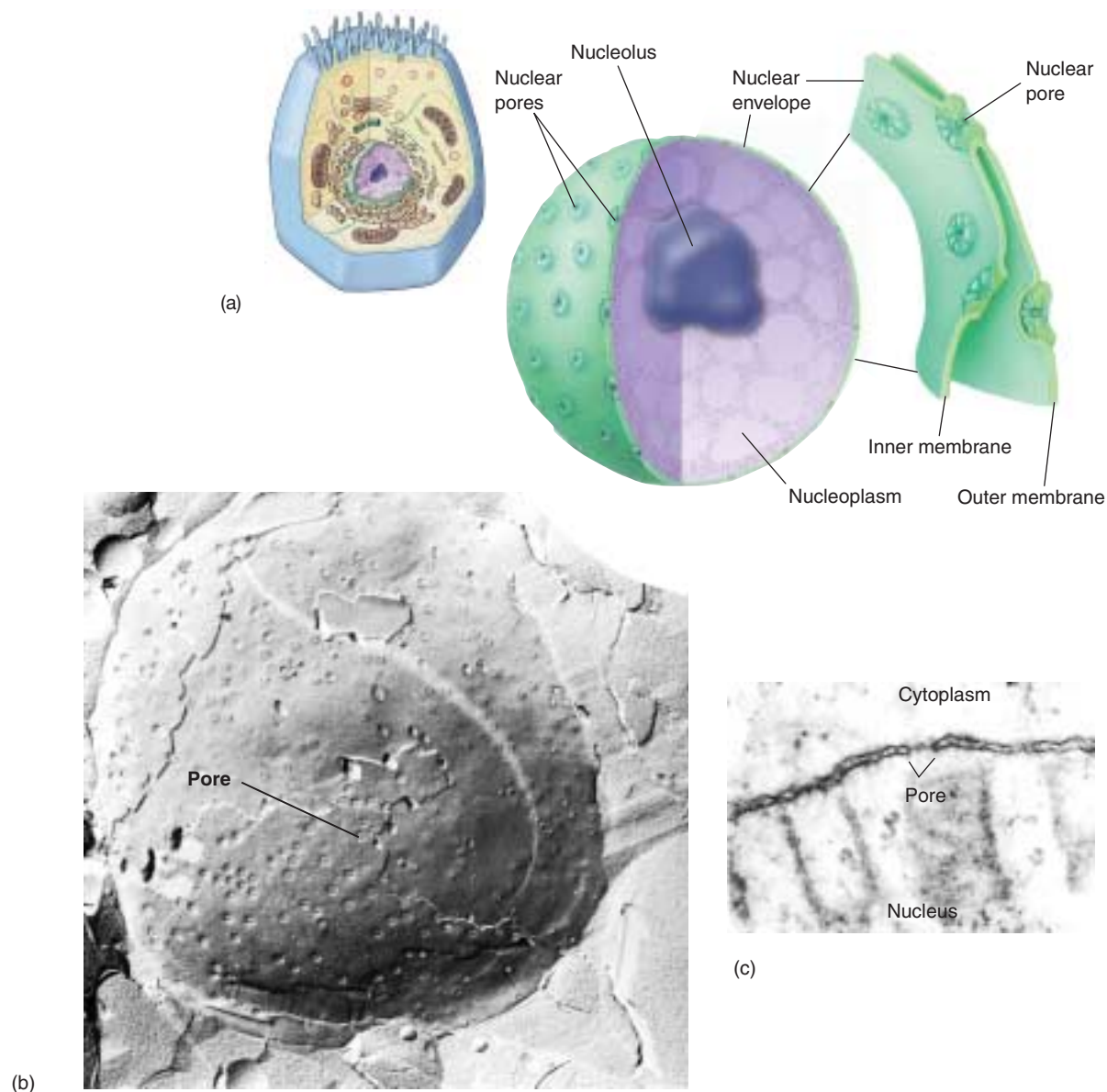


## 5.3 Take a tour of a eukaryotic cell.

### The Nucleus: Information Center for the Cell

The largest and most easily seen organelle within a eukaryotic cell is the **nucleus** (Latin, for kernel or nut), first described by the English botanist Robert Brown in 1831. Nuclei are roughly spherical in shape and, in animal cells, they are typically located in the central region of the cell (figure 5.10). In some cells, a network of fine cytoplasmic

filaments seems to cradle the nucleus in this position. The nucleus is the repository of the genetic information that directs all of the activities of a living eukaryotic cell. Most eukaryotic cells possess a single nucleus, although the cells of fungi and some other groups may have several to many nuclei. Mammalian erythrocytes (red blood cells) lose their nuclei when they mature. Many nuclei exhibit a dark-staining zone called the nucleolus, which is a region where intensive synthesis of ribosomal RNA is taking place.



**FIGURE 5.10**

**The nucleus.** (a) The nucleus is composed of a double membrane, called a nuclear envelope, enclosing a fluid-filled interior containing the chromosomes. In cross-section, the individual nuclear pores are seen to extend through the two membrane layers of the envelope; the dark material within the pore is protein, which acts to control access through the pore. (b) A freeze-fracture scanning electron micrograph of a cell nucleus showing nuclear pores (9500 $\times$ ). (c) A transmission electron micrograph (see figure 6.6) of the nuclear membrane showing a nuclear pore.

## The Nuclear Envelope: Getting In and Out

The surface of the nucleus is bounded by *two* phospholipid bilayer membranes, which together make up the **nuclear envelope** (see figure 5.10). The outer membrane of the nuclear envelope is continuous with the cytoplasm's interior membrane system, called the endoplasmic reticulum. Scattered over the surface of the nuclear envelope, like craters on the moon, are shallow depressions called **nuclear pores**. These pores form 50 to 80 nanometers apart at locations where the two membrane layers of the nuclear envelope pinch together. Rather than being empty, nuclear pores are filled with proteins that act as molecular channels, permitting certain molecules to pass into and out of the nucleus. Passage is restricted primarily to two kinds of molecules: (1) proteins moving into the nucleus to be incorporated into nuclear structures or to catalyze nuclear activities; and (2) RNA and protein-RNA complexes formed in the nucleus and exported to the cytoplasm.

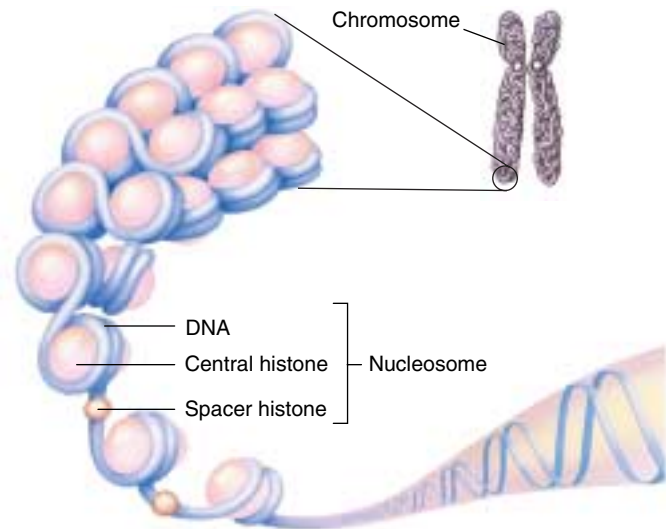
## The Chromosomes: Packaging the DNA

In both bacteria and eukaryotes, DNA contains the hereditary information specifying cell structure and function. However, unlike the circular DNA of bacteria, the DNA of eukaryotes is divided into several linear **chromosomes**. Except when a cell is dividing, its chromosomes are fully extended into threadlike strands, called **chromatin**, of DNA complexed with protein. This open arrangement allows proteins to attach to specific nucleotide sequences along the DNA. Without this access, DNA could not direct the day-to-day activities of the cell. The chromosomes are associated with packaging proteins called **histones**. When a cell prepares to divide, the DNA coils up around the histones into a highly condensed form. In the initial stages of this condensation, units of histone can be seen with DNA wrapped around like a sash. Called **nucleosomes**, these initial aggregations resemble beads on a string (figure 5.11). Coiling continues until the DNA is in a compact mass. Under a light microscope, these fully condensed chromosomes are readily seen in dividing cells as densely staining rods (figure 5.12). After cell division, eukaryotic chromosomes uncoil and can no longer be individually distinguished with a light microscope. Uncoiling the chromosomes into a more extended form permits enzymes to make RNA copies of DNA. Only by means of these RNA copies can the information in the DNA be used to direct the synthesis of proteins.

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**The nucleus of a eukaryotic cell contains the cell's hereditary apparatus and isolates it from the rest of the cell. A distinctive feature of eukaryotes is the organization of their DNA into complex chromosomes.**

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**FIGURE 5.11**  
**Nucleosomes.** Each nucleosome is a region in which the DNA is wrapped tightly around a cluster of histone proteins.



**FIGURE 5.12**  
**Eukaryotic chromosomes.** These condensed chromosomes within an onion root tip are visible under the light microscope (500 $\times$ ).

## The Endoplasmic Reticulum: Compartmentalizing the Cell

The interior of a eukaryotic cell is packed with membranes (table 5.1). So thin that they are invisible under the low resolving power of light microscopes, this **endomembrane system** fills the cell, dividing it into compartments, channeling the passage of molecules through the interior of the cell, and providing surfaces for the synthesis of lipids and some proteins. The presence of these membranes in eukaryotic cells constitutes one of the most fundamental distinctions between eukaryotes and prokaryotes.

The largest of the internal membranes is called the **endoplasmic reticulum (ER)**. The term *endoplasmic* means “within the cytoplasm,” and the term *reticulum* is Latin for “a little net.” Like the plasma membrane, the ER is composed of a lipid bilayer embedded with proteins. It weaves in sheets through the interior of the cell, creating a series of channels between its folds (figure 5.13). Of the many compartments in eukaryotic cells, the two largest are the inner region of the ER, called the **cisternal space**, and the region exterior to it, the **cytosol**.

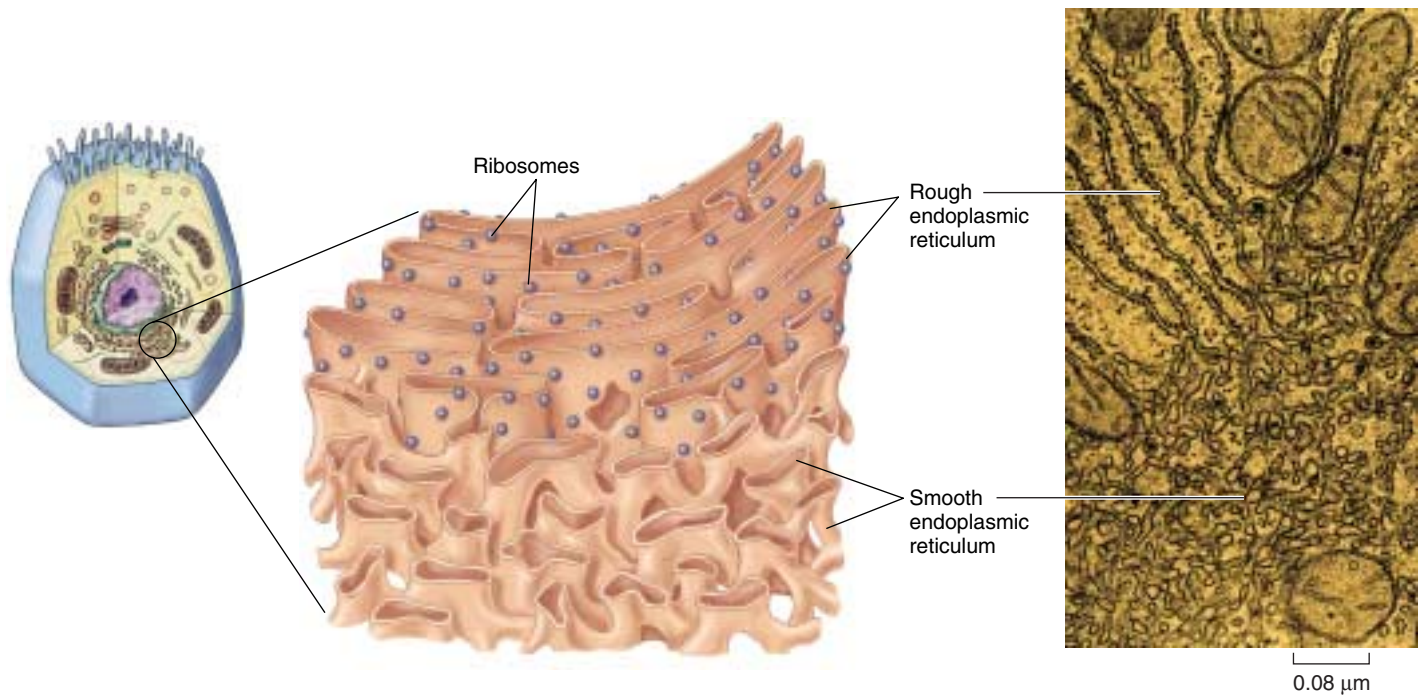
## Rough ER: Manufacturing Proteins for Export

The ER surface regions that are devoted to protein synthesis are heavily studded with **ribosomes**, large molecular aggregates of protein and ribonucleic acid (RNA) that translate RNA copies of genes into protein (we will examine ribosomes in detail later in this chapter). Through the electron microscope, these ribosome-rich regions of the ER appear pebbly, like the surface of sandpaper, and they are therefore called **rough ER** (see figure 5.13).

The proteins synthesized on the surface of the rough ER are destined to be exported from the cell. Proteins to be exported contain special amino acid sequences called **signal sequences**. As a new protein is made by a free ribosome (one not attached to a membrane), the signal sequence of the growing polypeptide attaches to a recognition factor that carries the ribosome and its partially completed protein to a “docking site” on the surface of the ER. As the protein is assembled it passes through the ER membrane into the interior ER compartment, the cisternal space, from which it is transported by vesicles to the Golgi apparatus (figure 5.14). The protein then travels within vesicles to the inner surface of the plasma membrane, where it is released to the outside of the cell.

Table 5.1 Eukaryotic Cell Structures and Their Functions

Structure	Description	Function
Cell wall	Outer layer of cellulose or chitin; or absent	Protection; support
Cytoskeleton	Network of protein filaments	Structural support; cell movement
Flagella (cilia)	Cellular extensions with 9 + 2 arrangement of pairs of microtubules	Motility or moving fluids over surfaces
Plasma membrane	Lipid bilayer with embedded proteins	Regulates what passes into and out of cell; cell-to-cell recognition
Endoplasmic reticulum	Network of internal membranes	Forms compartments and vesicles; participates in protein and lipid synthesis
Nucleus	Structure (usually spherical) surrounded by double membrane that contains chromosomes	Control center of cell; directs protein synthesis and cell reproduction
Golgi apparatus	Stacks of flattened vesicles	Packages proteins for export from cell; forms secretory vesicles
Lysosomes	Vesicles derived from Golgi apparatus that contain hydrolytic digestive enzymes	Digest worn-out organelles and cell debris; play role in cell death
Microbodies	Vesicles formed from incorporation of lipids and proteins containing oxidative and other enzymes	Isolate particular chemical activities from rest of cell
Mitochondria	Bacteria-like elements with double membrane	“Power plants” of the cell; sites of oxidative metabolism
Chloroplasts	Bacteria-like elements with membranes containing chlorophyll, a photosynthetic pigment	Sites of photosynthesis
Chromosomes	Long threads of DNA that form a complex with protein	Contain hereditary information
Nucleolus	Site of genes for rRNA synthesis	Assembles ribosomes
Ribosomes	Small, complex assemblies of protein and RNA, often bound to endoplasmic reticulum	Sites of protein synthesis



**FIGURE 5.13**

**The endoplasmic reticulum.** Ribosomes are associated with only one side of the rough ER; the other side is the boundary of a separate compartment within the cell into which the ribosomes extrude newly made proteins destined for secretion. Smooth endoplasmic reticulum has few to no bound ribosomes.

### Smooth ER: Organizing Internal Activities

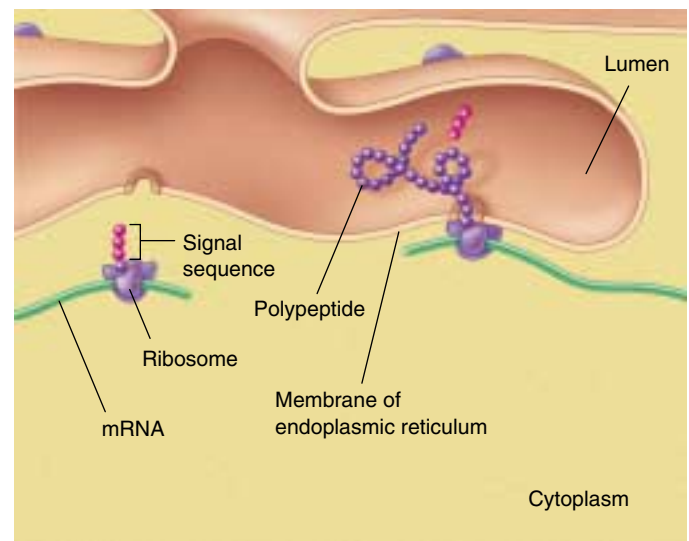
Regions of the ER with relatively few bound ribosomes are referred to as **smooth ER**. The membranes of the smooth ER contain many embedded enzymes, most of them active only when associated with a membrane. Enzymes anchored within the ER, for example, catalyze the synthesis of a variety of carbohydrates and lipids. In cells that carry out extensive lipid synthesis, such as those in the testes, intestine, and brain, smooth ER is particularly abundant. In the liver, the enzymes of the smooth ER are involved in the detoxification of drugs including amphetamines, morphine, codeine, and phenobarbital.

Some vesicles form at the plasma membrane by budding inward, a process called endocytosis. Some then move into the cytoplasm and fuse with the smooth endoplasmic reticulum. Others form secondary lysosomes or other interior vesicles.

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**The endoplasmic reticulum (ER) is an extensive system of folded membranes that divides the interior of eukaryotic cells into compartments and channels. Rough ER synthesizes proteins, while smooth ER organizes the synthesis of lipids and other biosynthetic activities.**

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**FIGURE 5.14**

**Signal sequences direct proteins to their destinations in the cell.** In this example, a sequence of hydrophobic amino acids (the signal sequence) on a secretory protein attaches them (and the ribosomes making them) to the membrane of the ER. As the protein is synthesized, it passes into the lumen (internal chamber) of the ER. The signal sequence is clipped off after the leading edge of the protein enters the lumen.

## The Golgi Apparatus: Delivery System of the Cell

At various locations within the endomembrane system, flattened stacks of membranes called **Golgi bodies** occur, often interconnected with one another. These structures are named for Camillo Golgi, the nineteenth-century Italian physician who first called attention to them. The numbers of Golgi bodies a cell contains ranges from 1 or a few in protists, to 20 or more in animal cells and several hundred in plant cells. They are especially abundant in glandular cells, which manufacture and secrete substances. Collectively the Golgi bodies are referred to as the **Golgi apparatus** (figure 5.15).

The Golgi apparatus functions in the collection, packaging, and distribution of molecules synthesized at one place in the cell and utilized at another location in the cell. A Golgi body has a front and a back, with distinctly different membrane compositions at the opposite ends. The front, or receiving end, is called the *cis* face, and is usually located near ER. Materials move to the *cis* face in transport vesicles that bud off of the ER. These vesicles fuse with the *cis* face, emptying their contents into the interior, or lumen, of the Golgi apparatus. These ER-synthesized molecules then pass through the channels of the Golgi apparatus until they reach the back, or discharging end, called the *trans* face, where they are discharged in secretory vesicles (figure 5.16).

Proteins and lipids manufactured on the rough and smooth ER membranes are transported into the Golgi ap-

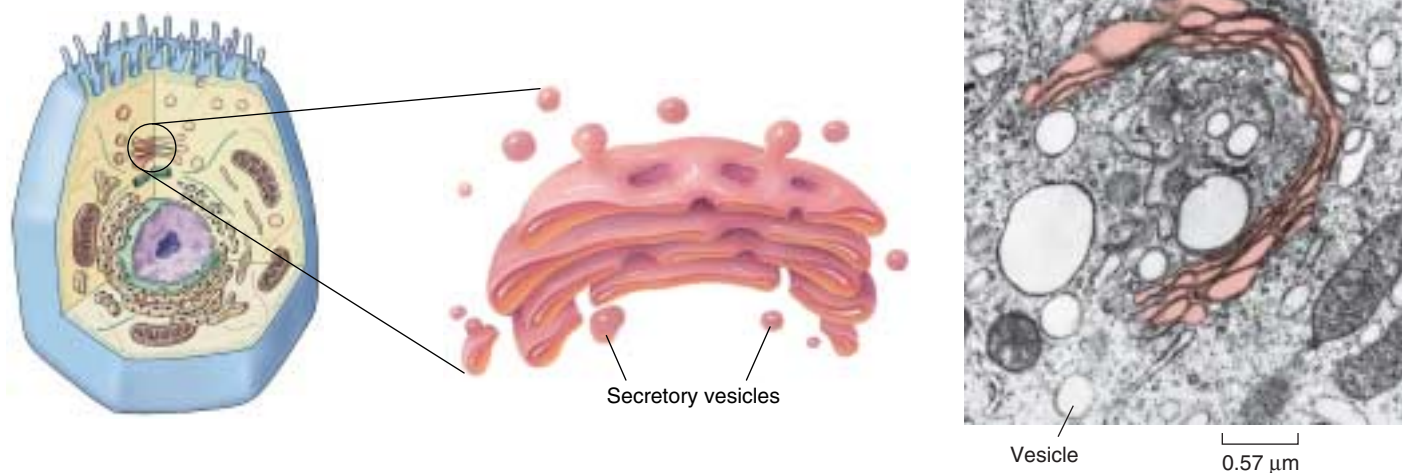
paratus and modified as they pass through it. The most common alteration is the addition or modification of short sugar chains, forming a *glycoprotein* when sugars are complexed to a protein and a *glycolipid* when sugars are bound to a lipid. In many instances, enzymes in the Golgi apparatus modify existing glycoproteins and glycolipids made in the ER by cleaving a sugar from their sugar chain or modifying one or more of the sugars.

The newly formed or altered glycoproteins and glycolipids collect at the ends of the Golgi bodies, in flattened stacked membrane folds called **cisternae** (Latin, “collecting vessels”). Periodically, the membranes of the cisternae push together, pinching off small, membrane-bounded secretory vesicles containing the glycoprotein and glycolipid molecules. These vesicles then move to other locations in the cell, distributing the newly synthesized molecules to their appropriate destinations. **Liposomes** are synthetically manufactured vesicles that contain any variety of desirable substances (such as drugs), and can be injected into the body. Because the membrane of liposomes is similar to plasma and organellar membranes, these liposomes serve as an effective and natural delivery system to cells and may prove to be of great therapeutic value.

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**The Golgi apparatus is the delivery system of the eukaryotic cell. It collects, packages, modifies, and distributes molecules that are synthesized at one location within the cell and used at another.**

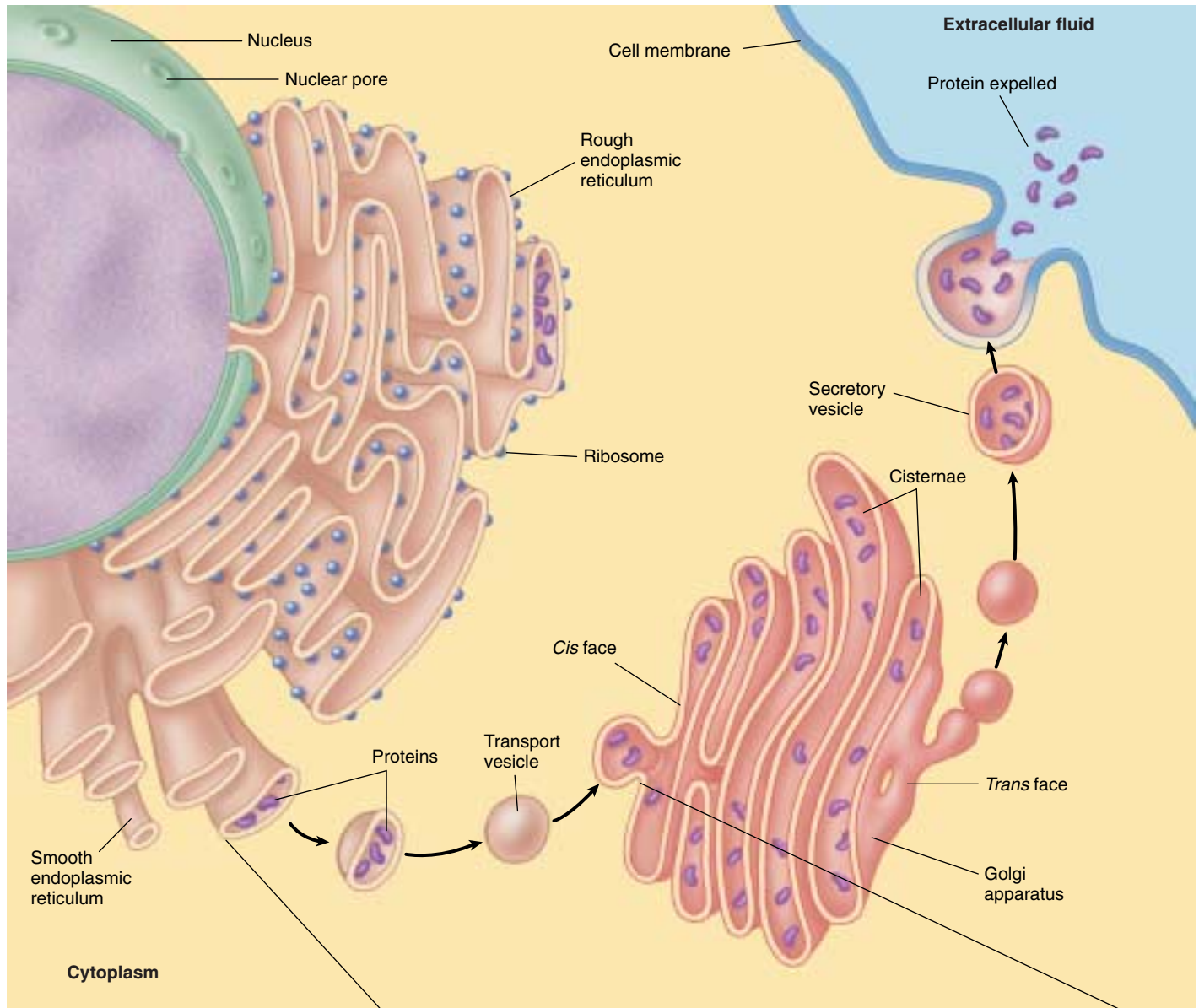
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**FIGURE 5.15**

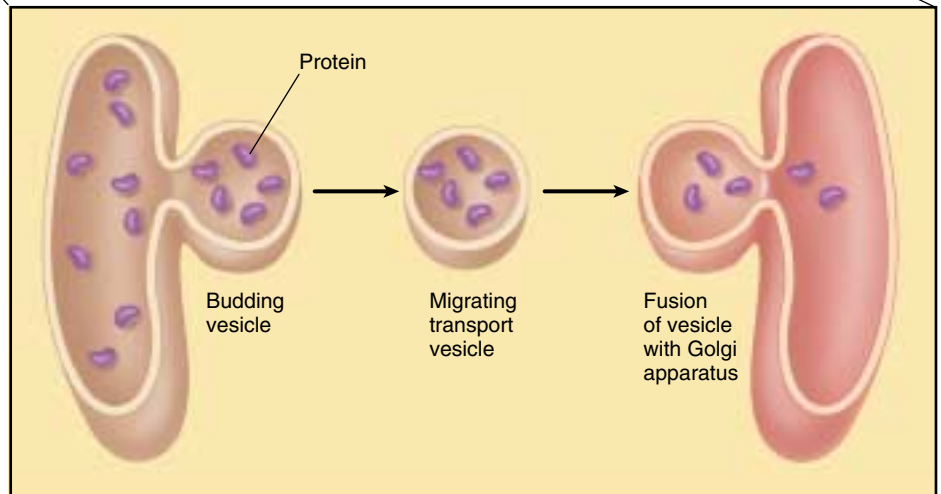
**The Golgi apparatus.** The Golgi apparatus is a smooth, concave membranous structure located near the middle of the cell. It receives material for processing on one surface and sends the material packaged in vesicles off the other. The substance in a vesicle could be for export out of the cell or for distribution to another region within the same cell.





**FIGURE 5.16**

**How proteins are transported within the cell.** Proteins are manufactured at the ribosome and then released into the internal compartments of the rough ER. If the newly synthesized proteins are to be used at a distant location in or outside of the cell, they are transported within vesicles that bud off the rough ER and travel to the *cis* face, or receiving end, of the Golgi apparatus. There they are modified and packaged into secretory vesicles. The secretory vesicles then migrate from the *trans* face, or discharging end, of the Golgi apparatus to other locations in the cell, or they fuse with the cell membrane, releasing their contents to the external cellular environment.



## Vesicles: Enzyme Storehouses

### Lysosomes: Intracellular Digestion Centers

**Lysosomes**, membrane-bounded digestive vesicles, are also components of the endomembrane system that arise from the Golgi apparatus. They contain high levels of degrading enzymes, which catalyze the rapid breakdown of proteins, nucleic acids, lipids, and carbohydrates. Throughout the lives of eukaryotic cells, lysosomal enzymes break down old organelles, recycling their component molecules and making room for newly formed organelles. For example, mitochondria are replaced in some tissues every 10 days.

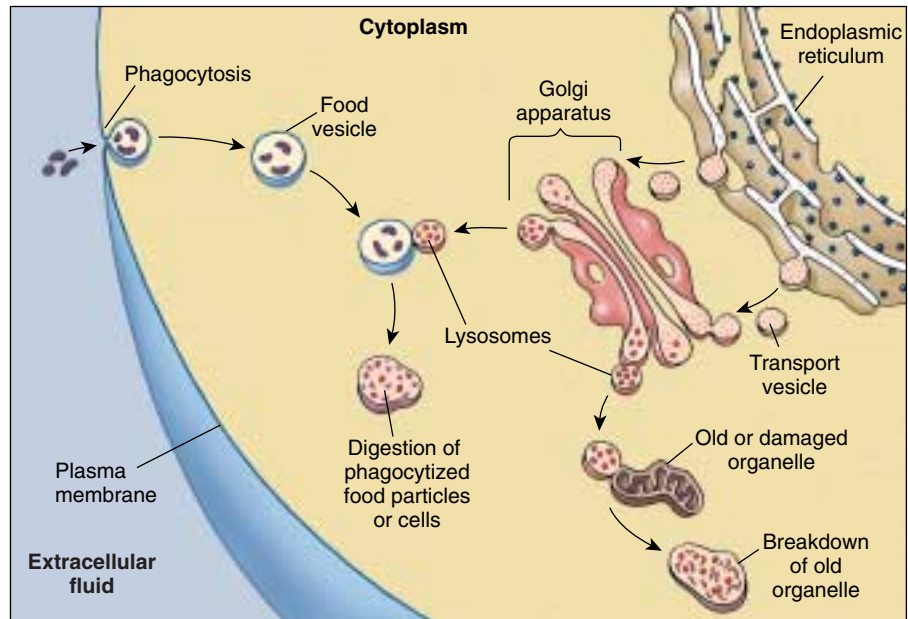
The digestive enzymes in lysosomes function best in an acidic environment. Lysosomes actively engaged in digestion keep their battery of hydrolytic enzymes (enzymes that catalyze the hydrolysis of molecules) fully active by pumping protons into their interiors and thereby maintaining a low internal pH. Lysosomes that are not functioning actively do not maintain an acidic internal pH and are called *primary lysosomes*. When a primary lysosome fuses with a food vesicle or other organelle, its pH falls and its arsenal of hydrolytic enzymes is activated; it is then called a *secondary lysosome*.

In addition to breaking down organelles and other structures within cells, lysosomes also eliminate other cells that the cell has engulfed in a process called *phagocytosis*, a specific type of endocytosis (see chapter 6). When a white blood cell, for example, phagocytizes a passing pathogen, lysosomes fuse with the resulting “food vesicle,” releasing their enzymes into the vesicle and degrading the material within (figure 5.17).

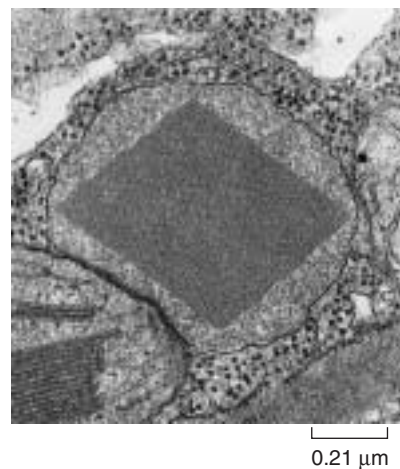
### Microbodies

Eukaryotic cells contain a variety of enzyme-bearing, membrane-enclosed vesicles called **microbodies**. Microbodies are found in the cells of plants, animals, fungi, and protists. The distribution of enzymes into microbodies is one of the principal ways in which eukaryotic cells organize their metabolism.

While lysosomes bud from the endomembrane system, microbodies grow by incorporating lipids and protein, then dividing. Plant cells have a special type of microbody called a **glyoxysome** that contains enzymes that convert fats into carbohydrates. Another type of microbody, a **peroxisome**, contains enzymes that catalyze the removal of electrons and associated hydrogen atoms (figure 5.18).



**FIGURE 5.17**  
**Lysosomes.** Lysosomes contain hydrolytic enzymes that digest particles or cells taken into the cell by phagocytosis and break down old organelles.



**FIGURE 5.18**  
**A peroxisome.** Peroxisomes are spherical organelles that may contain a large diamond-shaped crystal composed of protein. Peroxisomes contain digestive and detoxifying enzymes that produce hydrogen peroxide as a by-product.

If these oxidative enzymes were not isolated within microbodies, they would tend to short-circuit the metabolism of the cytoplasm, which often involves adding hydrogen atoms to oxygen. The name *peroxisome* refers to the hydrogen peroxide produced as a by-product of the activities of the oxidative enzymes in the microbody. Hydrogen peroxide is dangerous to cells because of its violent chemical reactivity. However, peroxisomes also contain the enzyme catalase, which breaks down hydrogen peroxide into harmless water and oxygen.

**Lysosomes and peroxisomes are vesicles that contain digestive and detoxifying enzymes. The isolation of these enzymes in vesicles protects the rest of the cell from inappropriate digestive activity.**

## Ribosomes: Sites of Protein Synthesis

Although the DNA in a cell's nucleus encodes the amino acid sequence of each protein in the cell, the proteins are not assembled there. A simple experiment demonstrates this: if a brief pulse of radioactive amino acid is administered to a cell, the radioactivity shows up associated with newly made protein, not in the nucleus, but in the cytoplasm. When investigators first carried out these experiments, they found that protein synthesis was associated with large RNA-protein complexes they called **ribosomes**.

Ribosomes are made up of several molecules of a special form of RNA called ribosomal RNA, or rRNA, bound within a complex of several dozen different proteins. Ribosomes are among the most complex molecular assemblies found in cells. Each ribosome is composed of two subunits (figure 5.19). The subunits join to form a functional ribosome only when they attach to another kind of RNA, called messenger RNA (mRNA) in the cytoplasm. To make proteins, the ribosome attaches to the mRNA, which is a transcribed copy of a portion of DNA, and uses the information to direct the synthesis of a protein.

Bacterial ribosomes are smaller than eukaryotic ribosomes. Also, a bacterial cell typically has only a few thousand ribosomes, while a metabolically active eukaryotic cell, such as a human liver cell, contains several million. Proteins that function in the cytoplasm are made by free ribosomes suspended there, while proteins bound within membranes or destined for export from the cell are assembled by ribosomes bound to rough ER.

### The Nucleolus Manufactures Ribosomal Subunits

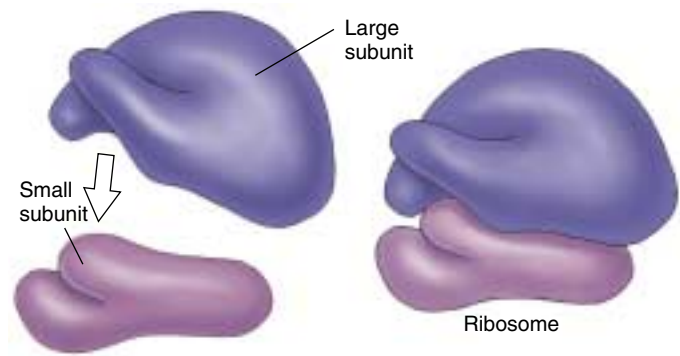
When cells are synthesizing a large number of proteins, they must first make a large number of ribosomes. To facilitate this, many hundreds of copies of the portion of the DNA encoding the rRNA are clustered together on the chromosome. By transcribing RNA molecules from this cluster, the cell rapidly generates large numbers of the molecules needed to produce ribosomes.

At any given moment, many rRNA molecules dangle from the chromosome at the sites of these clusters of genes that encode rRNA. Proteins associate with the dangling rRNA molecules. These areas where ribosomes are being assembled are easily visible within the nucleus as one or more dark-staining regions, called **nucleoli** (singular, nucleolus; figure 5.20). Nucleoli can be seen under the light microscope even when the chromosomes are extended, unlike the rest of the chromosomes, which are visible only when condensed.

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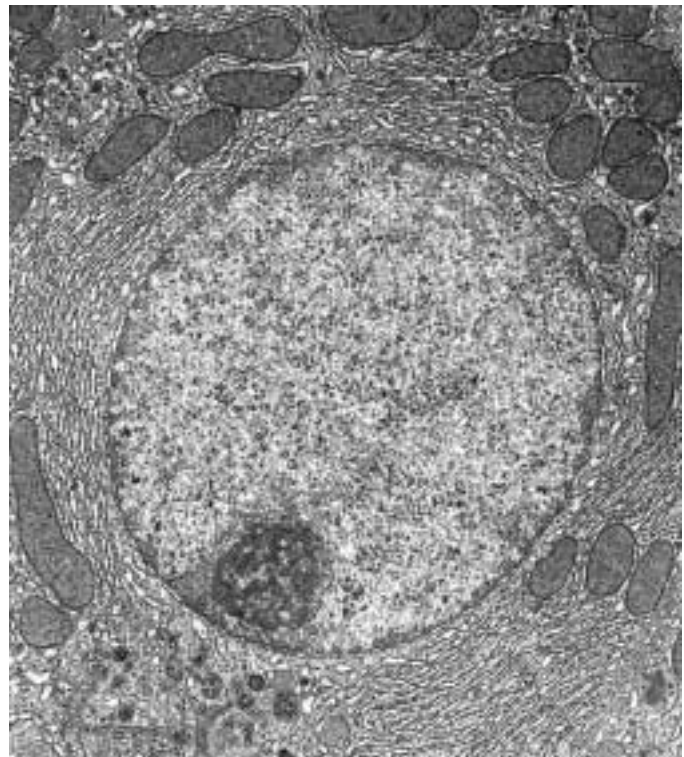
**Ribosomes are the sites of protein synthesis in the cytoplasm.**

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**FIGURE 5.19**

**A ribosome.** Ribosomes consist of a large and a small subunit composed of rRNA and protein. The individual subunits are synthesized in the nucleolus and then move through the nuclear pores to the cytoplasm, where they assemble. Ribosomes serve as sites of protein synthesis.



**FIGURE 5.20**

**The nucleolus.** This is the interior of a rat liver cell, magnified about 6000 times. A single large nucleus occupies the center of the micrograph. The electron-dense area in the lower left of the nucleus is the nucleolus, the area where the major components of the ribosomes are produced. Partly formed ribosomes can be seen around the nucleolus.

## Organelles That Contain DNA

Among the most interesting cell organelles are those in addition to the nucleus that contain DNA.

### Mitochondria: The Cell's Chemical Furnaces

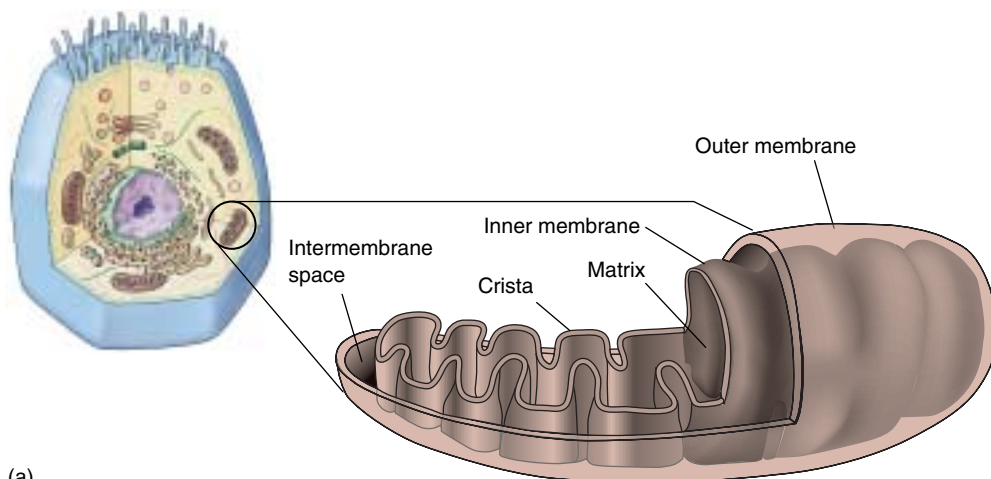
**Mitochondria** (singular, *mitochondrion*) are typically tubular or sausage-shaped organelles about the size of bacteria and found in all types of eukaryotic cells (figure 5.21). Mitochondria are bounded by two membranes: a smooth outer membrane and an inner one folded into numerous contiguous layers called **cristae** (singular, *crista*). The cristae partition the mitochondrion into two compartments: a **matrix**, lying inside the inner membrane; and an outer compartment, or **intermembrane space**, lying between the two mitochondrial membranes. On the surface of the inner membrane, and also embedded within it, are proteins that carry out oxidative metabolism, the oxygen-requiring process by which energy in macromolecules is stored in ATP. (a)

Mitochondria have their own DNA; this DNA contains several genes that produce proteins essential to the mitochondrion's role in oxidative metabolism. All of these genes are copied into RNA and used to make proteins within the mitochondrion. In this process, the mitochondria employ small RNA molecules and ribosomal components that the mitochondrial DNA also encodes. However, most of the genes that produce the enzymes used in oxidative metabolism are located in the nucleus.

A eukaryotic cell does not produce brand new mitochondria each time the cell divides. Instead, the mitochondria themselves divide in two, doubling in number, and these are partitioned between the new cells. Most of the components required for mitochondrial division are encoded by genes in the nucleus and translated into proteins by cytoplasmic ribosomes. Mitochondrial replication is, therefore, impossible without nuclear participation, and mitochondria thus cannot be grown in a cell-free culture.

### Chloroplasts: Where Photosynthesis Takes Place

Plants and other eukaryotic organisms that carry out photosynthesis typically contain from one to several hundred **chloroplasts**. Chloroplasts bestow an obvious advantage on the organisms that possess them: they can manufacture their own food. Chloroplasts contain the photosynthetic pigment chlorophyll that gives most plants their green color.



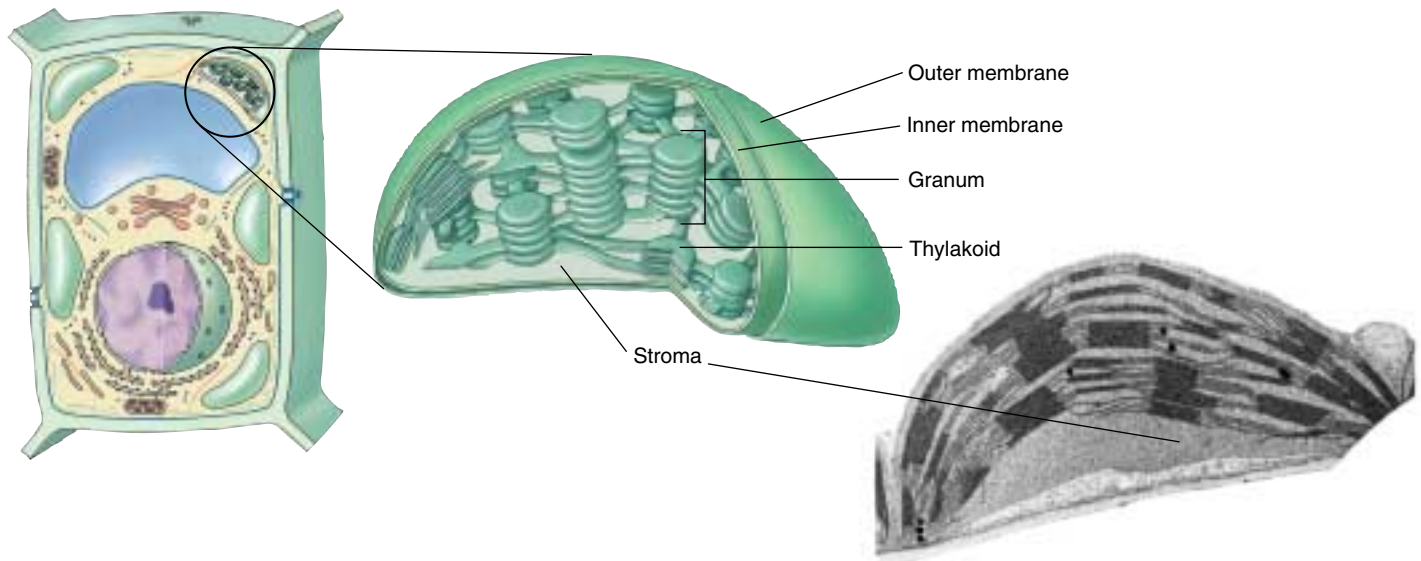
(b)

**FIGURE 5.21**

**Mitochondria.** (a) The inner membrane of a mitochondrion is shaped into folds called cristae, which greatly increase the surface area for oxidative metabolism. (b) Mitochondria in cross-section and cut lengthwise (70,000 $\times$ ).

The chloroplast body is enclosed, like the mitochondrion, within two membranes that resemble those of mitochondria (figure 5.22). However, chloroplasts are larger and more complex than mitochondria. In addition to the outer and inner membranes, which lie in close association with each other, chloroplasts have a closed compartment of stacked membranes called **grana** (singular, *granum*), which lie internal to the inner membrane. A chloroplast may contain a hundred or more grana, and each granum may contain from a few to several dozen disk-shaped structures called **thylakoids**. On the surface of the thylakoids are the light-capturing photosynthetic pigments, to be discussed in depth in chapter 10. Surrounding the thylakoid is a fluid matrix called the *stroma*.

Like mitochondria, chloroplasts contain DNA, but many of the genes that specify chloroplast components are also located in the nucleus. Some of the elements used in the photosynthetic process, including the specific protein components necessary to accomplish the reaction, are synthesized entirely within the chloroplast.



**FIGURE 5.22**

**Chloroplast structure.** The inner membrane of a chloroplast is fused to form stacks of closed vesicles called thylakoids. Within these thylakoids, photosynthesis takes place. Thylakoids are typically stacked one on top of the other in columns called grana.

Other DNA-containing organelles in plants are called leucoplasts, which lack pigment and a complex internal structure. In root cells and some other plant cells, leucoplasts may serve as starch storage sites. A leucoplast that stores starch (amylose) is sometimes termed an **amyloplast**. These organelles—chloroplasts, leucoplasts, and amyloplasts—are collectively called **plastids**. All plastids come from the division of existing plastids.

### Centrioles: Microtubule Assembly Centers

**Centrioles** are barrel-shaped organelles found in the cells of animals and most protists. They occur in pairs, usually located at right angles to each other near the nuclear membranes (figure 5.23); the region surrounding the pair in almost all animal cells is referred to as a **centrosome**. Although the matter is in some dispute, at least some centrioles seem to contain DNA, which apparently is involved in producing their structural proteins. Centrioles help to assemble **microtubules**, long, hollow cylinders of the protein tubulin. Microtubules influence cell shape, move the chromosomes in cell division, and provide the functional internal structure of flagella and cilia, as we will discuss later. Centrioles may be contained in areas called **microtubule-organizing centers (MTOCs)**. The cells of plants and fungi lack centrioles, and cell biologists are still in the process of characterizing their MTOCs.

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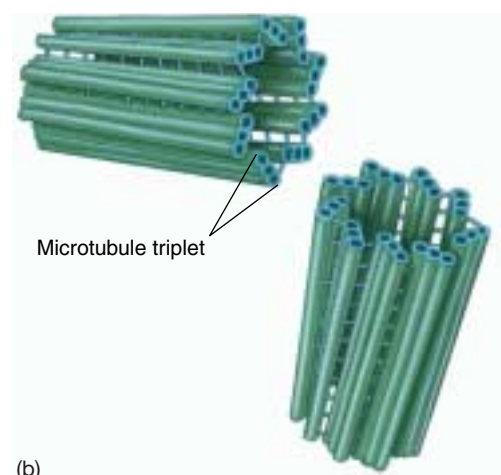
Both mitochondria and chloroplasts contain specific genes related to some of their functions, but both depend on nuclear genes for other functions. Some centrioles also contain DNA, which apparently helps control the synthesis of their structural proteins.

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(a)

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(b)

**FIGURE 5.23**

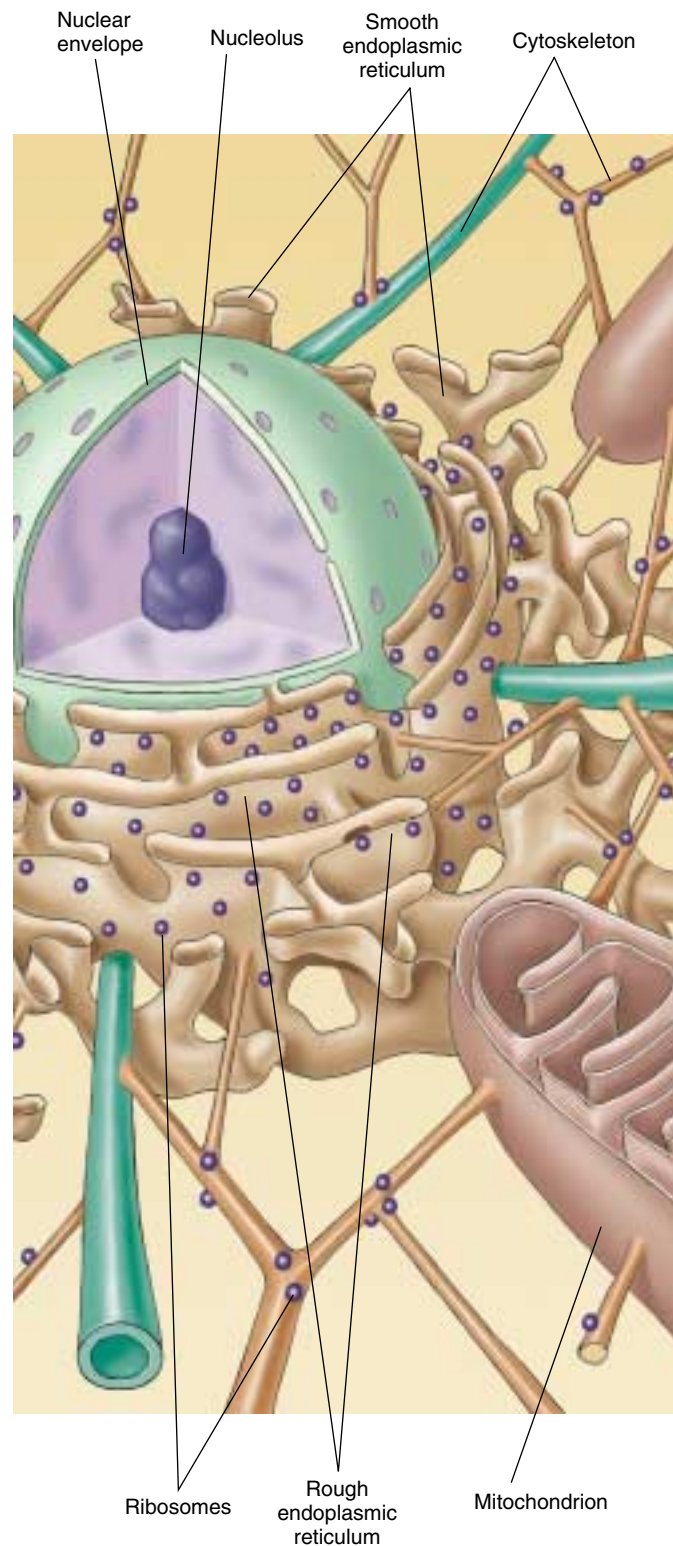
**Centrioles.** (a) This electron micrograph shows a pair of centrioles (75,000 $\times$ ). The round shape is a centriole in cross-section; the rectangular shape is a centriole in longitudinal section. (b) Each centriole is composed of nine triplets of microtubules.

## The Cytoskeleton: Interior Framework of the Cell

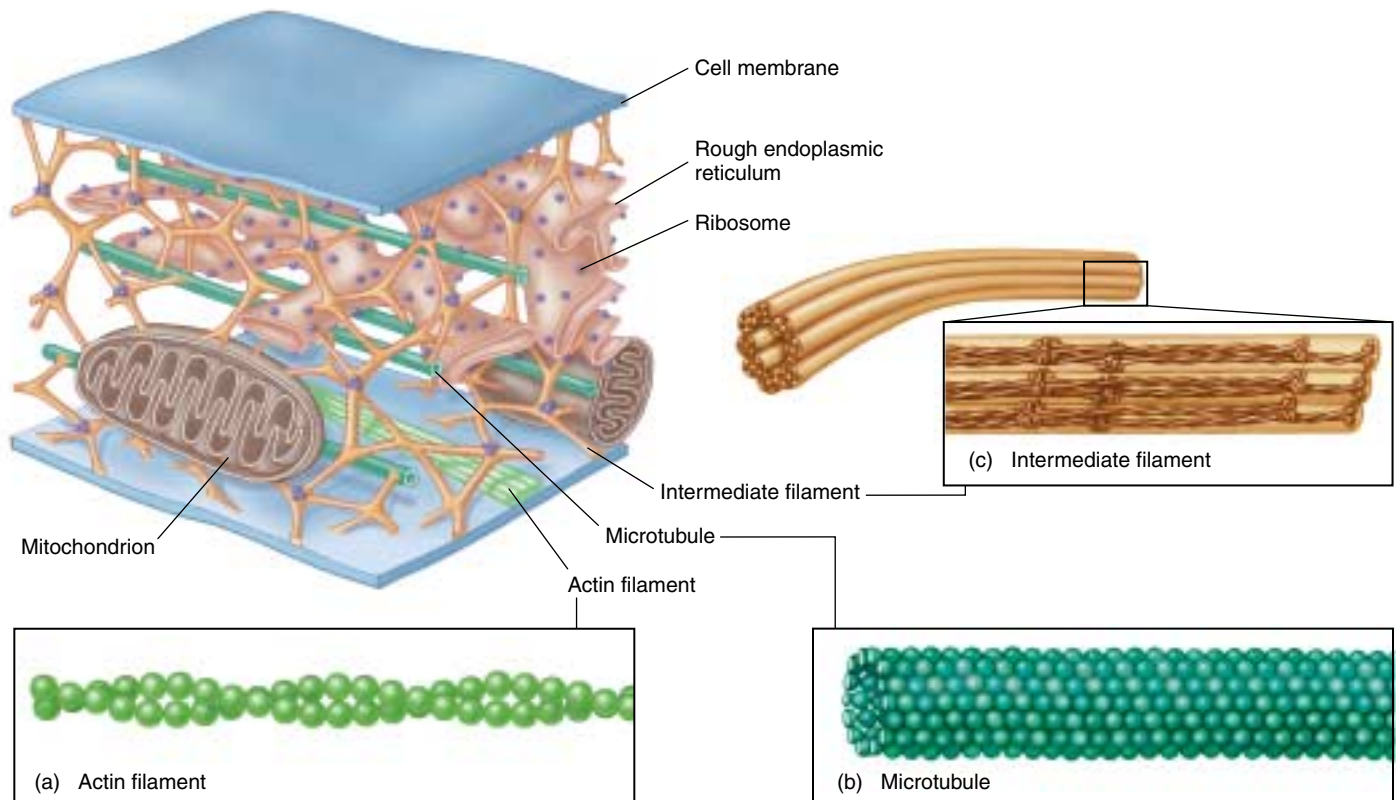
The cytoplasm of all eukaryotic cells is crisscrossed by a network of protein fibers that supports the shape of the cell and anchors organelles to fixed locations. This network, called the **cytoskeleton** (figure 5.24), is a dynamic system, constantly forming and disassembling. Individual fibers form by **polymerization**, as identical protein subunits attract one another chemically and spontaneously assemble into long chains. Fibers disassemble in the same way, as one subunit after another breaks away from one end of the chain.

Eukaryotic cells may contain three types of cytoskeletal fibers, each formed from a different kind of subunit:

- 1. Actin filaments.** Actin filaments are long fibers about 7 nanometers in diameter. Each filament is composed of two protein chains loosely twined together like two strands of pearls (figure 5.25a). Each “pearl,” or subunit, on the chains is the globular protein **actin**. Actin molecules spontaneously form these filaments, even in a test tube; a cell regulates the rate of their formation through other proteins that act as switches, turning on polymerization when appropriate. Actin filaments are responsible for cellular movements such as contraction, crawling, “pinching” during division, and formation of cellular extensions.
- 2. Microtubules.** Microtubules are hollow tubes about 25 nanometers in diameter, each composed of a ring of 13 protein protofilaments (figure 5.25b). Globular proteins consisting of dimers of alpha and beta *tubulin* subunits polymerize to form the 13 protofilaments. The protofilaments are arrayed side by side around a central core, giving the microtubule its characteristic tube shape. In many cells, microtubules form from MTOC nucleation centers near the center of the cell and radiate toward the periphery. They are in a constant state of flux, continually polymerizing and depolymerizing (the average half-life of a microtubule ranges from 10 minutes in a nondividing animal cell to as short as 20 seconds in a dividing animal cell), unless stabilized by the binding of guanosine triphosphate (GTP) to the ends, which inhibits depolymerization. The ends of the microtubule are designated as “+” (away from the nucleation center) or “-” (toward the nucleation center). Along with allowing for cellular movement, microtubules are responsible for moving materials within the cell itself. Special motor proteins, discussed later in this chapter, move cellular organelles around the cell on microtubular “tracks.” *Kinesin* proteins move organelles toward the “+” end (toward the cell periphery), and *dyneins* move them toward the “-” end.



**FIGURE 5.24**  
**The cytoskeleton.** In this diagrammatic cross-section of a eukaryotic cell, the cytoskeleton, a network of fibers, supports organelles such as mitochondria.



**FIGURE 5.25**

**Molecules that make up the cytoskeleton.** (a) Actin filaments. Actin filaments are made of two strands of the fibrous protein actin twisted together and usually occur in bundles. Actin filaments are ubiquitous, although they are concentrated below the plasma membrane in bundles known as stress fibers, which may have a contractile function. (b) Microtubules. Microtubules are composed of 13 stacks of tubulin protein subunits arranged side by side to form a tube. Microtubules are comparatively stiff cytoskeletal elements that serve to organize metabolism and intracellular transport in the nondividing cell. (c) Intermediate filaments. Intermediate filaments are composed of overlapping staggered tetramers of protein. This molecular arrangement allows for a ropelike structure that imparts tremendous mechanical strength to the cell.

**3. Intermediate filaments.** The most durable element of the cytoskeleton in animal cells is a system of tough, fibrous protein molecules twined together in an overlapping arrangement (figure 5.25c). These fibers are characteristically 8 to 10 nanometers in diameter, intermediate in size between actin filaments and microtubules (which is why they are called intermediate filaments). Once formed, intermediate filaments are stable and usually do not break down. Intermediate filaments constitute a heterogeneous group of cytoskeletal fibers. The most common type, composed of protein subunits called *vimentin*, provides structural stability for many kinds of cells. *Keratin*, another class of intermediate filament, is found in epithelial cells (cells that line organs and body cavities) and associated structures such as hair

and fingernails. The intermediate filaments of nerve cells are called *neurofilaments*.

As we will discuss in the next section, the cytoskeleton provides an interior framework that supports the shape of the cell, stretching the plasma membrane much as the poles of a circus tent. Changing the relative length of cytoskeleton filaments allows cells to rapidly alter their shape, extending projections out or folding inward. Within the cell, the framework of filaments provides a molecular highway along which molecules can be transported.

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**Elements of the cytoskeleton crisscross the cytoplasm, supporting the cell shape and anchoring organelles in place. There are three principal types of fibers: actin filaments, microtubules, and intermediate filaments.**

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## Cell Movement

Essentially all cell motion is tied to the movement of actin filaments, microtubules, or both. Intermediate filaments act as intracellular tendons, preventing excessive stretching of cells, and actin filaments play a major role in determining the shape of cells. Because actin filaments can form and dissolve so readily, they enable some cells to change shape quickly. If you look at the surfaces of such cells under a microscope, you will find them alive with motion, as projections, called **microvilli** in animal cells, shoot outward from the surface and then retract, only to shoot out elsewhere moments later (figure 5.26).

### Some Cells Crawl

It is the arrangement of actin filaments within the cell cytoplasm that allows cells to “crawl,” *literally!* Crawling is a significant cellular phenomenon, essential to inflammation, clotting, wound healing, and the spread of cancer. White blood cells in particular exhibit this ability. Produced in the bone marrow, these cells are released into the circulatory system and then eventually crawl out of capillaries and into the tissues to destroy potential pathogens.

Cells exist in a *gel-sol* state; that is, at any given time, some regions of the cell are rigid (*gel*) and some are more fluid (*sol*). The cell is typically more sol-like in its interior, and more gel-like at its perimeter. To crawl, the cell creates a weak area in the gel perimeter, and then forces the fluid (*sol*) interior through the weak area, forming a **pseudopod** (“false foot”). As a result a large section of cytoplasm oozes off in a different direction, but still remains within the plasma membrane. Once extended, the pseudopod stabilizes into a gel state, assembling actin filaments. Specific membrane proteins in the pseudopod stick to the surface the cell is crawling on, and the rest of the cell is dragged in that direction. The pressure required to force out a developing pseudopod is created when actin filaments in the trailing end of the cell contract, just as squeezing a water balloon at one end forces the balloon to bulge out at the other end.

### Moving Material within the Cell

Actin filaments and microtubules often orchestrate their activities to affect cellular processes. For example, during cell reproduction (see chapter 11), newly replicated chromosomes move to opposite sides of a dividing cell because they are attached to shortening microtubules. Then, in animal cells, a belt of actin pinches the cell in two by contracting like a purse string. Muscle cells also use actin filaments to contract their cytoskeletons. The fluttering of an eyelash, the flight of an eagle, and the awkward crawling of a baby all depend on these cytoskeletal movements within muscle cells.



**FIGURE 5.26**

**The surfaces of some cells are in constant motion.** This amoeba, a single-celled protist, is advancing toward you, its advancing edges extending projections outward. The moving edges have been said to resemble the ruffled edges of a skirt.

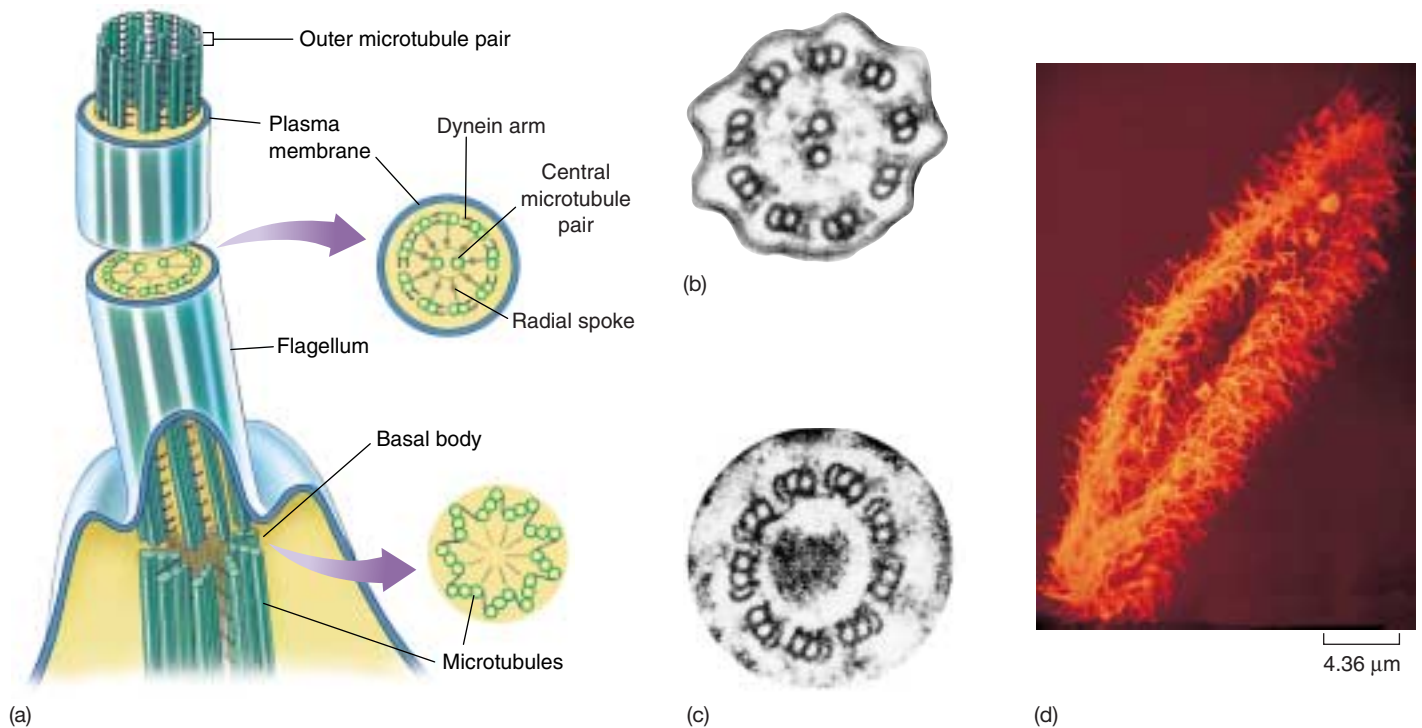
Not only is the cytoskeleton responsible for the cell’s shape and movement, but it also provides a scaffold that holds certain enzymes and other macromolecules in defined areas of the cytoplasm. Many of the enzymes involved in cell metabolism, for example, bind to actin filaments; so do ribosomes. By moving and anchoring particular enzymes near one another, the cytoskeleton, like the endoplasmic reticulum, organizes the cell’s activities.

### Intracellular Molecular Motors

Certain eukaryotic cells must move materials from one place to another in the cytoplasm. Most cells use the endomembrane system as an intracellular highway; the Golgi apparatus packages materials into vesicles that move through the channels of the endoplasmic reticulum to the far reaches of the cell. However, this highway is only effective over short distances. When a cell has to transport materials through long extensions like the axon of a nerve cell, the ER highways are too slow. For these situations, eukaryotic cells have developed high-speed locomotives that run along microtubular tracks.

Four components are required: (1) a **vesicle** or organelle that is to be transported, (2) a **motor molecule** that provides the energy-driven motion, (3) a **connector molecule** that connects the vesicle to the motor molecule, and (4) **microtubules** on which the vesicle will ride like a train on a rail. For example, embedded within the membranes of endoplasmic reticulum is a protein called *kinectin* that bind the ER vesicles to the motor protein *kinesin*. As nature’s tiniest motors, these motor proteins literally pull the transport vesicles along the microtubular tracks. Kinesin uses ATP to power its movement toward





**FIGURE 5.27**

**Flagella and cilia.** (a) A eukaryotic flagellum originates directly from a basal body. (b) The flagellum has two microtubules in its core connected by radial spokes to an outer ring of nine paired microtubules with dynein arms. (c) The basal body consists of nine microtubule triplets connected by short protein segments. The structure of cilia is similar to that of flagella, but cilia are usually shorter. (d) The surface of this *Paramecium* is covered with a dense forest of cilia.

the cell periphery, dragging the vesicle with it as it travels along the microtubule. Another vesicle protein (or perhaps a slight modification of kinesin—further research is needed to determine which) binds vesicles to the motor protein dynein, which directs movement in the opposite direction, inward toward the cell's center. (Dynein is also involved in the movement of eukaryotic flagella, as discussed below.) The destination of a particular transport vesicle and its contents is thus determined by the nature of the linking protein embedded within the vesicle's membrane.

### Swimming with Flagella and Cilia

Earlier in this chapter, we described the structure of bacterial flagella. Eukaryotic cells have a *completely different* kind of flagellum, consisting of a circle of nine microtubule pairs surrounding two central microtubules; this arrangement is referred to as the **9 + 2 structure** (figure 5.27). As pairs of microtubules move past one another using arms composed of the motor protein dynein, the eukaryotic flagellum undulates rather than rotates. When examined carefully, each flagellum proves to be an outward projection of the cell's interior, containing cytoplasm and enclosed by the plasma membrane. The microtubules of the flagellum are derived

from a **basal body**, situated just below the point where the flagellum protrudes from the surface of the cell.

The flagellum's complex microtubular apparatus evolved early in the history of eukaryotes. Although the cells of many multicellular and some unicellular eukaryotes today no longer possess flagella and are nonmotile, an organization similar to the 9 + 2 arrangement of microtubules can still be found within them, in structures called **cilia** (singular, *cilium*). Cilia are short cellular projections that are often organized in rows (see figure 5.1). They are more numerous than flagella on the cell surface, but have the same internal structure. In many multicellular organisms, cilia carry out tasks far removed from their original function of propelling cells through water. In several kinds of vertebrate tissues, for example, the beating of rows of cilia moves water over the tissue surface. The sensory cells of the vertebrate ear also contain cilia; sound waves bend these cilia, the initial sensory input of hearing. Thus, the 9 + 2 structure of flagella and cilia appears to be a fundamental component of eukaryotic cells.

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**Some eukaryotic cells use pseudopodia to crawl about within multicellular organisms, while many protists swim using flagella and cilia. Materials are transported within cells by special motor proteins.**

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## Special Things about Plant Cells

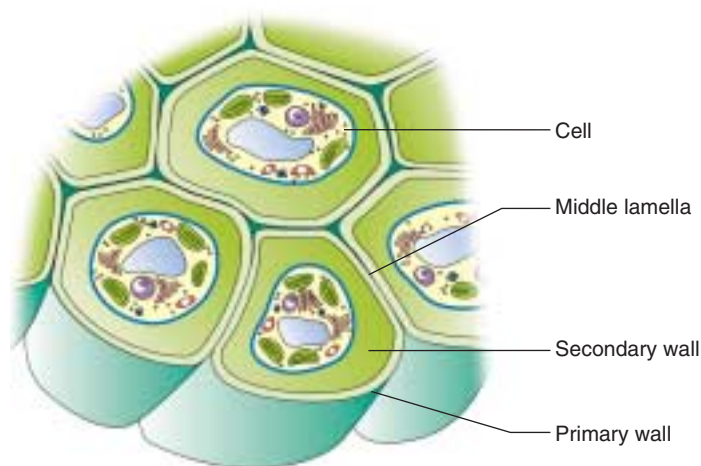
### Vacuoles: A Central Storage Compartment

The center of a plant cell usually contains a large, apparently empty space, called the **central vacuole** (figure 5.28). This vacuole is not really empty; it contains large amounts of water and other materials, such as sugars, ions, and pigments. The central vacuole functions as a storage center for these important substances and also helps to increase the surface-to-volume ratio of the plant cell by applying pressure to the cell membrane. The cell membrane expands outward under this pressure, thereby increasing its surface area.

### Cell Walls: Protection and Support

Plant cells share a characteristic with bacteria that is not shared with animal cells—that is, plants have **cell walls**, which protect and support the plant cell. Although bacteria also have cell walls, plant cell walls are chemically and structurally different from bacterial cell walls. Cell walls are also present in fungi and some protists. In plants, cell walls are composed of fibers of the polysaccharide cellulose. **Primary walls** are laid down when the cell is still growing, and between the walls of adjacent cells is a sticky substance called the **middle lamella**, which glues the cells together (figure 5.29). Some plant cells produce strong **secondary walls**, which are deposited inside the primary walls of fully expanded cells.

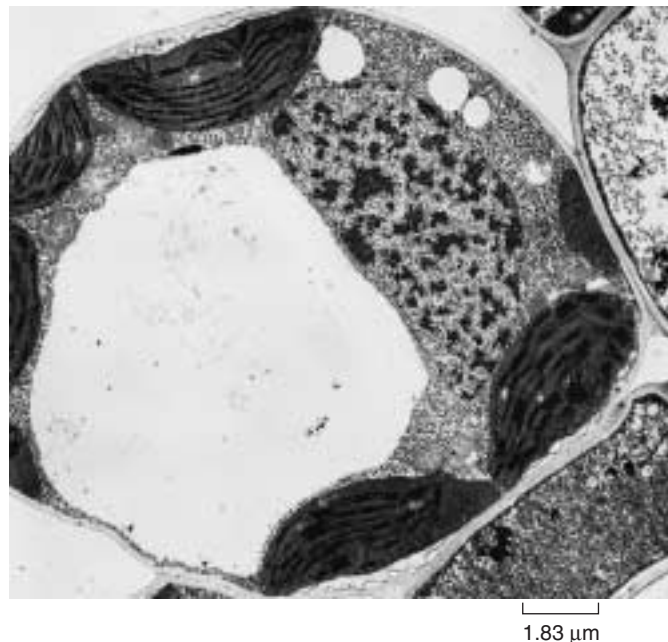
**Plant cells store substances in a large central vacuole, and encase themselves within a strong cellulose cell wall.**



(a)

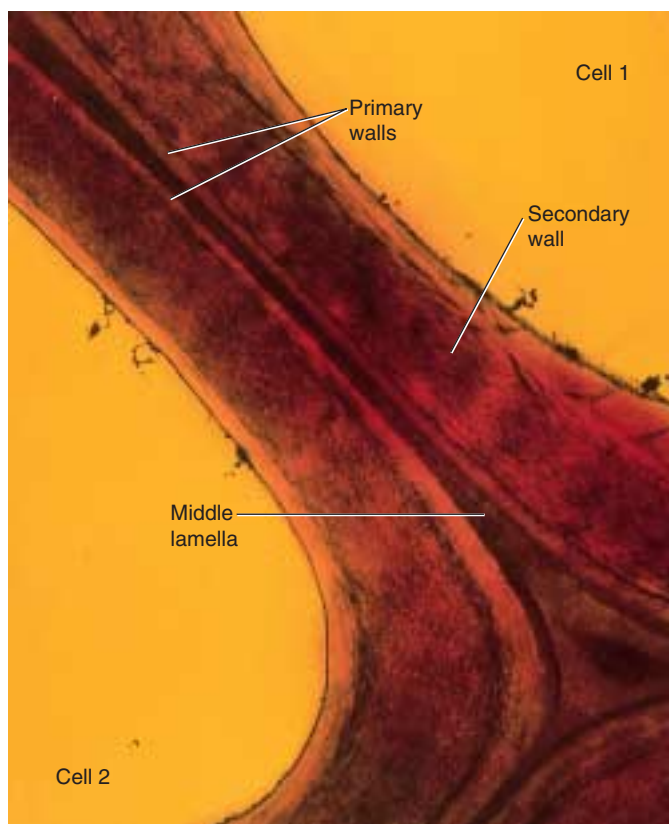
**FIGURE 5.29**

**Cell walls in plants.** As shown in this drawing (a) and transmission electron micrograph (b), plant cell walls are thicker, stronger, and more rigid than those of bacteria. Primary cell walls are laid down when the cell is young. Thicker secondary cell walls may be added later when the cell is fully grown.



**FIGURE 5.28**

**The central vacuole.** A plant's central vacuole stores dissolved substances and can increase in size to increase the surface area of a plant cell.



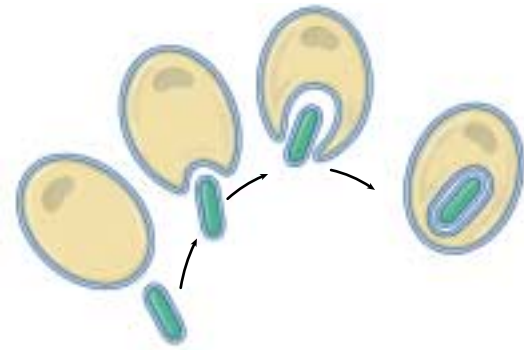
(b)

## 5.4 Symbiosis played a key role in the origin of some eukaryotic organelles.

### Endosymbiosis

Symbiosis is a close relationship between organisms of different species that live together. The theory of **endosymbiosis** proposes that some of today's eukaryotic organelles evolved by a symbiosis in which one species of prokaryote was engulfed by and lived inside another species of prokaryote that was a precursor to eukaryotes (figure 5.30). According to the endosymbiont theory, the engulfed prokaryotes provided their hosts with certain advantages associated with their special metabolic abilities. Two key eukaryotic organelles are believed to be the descendants of these endosymbiotic prokaryotes: mitochondria, which are thought to have originated as bacteria capable of carrying out oxidative metabolism; and chloroplasts, which apparently arose from photosynthetic bacteria.

The endosymbiont theory is supported by a wealth of evidence. Both mitochondria and chloroplasts are surrounded by two membranes; the inner membrane probably evolved from the plasma membrane of the engulfed bacterium, while the outer membrane is probably derived from the plasma membrane or endoplasmic reticulum of the host cell. Mitochondria are about the same size as most bacteria, and the cristae formed by their inner membranes resemble the folded membranes in various groups of bacteria. Mitochondrial ribosomes are also similar to bacterial ribosomes in size and structure. Both mitochondria and



**FIGURE 5.30**  
**Endosymbiosis.** This figure shows how a double membrane may have been created during the symbiotic origin of mitochondria or chloroplasts.

chloroplasts contain circular molecules of DNA similar to those in bacteria. Finally, mitochondria divide by simple fission, splitting in two just as bacterial cells do, and they apparently replicate and partition their DNA in much the same way as bacteria. Table 5.2 compares and reviews the features of three types of cells.

**Some eukaryotic organelles are thought to have arisen by endosymbiosis.**

**Table 5.2 A Comparison of Bacterial, Animal, and Plant Cells**

	<b>Bacterium</b>	<b>Animal</b>	<b>Plant</b>
<b>EXTERIOR STRUCTURES</b>			
Cell wall	Present (protein-polysaccharide)	Absent	Present (cellulose)
Cell membrane	Present	Present	Present
Flagella	May be present (single strand)	May be present	Absent except in sperm of a few species
<b>INTERIOR STRUCTURES</b>			
ER	Absent	Usually present	Usually present
Ribosomes	Present	Present	Present
Microtubules	Absent	Present	Present
Centrioles	Absent	Present	Absent
Golgi apparatus	Absent	Present	Present
Nucleus	Absent	Present	Present
Mitochondria	Absent	Present	Present
Chloroplasts	Absent	Absent	Present
Chromosomes	A single circle of DNA	Multiple; DNA-protein complex	Multiple; DNA-protein complex
Lysosomes	Absent	Usually present	Present
Vacuoles	Absent	Absent or small	Usually a large single vacuole



# Chapter 5

## Summary Questions Media Resources

### 5.1 All organisms are composed of cells.

- The cell is the smallest unit of life. All living things are made of cells.
- The cell is composed of a nuclear region, which holds the hereditary apparatus, enclosed within the cytoplasm.
- In all cells, the cytoplasm is bounded by a membrane composed of phospholipid and protein.

1. What are the three principles of the cell theory?
2. How does the surface area-to-volume ratio of cells limit the size that cells can attain?



- Exploration: Cell Size



- Surface to Volume

### 5.2 Eukaryotic cells are far more complex than bacterial cells.

- Bacteria, which have prokaryotic cell structure, do not have membrane-bounded organelles within their cells. Their DNA molecule is circular.
- The eukaryotic cell is larger and more complex, with many internal compartments.

3. How are prokaryotes different from eukaryotes in terms of their cell walls, interior organization, and flagella?



- Art Activities:
  - Animal Cell Structure
  - Plant Cell Structure
  - Nonphotosynthetic Bacterium
  - Cyanobacterium

### 5.3 Take a tour of a eukaryotic cell.

- A eukaryotic cell is organized into three principal zones: the nucleus, the cytoplasm, and the plasma membrane. Located in the cytoplasm are numerous organelles, which perform specific functions for the cell.
- Many of these organelles, such as the endoplasmic reticulum, Golgi apparatus (which gives rise to lysosomes), and nucleus, are part of a complex endomembrane system.
- Mitochondria and chloroplasts are part of the energy-processing system of the cell.
- The cytoskeleton encompasses a variety of fibrous proteins that provide structural support and perform other functions for the cell.
- Many eukaryotic cells possess flagella or cilia having a 9 + 2 arrangement of microtubules; sliding of the microtubules past one another bends these cellular appendages.
- Cells transport materials long distances within the cytoplasm by packaging them into vesicles that are pulled by motor proteins along microtubule tracks.

4. What is the endoplasmic reticulum? What is its function? How does rough ER differ from smooth ER?



- Art Activities:
  - Anatomy of the Nucleus
  - Golgi Apparatus Structure
  - Mitochondrion Structure
  - Organization of Cristae
  - Chloroplast Structure
  - The Cytoskeleton
  - Plant Cell

5. What is the function of the Golgi apparatus? How do the substances released by the Golgi apparatus make their way to other locations in the cell?

6. What types of eukaryotic cells contain mitochondria? What function do mitochondria perform?



- Endomembrane
- Energy Organelles
- Cytoskeleton

7. What unique metabolic activity occurs in chloroplasts?

8. What cellular functions do centrioles participate in?



- Art Quizzes:
  - Nucleosomes
  - Rough ER and Protein Synthesis
  - Protein Transport

9. What kinds of cytoskeleton fibers are stable and which are changeable?

10. How do cilia compare with eukaryotic flagella?

### 5.4 Symbiosis played a key role in the origin of some eukaryotic organelles.

- Present-day mitochondria and chloroplasts probably evolved as a consequence of early endosymbiosis: the ancestor of the eukaryotic cell engulfed a bacterium, and the bacterium continued to function within the host cell.

11. What is the endosymbiont theory? What is the evidence supporting this theory?



- Scientists on Science: The Joy of Discovery

