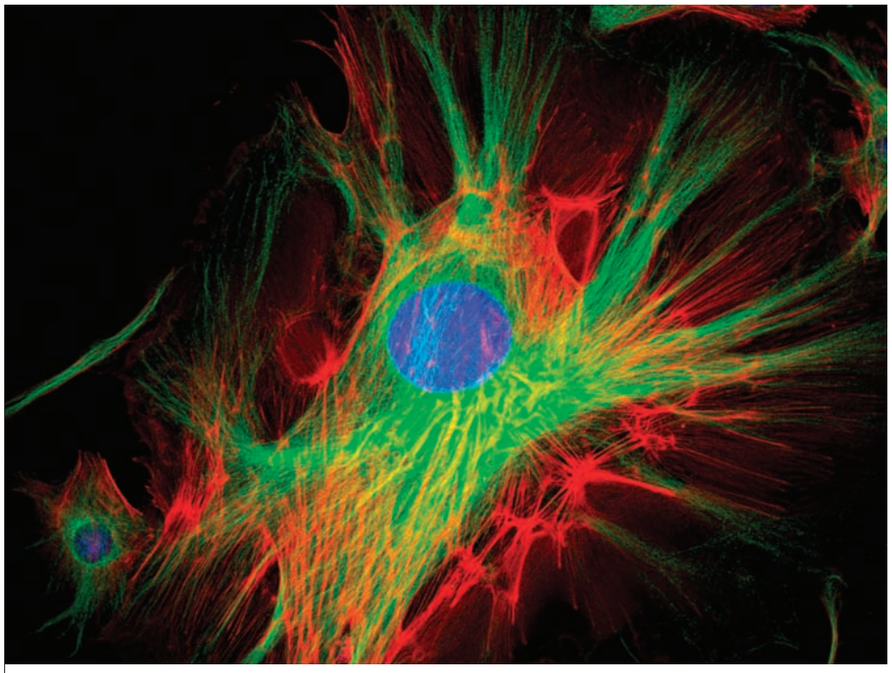


David Becker/Science Photo Library/Photo Researchers, Inc.

Cells fluorescently labeled to visualize their internal structure (confocal light micrograph). Cell nuclei are shown in blue and parts of the cytoskeleton in red and green.

Study Plan

5.1 Basic Features of Cell Structure and Function

Cells are small and are visualized using a microscope

Cells have a DNA-containing central region that is surrounded by cytoplasm

Cells occur in prokaryotic and eukaryotic forms, each with distinctive structures and organization

5.2 Prokaryotic Cells

Prokaryotic cells have little or no internal membrane structure

5.3 Eukaryotic Cells

Eukaryotic cells have a membrane-enclosed nucleus and cytoplasmic organelles

The eukaryotic nucleus contains much more DNA than the prokaryotic nucleoid

An endomembrane system divides the cytoplasm into functional and structural compartments

Mitochondria are the powerhouses of the cell

Microbodies carry out vital reactions that link metabolic pathways

The cytoskeleton supports and moves cell structures

Flagella propel cells, and cilia move materials over the cell surface

5.4 Specialized Structures of Plant Cells

Chloroplasts are biochemical factories powered by sunlight

Central vacuoles have diverse roles in storage, structural support, and cell growth

Cell walls support and protect plant cells

5.5 The Animal Cell Surface

Cell adhesion molecules organize animal cells into tissues and organs

Cell junctions reinforce cell adhesions and provide avenues of communication

The extracellular matrix organizes the cell exterior

5 The Cell: An Overview

Why It Matters

In the mid-1600s, Robert Hooke, Curator of Instruments for the Royal Society of England, was at the forefront of studies applying the newly invented light microscopes to biological materials. When Hooke looked at thinly sliced cork from a mature tree through a microscope, he observed tiny compartments **(Figure 5.1a).** He gave them the Latin name *cellulae,* meaning "small rooms"—hence, the origin of the biological term *cell*. Hooke was actually looking at the walls of dead cells, which is what cork consists of. Hooke also looked at the central pith of a plant stem, in which he found cells "fill'd with juices." Thus, he observed living cells, as well as dead and empty ones.

Reports of cells also came from other sources. By the late 1600s, Anton van Leeuwenhoek **(Figure 5.1b),** a Dutch shopkeeper, observed "many very little animalcules, very prettily a-moving," using a single-lens microscope of his own construction. Leeuwenhoek discovered and described diverse protists, sperm cells, and even bacteria, organisms so small that they would not be seen by others for another two centuries.

In the 1820s, improvements in microscopes brought cells into sharper focus. Robert Brown, an English botanist, noticed a discrete,

Figure 5.1
Investigations leading to the first descriptions of cells. **(a)** The cork cells drawn by Robert Hooke and the compound microscope he used to examine them. **(b)** Anton van Leeuwenhoek holding his microscope, which consisted of a single, small sphere of glass fixed in a holder. He viewed objects by holding them close to one side of the glass sphere and looking at them through the other side.

spherical body inside some cells; he called it a *nucleus*. In 1838, a German botanist, Matthias Schleiden, speculated that the nucleus had something to do with the development of a cell. The following year, the zoologist Theodor Schwann of Germany expanded Schleiden's idea to propose that all animals and plants consist of cells that contain a nucleus. He also proposed that even when a cell forms part of a larger organism, it has an individual life of its own. However, an important question remained: Where do cells come from? A decade later, the German physiologist Rudolf Virchow answered this question. From his studies of cell growth and reproduction, Virchow proposed that cells arise only from preexisting cells by a process of division.

Thus, by the middle of the nineteenth century, microscopic observations had yielded three profound generalizations, which together constitute what is now known as the **cell theory**:

1. All organisms are composed of one or more cells.
2. The cell is the smallest unit that has the properties of life.
3. Cells arise only from the growth and division of preexisting cells.

These tenets were fundamental to the development of biological science.

This chapter provides an overview of our current understanding of the structure and functions of cells, emphasizing both the similarities among all cells and some of the most basic differences among cells of various organisms. The variations in cells that help make particular groups of organisms distinctive are discussed in later chapters. This chapter also introduces some of the modern microscopes that transport us more deeply into the spectacular worlds of cells "fill'd with juices" and enable us to learn more about cell structure.

5.1 Basic Features of Cell Structure and Function

As the basic structural and functional units of all living organisms, cells carry out the essential processes of life. They contain highly organized systems of molecules, including the nucleic acids DNA and RNA, which carry hereditary information and direct the manufacture of cellular molecules. Cells use organic fuel molecules as energy sources for their activities. They use that energy to generate movements, and can alter their internal reactions in response to changes in their external environment. Cells can also duplicate and pass on their hereditary information as part of cellular reproduction. All these activities occur in cells that, in most cases, are invisible to the naked eye.

Some types of organisms, including bacteria, archaeans, and some protists such as the protozoa, are

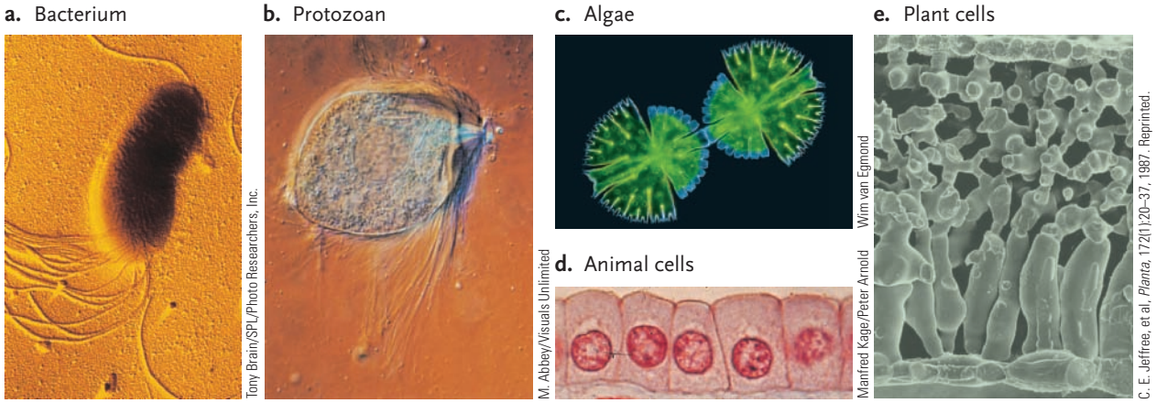


Figure 5.2
Examples of the varied kinds of cells. **(a)** A bacterial cell with flagella. **(b)** A trichomonad, a protist living in a termite's gut. **(c)** Two cells of *Micrasterias*, an alga. **(d)** Cells of a surface layer in the human kidney. **(e)** Cells in the leaf of a kidney bean plant *(Phaseolus)*.

unicellular. Each cell is a functionally independent organism capable of carrying out all life activities. In more complex multicellular organisms, including plants and animals, the activities of life are divided among varying numbers of specialized cells. However, individual cells of multicellular organisms are potentially capable of surviving by themselves if placed in a chemical medium that can sustain them.

If cells are broken open, the property of life is lost: they are unable to grow, reproduce, or respond to outside stimuli in a coordinated, potentially independent fashion. This fact confirms the second tenet of the cell theory: life as we know it does not exist in units more simple than individual cells. *Viruses,* which consist only of a nucleic acid molecule surrounded by a protein coat, cannot carry out all of the activities of life. Their only capacity is to infect living cells and direct them to make more virus particles of the same kind. (Viruses are discussed in Chapters 17 and 25.)

Cells Are Small and Are Visualized Using a Microscope

Cells assume a wide variety of forms in different microorganisms, plants, and animals **(Figure 5.2).** Individual cells range in size from tiny bacteria to an egg yolk, a single cell that can be several centimeters in diameter. Yet, all cells are organized according to the same basic plan, and all have structures that perform similar activities.

Most cells are too small to be seen by the unaided eye: humans cannot see objects smaller than about 0.1 mm in diameter. The smallest bacteria have diameters of about 0.5 μm (a micrometer is 1000 times smaller than a millimeter). The cells of multicellular animals range from about 5 to 30 μm in diameter. Your red blood cells are 7 to 8 μm across—a string of 2500 of these cells is needed to span the width of your thumbnail. Plant cells range from about 10 μm to a few hundred micrometers in diameter. (**Figure 5.3** explains the units of measurement used in biology to study molecules and cells.)

To see cells and the structures within them we use **microscopy**, a technique for producing visible images of objects, biological or otherwise, that are too small to be seen by the human eye **(Figure 5.4).** The instrument of microscopy is the **microscope.** The two common types of microscopes are **light microscopes**, which use light to illuminate the specimen (the object being viewed), and **electron microscopes**, which use electrons to illuminate the specimen. Different types of microscopes give different magnification and resolution of the specimen. Just as for a camera or a pair of binoculars, **magnification** is the ratio of the object as viewed to its real size, usually given as something like 1200×. **Resolution** is the minimum distance two points in the specimen can be separated and still be seen as two points. Resolution depends primarily on the wavelength of light or electrons used to illuminate the specimen; the shorter the wavelength, the better the resolution. Hence, electron microscopes have higher resolution than light microscopes. Biologists choose the type of microscopy technique based on what they need to see in the specimen; selected examples are shown in Figure 5.4.

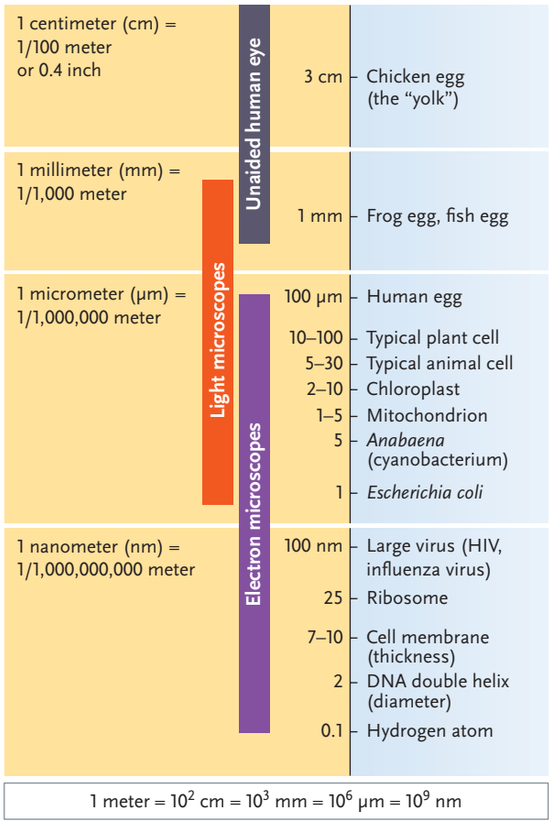


Figure 5.3
Units of measure and the ranges in which they are used in the study of molecules and cells. The vertical scale in each box is logarithmic.

Why are most cells so small? The answer depends partly on the change in the surface area-to-volume ratio of an object as its size increases **(Figure 5.5).** For example, doubling the diameter of a cell increases its volume by eight times but increases its surface area by only four times. The significance of this relationship is that the volume of a cell determines the amount of chemical activity that can take place within it, whereas the surface area determines the amount of substances that can be exchanged between the inside of the cell and the outside environment. Nutrients must constantly enter cells, and wastes must constantly leave; however, past a certain point, increasing the diameter of a cell gives a surface area that is insufficient to maintain an adequate nutrient–waste exchange for its entire volume.

Some cells increase their ability to exchange materials with their surroundings by flattening or by developing surface folds or extensions that increase their surface area. For example, human intestinal cells have closely packed, fingerlike extensions that increase their

Figure 5.4 Research Method

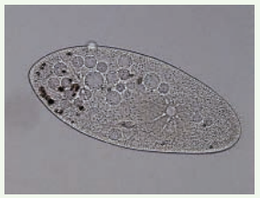
Light and Electron Microscopy

PURPOSE: Microscopy is a widely used technique in biology to view organisms, cells, and structures within cells in their natural state or after being treated (stained) so that specific structures can be seen more clearly. All of the photographs of cells and cell structures in this book were made using microscopy.

PROTOCOL: A light microscope uses a beam of light to illuminate the specimen and forms a magnified image of the specimen with glass lenses. An electron microscope uses a beam of electrons to illuminate the specimen and forms a magnified image with magnetic fields. Electron microscopy provides higher resolution and higher magnification than light microscopy.

Light microscopy

Micrographs are of the protist *Paramecium*.



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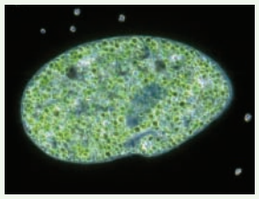
Bright field microscopy: Light passes directly through the specimen. Many cell structures have insufficient contrast to be discerned. Staining with a dye is used to enhance contrast in a specimen as shown here, but this treatment usually fixes and kills the cells.



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Dark field microscopy: Light illuminates the specimen at an angle, and only light scattered by the specimen reaches the viewing lens of the microscope. This gives a bright image of the cell against a black background.

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Phase-contrast microscopy: Differences in refraction (the way light is bent) caused by variations in the density of the specimen are visualized as differences in contrast. Otherwise invisible structures are revealed with this technique, and living cells in action can be photographed or filmed.

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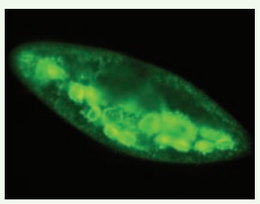
Nomarski (differential interference contrast): Similar to phase-contrast microscopy, special lenses enhance differences in density, giving a cell a 3D appearance.



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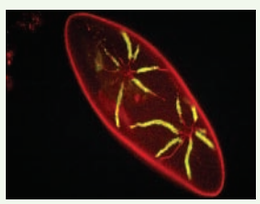
Fluorescence microscopy: Different structures or molecules in cells are stained with specific fluorescent dyes. The stained structures or molecules fluoresce when the microscope illuminates them with ultraviolet light, and their locations are seen by viewing the emitted visible light.



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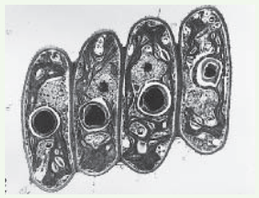
Confocal laser scanning microscopy: Lasers scan across a fluorescently stained specimen, and a computer focuses the light to show a single plane through the cell. This provides a sharper 3D image than other light microscopy techniques.

Electron microscopy

Micrographs are of the green alga *Scenedesmus*.



Jeremy Pickett-Heaps, University of Colorado

Transmission electron microscopy (TEM): A beam of electrons is focused on a thin section of a specimen in a vacuum. Electrons that pass through form the image; structures that scatter electrons appear dark. TEM is used primarily to examine structures within cells. Various staining and fixing methods are used to highlight structures of interest.

Jeremy Pickett-Heaps, University of Colorado

Scanning electron microscopy (SEM): A beam of electrons is scanned across a whole cell or organism, and the electrons excited on the specimen surface are converted to a 3D-appearing image.

INTERPRETING THE RESULTS: Different techniques of light and electron microscopy produce images that reveal different structures or functions of the specimen. A micrograph is a photograph of an image formed by a microscope.

surface area, which greatly enhances their ability to absorb digested food molecules.

Cells Have a DNA-Containing Central Region That Is Surrounded by Cytoplasm

All cells have a central region that contains DNA molecules, which store hereditary information. The hereditary information is organized in the form of *genes*—segments of DNA that code for individual proteins. The central region also contains proteins that help maintain the DNA structure and enzymes that duplicate DNA and copy its information into RNA.

All the parts of the cell that surround the central region comprise the **cytoplasm.** The cytoplasm consists of the **cytosol**, which is an aqueous (water) solution containing ions and various organic molecules, and **organelles** ("little organs"), which are small, organized structures important for cell function. The outer limit of the cytoplasm is the **plasma membrane**, a bilayer made of lipids with embedded protein molecules **(Figure 5.6).**

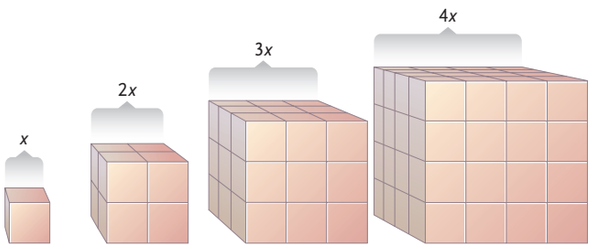
The lipid bilayer of the plasma membrane is a hydrophobic barrier to the passage of water-soluble substances, but selected water-soluble substances can penetrate cell membranes through transport protein channels. The selective movement of ions and water-soluble molecules through the transport proteins maintains the specialized internal ionic and molecular environments required for cellular life. (Membrane structure and functions are discussed further in Chapter 6.)

Many of the cell's vital activities occur in the cytoplasm, including the synthesis and assembly of most of the molecules required for growth and reproduction (except those made in the central region) and the conversion of chemical and light energy into forms that can be used by cells. The cytoplasm also conducts stimulatory signals from the outside into the cell interior and carries out chemical reactions that respond to these signals.

Cells Occur in Prokaryotic and Eukaryotic Forms, Each with Distinctive Structures and Organization

Organisms fall into two fundamental groups, prokaryotes and eukaryotes, based on the organization of their cells. **Prokaryotes** (*pro* = before; *karyon* = nucleus) make up two domains of organisms, the Bacteria and the Archaea. The central region of prokaryotic cells, the **nucleoid**, has no boundary membrane separating it from the cytoplasm. Prokaryotic membranes are limited to the plasma membrane and, in some cases, simple saclike membranes in the cytoplasm.

The **eukaryotes** (*eu* = true) make up the domain Eukarya, which includes all the remaining organisms. The central region of eukaryotic cells, a true **nucleus**, is separated by membranes from the surrounding cytoplasm. The cytoplasm of eukaryotic cells contains membrane systems that form organelles with their own distinct environments and specialized functions. As in prokaryotes, a plasma membrane surrounds eukaryotic cells as the outer limit of the cytoplasm.



Total surface area	$6x^2$	$6\ (2x)^2 = 24x^2$	$6\ (3x)^2 = 54x^2$	$6\ (4x)^2 = 96x^2$
Total volume	x^3	$(2x)^3 = 8x^3$	$(3x)^3 = 27x^3$	$(4x)^3 = 64x^3$
Surface area/ volume ratio	**6:1**	**3:1**	**2:1**	**1.5:1**

Figure 5.5
Relationship between surface area and volume. The surface area of an object increases as a square of the linear dimension, whereas the volume increases as a cube of that dimension.

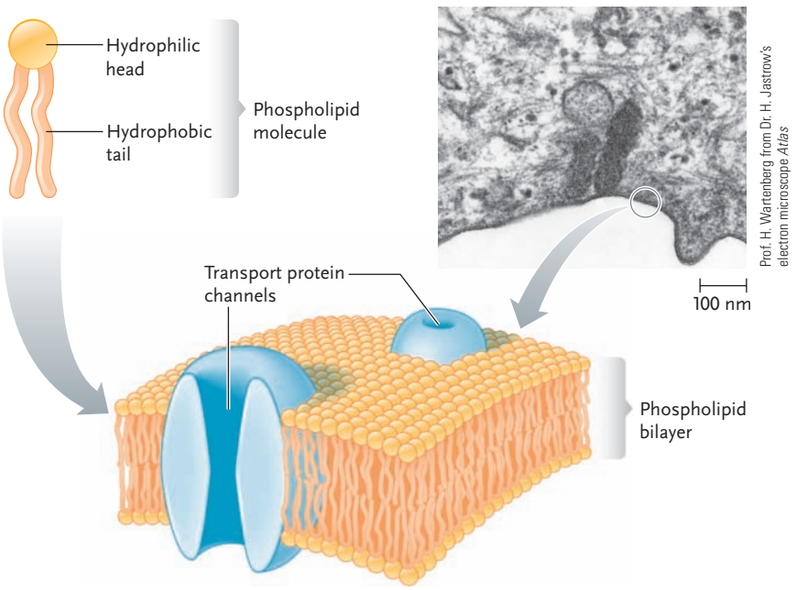


Figure 5.6
The plasma membrane, which forms the outer limit of a cell's cytoplasm. The plasma membrane consists of a phospholipid bilayer, an arrangement of phospholipids two molecules thick, which provides the framework of all biological membranes. Water-soluble substances cannot pass through the phospholipid part of the membrane. Instead, they pass through protein channels in the membrane; two proteins that transport substances across the membrane are shown. Other types of proteins are also associated with the plasma membrane. *(Inset)* Electron micrograph of part of an animal cell, showing the plasma membrane (circled).

Table 5.1 Components of Prokaryotic and Eukaryotic Cells

		Prokaryotes		Eukaryotes			
Cell Component	Major Functions	Bacteria	Archaea	Protists	Fungi	Plants	Animals
Nucleoid	DNA replication and RNA transcription	■	■				
Nucleus	DNA replication and RNA transcription			■	■	■	■
Nuclear envelope	Separation of nucleus from cytoplasm			■	■	■	■
Nucleolus	Ribosomal RNA synthesis and assembly of ribosomal subunits			■	■	■	■
Plasma membrane	Regulation of substances moving into and out of cells	■	■	■	■	■	■
Cell wall	Cell protection and support	■	■	Some	■	■	
Ribosomes	Protein synthesis	■	■	■	■	■	■
Endoplasmic reticulum	Synthesis, transport, and initial modification of membrane proteins, lipids, and secreted proteins			■	■	■	■
Golgi complex	Final modification, sorting, and distribution of membrane lipids, proteins, and secreted proteins			■	■	■	■
Lysosome	Digestion of biological molecules and structures			■	Some	■	■
Mitochondrion	Conversion of energy associated with glucose into ATP			■	■	■	■
Microbody	Housing of reactions that link major pathways			?	?	■	■
Chloroplast	Conversion of light energy to chemical energy of organic molecules			Some		■	
Central vacuole	Storage, cell growth, and support					■	
Microfilament	Reinforcement of cell shape, motility			■	■	■	■
Microtubule	Reinforcement of cell shape, motility			■	■	■	■
Intermediate filament	Reinforcement of cell shape			■			■
Flagellum or cilium with 9 + 2 system of microtubules	Cell motility			Some	Some	Some	■

■ Bullets denote presence of cell component in designated group.

The remainder of this chapter surveys the components of prokaryotic and eukaryotic cells in more detail. **Table 5.1** summarizes these cellular components and notes the organisms in which they appear.

Study Break

What is the plasma membrane, and what are its main functions?

5.2 Prokaryotic Cells

Prokaryotic Cells Have Little or No Internal Membrane Structure

Prokaryotic cells **(Figure 5.7)** are relatively small, usually not much more than a few micrometers in length and a micrometer or less in diameter; they have little or no internal membrane structure. In almost all prokaryotes, the plasma membrane is surrounded by a rigid external layer of material, the **cell wall**, which ranges in thickness from 15 to 100 nm or more (a nanometer is one-billionth of a meter). In many prokaryotic cells, the wall is coated with an external layer of sticky or slimy polysaccharides called a **capsule.** The cell wall provides rigidity to prokaryotic cells and, with the capsule, protects the cell from physical damage.

The plasma membrane performs several vital functions in prokaryotes. Besides transporting materials into and out of the cells, it contains most of the molecular systems that metabolize food molecules into the chemical energy of ATP. In photosynthetic prokaryotes, the molecules that absorb light energy and convert it to the chemical energy of ATP are also associated with the plasma membrane or with internal, saclike membranes derived from the plasma membrane.

In an electron microscope, the nucleoid of a prokaryotic cell is seen to contain a folded mass of DNA (see Figure 5.7). For most species, the DNA is a single,

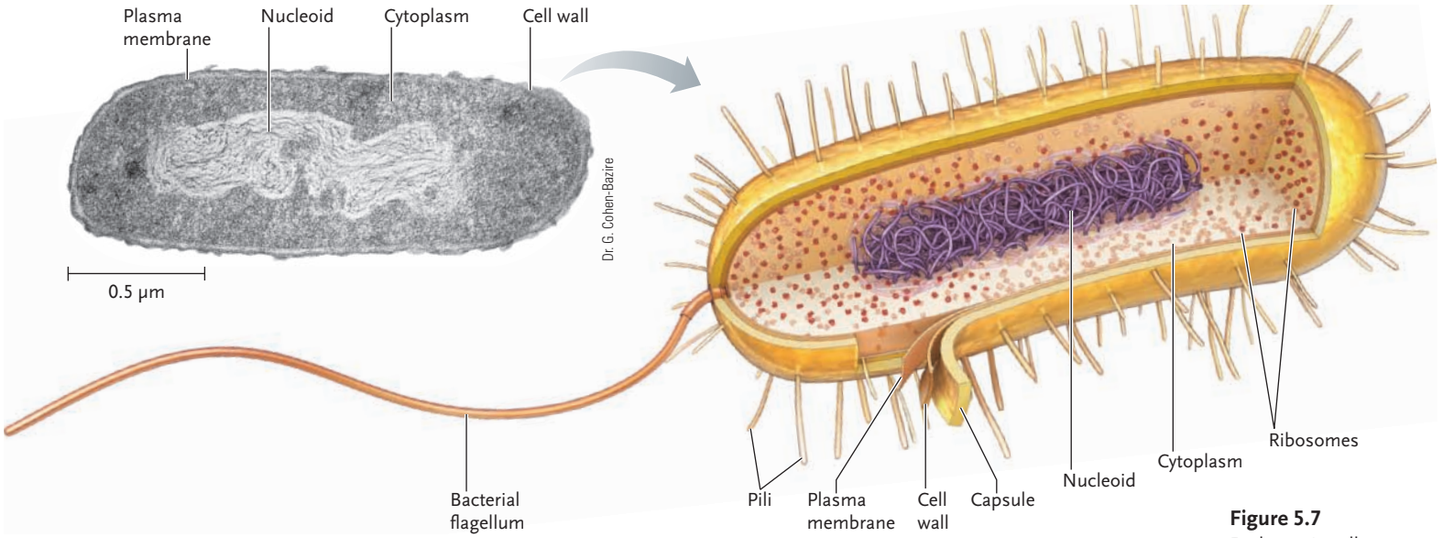


Figure 5.7 **Prokaryotic cell structure.** An electron micrograph (left) and a diagram (right) of the bacterium *Escherichia coli*. The pili extending from the cell wall attach bacterial cells to other cells of the same species or to eukaryotic cells as a part of infection. A typical *E. coli* has four flagella.

circular molecule that unfolds when released from the cell. This DNA molecule is the **prokaryotic chromosome.** (Chapter 17 discusses the genetics of prokaryotes.)

Individual genes in the DNA molecule encode the information required to make proteins. This information is copied into a type of RNA molecule called *messenger RNA*. Small, roughly spherical particles in the cytoplasm, the **ribosomes**, are organelles that use the information in the messenger RNA to assemble amino acids into proteins. A prokaryotic ribosome consists of a large and a small subunit, each formed from a combination of *ribosomal RNA* and protein molecules. In all, each prokaryotic ribosome contains three types of ribosomal RNA molecules, which are also copied from the DNA, and more than 50 proteins.

Many prokaryotes swim by means of long, thread-like protein fibers called **flagella** (singular, *flagellum*), which extend from the cell surface (see Figure 5.2a). The **prokaryotic flagellum**, which is helically shaped, rotates in a socket in the plasma membrane and cell wall to push the cell through a liquid medium (see Section 25.1). Prokaryotic flagella are fundamentally different from the much larger and more complex flagella of eukaryotic cells, which are described in Section 5.3.

Although prokaryotic cells appear relatively simple, their simplicity is deceptive. Most can use a variety of substances as energy and carbon sources, and they are able to synthesize almost all of their required organic molecules from simple inorganic raw materials. In many respects, prokaryotes are more versatile biochemically than eukaryotes. Their small size and metabolic versatility are reflected in their abundance; prokaryotes vastly outnumber all other types of organisms and live successfully in almost all regions of Earth's surface. (Chapter 25 outlines the diversity of prokaryotes and extends the discussion of prokaryotic structure.)

The two domains of the prokaryotes, the Bacteria and the Archaea, share many biochemical and molecular features. However, the archaeans also share some features with eukaryotes and have other characteristics that are unique to their group. *Insights from the Molecular Revolution* describes the discovery of features that support the classification of the Archaea as a separate domain.

Study Break

Where in a prokaryotic cell is DNA found? How is that DNA organized?

5.3 Eukaryotic Cells

Eukaryotic Cells Have a Membrane-Enclosed Nucleus and Cytoplasmic Organelles

The domain of the eukaryotes, Eukarya, is divided into four major groups: the protists, fungi, animals, and plants. The cells of all eukaryotes have a true nucleus enclosed by membranes. The cytoplasm surrounding the nucleus contains a remarkable system of membranous organelles, each specialized to carry out one or more major functions of energy metabolism and molecular synthesis, storage, and transport. The cytosol, the cytoplasmic solution surrounding the organelles, participates in energy metabolism and molecular synthesis and performs specialized functions in support and motility.

The eukaryotic plasma membrane carries out various functions through embedded proteins. Proteins that form channels through the membrane transport

Insights from the Molecular Revolution

An Old Kingdom in a New Domain

In 1996, Carol J. Bult, Carl R. Woese, J. Craig Venter, and 37 other scientists at the Institute for Genomic Research published the complete DNA sequence of *Methanococcus jannaschii*, a member of the prokaryotic domain Archaea. Information obtained from the DNA sequence clearly supports the conclusion that archaeans are as different from the Bacteria, the other prokaryotic domain, as they are from the eukaryotes.

Many archaeans live in extreme environments that can be tolerated by no other organisms, suggesting that they might belong in a distinct domain. For example, *Methanococcus* was first found in an oceanic hot water vent at a depth of more than 2600 m (8500 feet). It can live at temperatures as high as 94°C, which is almost the temperature of boiling water, and can tolerate pressures as high as 200 times the pressure of air at sea level!

The complete DNA sequence of *Methanococcus* was obtained using techniques outlined in Chapter 18. Using computer algorithms, the scientists compared the final sequence with the already known sequences of several bacteria and of brewer's yeast *(Saccharomyces cerevisiae)*, the first eukaryote to be sequenced completely. They found genes coding for 1738 proteins in the *Methanococcus* DNA. Of these, only 38% were related to genes coding for known proteins in either bacteria or eukaryotes. The remaining 62%, representing sequences with no known relatives in organisms of the other domains, demonstrated the unique character of the archaeans.

Some features of *Methanococcus* DNA are typically prokaryotic. Its single, circular chromosome is in a nucleoid, which is not bounded by a membrane. Its genes are organized into functional groups called *operons*, each having several genes copied as a unit into a single messenger RNA molecule (see discussion in Section 16.1). By contrast, each gene in eukaryotes is copied into a separate messenger RNA molecule. Some of the proteins encoded in *Methanococcus* DNA, including enzymes active in energy metabolism, membrane transport, and cell division, are similar to those of bacteria. Other proteins encoded in the *Methanococcus* DNA are similar to those of eukaryotes, including enzymes and other proteins that carry out DNA replication and the copying of genes into messenger RNA.

Thus, *Methanococcus* has a majority of genes that are unique, some that are typically bacterial, and some that are typically eukaryotic. This finding supports the proposal, first advanced by Woese, that *Methanococcus* and its archaean relatives are a separate domain of life, with the Bacteria and the Eukarya as the other domains. Woese's three-domain system is used in this book.

substances into and out of the cell. Other proteins in the plasma membrane act as receptors; they recognize and bind specific signal molecules in the cellular environment and trigger internal responses. In some eukaryotes, particularly animals, other plasma membrane proteins recognize and adhere to molecules on the surfaces of other cells. Other plasma membrane proteins are important markers in the immune system, labeling cells as "self," that is, belonging to the organism. Therefore, the immune system can identify cells without those markers as being foreign, most likely *pathogens* (disease-causing organisms or viruses).

A supportive cell wall surrounds the plasma membrane of fungal, plant, and many cells of protists. Because the cell wall lies outside the plasma membrane, it is an *extracellular* structure (*extra* = outside). Although animal cells do not have cell walls, they also form extracellular material with supportive and other functions.

Figure 5.8 show where the nucleus, cytoplasmic organelles, and other structures are located in representative animal cells. **Figure 5.9** show their locations in plant cells. The following sections discuss the structure and function of eukaryotic cell parts in more detail, beginning with the nucleus.

The Eukaryotic Nucleus Contains Much More DNA Than the Prokaryotic Nucleoid

The nucleus (see Figures 5.8 and 5.9) is separated from the cytoplasm by the **nuclear envelope**, which consists of two membranes, one layered just inside the other and separated by a narrow space **(Figure 5.10). Nuclear pores** form openings through both membranes. The pores are made of protein structures that control the movement of large molecules, such as RNA and proteins, between the nucleus and cytoplasm. A network of protein filaments called *lamins* lines and reinforces the inner surface of the nuclear envelope in animal cells. Other, unrelated reinforcing proteins line the inner surface of the nuclear envelope in many protists, fungi, and plants.

The liquid or semiliquid substance within the nucleus is called the **nucleoplasm.** Most of the space inside the nucleus is filled with **chromatin**, a combination of DNA and proteins. By contrast with most prokaryotes, most of the hereditary information of a eukaryote is distributed among several to many linear DNA molecules in the nucleus. Each individual DNA molecule with its associated proteins is a **eukaryotic chromosome.** The terms *chromatin* and *chromosome* are similar but have distinct meanings. *Chromatin*

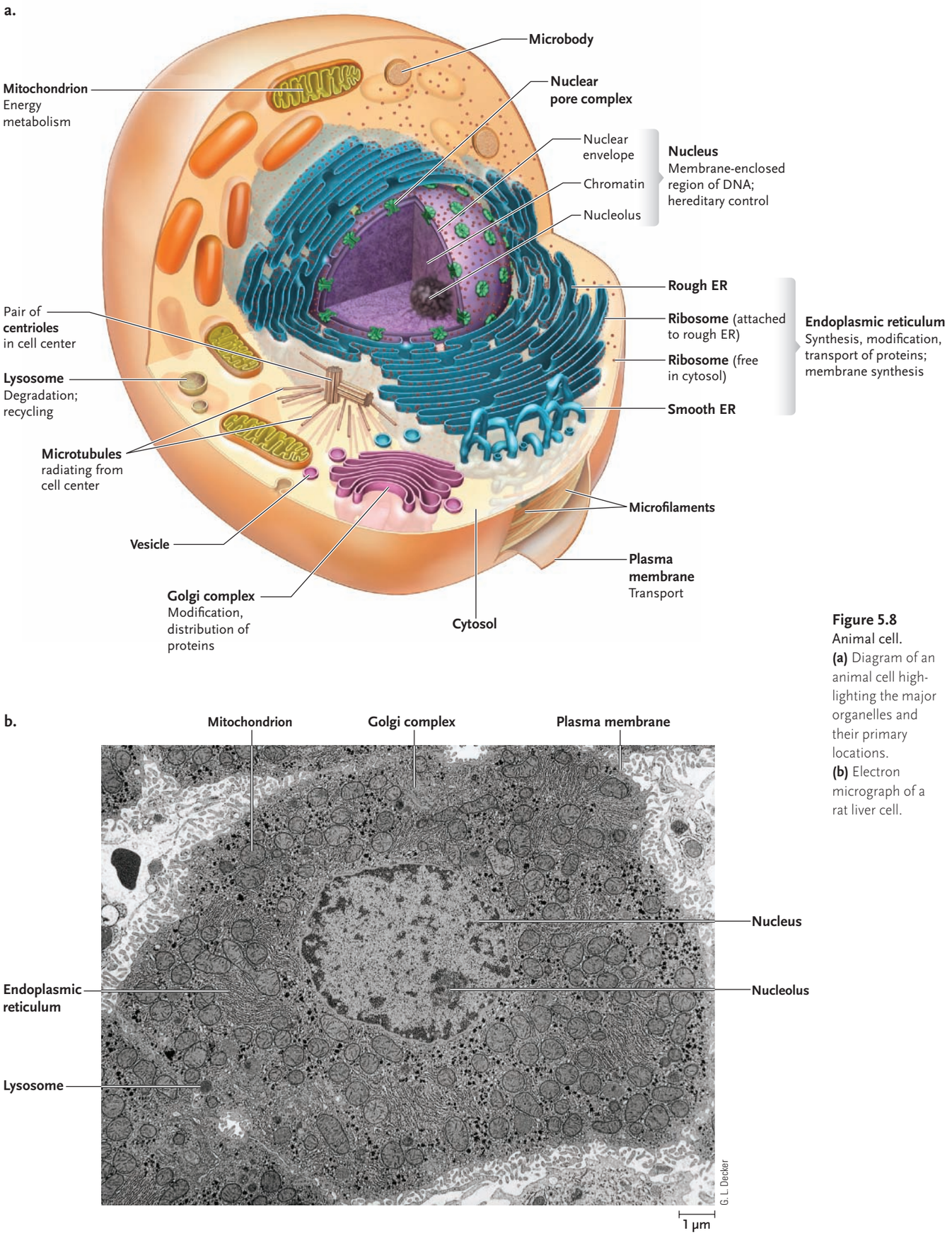


Figure 5.8
Animal cell.
(a) Diagram of an animal cell highlighting the major organelles and their primary locations.
(b) Electron micrograph of a rat liver cell.

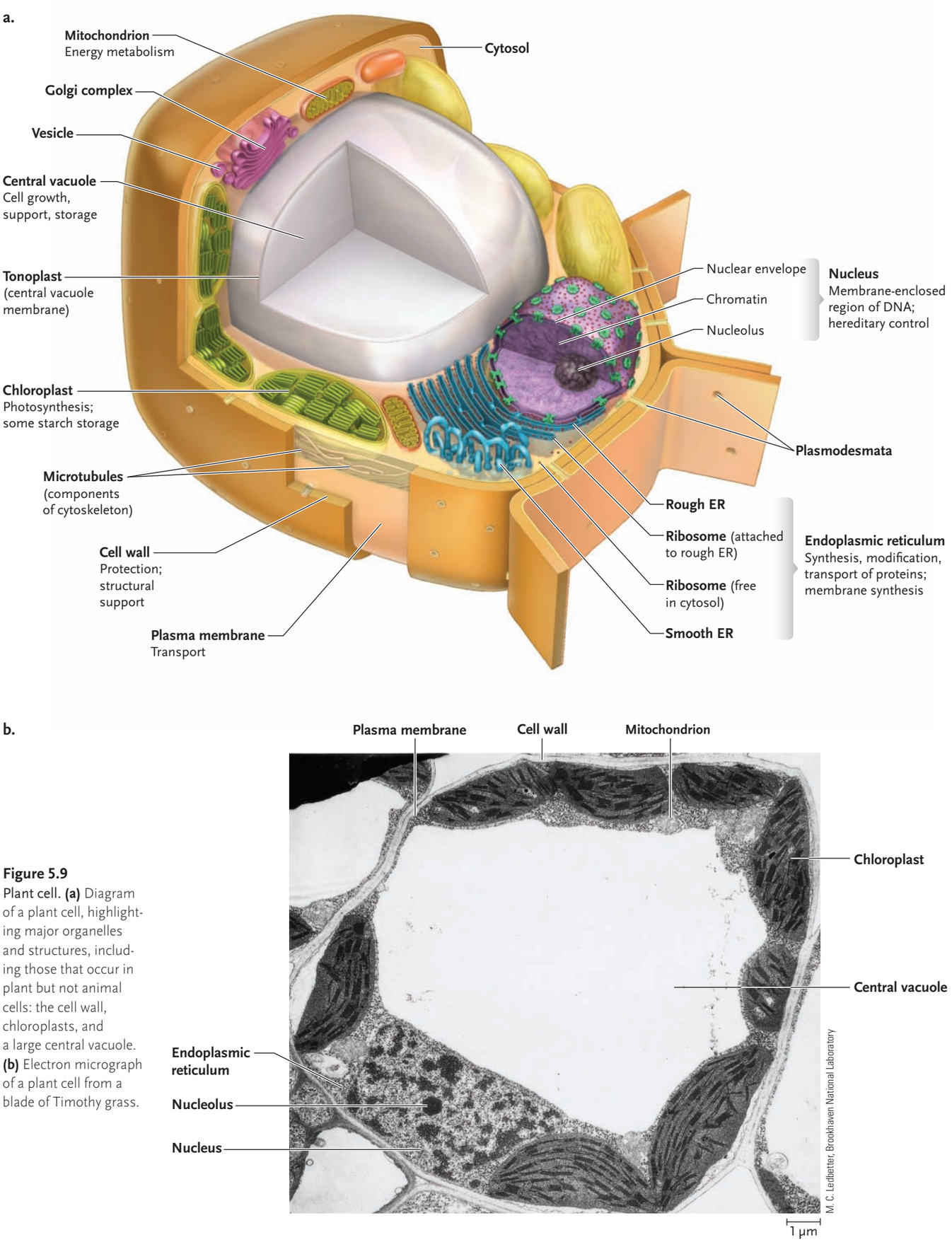


Figure 5.9
Plant cell. **(a)** Diagram of a plant cell, highlighting major organelles and structures, including those that occur in plant but not animal cells: the cell wall, chloroplasts, and a large central vacuole. **(b)** Electron micrograph of a plant cell from a blade of Timothy grass.

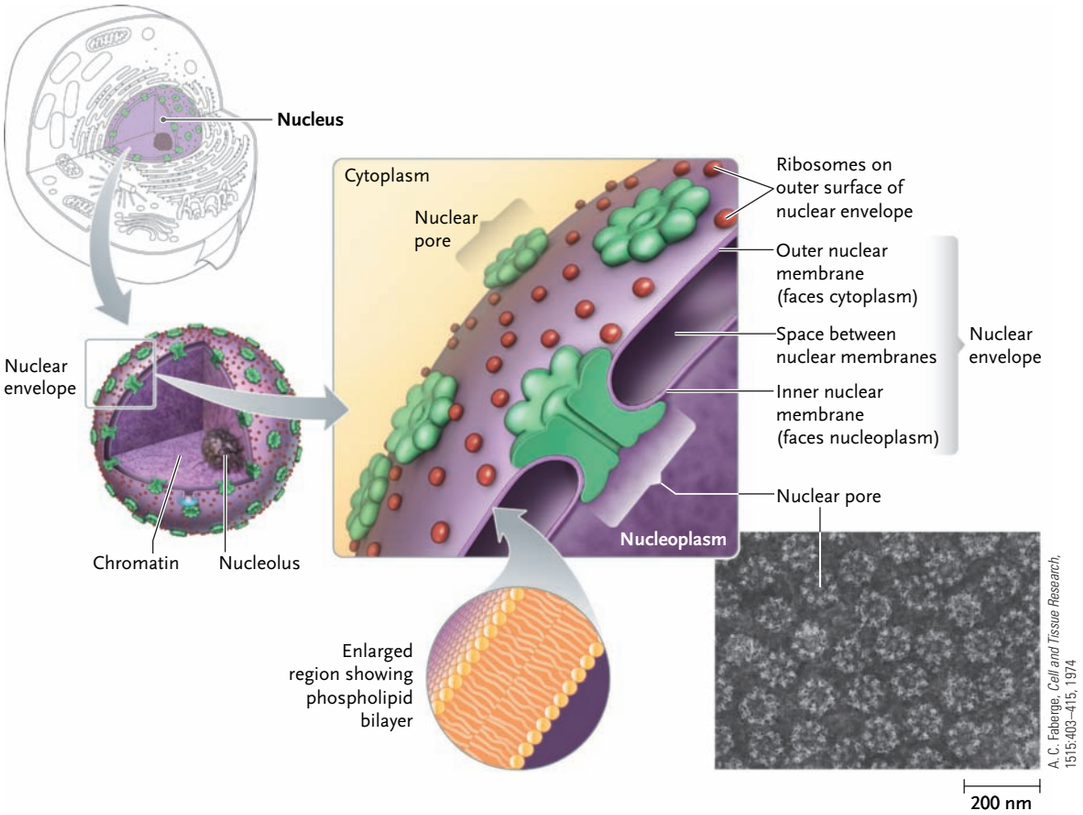


Figure 5.10
The nuclear envelope, which consists of a system of two concentric membranes perforated by nuclear pores. The electron micrograph shows nuclear pores; each pore is an organized cluster of membrane proteins that spans the membrane and facilitates transport of molecules between the nucleus and cytoplasm.

refers to any collection of eukaryotic DNA molecules with their associated proteins. *Chromosome* refers to one complete DNA molecule with its associated proteins.

Eukaryotic nuclei contain much more DNA than do prokaryotic nucleoids. For example, the entire complement of 46 chromosomes in the nucleus of a human cell has a total DNA length of about 2 meters (m), compared with about 1500 μm in prokaryotic cells with the most DNA. Some eukaryotic cells contain even more DNA; for example, a single frog or salamander nucleus, although of microscopic diameter, is packed with about 10 m of DNA!

A eukaryotic nucleus also contains one or more **nucleoli** (singular, *nucleolus*), which look like irregular masses of small fibers and granules in the electron microscope (see Figures 5.8b and 5.9b). These structures form around the genes coding for the ribosomal RNA molecules of ribosomes. Within the nucleolus, the information in ribosomal RNA genes is copied into the ribosomal RNA molecules, which combine with proteins to form ribosomal subunits. The ribosomal subunits then leave the nucleoli and exit the nucleus through the nuclear pores to enter the cytoplasm, where they join to form complete ribosomes.

The genes for most of the proteins that the organism can make are found within the chromatin, as are the genes for specialized RNA molecules such as ribosomal RNA molecules. Expression of these genes is carefully controlled as required for the function of each cell. (The other proteins in the cell are specified by DNA in the mitochondria and chloroplasts.)

An Endomembrane System Divides the Cytoplasm into Functional and Structural Compartments

Eukaryotic cells are characterized by an **endomembrane system** (*endo* = within), a collection of interrelated internal membranous sacs that divide the cell into functional and structural compartments. The endomembrane system has a number of functions, including the synthesis and modification of proteins and their transport into membranes and organelles or to the outside of the cell, the synthesis of lipids, and the detoxification of some toxins. The membranes of the system are connected either directly in the physical sense or indirectly by **vesicles**, which are small membrane-bound compartments that transfer substances between parts of the system.

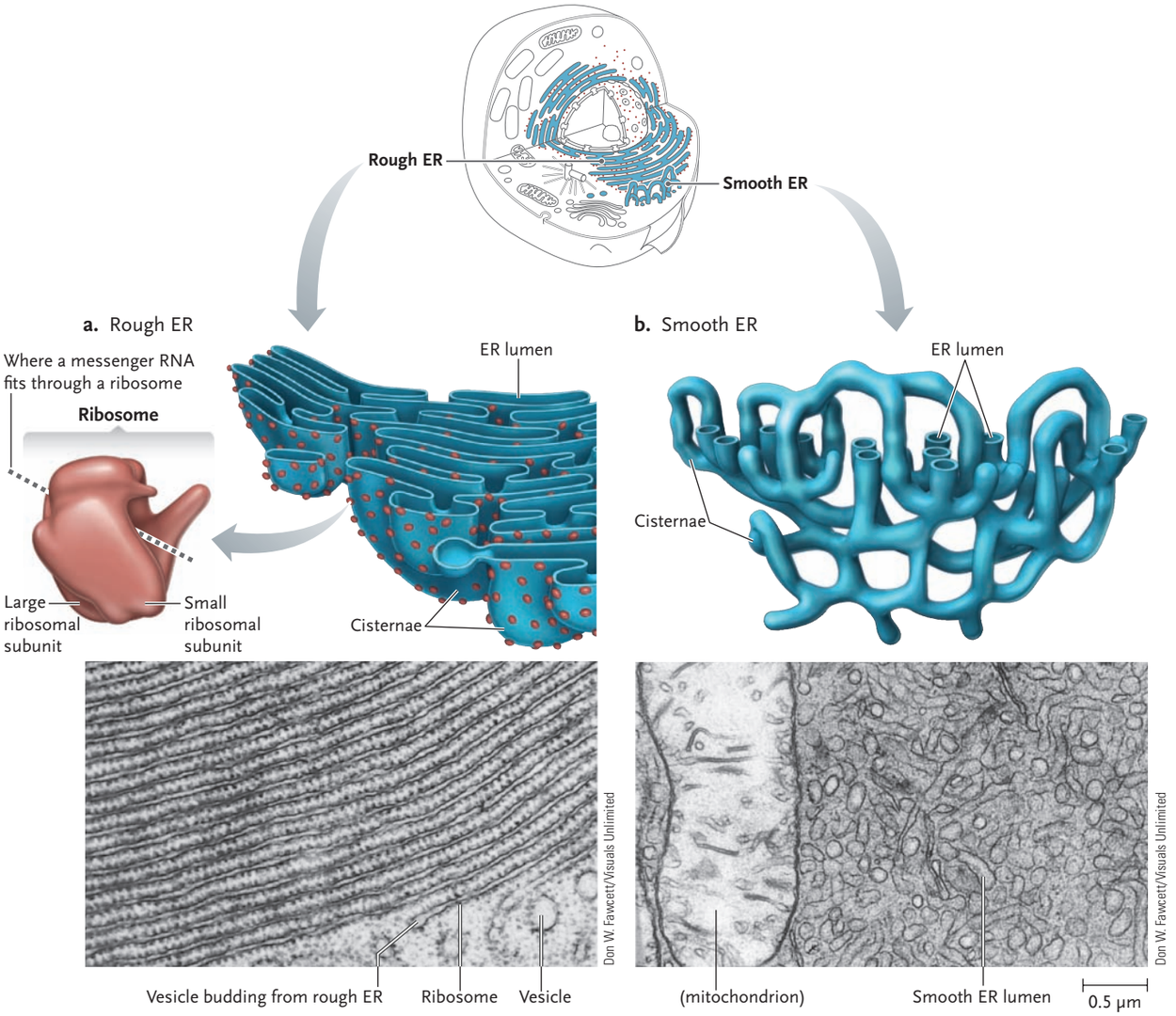


Figure 5.11
The endoplasmic reticulum.
(a) Rough ER, showing the ribosomes that stud the membrane surfaces facing the cytoplasm. The structure of a single ribosome is shown on the top left. **(b)** Smooth ER membranes.

The components of the endomembrane system include the endoplasmic reticulum, Golgi complex, nuclear envelope, lysosomes, vesicles, and plasma membrane. The plasma membrane and the nuclear envelope are discussed earlier in this chapter. The functions of the other organelles are described in the following sections.

Endoplasmic Reticulum. The **endoplasmic reticulum (ER)** is an extensive interconnected network (*reticulum* = little net) of membranous channels and vesicles called **cisternae** (singular, *cisterna*). Each cisterna is formed by a single membrane that surrounds an enclosed space called the **ER lumen (Figure 5.11).** The ER occurs in two forms: rough ER and smooth ER, each with specialized structure and function.

The **rough ER** gets its name from the many ribosomes that stud its outer surface. Like a prokaryotic ribosome, a eukaryotic ribosome consists of a large and a small subunit (see Figure 5.11a). Eukaryotic ribosomes are larger than prokaryotic ribosomes and contain four types of ribosomal RNA molecules and more than 80 proteins. Their function is identical to that of prokaryotic ribosomes: they use the information in messenger RNA to assemble amino acids into proteins.

The proteins made on ribosomes attached to the ER enter the ER lumen, where they fold into their final form. Chemical modifications of these proteins, such as addition of carbohydrate groups to produce glycoproteins, occur in the lumen. The proteins are then delivered to other regions of the cell within small vesicles that pinch off from the ER, travel through the cytosol, and join with the organelle that performs the next steps in their modification and distribution. For most of the proteins made on the rough ER, the next destination is the Golgi complex, which packages and sorts them for delivery to their final destinations.

The outer membrane of the nuclear envelope is closely related in structure and function to the rough

ER, to which it is often connected. This membrane is also a "rough" membrane, covered with ribosomes attached to the surface facing the cytoplasm. The proteins made on these ribosomes enter the space between the two nuclear envelope membranes. From there, the proteins can move into the ER and on to other cellular locations.

Proteins made on ribosomes that are freely suspended in the cytosol may remain in the cytosol, pass through the nuclear pores to enter the nucleus, or become parts of mitochondria, chloroplasts, the cytoskeleton, or other cytoplasmic structures. Proteins that enter the nucleus become part of chromatin or remain in solution in the nucleoplasm.

The **smooth ER** is so called because its membranes have no ribosomes attached to their surfaces (see Figure 5.11b). The smooth ER has various functions in the cytoplasm, including synthesis of lipids that become part of cell membranes. In some cells, such as those of the liver, smooth ER membranes contain enzymes that convert drugs, poisons, and toxic by-products of cellular metabolism into substances that can be tolerated or more easily removed from the body.

The rough and smooth ER membranes are often connected, making the entire ER system a continuous network of interconnected channels in the cytoplasm. The relative proportions of rough and smooth ER reflect cellular activities in protein and lipid synthesis. Cells that are highly active in making proteins to be released outside the cell, such as pancreatic cells that make digestive enzymes, are packed with rough ER but have relatively little smooth ER. By contrast, cells that primarily synthesize lipids or break down toxic substances are packed with smooth ER but contain little rough ER.

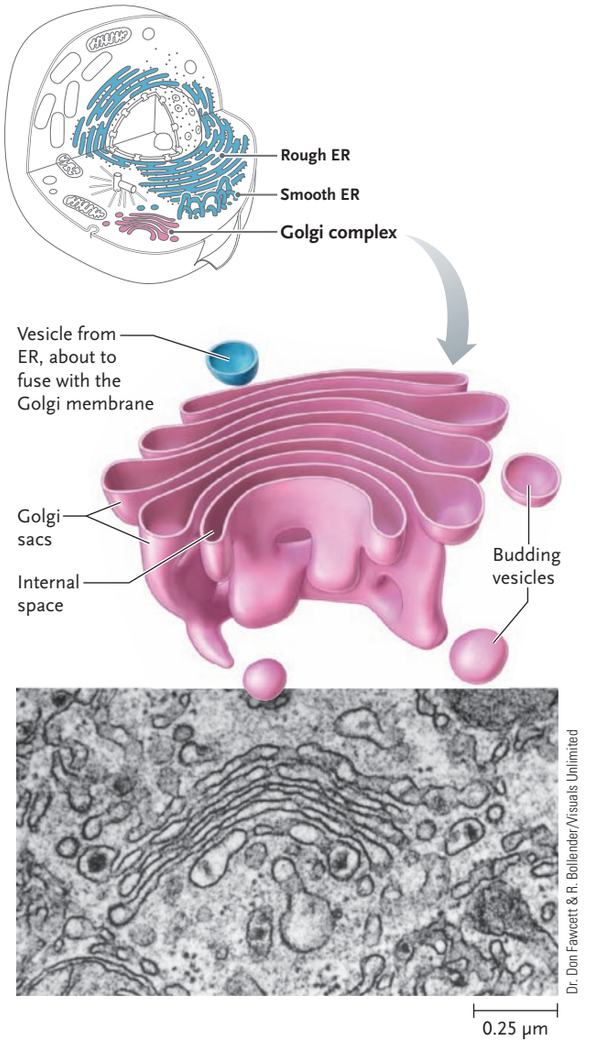


Figure 5.12
The Golgi complex.

Golgi Complex. Camillo Golgi, a late-nineteenth-century Italian neuroscientist and Nobel laureate, discovered the Golgi complex. The **Golgi complex** consists of a stack of flattened, membranous sacs without attached ribosomes. In most cells, the complex looks like a stack of cupped pancakes **(Figure 5.12).** The Golgi complex is usually located near concentrations of rough ER membranes, between the ER and the plasma membrane.

The Golgi complex receives proteins that were made in the ER and transported to the complex in vesicles. Within the Golgi complex, further chemical modifications of the proteins occur, for example, removal of segments of the amino acid chain, addition of small functional groups, or addition of lipid or carbohydrate units. The modified proteins then are sorted into vesicles that pinch off from the margins of Golgi sacs on the side of the complex that faces the plasma membrane.

The Golgi complex regulates the movement of several types of proteins. Some are secreted from the cell, others become embedded in the plasma membrane as integral membrane proteins, and yet others are placed in lysosomes. For instance, proteins secreted from the cell are transported to the plasma membrane by **secretory vesicles**, which release their contents to the exterior by **exocytosis (Figure 5.13a).** In this process, a secretory vesicle fuses with the plasma membrane and spills the vesicle contents to the outside.

Vesicles also may form by the reverse process, called **endocytosis**, which brings molecules into the cell from the exterior **(Figure 5.13b).** In this process, the plasma membrane forms a pocket, which bulges inward and pinches off into the cytoplasm as an **endocytic vesicle.** Once in the cytoplasm, endocytic vesicles, which contain segments of the plasma membrane as well as proteins and other molecules, are carried to the Golgi complex or to other destinations such as lysosomes in animal cells. The substances carried to the Golgi complex are sorted and placed into vesicles for routing to other locations, which may include lysosomes. Those routed to lysosomes are digested into molecular subunits that may be recycled as the building blocks for the biological molecules of the cell. Exo-

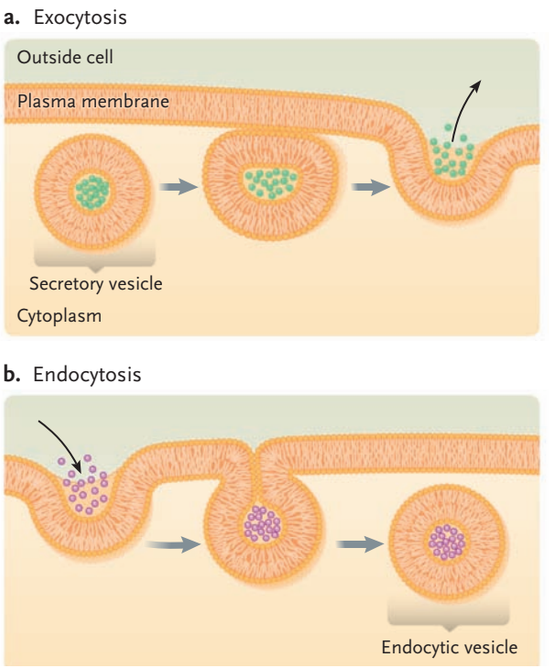


Figure 5.13
Exocytosis and endocytosis.

cytosis and endocytosis are discussed in more detail in Chapter 6.

Lysosomes. **Lysosomes** are membrane-bound vesicles that contain more than 30 hydrolytic enzymes for the digestion of many complex molecules, including proteins, lipids, nucleic acids, and polysaccharides **(Figure 5.14).** The cell recycles the subunits of these molecules.

Lysosomes are formed by budding from the Golgi complex. Their hydrolytic enzymes are synthesized in the rough ER, modified in the lumen of the ER to identify them as being bound for a lysosome, transported to the Golgi complex in a vesicle, and then packaged in the budding lysosome.

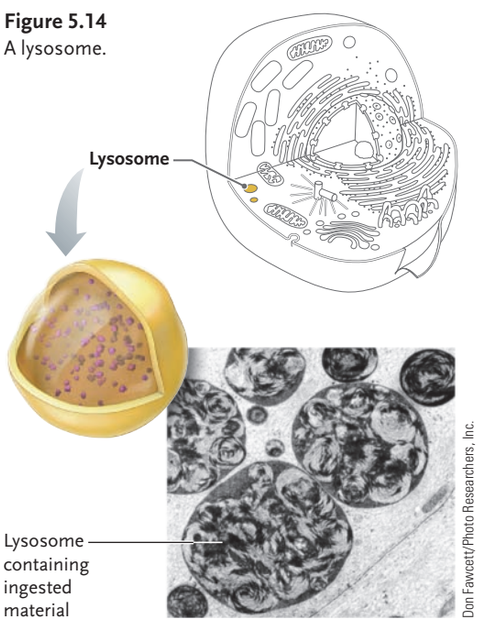


Figure 5.14
A lysosome.

The pH within lysosomes is acidic (pH ~5) and is significantly lower than the pH of the cytosol (pH ~7.2). The hydrolytic enzymes in the lysosomes function optimally at the acidic pH within the organelle, but they do not function well at the pH of the cytosol; this difference reduces the risk to the viability of the cell should the enzymes be released from the vesicle.

Lysosomal enzymes can digest several types of materials. They digest food molecules entering the cell by endocytosis when an endocytic vesicle fuses with a lysosome. In a process called *autophagy,* they digest organelles that are not functioning correctly. A membrane surrounds the defective organelle, forming a large vesicle that fuses with one or more lysosomes; the organelle then is degraded by the hydrolytic enzymes. They also play a role in **phagocytosis**, a process in which some types of cells engulf bacteria or other cellular debris to break them down. These cells include the white blood cells known as *phagocytes,* which play an important role in the immune system (see Chapter 43). Phagocytosis produces a large vesicle that contains the engulfed materials until lysosomes fuse with the vesicle and release the hydrolytic enzymes necessary for degrading them.

In certain human genetic diseases known as *lysosomal storage diseases,* one of the hydrolytic enzymes normally found in the lysosome is absent. As a result, the substrate of that enzyme accumulates in the lysosomes, and this accumulation eventually interferes with normal cellular activities. An example is Tay–Sachs disease, which is a fatal disease of the central nervous system caused by the failure to synthesize the enzyme needed for hydrolysis of fatty acid derivatives found in brain and nerve cells.

Summary. In summary, the endomembrane system is a major traffic network for proteins and other substances within the cell. The Golgi complex in particular is a key distribution station for membranes and proteins **(Figure 5.15).** From the Golgi complex, lipids and proteins may move to storage or secretory vesicles, and from the secretory vesicles, they may move to the cell exterior by exocytosis. Membranes and proteins may also move between the nuclear envelope and the endomembrane system. Proteins and other materials that enter cells by endocytosis also enter the endomembrane system to travel to the Golgi complex for sorting and distribution to other locations. Details of how proteins are routed within cells to their final destinations are presented in Chapter 7.

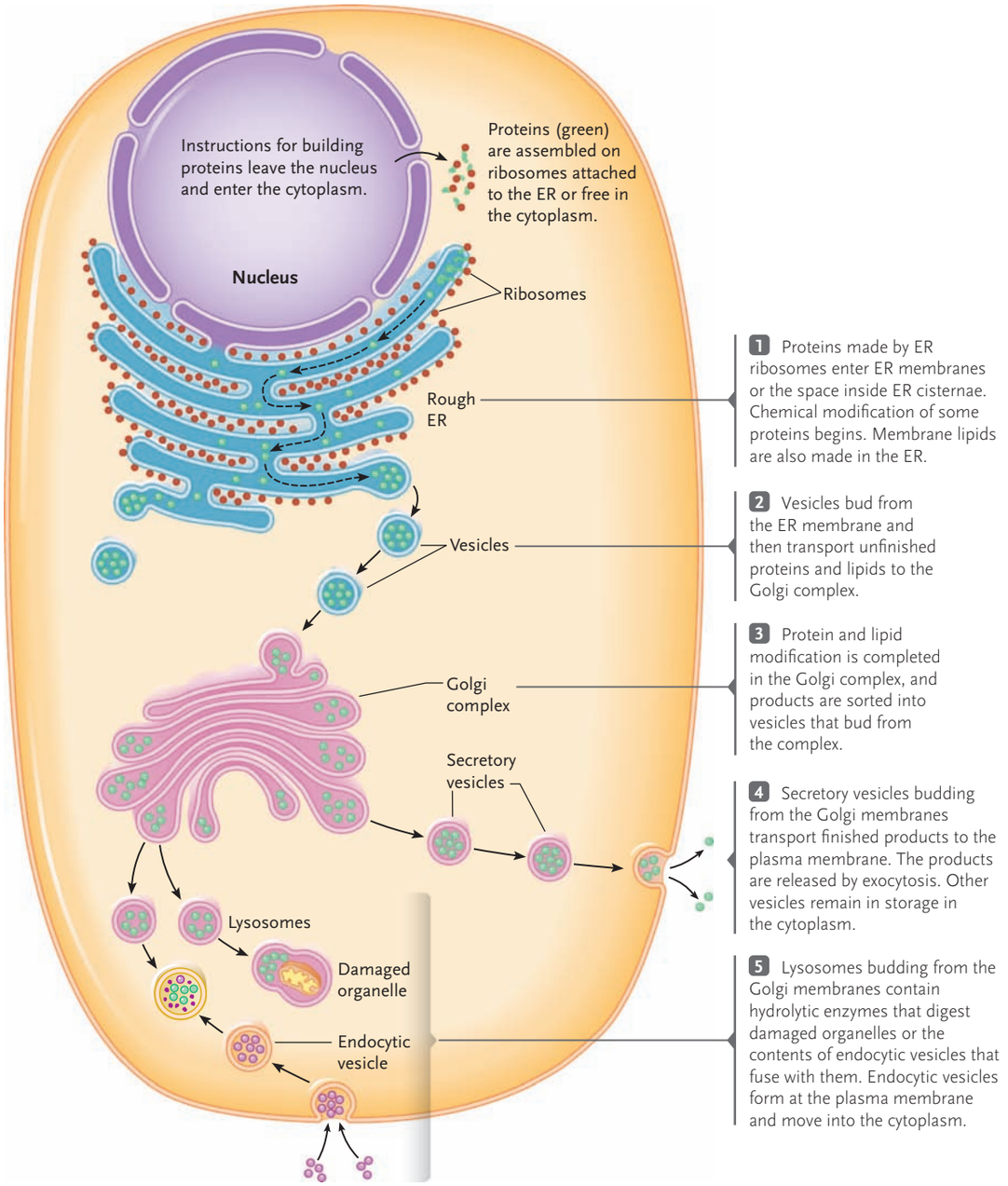


Figure 5.15
Vesicle traffic in the cytoplasm. The ER and Golgi complex are part of the endomembrane system, which releases proteins and other substances to the cell exterior and gathers materials from outside the cell.

Mitochondria Are the Powerhouses of the Cell

Mitochondria (singular, *mitochondrion*) are the membrane-bound organelles in which cellular respiration occurs. *Cellular respiration* is the process by which energy-rich molecules such as sugars, fats, and other fuels are broken down to water and carbon dioxide by mitochondrial reactions, with the release of energy. Much of the energy released by the breakdown is captured in ATP. Mitochondria require oxygen for this process—when you breathe, you are taking in oxygen primarily for your mitochondrial reactions (see Chapter 8). Mitochondria are frequently called the powerhouses of the cell because of their ATP-generating activities.

Mitochondria are enclosed by two membranes **(Figure 5.16).** The **outer mitochondrial membrane** is smooth and covers the outside of the organelle. The surface area of the **inner mitochondrial membrane** is expanded by folds called **cristae** (singular, *crista*). Both membranes surround the innermost compartment of the mitochondrion, called the **mitochondrial matrix.** The ATP-generating reactions of mitochondria occur in the cristae and matrix.

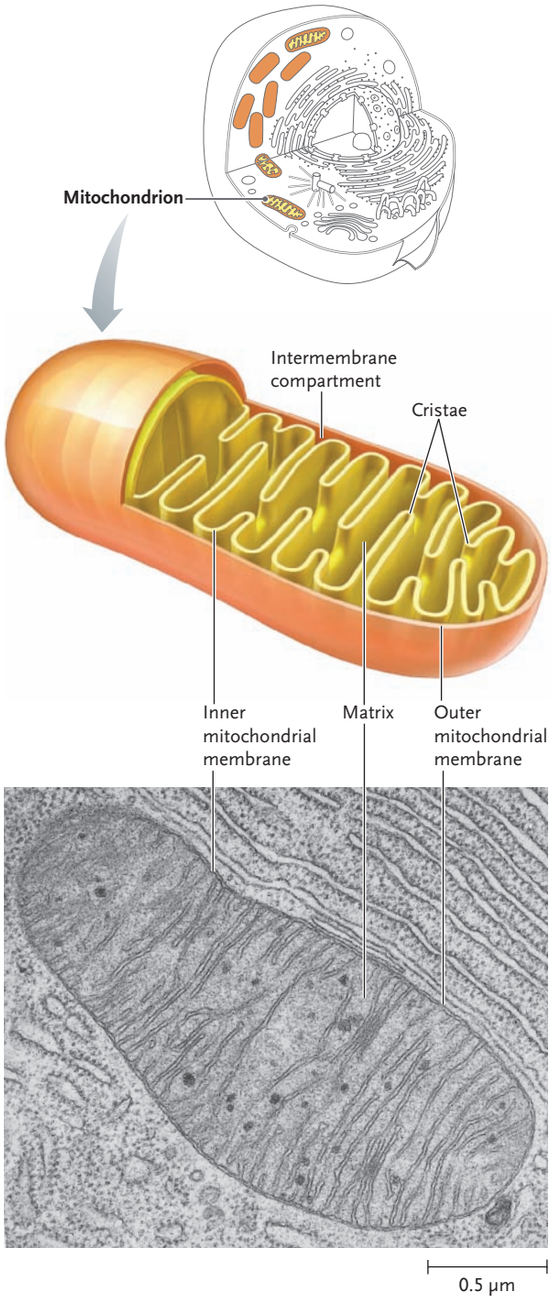


Figure 5.16
Mitochondria. The electron micrograph shows a mitochondrion from bat pancreas, surrounded by cytoplasm that contains rough ER. Cristae extend into the interior of the mitochondrion as folds from the inner mitochondrial membrane. The darkly stained granules inside the mitochondrion are probably lipid deposits.

The mitochondrial matrix also contains DNA and ribosomes that resemble the equivalent structures in bacteria. These and other similarities suggest that mitochondria originated from ancient bacteria that became permanent residents of the cytoplasm during the evolution of eukaryotic cells (see Chapter 24 for further discussion).

Microbodies Carry Out Vital Reactions That Link Metabolic Pathways

Microbodies are small, relatively simple membrane-bound organelles found in various forms in essentially all eukaryotic cells. They consist of a single boundary membrane that encloses a collection of enzymes and other proteins **(Figure 5.17).** Recent research has shown that the ER is involved in microbody production. Proteins and phospholipids are continuously imported into microbodies. The phospholipids are used for new membrane synthesis, leading to growth of the microbody. Division of a microbody then produces new microbodies.

Microbodies have various functions that are often specific to an organism or cell type. Commonly, microbodies contain enzymes that conduct preparatory or intermediate reactions linking major biochemical pathways. For example, the series of reactions that allows cells to use fats as an energy source begins in microbodies and continues in mitochondria. Beginning or intermediate steps in the breakdown of some amino acids and alcohols also take place in microbodies, including about half of the ethyl alcohol that humans consume. Many types of microbodies produce as a by-product the toxic substance hydrogen peroxide (H_2O_2), which is broken down into water and oxygen by the enzyme *catalase*. Microbodies with this reaction are often termed **peroxisomes.**

Microbodies in plants convert oils or fats to sugars that can be used directly for energy-releasing reactions in mitochondria or for reactions that require sugars as chemical building blocks. These microbody reactions are particularly important in plant embryos that develop from oily seeds, such as those of the peanut or soybean. Depending on the particular reaction pathways they carry out, plant microbodies are called peroxisomes, *glyoxysomes,* or *glycosomes*.

The Cytoskeleton Supports and Moves Cell Structures

The characteristic shape and internal organization of each type of cell is maintained in part by its **cytoskeleton,** the interconnected system of protein fibers and tubes that extends throughout the cytoplasm. The cytoskeleton also reinforces the plasma membrane and functions in movement, both of structures within the cell and of the cell as a whole. It is most highly developed in animal cells, in which it fills and supports the cytoplasm from the plasma membrane to the nuclear envelope **(Figure 5.18).** Although cytoskeletal structures are also present in plant cells, the fibers and tubes of the system are less prominent; much of cellular support in plants is provided by the cell wall and a large central vacuole (described in Section 5.4).

The cytoskeleton of animal cells contains structural elements of three major types: microtubules,

intermediate filaments, and microfilaments. Plant cytoskeletons contain only microtubules and microfilaments. **Microtubules (Figure 5.19a)** are microscopic tubes about 25 nm in diameter; they function much like the tubes used by human engineers to construct supportive structures. **Intermediate filaments (Figure 5.19b)** are fibers with diameters of about 8 to 12 nm. These fibers occur singly, in parallel bundles, and in interlinked networks, either alone or in combination with microtubules, microfilaments, or both. **Microfilaments (Figure 5.19c)** are thin fibers 5 to 7 nm in diameter that consist of two rows of protein subunits wound around each other in a long spiral.

Each cytoskeletal element is assembled from proteins—microtubules from *tubulins,* intermediate filaments from a large and varied group of *intermediate filament proteins,* and microfilaments from *actins* (see Figure 5.19). The keratins of animal hair, nails, and claws contain a common form of intermediate filament proteins known as the *cytokeratins*. For example, human hair consists of thick bundles of cytokeratin fibers extruded from hair follicle cells. The lamins that line the inner surface of the nuclear envelope in animal cells are also assembled from intermediate filament proteins.

Many of the cytoskeletal microtubules in animal cells are formed and radiate outward from a site near the nucleus termed the **cell center** or **centrosome** (see Figure 5.8a). At its midpoint are two short, barrel-shaped structures also formed from microtubules called the **centrioles** (see Figure 5.23). Often, intermediate filaments extend from the cell center as well, apparently held in the same radiating pattern by linkage to microtubules. Microtubules that radiate from the cell center anchor the ER, Golgi complex, lysosomes, secretory vesicles, and at least some mitochondria in position. The microtubules also provide tracks along which vesicles move from the cell interior to the plasma membrane and in the reverse direction. The intermediate filaments probably add support to the microtubule arrays.

Eukaryotic cell movements are generated by "motor" proteins that push or pull against microtubules or microfilaments, much as our muscles produce body movements by acting on bones of the skeleton. One end of a motor protein is firmly fixed to a cell structure such as a vesicle or to a microtubule or microfilament. The other end has reactive groups that "walk" along another microtubule or microfilament by making an attachment, forcefully swiveling a short distance, and then releasing **(Figure 5.20).** ATP supplies the energy

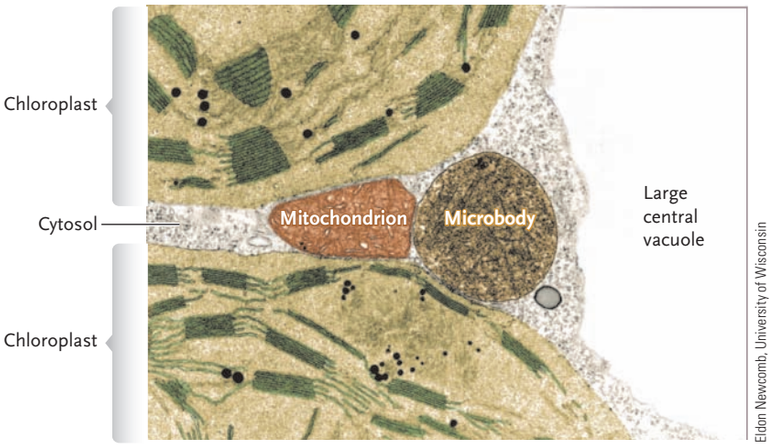
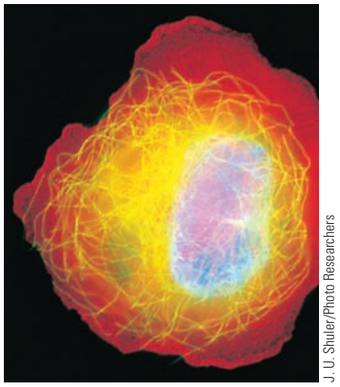
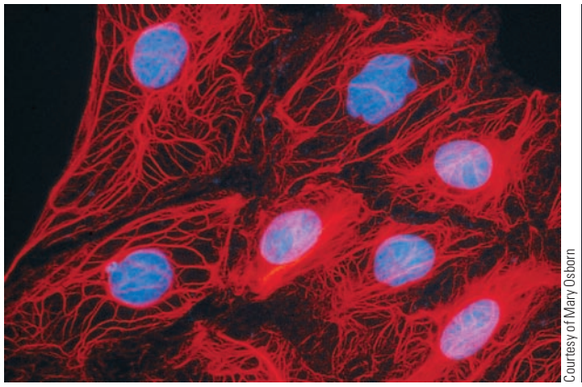


Figure 5.17
A microbody in the cytoplasm of a tobacco leaf cell. The EM has been colorized to make the structures easier to identify.

a. Microtubules



b. Intermediate filaments



c. Microfilaments

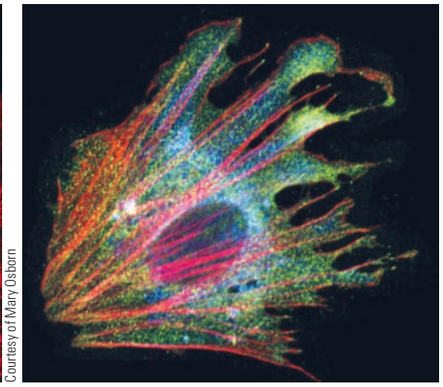


Figure 5.18
Cytoskeletons of eukaryotic cells, as seen in cells stained for light microscopy. (a) Microtubules (yellow) and microfilaments (red) in a pancreatic cell. **(b)** Intermediate filaments assembled from keratin proteins in cells of the kangaroo rat. The nucleus is stained blue in these cells. **(c)** Microfilaments (red) in a migrating mammalian cell.

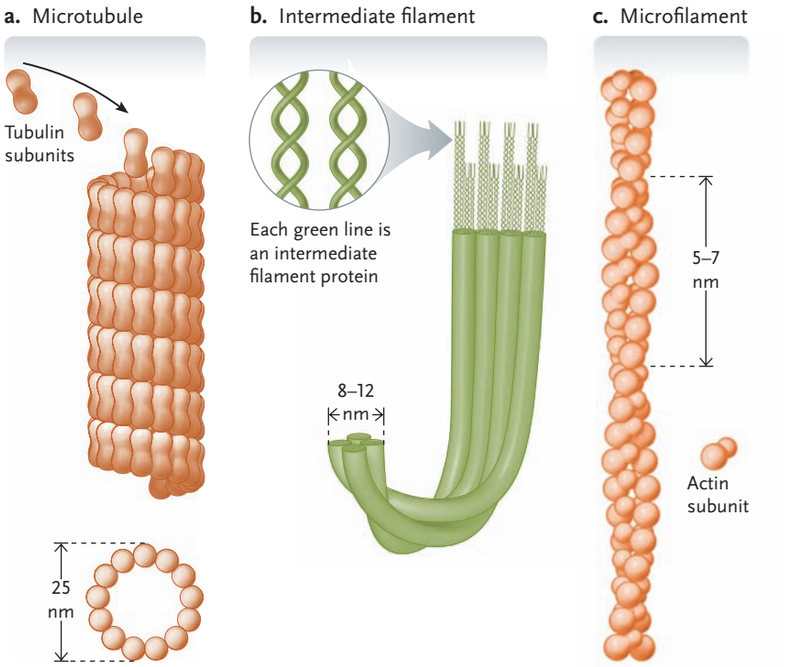


Figure 5.19
The major components of the cytoskeleton. **(a)** A microtubule, assembled from tubulin proteins. **(b)** An intermediate filament. Eight protein chains wind together to form each subunit shown as a green cylinder. **(c)** A microfilament, assembled from two rows of actin proteins, wound around each other into a double helix.

for the walking movements. The motor proteins that walk along microfilaments are called *myosins,* and the ones that walk along microtubules are called *dyneins* and *kinesins.*

Some cell movements, such as the whipping motions of sperm tails, depend entirely on microtubules and their motor proteins. Microfilaments are solely responsible for other types of movements, including *amoeboid motion,* the actively flowing motion of cytoplasm called *cytoplasmic streaming,* and the contraction of muscle cells (the roles of myosin and microfilaments in muscle contraction are discussed further in Chapter 41). When animal cells divide, both microtubules and microfilaments are active—the chromosomes are separated and moved by microtubules, and the cytoplasm is divided by microfilaments (see Chapter 10 for further discussion).

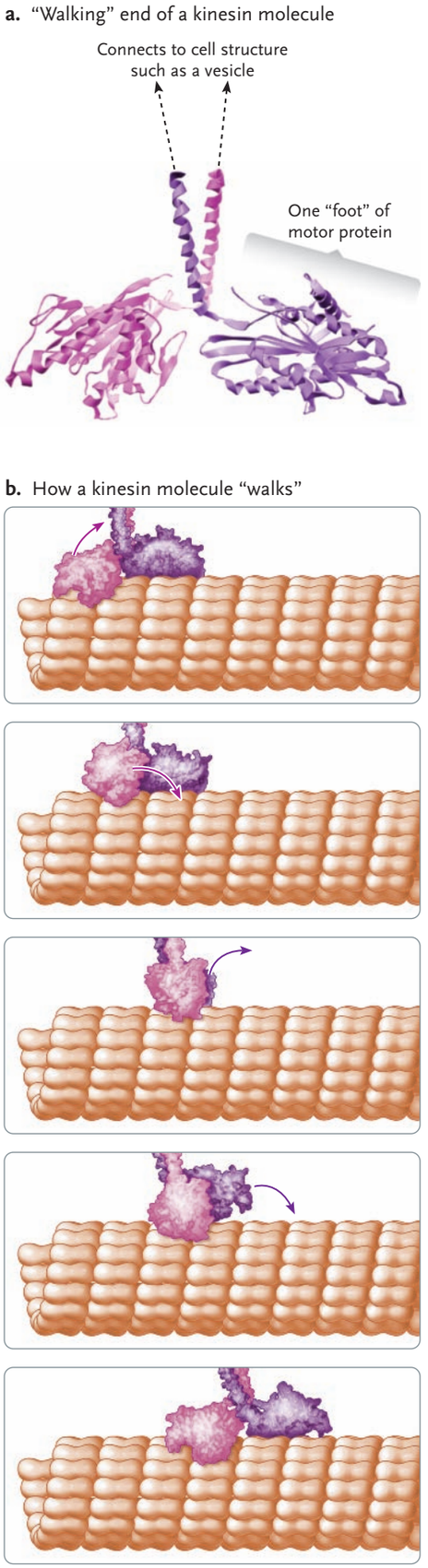


Figure 5.20
The microtubule motor protein kinesin. **(a)** Structure of the end of a kinesin molecule that "walks" along a microtubule, with α-helical segments shown as spirals and β strands as flat ribbons. **(b)** How a kinesin molecule walks along the surface of a molecule by alternately attaching and releasing its "feet."

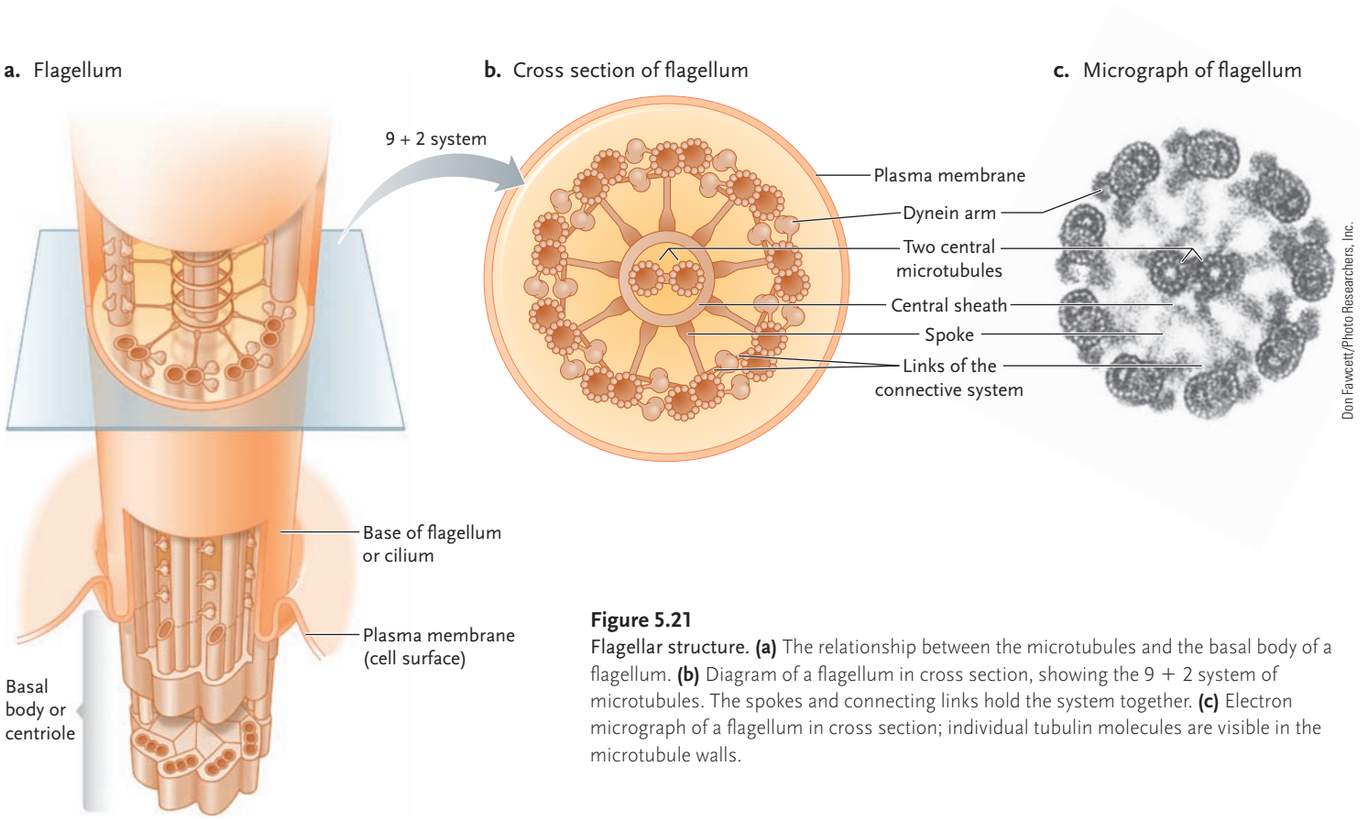


Figure 5.21
Flagellar structure. **(a)** The relationship between the microtubules and the basal body of a flagellum. **(b)** Diagram of a flagellum in cross section, showing the 9 + 2 system of microtubules. The spokes and connecting links hold the system together. **(c)** Electron micrograph of a flagellum in cross section; individual tubulin molecules are visible in the microtubule walls.

Flagella Propel Cells, and Cilia Move Materials over the Cell Surface

Flagella and **cilia** (singular, *cilium*) are elongated, slender, motile structures that extend from the cell surface. They are identical in structure except that cilia are usually shorter than flagella and occur on cells in greater numbers. Whiplike or oarlike movements of a flagellum propel a cell through a watery medium, and cilia move fluids over the cell surface.

A bundle of microtubules extends from the base to the tip of a flagellum or cilium **(Figure 5.21).** In the bundle, a circle of nine double microtubules surrounds a central pair of single microtubules, forming what is known as the 9 + 2 complex. Dynein motor proteins slide the microtubules of the 9 + 2 complex over each other to produce the movements of a flagellum or cilium **(Figure 5.22).**

Flagella and cilia arise from the centrioles. These barrel-shaped structures contain a bundle of microtubules similar to the 9 + 2 complex, except that the central pair of microtubules is missing and the outer circle is formed from a ring of nine triple rather than double microtubules (compare Figure 5.21 and **Figure 5.23**). During the formation of a flagellum or cilium, a centriole moves to a position just under the plasma membrane. Then two of the three microtubules of each triplet grow outward from one end of the centriole to form the ring of nine double microtubules. The two central microtubules of the 9 + 2 complex also grow

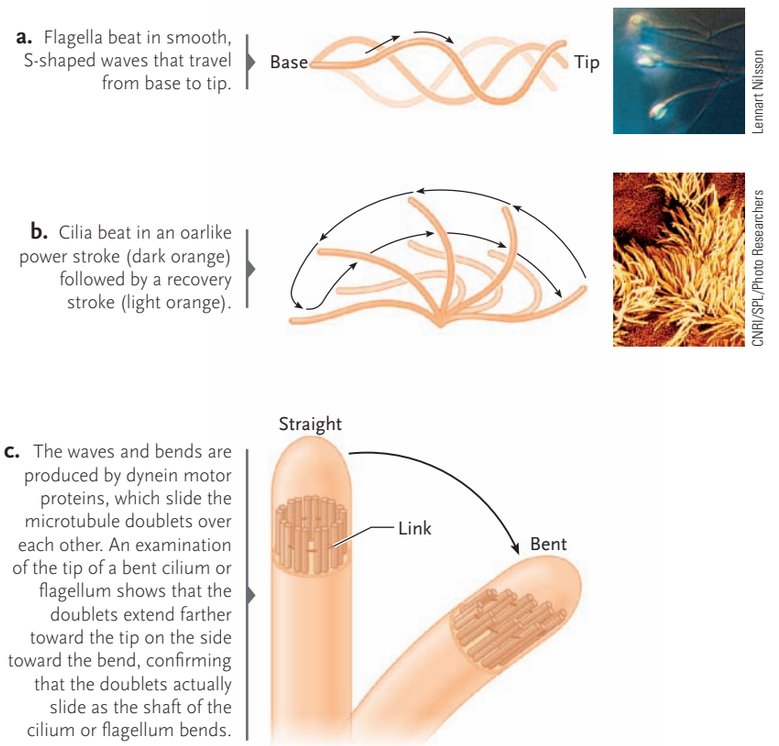
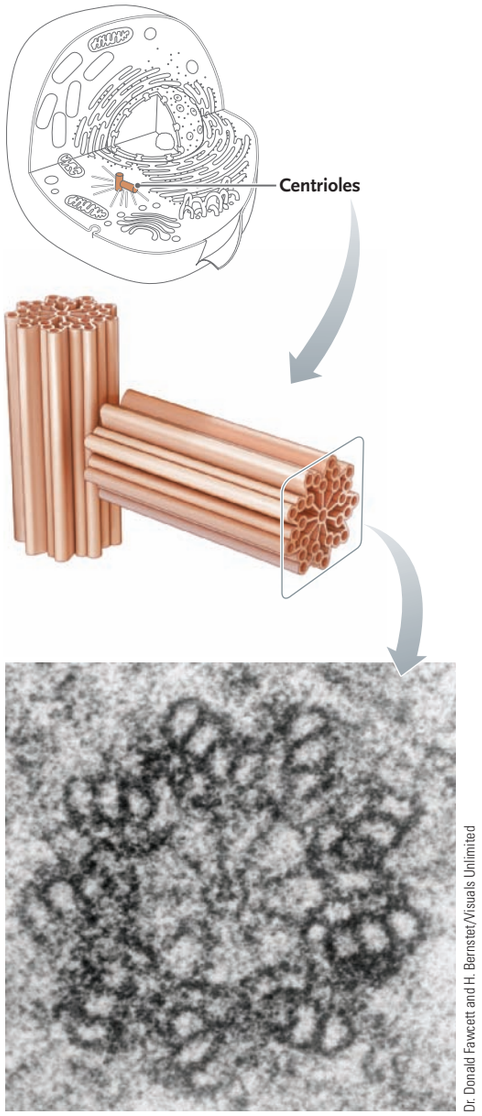


Figure 5.22
Flagellar and ciliary beating patterns. The micrographs show a few human sperm, each with a flagellum (top), and cilia from the lining of an airway in the lungs (bottom).



Dr. Donald Fawcett and H. Bernstet/Visuals Unlimited

Figure 5.23
Centrioles. The two centrioles of the pair at the cell center usually lie at right angles to each other as shown. The electron micrograph shows a centriole from a mouse cell in cross section. A centriole gives rise to the 9 + 2 system of a flagellum and persists as the basal body at the inner end of the flagellum.

from the end of the centriole, but without direct connection to any centriole microtubules. The centriole remains at the innermost end of a flagellum or cilium when its development is complete as the **basal body** of the structure (see Figure 5.21).

Cilia and flagella are found in protozoa and algae, and many types of animal cells have flagella—the tail of a sperm cell is a flagellum—as do the reproductive cells of some plants. In humans, cilia cover the surfaces of cells lining cavities or tubes in some parts of the body. For example, cilia on cells lining the ventricles (cavities) of the brain circulate fluid through the brain, and cilia in the oviducts conduct eggs from the ovaries to the uterus. Cilia covering cells that line the air passages of the lungs sweep out mucus containing bacteria, dust particles, and other contaminants.

Although the purpose of the eukaryotic flagellum is the same as that of prokaryotic flagella, the genes that encode the components of the flagellar apparatus of cells of Bacteria, Archaea, and Eukarya are different in each case. Thus, the three types of flagella are analogous, not homologous, structures, and they must have evolved independently.

With a few exceptions, the cell structures described so far in this chapter occur in all eukaryotic cells. The major exception is intermediate filaments, which appear to be restricted to animal cells. The next section describes three additional structures that are characteristic of plant cells.

Study Break

1. Where in a eukaryotic cell is DNA found? How is that DNA organized?
2. What is the nucleolus, and what is its function?
3. Explain the structure and function of the endomembrane system.
4. What is the structure and function of a mitochondrion?
5. What is the structure and function of the cytoskeleton?

5.4 Specialized Structures of Plant Cells

Chloroplasts, a large and highly specialized central vacuole, and cell walls give plant cells their distinctive characteristics, but these structures also occur in some other eukaryotes—chloroplasts in algal protists and cell walls in algal protists and fungi. They are shown in Figure 5.9 and described in the following sections.

Chloroplasts Are Biochemical Factories Powered by Sunlight

Chloroplasts (Figure 5.24), like mitochondria, are usually lens- or disc-shaped and are surrounded by a smooth **outer boundary membrane**, and an **inner boundary membrane,** which lies just inside the outer membrane. These two boundary membranes completely enclose an inner compartment, the **stroma.** Within the stroma is a third membrane system that consists of flattened, closed sacs called **thylakoids.** In higher plants, the thylakoids are stacked, one on top of another, forming structures called **grana** (singular, *granum*).

Chloroplasts are the sites of photosynthesis in plant cells. The thylakoid membranes contain molecules that absorb light energy and convert it to chemical energy. The primary molecule absorbing light is

chlorophyll, a green pigment that is present in all chloroplasts. The chemical energy is used by enzymes in the stroma to make carbohydrates and other complex organic molecules from water, carbon dioxide, and other simple inorganic precursors. The organic molecules produced in chloroplasts, or from biochemical building blocks made in chloroplasts, are the ultimate food source for most organisms. (The physical and biochemical reactions of chloroplasts are described in Chapter 9.)

Chloroplasts are members of a family of plant organelles known collectively as **plastids.** Other members of the family include amyloplasts and chromoplasts. **Amyloplasts** (*amylo* = starch) are colorless plastids that store starch, a product of photosynthesis. They occur in great numbers in the roots or tubers of some plants, such as the potato. **Chromoplasts** (*chromo* = color) contain red and yellow pigments and are responsible for the colors of ripening fruits or autumn leaves.

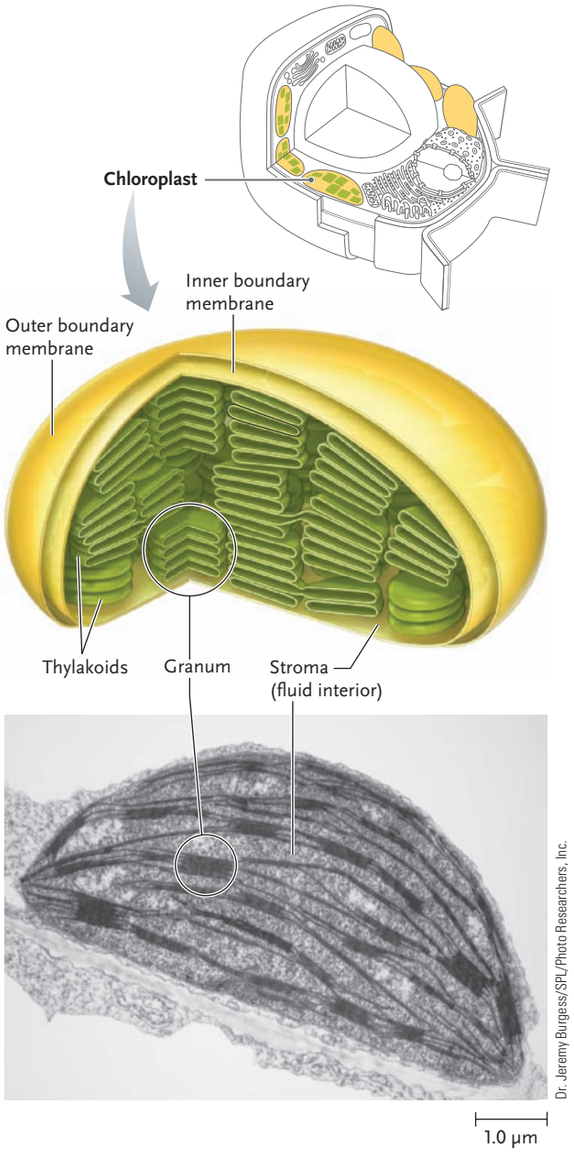
The chloroplast stroma contains DNA and ribosomes that resemble those of certain photosynthetic bacteria. Because of these similarities, chloroplasts, like mitochondria, are believed to have originated from ancient prokaryotes that became permanent residents of the eukaryotic cells ancestral to the plant lineage (see Chapter 24 for further discussion).

Central Vacuoles Have Diverse Roles in Storage, Structural Support, and Cell Growth

Central vacuoles (see Figure 5.9) are large vesicles that are identified as distinct organelles of plant cells because they perform specialized functions unique to plants. In a mature plant cell, 90% or more of the cell's volume may be occupied by one or more large central vacuoles. The remainder of the cytoplasm and the nucleus of these cells are restricted to a narrow zone between the central vacuole and the plasma membrane. The pressure within the central vacuole supports the cells.

The membrane that surrounds the central vacuole, the **tonoplast,** contains transport proteins that move substances into and out of the central vacuole. As plant cells mature, they grow primarily by increases in the pressure and volume of the central vacuole.

Central vacuoles conduct other vital functions. They store salts, organic acids, sugars, storage proteins, pigments, and, in some cells, waste products. Pigments concentrated in the vacuoles produce the colors of many flowers. Enzymes capable of breaking down biological molecules are present in some central vacuoles, giving them some of the properties of lysosomes. Molecules that provide chemical defenses against pathogenic organisms also occur in the central vacuoles of some plants.



Dr. Jeremy Burgess/SPL/Photo Researchers, Inc.

Figure 5.24 **Chloroplast structure.** The electron micrograph shows a maize (corn) chloroplast.

Cell Walls Support and Protect Plant Cells

The cell walls of plants are extracellular structures because they are located outside the plasma membrane **(Figure 5.25).** Cell walls provide support to individual cells, contain the pressure produced in the central vacuole, and protect cells against invading bacteria and fungi.

Cell walls consist of cellulose fibers (see Figure 3.7c), which give tensile strength to the walls, embedded in a network of highly branched carbohydrates. The initial cell wall laid down by a plant cell, the **primary cell wall,** is relatively soft and flexible. As the cell grows and matures, the primary wall expands and additional layers of cellulose fibers and branched carbohydrates are laid down between the primary wall and the plasma membrane. The added wall layer, which is

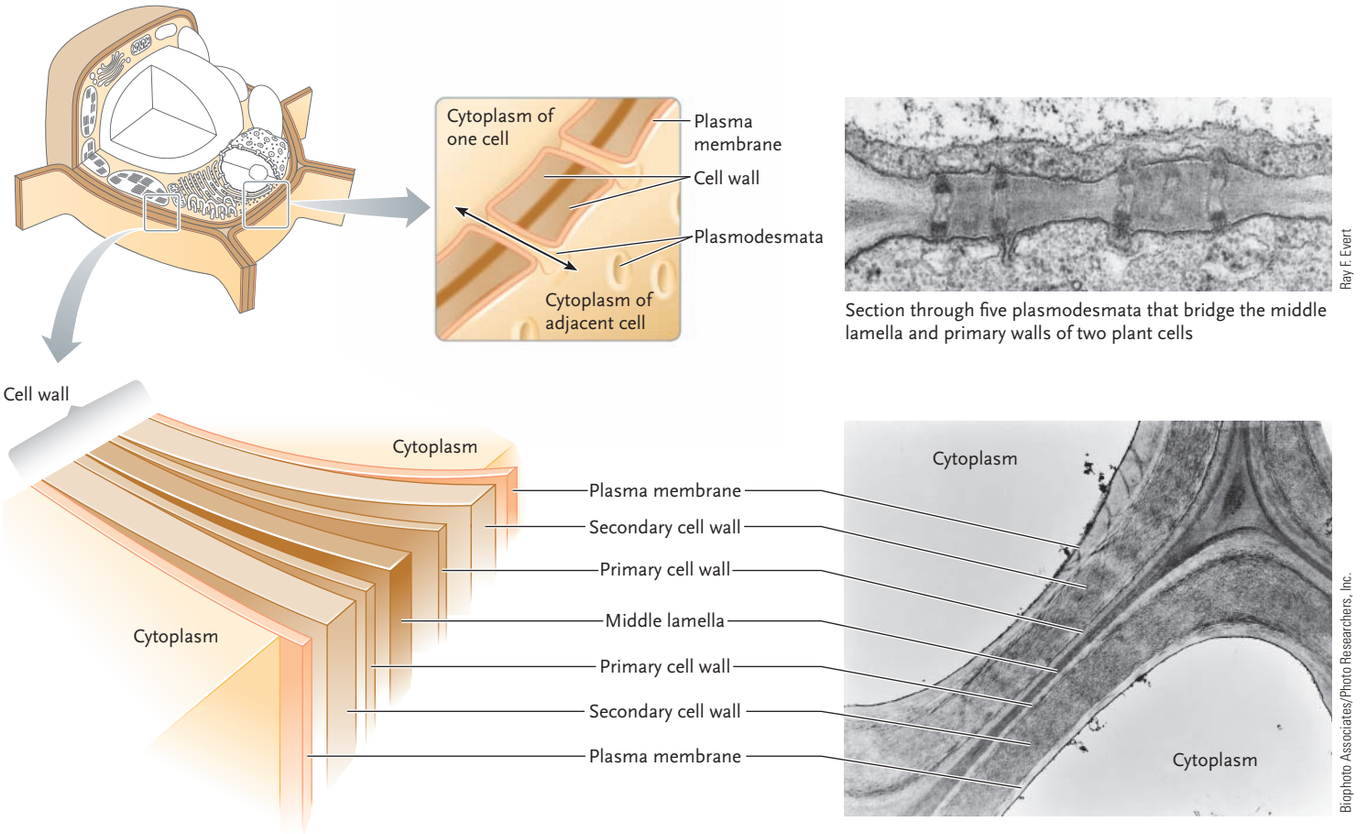


Figure 5.25
Cell wall structure. The upper right diagram and electron micrograph show plasmodesmata, which form openings in the cell wall that directly connect the cytoplasm of adjacent cells. The lower diagram and electron micrograph show the successive layers in the cell wall between two plant cells that have laid down secondary wall material.

more rigid and may become many times thicker than the primary wall, is the **secondary cell wall.** In woody plants and trees, secondary cell walls are reinforced by *lignin,* a hard, highly resistant substance assembled from complex alcohols, surrounding the cellulose fibers. Lignin-impregnated cell walls are actually stronger than reinforced concrete by weight; hence, trees can grow to substantial size, and the wood of trees is used extensively in human cultures to make many structures and objects, including houses, tables, and chairs.

The walls of adjacent cells are held together by a layer of gel-like polysaccharides called the **middle lamella**, which acts as an intercellular glue (see Figure 5.25). The polysaccharide material of the middle lamella, called *pectin,* is extracted from some plants and used to thicken jams and jellies.

Both primary and secondary cell walls are perforated by minute channels, the **plasmodesmata** (singular, *plasmodesma;* see Figure 5.25). These channels, lined by plasma membranes, contain extensions of the cytoplasm that directly connect adjacent plant cells. Plasmodesmata allow ions and small molecules to move directly from one cell to another, without having to penetrate the plasma membranes or cell walls.

Cell walls also surround the cells of fungi and algal protists. Carbohydrate molecules form the major framework of cell walls in most of these organisms, as they do in plants. In some, the wall fibers contain chitin (see Figure 3.7d) instead of cellulose. Details of cell wall structure in the algal protists and fungi, as well as in different subgroups of the plants, are presented in later chapters devoted to these organisms.

As noted earlier, animal cells do not form rigid, external, layered structures equivalent to the walls of plant cells. However, most animal cells secrete extracellular material and have other structures at the cell surface that play vital roles in the support and organization of animal body structures. The next section

describes these and other surface structures of animal cells.

Study Break

1. What is the structure and function of a chloroplast?
2. What is the function of the central vacuole in plants?

5.5 The Animal Cell Surface

Animal cells have specialized structures that help hold cells together, produce avenues of communication between cells, and organize body structures. Molecular systems that perform these functions are organized at three levels: individual **cell adhesion molecules** bind cells together, more complex **cell junctions** seal the spaces between cells and provide direct communication between cells, and the **extracellular matrix (ECM)** supports and protects cells and provides mechanical linkages, such as those between muscles and bone.

Cell Adhesion Molecules Organize Animal Cells into Tissues and Organs

Cell adhesion molecules are glycoproteins embedded in the plasma membrane. They help maintain body form and structure in animals ranging from sponges to the most complex invertebrates and vertebrates. Rather than acting as a generalized intercellular glue, cell adhesion molecules bind to specific molecules on other cells. Most cells in solid body tissues are held together by many different cell adhesion molecules.

Cell adhesion molecules make initial connections between cells early in embryonic development, but then attachments are broken and remade as individual cells or tissues change position in the developing embryo. As an embryo develops into an adult, the connections become permanent and are reinforced by cell junctions. Cancer cells typically lose these adhesions, allowing them to break loose from their original locations, migrate to new locations, and form additional tumors.

Some bacteria and viruses—such as the virus that causes the common cold—target cell adhesion molecules as attachment sites during infection. Cell adhesion molecules are also partially responsible for the ability of cells to recognize one another as being part of the same individual or foreign. For example, rejection of organ transplants in mammals results from an immune response triggered by the foreign cell-surface molecules.

Cell Junctions Reinforce Cell Adhesions and Provide Avenues of Communication

Three types of cell junctions are common in animal tissues **(Figure 5.26). Anchoring junctions** form buttonlike spots, or belts, that run entirely around cells, "welding" adjacent cells together. For some anchoring junctions known as **desmosomes**, intermediate filaments anchor the junction in the underlying cytoplasm; in other anchoring junctions known as **adherens junctions**, microfilaments are the anchoring cytoskeletal component. Anchoring junctions are most common in tissues that are subject to stretching, shear, or other mechanical forces—for example, heart muscle, skin, and the cell layers that cover organs or line body cavities and ducts.

Tight junctions, as the name indicates, are regions of tight connections between membranes of adjacent cells. The connection is so tight that it can keep particles as small as ions from moving between the cells in the layers.

Tight junctions seal the spaces between cells in the cell layers that cover internal organs and the outer surface of the body, or the layers that line internal cavities and ducts. For example, tight junctions between cells that line the stomach, intestine, and bladder keep the contents of these body cavities from leaking into surrounding tissues.

A tight junction is formed by direct fusion of proteins on the outer surfaces of the two plasma membranes of adjacent cells. Strands of the tight junction proteins form a complex network that gives the appearance of stitch work holding the cells together. Within a tight junction, the plasma membrane is not joined continuously; instead, there are regions of intercellular space. Nonetheless, the network of junction proteins is sufficient to make the tight cell connections characteristic of these junctions.

Gap junctions open direct channels that allow ions and small molecules to pass directly from one cell to another (see Figure 5.26). Hollow protein cylinders embedded in the plasma membranes of adjacent cells line up and form a sort of pipeline that connects the cytoplasm of one cell with the cytoplasm of the next. The flow of ions and small molecules through the channels provides almost instantaneous communication between animal cells, similar to the communication that plasmodesmata provide between plant cells.

In vertebrates, gap junctions occur between cells within almost all body tissues, but not between cells of different tissues. These junctions are particularly important in heart muscle tissues and in the smooth muscle tissues that form the uterus, where their pathways of communication allow cells of the organ to operate as a coordinated unit. Although most nerve tissues do not have gap junctions, nerve cells in dental pulp are connected by gap junctions; they are responsible for the

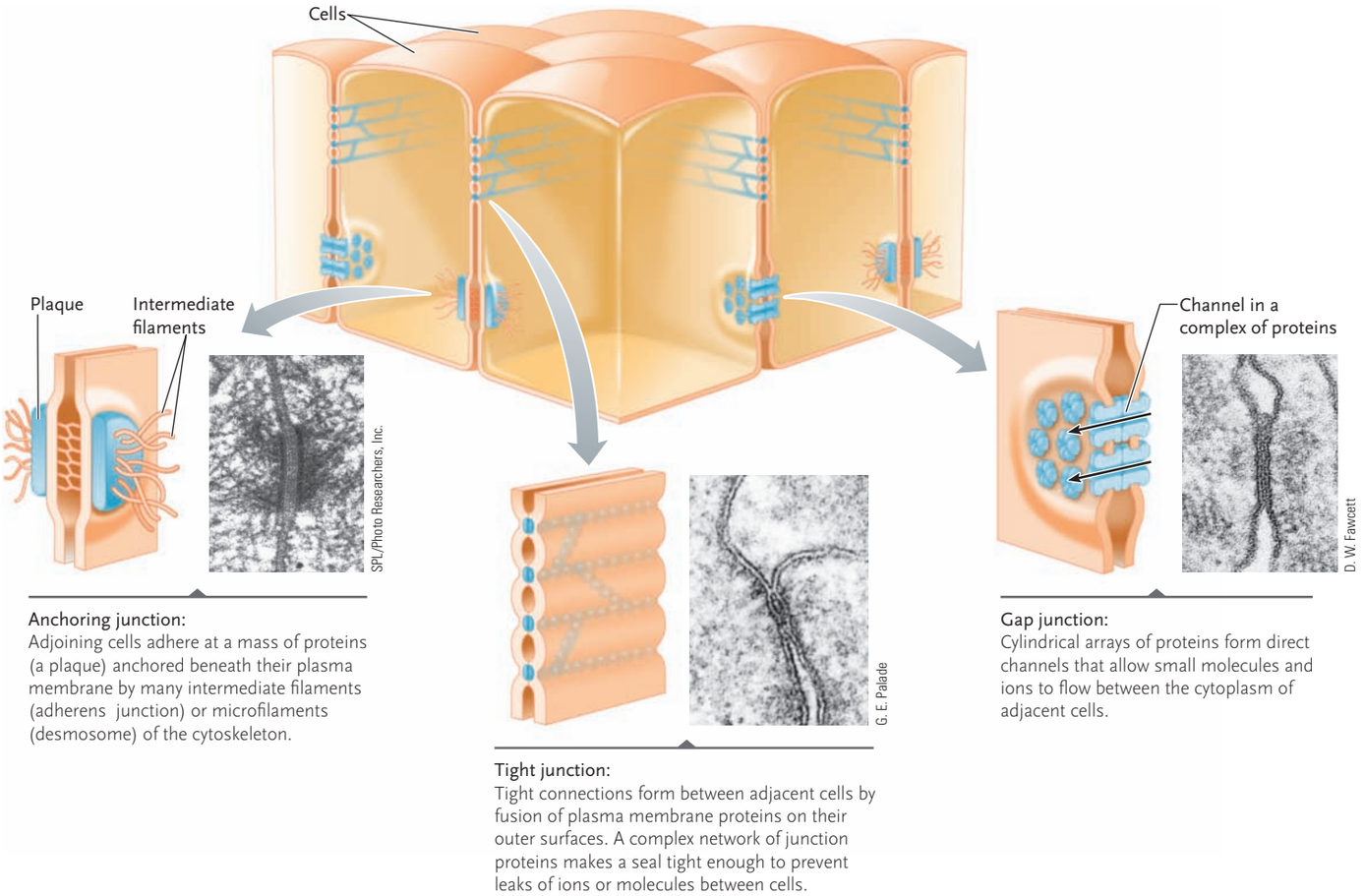


Figure 5.26
Anchoring junctions, tight junctions, and gap junctions, which connect cells in animal tissues. Anchoring junctions reinforce the cell-to-cell connections made by cell adhesion molecules, tight junctions seal the spaces between cells, and gap junctions create direct channels of communication between animal cells.

discomfort you feel if your teeth are disturbed or damaged, or when a dentist pokes a probe into a cavity.

The Extracellular Matrix Organizes the Cell Exterior

Many types of animal cells are embedded in an ECM that consists of proteins and polysaccharides secreted by the cells themselves **(Figure 5.27).** The primary function of the ECM is protection and support. The ECM forms the mass of skin, bones, and tendons; it also forms many highly specialized extracellular structures such as the cornea of the eye and filtering networks in the kidney. The ECM also affects cell division, adhesion, motility, and embryonic development, and it takes part in reactions to wounds and disease.

Glycoproteins are the main component of the ECM. In most animals, the most abundant ECM glycoprotein is *collagen,* which forms fibers with great tensile strength and elasticity. In vertebrates, the collagens of tendons, cartilage, and bone are the most abundant proteins of the body, making up about half of the total body protein by weight. (Collagens and their roles in body structures are described in further detail in Chapter 36.)

The consistency of the matrix, which may range from soft and jellylike to hard and elastic, depends on a network of proteoglycans that surrounds the collagen fibers. *Proteoglycans* are glycoproteins that consist of small proteins noncovalently attached to long polysaccharide molecules. Matrix consistency depends on the number of interlinks in this network, which determines how much water can be trapped in it. For example, cartilage, which contains a high proportion of interlinked glycoproteins, is relatively soft. Tendons, which are almost pure collagen, are tough and elastic. In bone, the glycoprotein network that surrounds collagen fibers is impregnated with mineral crystals, producing a dense and hard—but still elastic—structure that is about as strong as fiberglass or reinforced concrete.

Yet another class of glycoproteins is *fibronectins,* which aid in organizing the ECM and help cells attach

to it. Fibronectins bind to receptor proteins called *integrins* that span the plasma membrane. On the cytoplasmic side of the plasma membrane, the integrins bind to microfilaments of the cytoskeleton. Integrins integrate changes outside and inside the cell by communicating changes in the ECM to the cytoskeleton.

Having laid the groundwork for cell structure and function in this chapter, we next take up further details of individual cell structures, beginning with the roles of cell membranes in transport in the next chapter.

Study Break

1. Distinguish between anchoring junctions, tight junctions, and gap junctions.
2. What is the structure and function of the extracellular matrix?

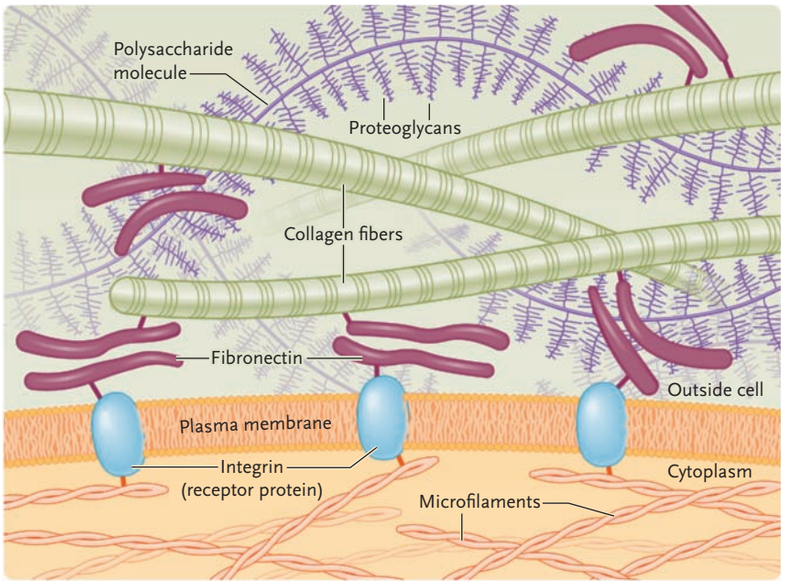


Figure 5.27
Components of the extracellular matrix.

Unanswered Questions

The study of cell structure and function is the focus of the field of cell biology. Research in cell biology includes an analysis of the physiological properties of cells, such as their structure at the whole-cell and subcellular levels, the reactions they conduct, their division, and their interactions with their environments. Understanding the structure and functions of cells is of core importance to all aspects of biology. Research on this topic is often closely allied with genetics, molecular biology, developmental biology, and biochemistry.

Many research questions are being addressed for both prokaryotes and eukaryotes. In prokaryotes, investigators are studying the nature of proteins that hold DNA in its structural conformations in the nucleoid, and the types of molecules found in many prokaryotes for which no function is currently known, including certain vesicles and molecular deposits. In eukaryotes, researchers are asking questions about every major eukaryotic structure described in this chapter.

What are the molecular mechanisms for protein insertion into lipid bilayers?

Stephen High's research group at the University of Manchester, England, is studying how proteins are inserted into lipid bilayers to form biologically functional membranes. They work with the ER, where many integral membrane proteins are synthesized. Using molecular approaches, High's team has identified several protein components of the ER that help regulate the integration of membrane proteins into the lipid bilayer of the ER. The Sec61 protein complex in particular plays a central role in this process, and High's group is studying the molecular mechanisms by which this protein works. They are also studying how the ER performs "quality control"—that is, how it deals with misfolded integral membrane proteins that have been inserted into the ER. Such proteins do not function properly, and it is important to remove them. Research on this problem is focused on identifying the ER components that recognize the aberrant proteins and on elucidating the molecular pathways by which those proteins are removed from the lipid bilayer and degraded.

How does the actin cytoskeleton regulate cell shape?

The ability to change shape and to move is critical for the function of a variety of cells, including single-celled amoebas and cells of the human immune system. The cellular structure responsible for shape changes and movement is the actin cytoskeleton; hence, many research groups are studying this cell component. For example, Matt Welch's research team at the University of California, Berkeley, is studying how the assembly of actin filaments in the cytoskeleton is initiated and regulated, how the actin cytoskeleton interacts with other cellular forces to drive shape change and movement, and how the actin cytoskeleton is targeted specifically by bacterial and viral pathogens to enhance their spread during infections in the organism.

Welch's work with pathogens draws from the fact that various bacterial and viral pathogens target the actin cytoskeleton of eukaryotic cells during infection. Determination of the mechanisms involved in these attacks is necessary to understand how pathogens infect cells and how to combat those infections. For instance, the spotted fever group of Rickettsia (Gram-negative, intracellular bacteria), which cause diseases such as Rocky Mountain spotted fever, enter the host cells and cause them to assemble actin filaments at their surfaces. The energy produced from this actin assembly powers the movement of the pathogen within the cell, and then its cell-to-cell spread. Currently, Welch's research team is trying to determine the mechanism by which these proteins initiate actin assembly and organize the actin into distinctive networks within infected cells.

Peter J. Russell

Review

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5.1 Basic Features of Cell Structure and Function

- According to the cell theory: (1) all living organisms are composed of cells, (2) cells are the functional units of life, and (3) cells arise only from preexisting cells by a process of division.
- Cells of all kinds are divided internally into a central region containing the genetic material, and the cytoplasm, which consists of the cytosol and organelles and is bounded by the plasma membrane.
- The plasma membrane is a lipid bilayer in which transport proteins are embedded (Figure 5.6).
- In the cytoplasm, proteins are made, most of the other molecules required for growth and reproduction are assembled, and energy absorbed from the surroundings is converted into energy usable by the cell.

Animation: Overview of cells

Animation: Surface-to-volume ratio

Animation: Cell membranes

5.2 Prokaryotic Cells

- Prokaryotic cells are surrounded by a plasma membrane and, in most groups, are enclosed by a cell wall. The genetic material, typically a single, circular DNA molecule, is located in the nucleoid. The cytoplasm contains masses of ribosomes (Figure 5.7).

Animation: Typical prokaryotic cell

5.3 Eukaryotic Cells

- Eukaryotic cells have a true nucleus, which is separated from the cytoplasm by the nuclear envelope perforated by nuclear pores. A plasma membrane forms the outer boundary of the cell. Other membrane systems enclose specialized compartments as organelles in the cytoplasm (Figures 5.8 and 5.9).
- The eukaryotic nucleus contains chromatin, a combination of DNA and proteins. A specialized segment of the chromatin forms the nucleolus, where ribosomal RNA molecules are made and combined with ribosomal proteins to make ribosomes. The nuclear envelope is perforated by pores that open channels between the nucleus and the cytoplasm (Figure 5.10).
- Eukaryotic cytoplasm contains ribosomes, an endomembrane system, mitochondria, microbodies, the cytoskeleton, and some organelles specific to certain organisms. The endomembrane system includes the ER, Golgi complex, nuclear envelope, lysosomes, vesicles, and plasma membrane.
- The endoplasmic reticulum (ER) occurs in two forms, as rough and smooth ER. The ribosome-studded rough ER makes proteins that become part of cell membranes or are released from the cell. Smooth ER synthesizes lipids and breaks down toxic substances (Figure 5.11).
- The Golgi complex chemically modifies proteins made in the rough ER and sorts finished proteins to be secreted from the cell, embedded in the plasma membrane, or included in lysosomes (Figures 5.12, 5.13, and 5.15).
- Lysosomes, specialized vesicles that contain hydrolytic enzymes, digest complex molecules such as food molecules that enter the cell by endocytosis, cellular organelles that are no longer functioning correctly, and engulfed bacteria and cell debris (Figure 5.14).
- Mitochondria carry out cellular respiration, the conversion of fuel molecules into the energy of ATP (Figure 5.16).
- Microbodies conduct the initial steps in fat breakdown and other reactions that link major biochemical pathways in the cytoplasm (Figure 5.17).
- The cytoskeleton is a supportive structure built from microtubules, intermediate filaments, and microfilaments in animal cells, but from only microtubules and microfilaments in plants. Motor proteins walking along microtubules and microfilaments produce most cell movements (Figures 5.18–5.20).
- Motor protein-controlled sliding of microtubules generates the movements of flagella and cilia. Flagella and cilia arise from centrioles (Figures 5.21–5.23).

Animation: Common eukaryotic organelles

Animation: Nuclear envelope

Animation: The endomembrane system

Practice: Structure of a mitochondrion

Animation: Cytoskeletal components

Animation: Motor proteins

Animation: Flagella structure

5.4 Specialized Structures of Plant Cells

- Plant cells contain all the eukaryotic structures found in animal cells except for intermediate filaments. They also contain three structures not found in animal cells: chloroplasts, a large central vacuole, and a cell wall (Figure 5.9).
- Chloroplasts contain pigments and molecular systems that absorb light energy and convert it to chemical energy. The chemical energy is used inside the chloroplasts to assemble carbohydrates and other organic molecules from simple inorganic raw materials (Figure 5.24).
- The large central vacuole, which consists of a tonoplast enclosing an inner space, develops pressure that supports plant cells, accounts for much of cellular growth by enlarging as cells mature, and serves as a storage site for substances including waste materials (Figure 5.9).
- A cellulose cell wall surrounds plant cells, providing support and protection. Plant cell walls are perforated by plasmodesmata, channels that provide direct pathways of communication between the cytoplasm of adjacent cells (Figure 5.25).

Practice: Structure of a chloroplast

Animation: Plant cell walls

5.5 The Animal Cell Surface

- Animal cells have specialized surface molecules and structures that function in cell adhesion, communication, and support.
- Cell adhesion molecules bind to specific molecules on other cells. The adhesions organize and hold together cells of the same type in body tissues.
- Cell adhesions are reinforced by various junctions. Anchoring junctions hold cells together. Tight junctions seal together the plasma membranes of adjacent cells, preventing ions and

molecules from moving between the cells. Gap junctions open direct channels between the cytoplasm of adjacent cells (Figure 5.26).

- The extracellular matrix, formed from collagen proteins embedded in a matrix of branched glycoproteins, functions primarily in cell and body protection and support but also affects cell division, motility, embryonic development, and wound healing (Figure 5.27).

Animation: Animal cell junctions

Questions

Self-Test Questions

1. A cell found on the surface of your textbook contains ribosomes, DNA, a plasma membrane, a cell wall, and mitochondria. What type of cell is it?
   a. lung cell
   b. bacterium
   c. sperm cell
   d. plant cell
   e. fingernail
2. A prokaryote converts food energy to ATP on/in its:
   a. chromosome.
   b. flagella.
   c. ribosomes.
   d. cell wall.
   e. plasma membrane.
3. Which of the following structures does *not* require an immediate source of energy to function?
   a. central vacuoles
   b. cilia
   c. microtubules
   d. microfilaments
   e. microbodies
4. Which of the following structures is *not* used in eukaryotic protein manufacture and secretion?
   a. ribosome
   b. lysosome
   c. rough ER
   d. smooth ER
   e. Golgi complex
5. When a person has an infection, white blood cells are summoned to roll, stick, and squeeze through the inner surface of blood vessels. The major components for this action are:
   a. plasmodesmata.
   b. desmosomes.
   c. cell adhesion molecules.
   d. flagella.
   e. cilia.
6. An electron micrograph shows that a cell has extensive amounts of rough ER throughout. One can deduce from this that the cell is:
   a. synthesizing and metabolizing carbohydrates.
   b. synthesizing and secreting proteins.
   c. synthesizing ATP.
   d. contracting.
   e. resting metabolically.
7. Which of the following contributes to the sealed lining of the digestive tract to keep food inside it?
   a. A central vacuole stores proteins.
   b. Tight junctions form a hollow tube for transport of molecules.
   c. Gap junctions communicate between cells of the stomach lining and its muscular wall.
   d. Desmosomes form buttonlike spots or a belt to keep cells joined together.
   e. Plasmodesmata help cells communicate their activities.
8. Which of the following structures are found in the same organelle?
   a. stroma and vacuole
   b. basal body and flagellum
   c. matrix and cristae
   d. DNA and ribosomes
   e. cytosol and plasma membrane
9. Which of the following statements about proteins is correct?
   a. Proteins are transported to the rough ER for use within the cell.
   b. Lipids and carbohydrates are added to proteins by the Golgi complex.
   c. Proteins are transported directly into the cytosol for secretion from the cell.
   d. Proteins that are to be stored by the cell are moved to the rough ER.
   e. Proteins are synthesized in vesicles.
10. Which of the following is *not* a component of the cytoskeleton?
    a. microtubules
    b. microfilaments
    c. cytokeratins
    d. actins
    e. cilia

Questions for Discussion

1. Many compound microscopes have a filter that eliminates all wavelengths except that of blue light, thereby allowing only blue light to pass through the microscope. Use the spectrum of visible light (see Figure 9.4) to explain why the filter improves the resolution of light microscopes.
2. Explain why aliens invading Earth are not likely to be giant cells the size of humans.
3. An electron micrograph of a cell shows the cytoplasm packed with rough ER membranes, a Golgi complex, and mitochondria. What activities might this cell concentrate on? Why would large numbers of mitochondria be required for these activities?
4. Assuming that mitochondria evolved from bacteria that entered cells by endocytosis, what are the likely origins of the outer and inner mitochondrial membranes?
5. Researchers have noticed that some men who were sterile because their sperm cells were unable to move also had chronic infections of the respiratory tract. What might be the connection between these two symptoms?

Experimental Analysis

The unicellular alga *Chlamydomonas reinhardtii* has two flagella assembled from tubulin proteins. If a researcher changes the pH from approximately neutral (their normal growing condition) to pH 4.5, *Chlamydomonas* cells spontaneously lose their flagella. After the cells are returned to neutral pH, they regrow the flagella—a process called reflagellation. Assuming that you have

deflagellated *Chlamydomonas* cells, devise experiments to answer the following questions:

1. Do new tubulin proteins need to be made for reflagellation to occur, or is there a reservoir of proteins in the cell?
2. Is the production of new messenger RNA for the tubulin proteins necessary for reflagellation?
3. What is the optimal pH for reflagellation?

Evolution Link

What aspects of cell structure suggest that prokaryotes and eukaryotes share a common ancestor in their evolutionary history?

How Would You Vote?

Researchers are modifying prokaryotes to identify what it takes to "be alive." They are creating "new" organisms by removing genes from living cells, one at a time. What are the potential advantages or bioethical pitfalls of this kind of research? Go to www.thomsonedu.com/login to investigate both sides of the issue and then vote.