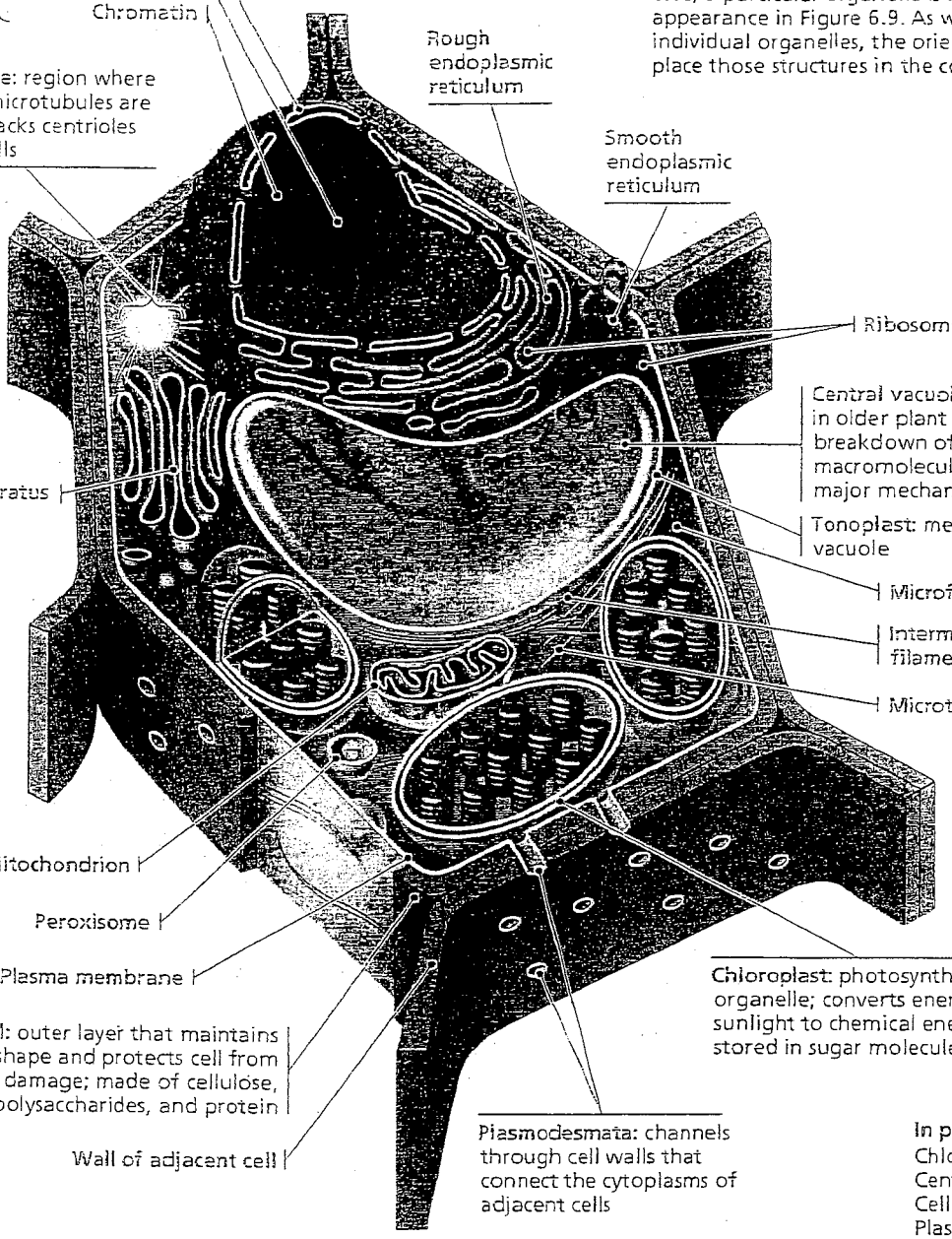
PLANT CELL

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

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



ICLEUS
Nuclear envelope
Nucleolus
Chromatin
Rough endoplasmic reticulum
ntrosome: region where e cell's microtubules are tiated; lacks centrioles plant cells
Smooth endoplasmic reticulum
Ribosomes (small brown dots)
Central vacuole: prominent organelle in older plant cells; functions include storage, breakdown of waste products, hydrolysis of macromolecules; enlargement of vacuole is a major mechanism of plant growth
gi apparatus
Tonoplast: membrane enclosing the central vacuole
Microfilaments
Intermediate filaments
Microtubules
CYTOSKELETON
Mitochondrion
Peroxisome
Plasma membrane
Chloroplast: photosynthetic organelle; converts energy of sunlight to chemical energy stored in sugar molecules
Cell wall: outer layer that maintains cell's shape and protects cell from hanical damage; made of cellulose, other polysaccharides, and protein
Wall of adjacent cell
Plasmodesmata: channels through cell walls that connect the cytoplasms of adjacent cells

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

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Concept Check

1. After carefully reviewing Figure 6.9, briefly describe the structure and function of each of the following organelles: nucleus, mitochondrion, chloroplast, central vacuole, endoplasmic reticulum, and Golgi apparatus.

For suggested answers, see Appendix A.

Concept 6.3

The eukaryotic cell's genetic instructions are housed in the nucleus and carried out by the ribosomes

In the first stop of our detailed tour of the cell, let's look at two organelles involved in the genetic control of the cell: the nucleus, which houses most of the cell's DNA, and the ribosomes, which use information from the DNA to make proteins.

The Nucleus: Genetic Library of the Cell

The nucleus contains most of the genes in the eukaryotic cell (some genes are located in mitochondria and chloroplasts). It is generally the most conspicuous organelle in a eukaryotic cell, averaging about 5 μm in diameter. The nuclear envelope encloses the nucleus (Figure 6.10), separating its contents from the cytoplasm.

The nuclear envelope is a *double* membrane. The two membranes, each a lipid bilayer with associated proteins, are separated by a space of 20–40 nm. The envelope is perforated by pores that are about 100 nm in diameter. At the lip of each pore, the inner and outer membranes of the nuclear envelope are continuous. An intricate protein structure called a *pore complex* lines each pore and regulates the entry and exit of certain large macromolecules and particles. Except at the pores, the nuclear side of the envelope is lined by the **nuclear lamina**, a netlike array of protein filaments that maintains the shape of the nucleus by mechanically supporting the nuclear envelope. There is also much evidence for a *nuclear matrix*, a framework of fibers extending throughout the nuclear interior. (In Chapter 19, we will examine possible functions of the nuclear lamina and matrix in organizing the genetic material.)

Within the nucleus, the DNA is organized into discrete units called chromosomes, structures that carry the genetic information. Each chromosome is made up of a material called chromatin, a complex of proteins and DNA. Stained chromatin usually appears through both light microscopes and electron microscopes as a diffuse mass. As a cell prepares to divide, however, the thin chromatin fibers coil up (condense), becoming thick enough to be distinguished as the familiar separate structures we know as chromosomes. Each eukaryotic species has a characteristic number of chromosomes. A typical human cell, for example, has 46 chromosomes in its nucleus; the exceptions are the sex cells (eggs and sperm), which have only 23 chromosomes in humans. A fruit fly cell has 8 chromosomes in most cells, with 4 in the sex cells.

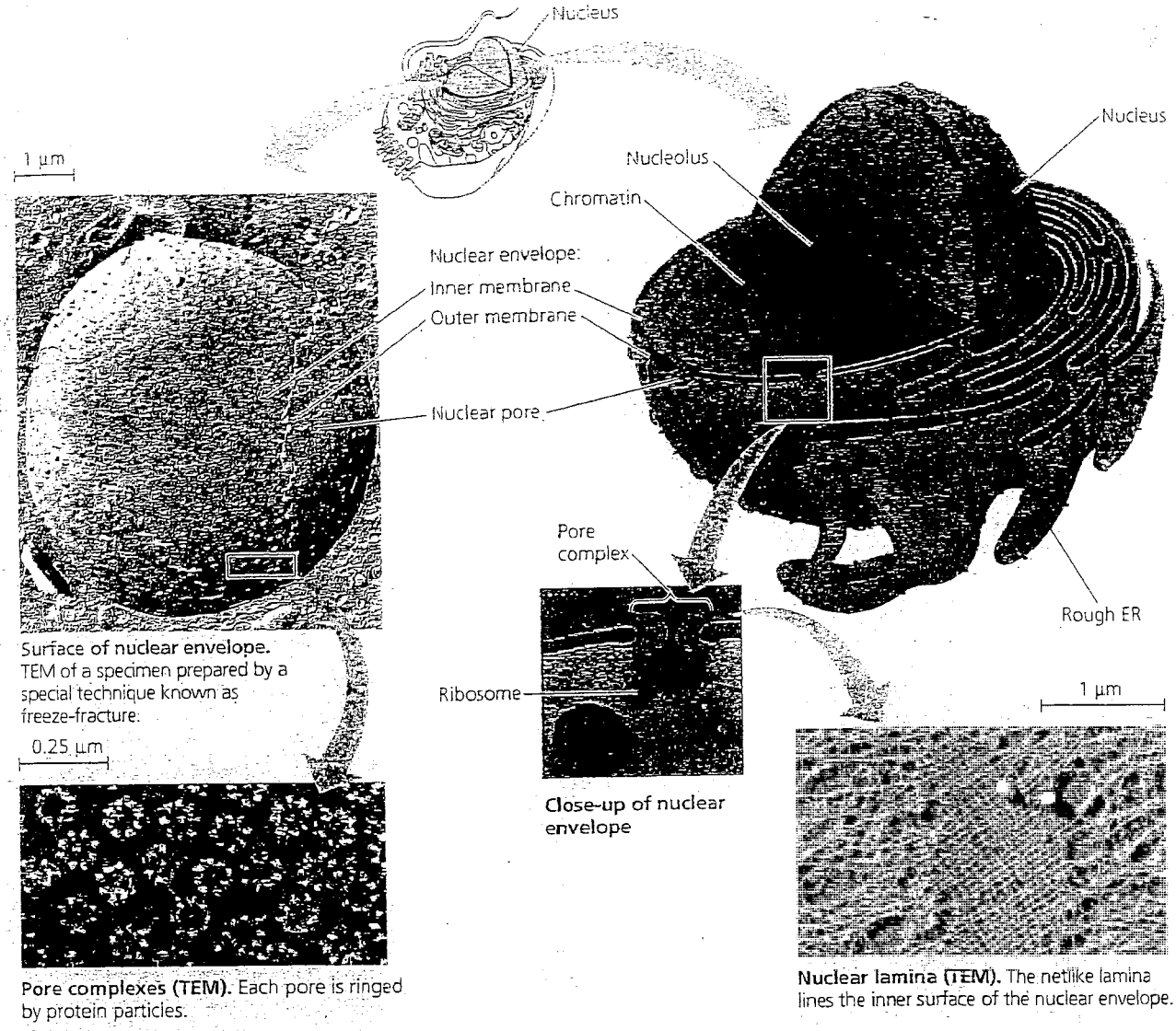
A prominent structure within the nondividing nucleus is the **nucleolus** (plural, *nucleoli*), which appears through the electron microscope as a mass of densely stained granules and fibers adjoining part of the chromatin. Here a special type of RNA called *ribosomal RNA* (rRNA) is synthesized from instructions in the DNA. Also, proteins imported from the cytoplasm are assembled with rRNA into large and small ribosomal subunits in the nucleolus. These subunits then exit the nucleus through the nuclear pores to the cytoplasm, where a large and a small subunit can assemble into a ribosome. Sometimes there are two or more nucleoli; the number depends on the species and the stage in the cell's reproductive cycle. Recent studies have suggested that the nucleolus may perform additional functions as well.

As we saw in Figure 5.25, the nucleus directs protein synthesis by synthesizing messenger RNA (mRNA) according to instructions provided by the DNA. The mRNA is then transported to the cytoplasm via the nuclear pores. Once an mRNA molecule reaches the cytoplasm, ribosomes translate the mRNA's genetic message into the primary structure of a specific polypeptide. This process of transcribing and translating genetic information is described in detail in Chapter 17.

Ribosomes: Protein Factories in the Cell

Ribosomes, particles made of ribosomal RNA and protein, are the organelles that carry out protein synthesis (Figure 6.11). Cells that have high rates of protein synthesis have a particularly large number of ribosomes. For example, a human pancreas cell has a few million ribosomes. Not surprisingly, cells active in protein synthesis also have prominent nucleoli. (Keep in mind that both nucleoli and ribosomes, unlike most other organelles, are not enclosed in membrane.)

Ribosomes build proteins in two cytoplasmic locales (see Figure 6.11). *Free ribosomes* are suspended in the cytosol, while *bound ribosomes* are attached to the outside of the endoplasmic reticulum or nuclear envelope. Most of the proteins made on free ribosomes function within the cytosol; examples are enzymes that catalyze the first steps of sugar breakdown. Bound ribosomes generally make proteins that are destined either for insertion into membranes, for packaging within certain organelles such as lysosomes (see Figure 6.9), or for export from the cell (secretion). Cells that specialize in protein secretion—for instance, the cells of the pancreas that secrete digestive enzymes—frequently have a high proportion of bound ribosomes. Bound and free ribosomes are structurally



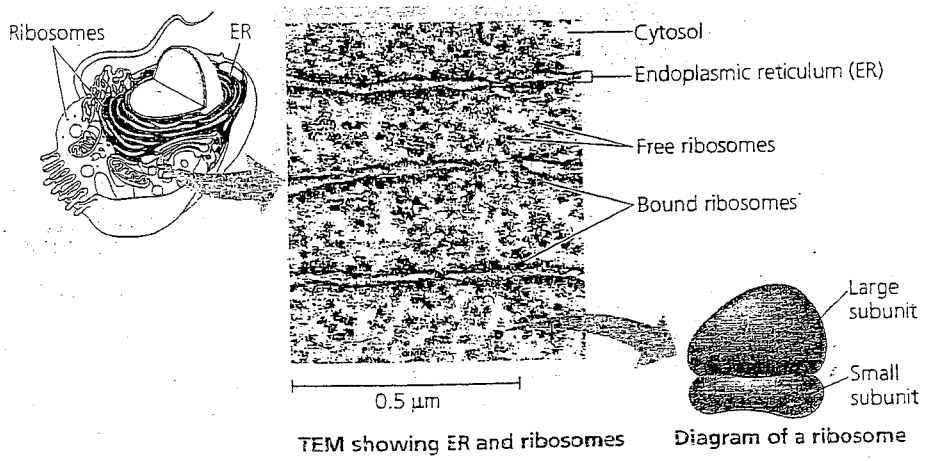
Surface of nuclear envelope. TEM of a specimen prepared by a special technique known as freeze-fracture.

Pore complexes (TEM). Each pore is ringed by protein particles.

Close-up of nuclear envelope

Nuclear lamina (TEM). The netlike lamina lines the inner surface of the nuclear envelope.

▲ **Figure 6.10 The nucleus and its envelope.** Within the nucleus are the chromosomes, which appear as a mass of chromatin (DNA and associated proteins), and one or more nucleoli (singular, nucleolus), which function in ribosome synthesis. The nuclear envelope, which consists of two membranes separated by a narrow space, is perforated with pores and lined by the nuclear lamina.



TEM showing ER and ribosomes

Diagram of a ribosome

◀ **Figure 6.11 Ribosomes.** This electron micrograph of part of a pancreas cell shows many ribosomes, both free (in the cytosol) and bound (to the endoplasmic reticulum). The simplified diagram of a ribosome shows its two subunits.

ntical and can alternate between the two roles; the cell adts the relative numbers of each as metabolic changes alter types of proteins that must be synthesized. You will learn ore about ribosome structure and function in Chapter 17.

Concept Check

1. What role do the ribosomes play in carrying out the genetic instructions?
2. Describe the composition of chromatin and of nucleoli and the function(s) of each.

For suggested answers, see Appendix A.

Concept

he endomembrane system gulates protein traffic and erforms metabolic functions the cell

ny of the different membranes of the eukaryotic cell are of an endomembrane system, which carries out a vari- of tasks in the cell. These tasks include synthesis of pros and their transport into membranes and organelles or of the cell, metabolism and movement of lipids, and detoxtion of poisons. The membranes of this system are related er through direct physical continuity or by the transfer of nbrane segments as tiny vesicles (sacs made of membrane). pite these relationships, the various membranes are not ıtical in structure and function. Moreover, the thickness, ecular composition, and types of chemical reactions car- out by proteins in a given membrane are not fixed, but be modified several times during the membrane's life. endomembrane system includes the nuclear envelope, oplasmic reticulum, Golgi apparatus, lysosomes, various ls of vacuoles, and the plasma membrane (not actually an membrane in physical location, but nevertheless related to endoplasmic reticulum and other internal membranes). have already discussed the nuclear envelope and will now s on the endoplasmic reticulum and the other endomemes to which the endoplasmic reticulum gives rise.

e Endoplasmic Reticulum: synthetic Factory

endoplasmic reticulum (ER) is such an extensive net- of membranes that it accounts for more than half the membrane in many eukaryotic cells. (The word *endoplasmic* means "within the cytoplasm," and *reticulum* is Latin for "little net.") The ER consists of a network of membranous tubules and sacs called cisternae (from the Latin *cisterna*, a reservoir for a liquid). The ER membrane separates the internal compartment of the ER, called the ER lumen (cavity) or cisternal space, from the cytosol. And because the ER membrane is continuous with the nuclear envelope, the space between the two membranes of the envelope is continuous with the lumen of the ER (Figure 6.12).

There are two distinct, though connected, regions of ER that differ in structure and function: smooth ER and rough ER. **Smooth ER** is so named because its outer surface lacks ribosomes. **Rough ER** has ribosomes that stud the outer surface of the membrane and thus appears rough through the electron microscope. As already mentioned, ribosomes are also attached to the cytoplasmic side of the nuclear envelope's outer membrane, which is continuous with rough ER.

Functions of Smooth ER

The smooth ER of various cell types functions in diverse metabolic processes. These processes include synthesis of lipids, metabolism of carbohydrates, and detoxification of drugs and poisons.

Enzymes of the smooth ER are important to the synthesis of lipids, including oils, phospholipids, and steroids. Among the steroids produced by the smooth ER in animal cells are the sex hormones of vertebrates and the various steroid hormones secreted by the adrenal glands. The cells that actually synthesize and secrete these hormones—in the testes and ovaries, for example—are rich in smooth ER, a structural feature that fits the function of these cells.

In the smooth ER, other enzymes help detoxify drugs and poisons, especially in liver cells. Detoxification usually involves adding hydroxyl groups to drugs, making them more soluble and easier to flush from the body. The sedative phenobarbital and other barbiturates are examples of drugs metabolized in this manner by smooth ER in liver cells. In fact, barbiturates, alcohol, and many other drugs induce the proliferation of smooth ER and its associated detoxification enzymes, thus increasing the rate of detoxification. This, in turn, increases tolerance to the drugs, meaning that higher doses are required to achieve a particular effect, such as sedation. Also, because some of the detoxification enzymes have relatively broad action, the proliferation of smooth ER in response to one drug can increase tolerance to other drugs as well. Barbiturate abuse, for example, may decrease the effectiveness of certain antibiotics and other useful drugs.

The smooth ER also stores calcium ions. In muscle cells, for example, a specialized smooth ER membrane pumps calcium ions from the cytosol into the ER lumen. When a muscle cell is stimulated by a nerve impulse, calcium ions rush back across the ER membrane into the cytosol and trigger

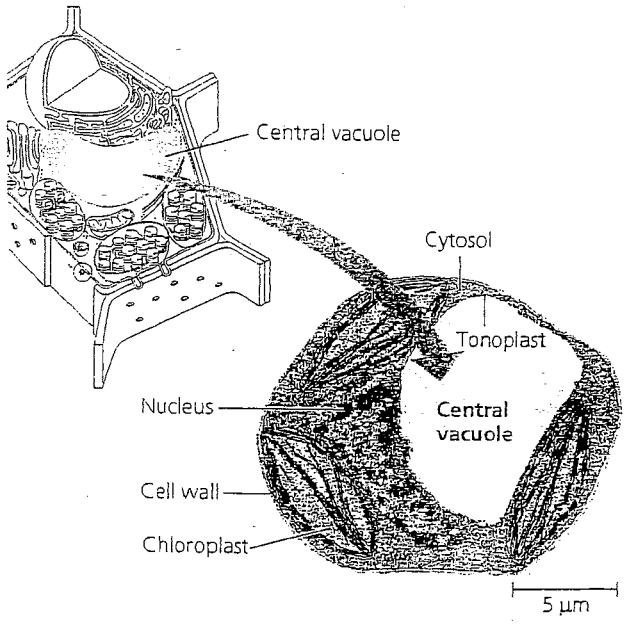
comes surrounded by a membrane, and a lysosome fuses th this vesicle (Figure 5.14b). The lysosomal enzymes dis-antle the enclosed material, and the organic monomers are turned to the cytosol for reuse. With the help of lysosomes, e cell continually renews itself. A human liver cell, for ex-iple, recycles half of its macromolecules each week.

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

.cuoles: Diverse Maintenance ompartments

lant or fungal cell may have one or several vacuoles. While uoles carry out hydrolysis and are thus similar to lyso-nes, they carry out other functions as well. Food vacuoles, med by phagocytosis, have already been mentioned (see ure 6.14a). Many freshwater protists have contractile vac-es that pump excess water out of the cell, thereby main-ting the appropriate concentration of salts and other mole-es (see Figure 7.14). Mature plant cells generally contain a e central vacuole (Figure 5.15) enclosed by a membrane ed the tonoplast. The central vacuole develops by the coalescence of smaller vacuoles, themselves derived from the endoplasmic reticulum and Golgi apparatus. The vacuole is in this way an integral part of a plant cell's endomembrane system. Like all cellular membranes, the tonoplast is selective in transporting solutes; as a result, the solution inside the vacuole, called cell sap, differs in composition from the cytosol.

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



gure 5.15 The plant cell vacuole. The central vacuole is ly the largest compartment in a plant cell; the rest of the lasm is generally confined to a narrow zone between the ular membrane (tonoplast) and the plasma membrane (TEM).

The Endomembrane System: *A Review*

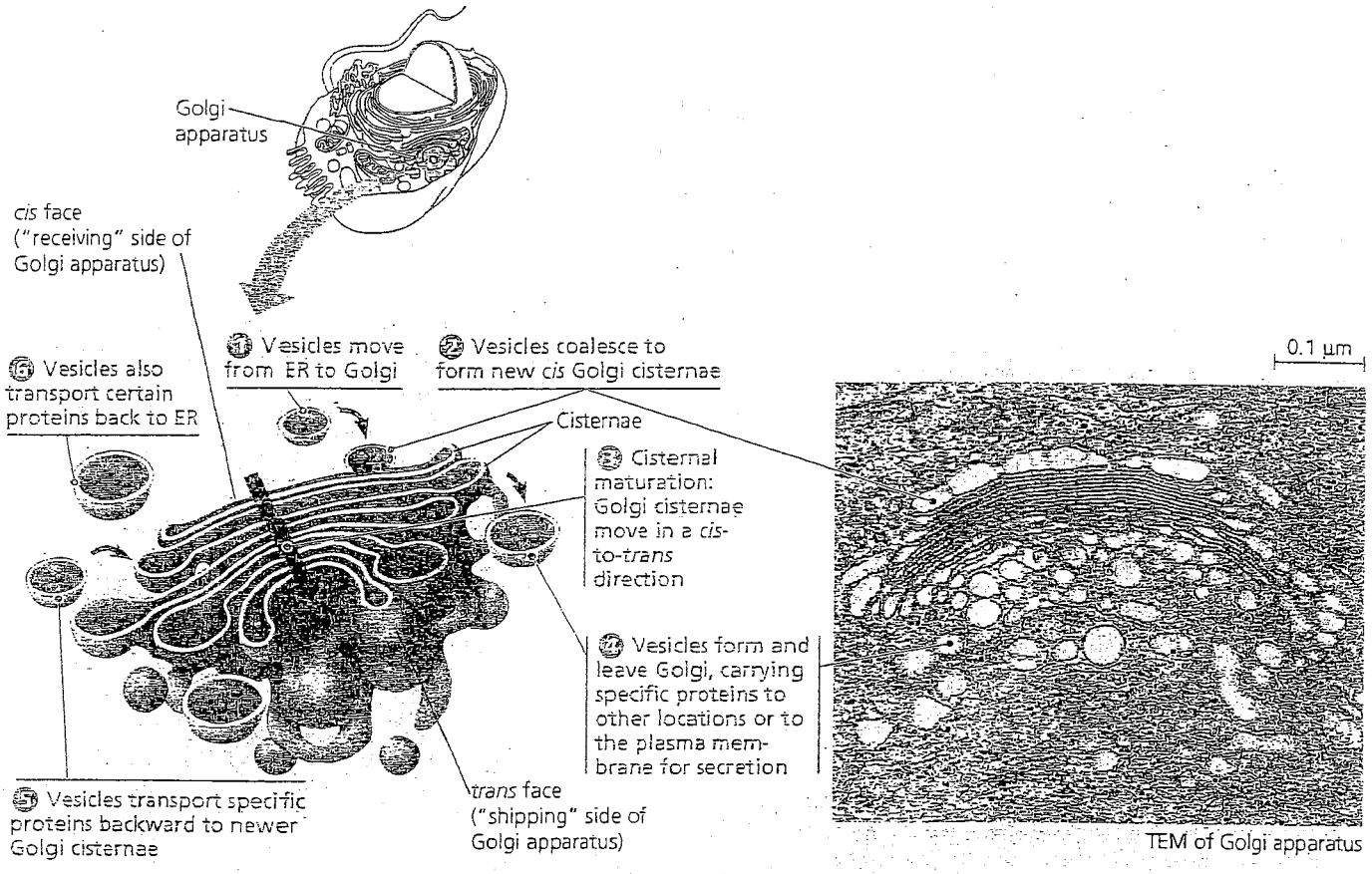
Figure 5.15 reviews the endomembrane system, showing the flow of membrane lipids and proteins through the various organelles. As the membrane moves from the ER to the Golgi and then elsewhere, its molecular composition and metabolic functions are modified, along with those of its contents. The endomembrane system is a complex and dynamic player in the cell's compartmental organization.

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

Concept Check

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

For suggested answers, see Appendix A.



▲ Figure 6.13 The Golgi apparatus. The Golgi apparatus consists of stacks of flattened sacs, or cisternae, which, unlike ER cisternae, are not physically connected. (The drawing is a cutaway view.) A Golgi stack receives and dispatches transport vesicles and the products they contain. A Golgi stack has a structural and functional polarity, with a *cis* face that receives vesicles containing ER products and a *trans* face that dispatches vesicles. The cisternal maturation model suggests that the Golgi cisternae themselves appear to "mature," moving from the *cis* to the *trans* face while carrying some proteins along. In addition, some vesicles recycle enzymes that had been carried forward, in moving cisternae, "backward" to a newer region where their functions are needed (TEM).

Golgi membrane. The *trans* face gives rise to vesicles, which pinch off and travel to other sites.

Products of the ER are usually modified during their transit from the *cis* region to the *trans* region of the Golgi. Proteins and phospholipids of membranes may be altered. For example, various Golgi enzymes modify the carbohydrate portions of glycoproteins. Carbohydrates are first added to proteins in the rough ER, often during the process of polypeptide synthesis. The carbohydrate on the resulting glycoprotein is then modified as it passes through the rest of the ER and the Golgi. The Golgi removes some sugar monomers and substitutes others, producing a large variety of carbohydrates.

In addition to its finishing work, the Golgi apparatus manufactures certain macromolecules by itself. Many polysaccharides secreted by cells are Golgi products, including pectins and certain other non-cellulose polysaccharides made by plant cells and incorporated along with cellulose into their cell walls. (Cellulose is made by enzymes located within the plasma membrane, which directly deposit this polysaccharide on the outside surface.) Golgi products that will be secreted depart from the *trans* face of the Golgi inside transport vesicles that eventually fuse with the plasma membrane.

The Golgi manufactures and refines its products in stages, with different cisternae between the *cis* and *trans* regions containing unique teams of enzymes. Until recently, we viewed the Golgi as a static structure, with products in various stages of processing transferred from one cisterna to the next by vesicles. While this may occur, recent research has given rise to a new model of the Golgi as a more dynamic structure. According to the model called the *cisternal maturation model*, the cisternae of the Golgi actually progress forward from the *cis* to the *trans* face of the Golgi, carrying and modifying their protein cargo as they move. Figure 6.13 shows the details of this model.

Before a Golgi stack dispatches its products by budding vesicles from the *trans* face, it sorts these products and targets them for various parts of the cell. Molecular identification tags, such as phosphate groups that have been added to the Golgi

products, aid in sorting by acting like ZIP codes on mailing labels. Finally, transport vesicles budded from the Golgi may have external molecules on their membranes that recognize "docking sites" on the surface of specific organelles or on the plasma membrane, thus targeting them appropriately.

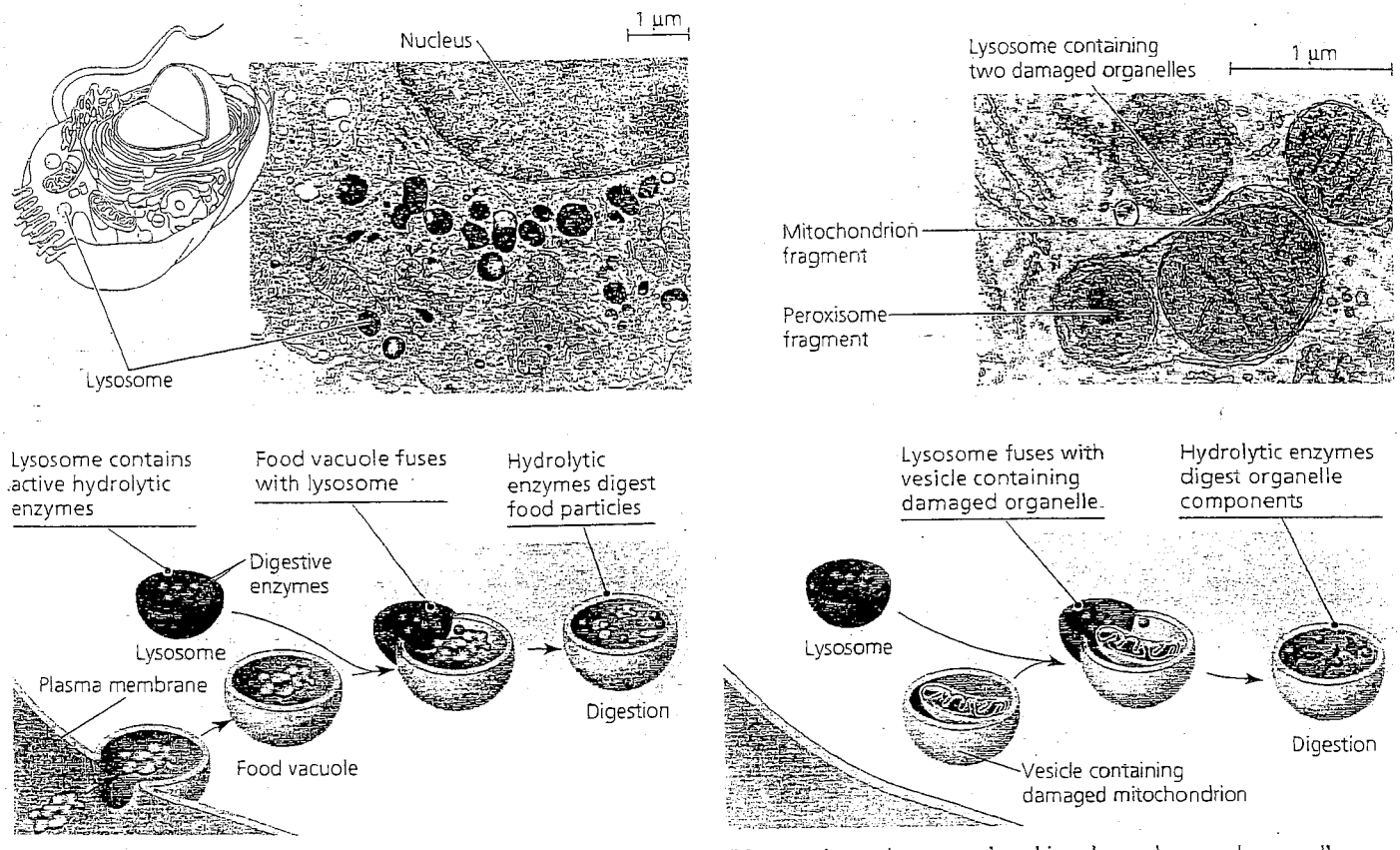
Lysosomes: Digestive Compartments

A lysosome is a membranous sac of hydrolytic enzymes that an animal cell uses to digest all kinds of macromolecules. Lysosomal enzymes work best in the acidic environment found in lysosomes. If a lysosome breaks open or leaks its contents, the released enzymes are not very active, because the cytosol has a neutral pH. However, excessive leakage from a large number of lysosomes can destroy a cell by autodigestion.

Hydrolytic enzymes and lysosomal membrane are made by rough ER and then transferred to the Golgi apparatus for further processing. At least some lysosomes probably arise by budding from the *trans* face of the Golgi apparatus (see Figure 6.13). Proteins of the inner surface of the lysosomal membrane and the digestive enzymes themselves are thought to be spared from destruction by having three-dimensional conformations that protect vulnerable bonds from enzymatic attack.

Lysosomes carry out intracellular digestion in a variety of circumstances. Amoebas and many other protists eat by engulfing smaller organisms or other food particles, a process called **phagocytosis** (from the Greek *phagein*, to eat, and *kytos*, vessel, referring here to the cell). The *food vacuole* formed in this way then fuses with a lysosome, whose enzymes digest the food (Figure 6.14a). Digestion products, including simple sugars, amino acids, and other monomers, pass into the cytosol and become nutrients for the cell. Some human cells also carry out phagocytosis. Among them are macrophages, a type of white blood cell that helps defend the body by engulfing and destroying bacteria and other invaders (see Figure 6.32).

Lysosomes also use their hydrolytic enzymes to recycle the cell's own organic material, a process called *autophagy*. During autophagy, a damaged organelle or small amount of cytosol



(a) Phagocytosis: lysosome digesting food

(b) Autophagy: lysosome breaking down damaged organelle

▲ Figure 6.14 Lysosomes. Lysosomes digest (hydrolyze) materials taken into the cell and recycle intracellular materials. **(a)** *Top* In this macrophage (a type of white blood cell) from a rat, the lysosomes are very dark because of a specific stain that reacts with one of the products of digestion within the lysosome (TEM). Macrophages ingest bacteria and viruses and destroy them using lysosomes. *Bottom* This diagram shows one lysosome fusing with a food vacuole during the process of phagocytosis. **(b)** *Top* In the cytoplasm of this rat liver cell, a lysosome has engulfed two disabled organelles, a mitochondrion and a peroxisome, in the process of autophagy (TEM). *Bottom* This diagram shows a lysosome fusing with a vesicle containing a damaged mitochondrion.

ontraction of the muscle cell. In other cell types, calcium ion release from the smooth ER can trigger different responses.

Functions of Rough ER

Many types of specialized cells secrete proteins produced by ribosomes attached to rough ER. For example, certain cells in the pancreas secrete the protein insulin, a hormone, into the bloodstream. As a polypeptide chain grows from a bound ribosome, it is threaded into the ER lumen through a pore formed by a protein complex in the ER membrane. As the new protein enters the ER lumen, it folds into its native conformation. Most secretory proteins are **glycoproteins**, proteins that have carbohydrates covalently bonded to them. The carbohydrate is attached to the protein in the ER by specialized molecules built into the ER membrane.

Once secretory proteins are formed, the ER membrane keeps them separate from the proteins, produced by free ribosomes, that will remain in the cytosol. Secretory proteins depart from the ER wrapped in the membranes of vesicles that bud like bubbles from a specialized region called transitional ER (see Figure 6.12). Vesicles in transit from one part of the cell to another are called **transport vesicles**; we will learn their fate in the next section.

In addition to making secretory proteins, rough ER is a membrane factory for the cell; it grows in place by adding membrane proteins and phospholipids to its own membrane. As polypeptides destined to be membrane proteins grow from the ribosomes, they are inserted into the ER membrane itself and are anchored there by their hydrophobic portions. The rough ER also makes its own membrane phospholipids; enzymes built into the ER membrane assemble phospholipids from precursors in the cytosol. The ER membrane expands and is transferred in the form of transport vesicles to other components of the endomembrane system.

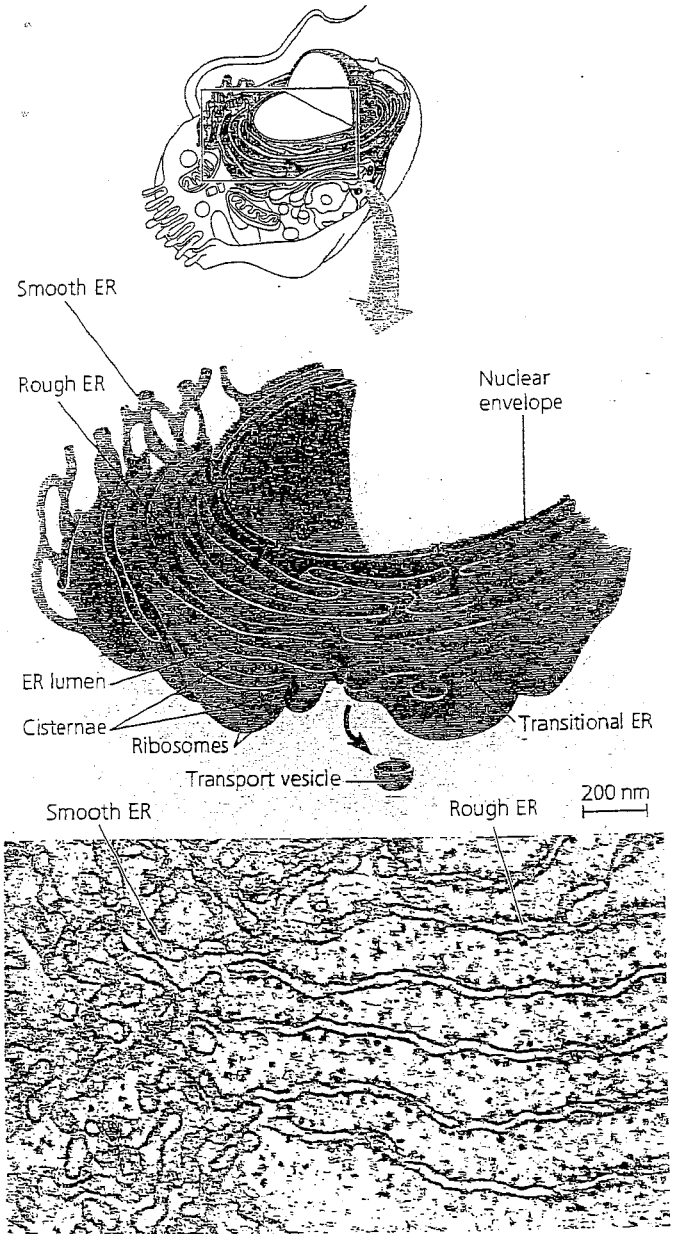


Figure 6.12 Endoplasmic reticulum (ER). A membranous system of interconnected tubules and flattened sacs called cisternae, the ER is also continuous with the nuclear envelope. (The drawing is a cutaway view.) The membrane of the ER encloses a continuous compartment called the ER lumen (or cisternal space). Rough ER, which is studded on its outer surface with ribosomes, can be distinguished from smooth ER in the electron micrograph (TEM). Transport vesicles bud off from a region of the rough ER called transitional ER and travel to the Golgi apparatus and other destinations.

The Golgi Apparatus: Shipping and Receiving Center

After leaving the ER, many transport vesicles travel to the Golgi apparatus. We can think of the Golgi as a center of manufacturing, warehousing, sorting, and shipping. Here, products of the ER are modified and stored and then sent to other destinations. Not surprisingly, the Golgi apparatus is especially extensive in cells specialized for secretion.

The Golgi apparatus consists of flattened membranous sacs—cisternae—looking like a stack of pita bread (**Figure 6.13**, on the next page). A cell may have many or even hundreds of these stacks. The membrane of each cisterna in a stack separates its internal space from the cytosol. Vesicles concentrated in the vicinity of the Golgi apparatus are engaged in the transfer of material between the parts of the Golgi and other structures.

A Golgi stack has a distinct polarity, with the membranes of cisternae on opposite sides of the stack differing in thickness and molecular composition. The two poles of a Golgi stack are referred to as the *cis* face and the *trans* face; these act, respectively, as the receiving and shipping departments of the Golgi apparatus. The *cis* face is usually located near the ER. Transport vesicles move material from the ER to the Golgi apparatus. A vesicle that buds from the ER can add its membrane and the contents of its lumen to the *cis* face by fusing with a

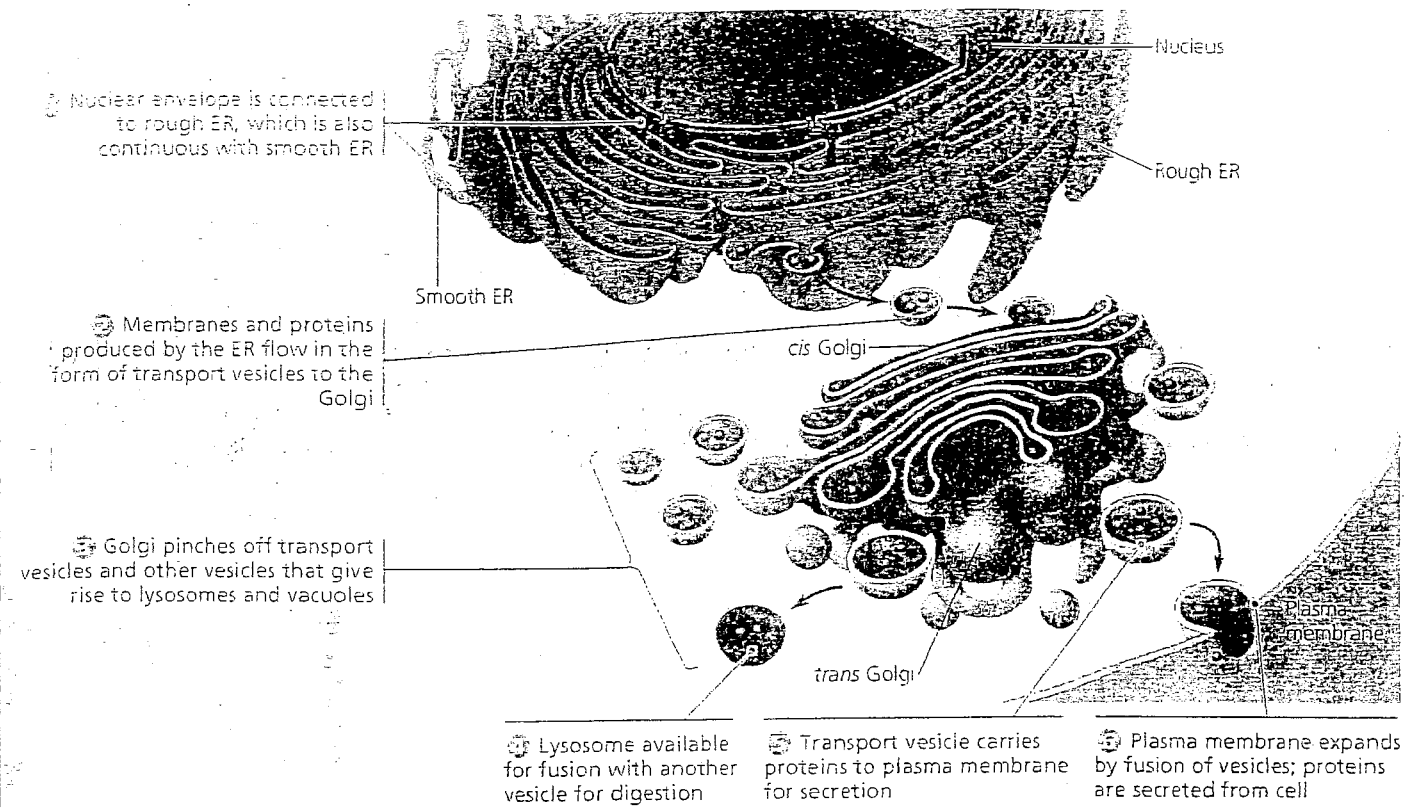


Figure 6.15 Review: relationships among organelles of the endomembrane system. The red arrows show some of the migration pathways for membranes and the materials they enclose.

Concept 6.5

Mitochondria and chloroplasts change energy from one form to another

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

Although mitochondria and chloroplasts are enclosed by membranes, they are not part of the endomembrane system. In contrast to organelles of the endomembrane system, each of these organelles has at least two membranes separating the innermost space from the cytosol. Their membrane proteins are made not by the ER, but by free ribosomes in the cytosol and by ribosomes contained within these organelles themselves. Not only do these organelles have ribosomes, but they also contain a small amount of DNA. It is this DNA that programs the synthesis of the proteins made on the organelle's own ribosomes. (Proteins imported from the cytosol—constituting most of the organelle's proteins—are programmed by nuclear DNA.) Mitochondria and chloroplasts are semiautonomous organelles that grow and reproduce within the cell. In Chapters 9 and 10, we will focus on how mitochondria and chloroplasts function. We will consider the evolution of these organelles in Chapter 26. Here we are concerned mainly with the structure of these energy transformers.

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

Mitochondria: Chemical Energy Conversion

Mitochondria are found in nearly all eukaryotic cells, including those of plants, animals, fungi, and protists. Some cells have a single large mitochondrion, but more often a cell has

hundreds or even thousands of mitochondria; the number is correlated with the cell's level of metabolic activity. For example, motile or contractile cells have proportionally more mitochondria per volume than less active cells. Mitochondria are about 1–10 μm long. Time-lapse films of living cells reveal mitochondria moving around, changing their shapes, and dividing in two, unlike the static cylinders seen in electron micrographs of dead cells.

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

Chloroplasts: Capture of Light Energy

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

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

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

Peroxisomes: Oxidation

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

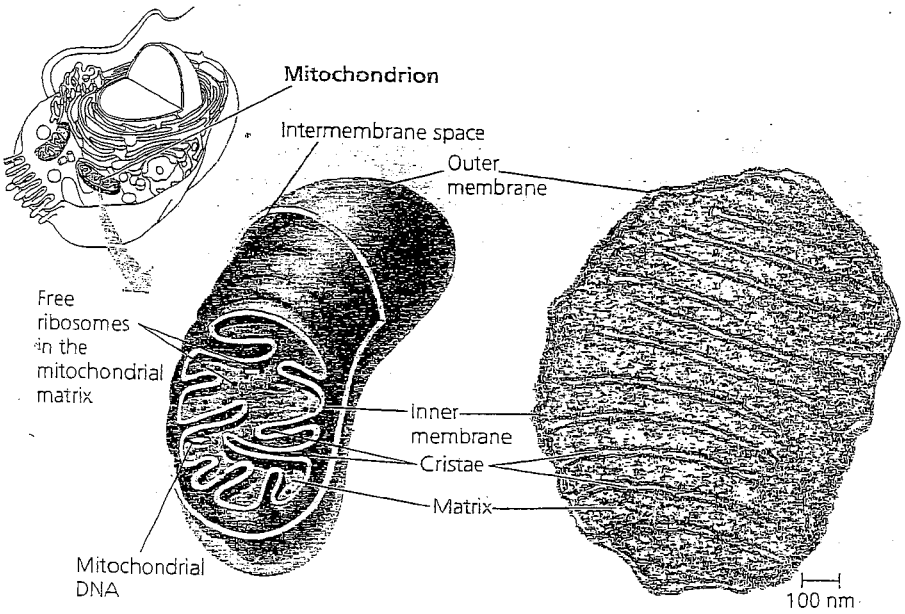


Figure 6.17 The mitochondrion, site of cellular respiration. The inner and outer membranes of the mitochondrion are evident in the drawing and micrograph (TEM). The cristae are infoldings of the inner membrane. The cutaway drawing shows the two compartments bounded by the membranes: the intermembrane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

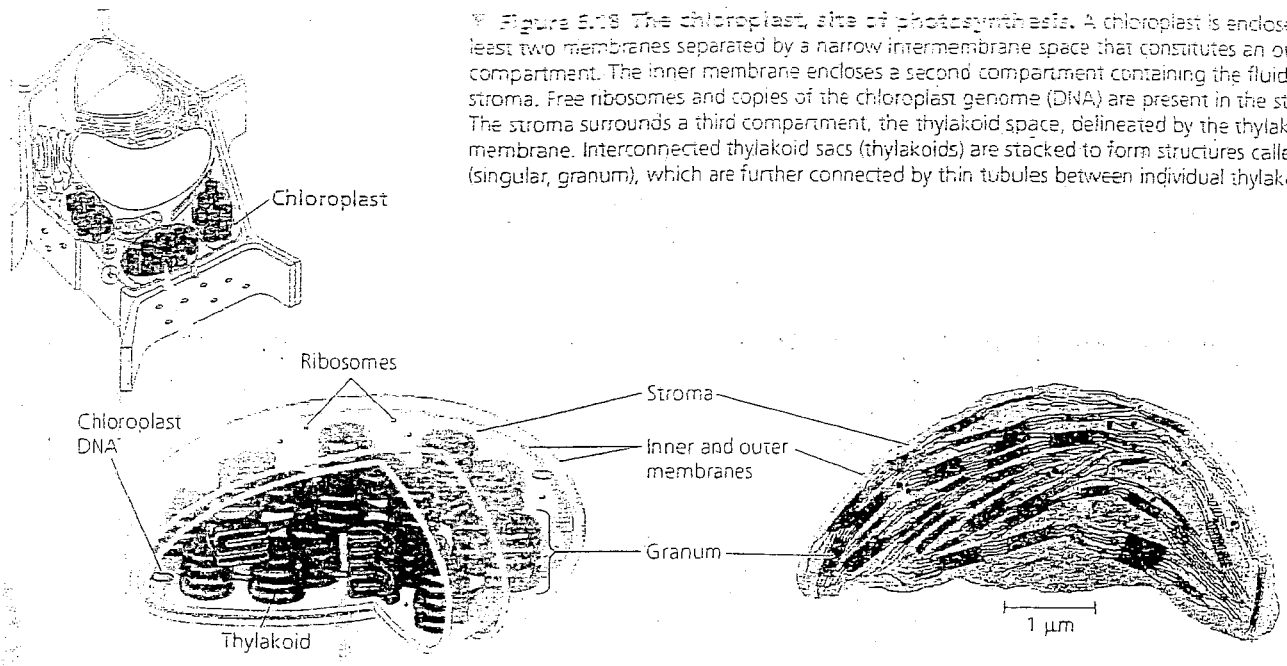


Figure 6.18 The chloroplast, site of photosynthesis. A chloroplast is enclosed by at least two membranes separated by a narrow intermembrane space that constitutes an outer compartment. The inner membrane encloses a second compartment containing the fluid called stroma. Free ribosomes and copies of the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

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

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

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

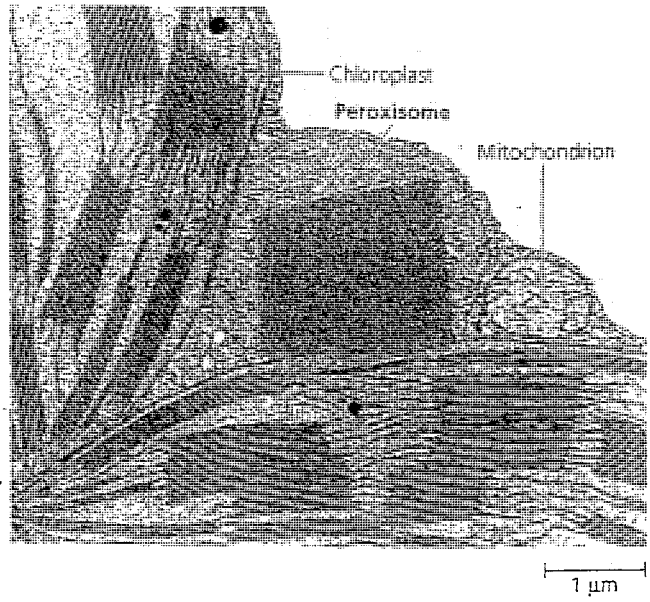


Figure 6.19 A peroxisome. Peroxisomes are roughly spherical and often have a granular or crystalline core that is thought to be a dense collection of enzyme molecules. This peroxisome is in a leaf cell. Notice its proximity to two chloroplasts and a mitochondrion. These organelles cooperate with peroxisomes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

Concept Check

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

For suggested answers, see Appendix A.

Concept 6.3

The cytoskeleton is a network of fibers that organizes structures and activities in the cell

In the early days of electron microscopy, biologists thought that the organelles of a eukaryotic cell floated freely in the cytosol. But improvements in both light microscopy and electron microscopy have revealed the cytoskeleton, a network of fibers extending throughout the cytoplasm (Figure 6.20). The cytoskeleton, which plays a major role in organizing the structures and activities of the cell, is composed of three types of molecular structures: microtubules, microfilaments, and intermediate filaments (Table 6.1).

Roles of the Cytoskeleton: Support, Motility, and Regulation

The most obvious function of the cytoskeleton is to give mechanical support to the cell and maintain its shape. This is especially important for animal cells, which lack walls. The remarkable strength and resilience of the cytoskeleton as a whole is based on its architecture. Like a geodesic dome, the cytoskeleton is stabilized by a balance between opposing forces exerted by its elements. And just as the skeleton of an animal helps fix the positions of other body parts, the cytoskeleton provides anchorage for many organelles and even cytosolic enzyme molecules. The cytoskeleton is more dynamic than an animal skeleton, however. It can be quickly dismantled in one part of the cell and reassembled in a new location, changing the shape of the cell.

The cytoskeleton is also involved in several types of cell motility (movement). The term *cell motility* encompasses both changes in cell location and more limited movements of parts of the cell. Cell motility generally requires the interaction of the cytoskeleton with proteins called motor proteins. Examples of such cell motility abound. Cytoskeletal elements and motor proteins work together with plasma membrane molecules to allow whole cells to move along fibers outside the cell. Motor proteins bring about the movements of cilia and flagella by gripping microtubules within those organelles and propelling them past each other. A similar mechanism involving microfilaments causes muscle cells to contract. Inside the cell, vesicles often travel to their destinations along "monorails" provided by the cytoskeleton. For example, this is how vesicles containing neurotransmitter molecules migrate to the tips of axons, the long extensions of nerve cells that release these molecules as chemical signals to adjacent nerve cells (Figure 6.21). The vesicles that bud off from the ER travel to the Golgi along tracks built of cytoskeletal elements. It is the cytoskeleton that manipulates the plasma membrane to form food vacuoles during phagocytosis. Finally, the streaming of cytoplasm that circulates materials within many large plant cells is yet another kind of cellular movement brought about by components of the cytoskeleton.

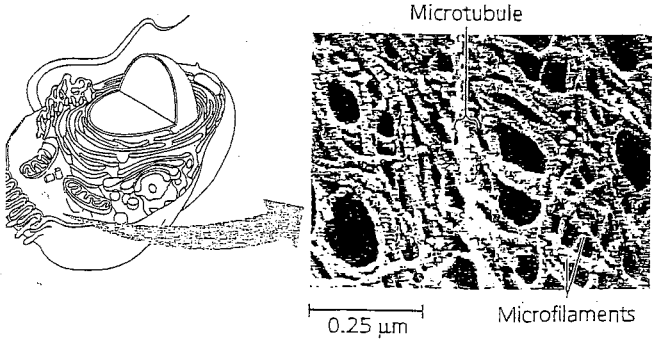
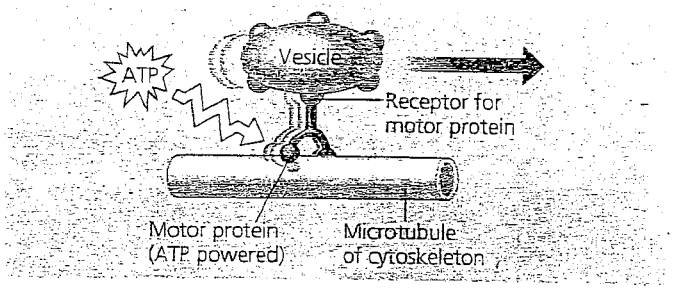
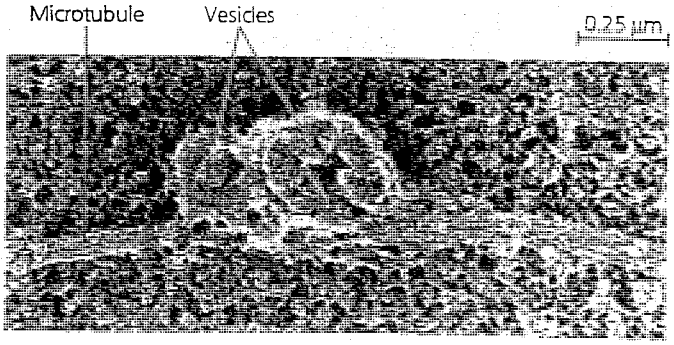


Figure 6.20 The cytoskeleton. In this TEM, prepared by a method known as deep-etching, the thicker, hollow microtubules and the thinner, solid microfilaments are visible. A third component of the cytoskeleton, intermediate filaments, is not evident here.



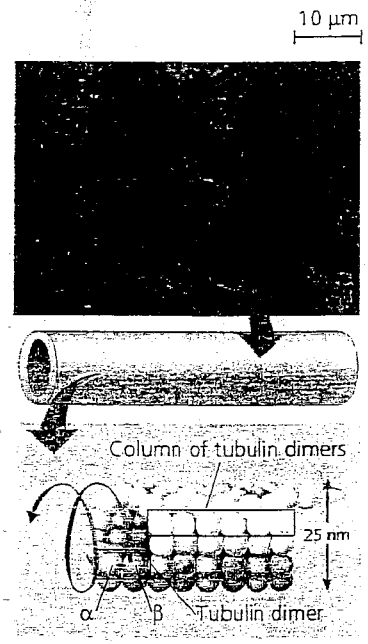
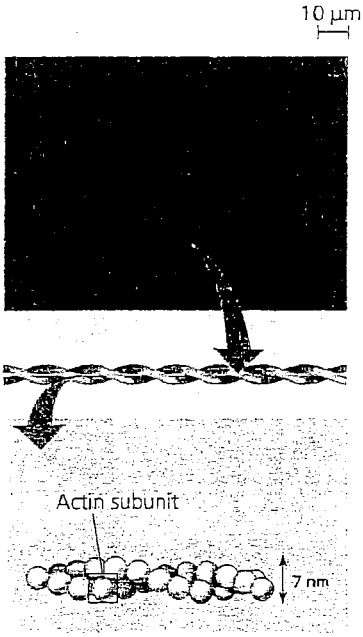
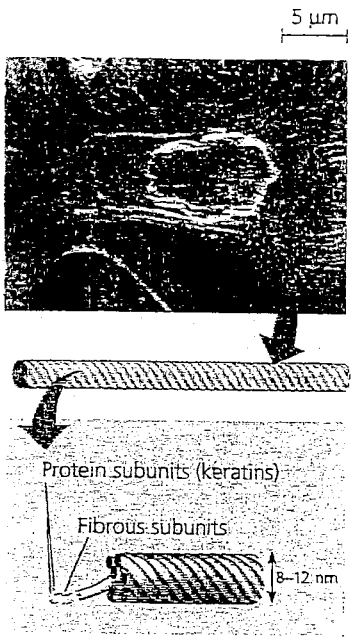
(a) Motor proteins that attach to receptors on organelles can "walk" the organelles along microtubules or, in some cases, microfilaments.



(b) Vesicles containing neurotransmitters migrate to the tips of nerve cell axons via the mechanism in (a). In this SEM of a squid giant axon, two vesicles can be seen moving along a microtubule. (A separate part of the experiment provided the evidence that they were in fact moving.)

Figure 6.21 Motor proteins and the cytoskeleton.

Table 6.1 The Structure and Function of the Cytoskeleton

Property	Microtubules (Tubulin Polymers)	Microfilaments (Actin Filaments)	Intermediate Filaments
Structure	Hollow tubes; wall consists of 13 columns of tubulin molecules	Two intertwined strands of actin, each a polymer of actin subunits	Fibrous proteins supercoiled into thicker cables
Diameter	25 nm with 15-nm lumen	7 nm	8–12 nm
Protein subunits	Tubulin, consisting of α-tubulin and β-tubulin	Actin	One of several different proteins of the keratin family, depending on cell type
Main functions	Maintenance of cell shape (compression-resisting "girders") Cell motility (as in cilia or flagella) Chromosome movements in cell division Organelle movements	Maintenance of cell shape (tension-bearing elements) Changes in cell shape Muscle contraction Cytoplasmic streaming Cell motility (as in pseudopodia) Cell division (cleavage furrow formation)	Maintenance of cell shape (tension-bearing elements) Anchorage of nucleus and certain other organelles Formation of nuclear lamina
Micrographs of fibroblasts, a favorite cell type for cell biology studies. Each has been experimentally treated to fluorescently tag the structure of interest.			

The most recent addition to the list of possible cytoskeletal unctions is the regulation of biochemical activities in the cell. Mounting evidence suggests that the cytoskeleton can transmit mechanical forces exerted by extracellular molecules via urface proteins of the cell to its interior—and even into the ucleus. In one experiment, investigators used a micromanipulation device to pull on certain plasma membrane proeins attached to the cytoskeleton. A video microscope captured lmost instantaneous rearrangements of nucleoli and other tructures in the nucleus. In this way, the transmission of naturally occurring mechanical signals by the cytoskeleton may help regulate cell function.

Components of the Cytoskeleton

Now let's look more closely at the three main types of fibers that make up the cytoskeleton (see Table 6.1). Microtubules are the thickest of the three types; microfilaments (also called actin filaments) are the thinnest; and intermediate filaments are fibers with diameters in a middle range.

Microtubules

Microtubules are found in the cytoplasm of all eukaryotic cells. They are hollow rods measuring about 25 nm in diameter and from 200 nm to 25 μm in length. The wall of the hollow tube is constructed from a globular protein called tubulin. Each tubulin molecule is a dimer consisting of two slightly different polypeptide subunits, α-tubulin and β-tubulin. A microtubule grows in length by adding tubulin dimers to its ends. Microtubules can be disassembled and their tubulin used to build microtubules elsewhere in the cell.

Microtubules shape and support the cell and also serve as tracks along which organelles equipped with motor proteins can move (see Figure 6.21). For example, microtubules guide secretory vesicles from the Golgi apparatus to the plasma membrane. Microtubules are also responsible for the separation of chromosomes during cell division (see Chapter 12).

Centrosomes and Centrioles. In many cells, microtubules grow out from a **centrosome**, a region often located near the nucleus that is considered to be a "microtubule-organizing center." These microtubules function as compression-resisting girders of the cytoskeleton. Within the centrosome of an animal cell are a pair of **centrioles**, each composed of nine sets of triplet microtubules arranged in a ring **(Figure 6.22)**. Before a cell divides, the centrioles replicate. Although centrioles may help organize microtubule assembly, they are not essential for this function in all eukaryotes; centrosomes of most plants lack centrioles, but have well-organized microtubules.

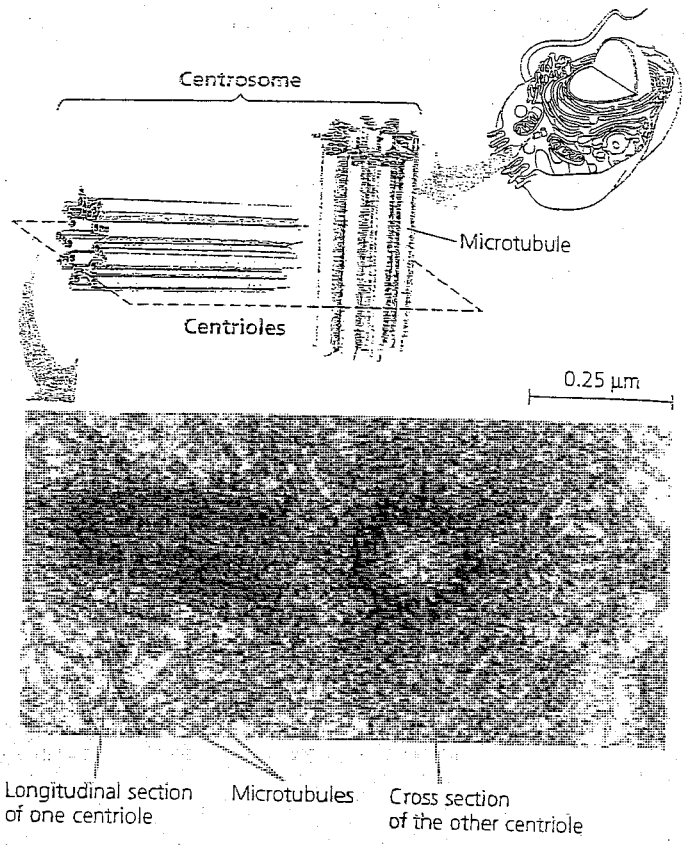
Cilia and Flagella. In eukaryotes, a specialized arrangement of microtubules is responsible for the beating of **flagella** (singular, *flagellum*) and **cilia** (singular, *cilium*), locomotor appendages that protrude from some cells. Many unicellular eukaryotic organisms are propelled through water by cilia or flagella, and the sperm of animals, algae, and some plants have flagella. When cilia or flagella extend from cells that are held in place as part of a tissue layer, they can move fluid over the surface of the tissue. For example, the ciliated lining of the windpipe sweeps mucus containing trapped debris out of the lungs (see Figure 6.4). In a woman's reproductive tract, the cilia lining the oviducts (fallopian tubes) help move an egg toward the uterus.

Cilia usually occur in large numbers on the cell surface. They are about 0.25 μm in diameter and about 2–20 μm in length. Flagella are the same diameter but longer than cilia, measuring 10–200 μm in length. Also, flagella are usually limited to just one or a few per cell.

Flagella and cilia differ in their beating patterns **(Figure 6.23)**. A flagellum has an undulating motion that generates force in the same direction as the flagellum's axis. In contrast, cilia work more like oars, with alternating power and recovery strokes generating force in a direction perpendicular to the cilium's axis.

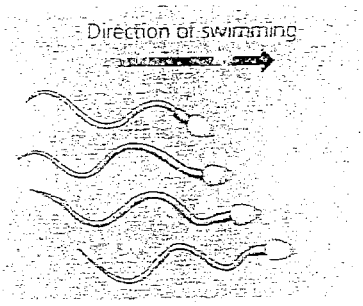
Though different in length, number per cell, and beating pattern, cilia and flagella share a common ultrastructure. A cilium or flagellum has a core of microtubules sheathed in an extension of the plasma membrane **(Figure 6.24)**. Nine doublets of microtubules, the members of each pair sharing part of their walls, are arranged in a ring. In the center of the ring are two single microtubules. This arrangement, referred to as the "9 + 2" pattern, is found in nearly all eukaryotic flagella and cilia. (The flagella of motile prokaryotes, discussed in Chapter 27, do not contain microtubules.) Flexible "wagon wheels" of cross-linking proteins, evenly spaced along the length of the cilium or flagellum, connect the outer doublets to each other (the wheel rim) and to the two central microtubules (the wheel spokes). Each outer doublet also has pairs of side-arms spaced along its length and reaching toward the neighboring doublet; these are motor proteins. The microtubule assembly of a cilium or flagellum is anchored in the cell by a **basal body**, which is structurally identical to a centriole. In fact, in many animals (including humans), the basal body of the fertilizing sperm's flagellum enters the egg and becomes a centriole.

Each motor protein extending from one microtubule doublet to the next is a large protein called dynein, which is composed



▲ Figure 6.22 Centrosome containing a pair of centrioles. An animal cell has a pair of centrioles within its centrosome, the region near the nucleus where the cell's microtubules are initiated. The centrioles, each about 250 nm (0.25 μm) in diameter, are found at right angles to each other, and each is made up of nine sets of three microtubules. The blue portions of the drawing represent nontubulin proteins that connect the microtubule triplets (TEM).

(a) Motion of flagella. A flagellum usually undulates, its snakelike motion driving a cell in the same direction as the axis of the flagellum. Propulsion of a human sperm cell is an example of flagellate locomotion (LM).



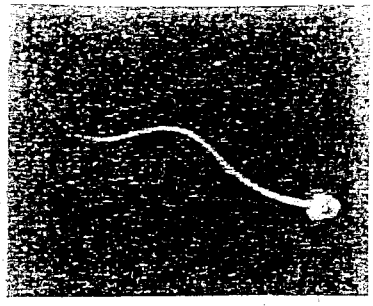
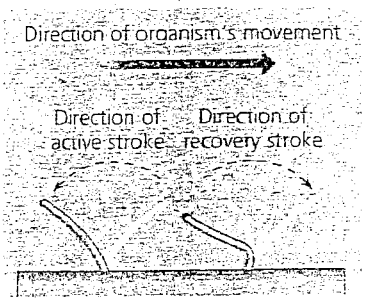
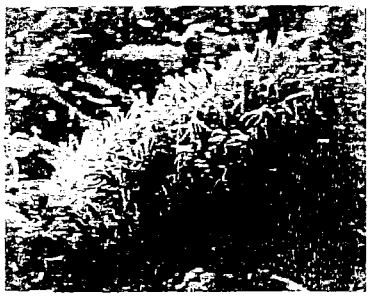
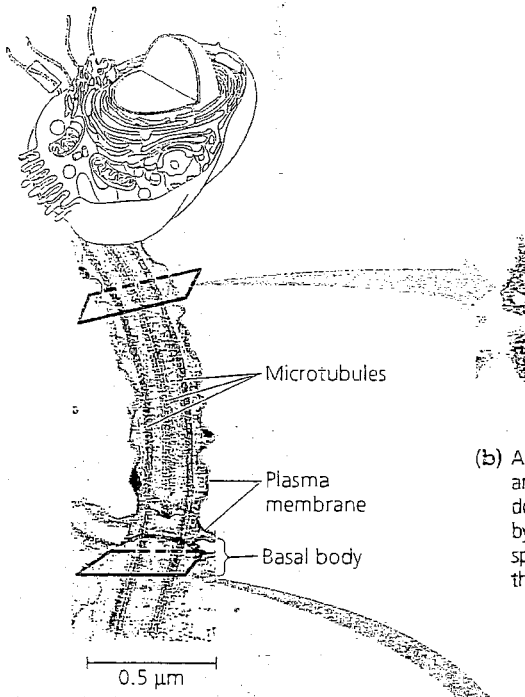


Figure 6.23 A comparison of the beating of flagella and cilia.

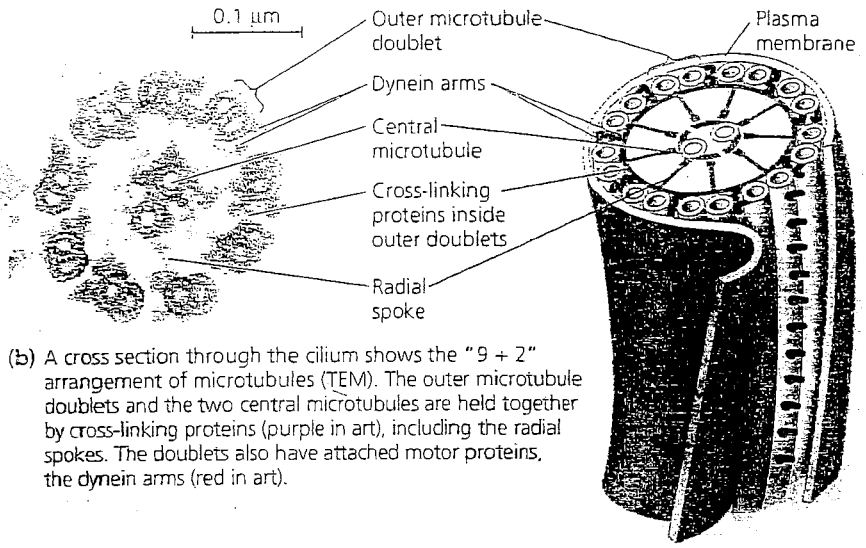
(b) Motion of cilia. Cilia have a back-and-forth motion that moves the cell in a direction perpendicular to the axis of the cilium. A dense nap of cilia, beating at a rate of about 40 to 60 strokes a second, covers this *Colpidium*, a freshwater protozoan (colorized SEM).



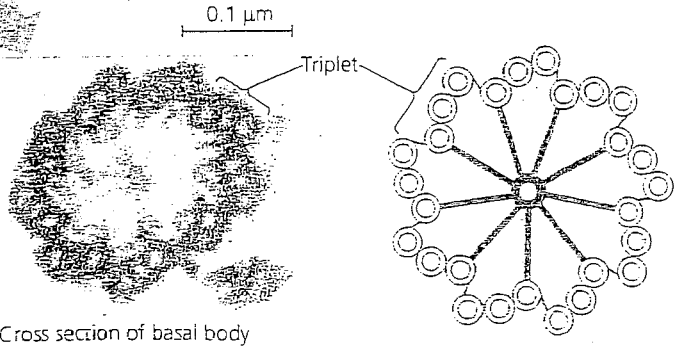




(a) A longitudinal section of a cilium shows microtubules running the length of the structure (TEM).



(b) A cross section through the cilium shows the "9 + 2" arrangement of microtubules (TEM). The outer microtubule doublets and the two central microtubules are held together by cross-linking proteins (purple in art), including the radial spokes. The doublets also have attached motor proteins, the dynein arms (red in art).



(c) Basal body: The nine outer doublets of a cilium or flagellum extend into the basal body, where each doublet joins another microtubule to form a ring of nine triplets. Each triplet is connected to the next by nontubulin proteins (blue). The two central microtubules terminate above the basal body (TEM).

Figure 6.24 Ultrastructure of a eukaryotic flagellum or cilium.

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of several polypeptides. These dynein arms are responsible for the bending movements of cilia and flagella. A dynein arm performs a complex cycle of movements caused by changes in the conformation of the protein, with ATP providing the energy for these changes (Figure 6.25).

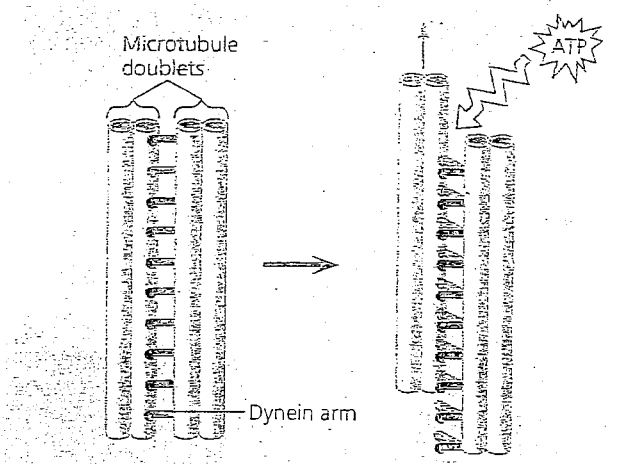
The mechanics of dynein "walking" are reminiscent of a cat climbing a tree by attaching its claws, moving its legs, releasing its front claws, and grabbing again farther up the tree. Similarly, the dynein arms of one doublet attach to an adjacent doublet and pull so that the doublets slide past each other in opposite directions. The arms then release from the other doublet and reattach a little farther along its length. Without any restraints on the movement of the microtubule doublets, one doublet would continue to "walk" along and slide past the surface of the other, elongating the cilium or flagellum rather than bending it (see Figure 6.25a). For lateral movement of a cilium or flagellum, the dynein "walking" must have something to pull against, as when the muscles in your leg pull against your bones to move your knee. In cilia and flagella, the microtubule doublets seem to be held in place by the cross-linking proteins just inside the outer doublets and by the radial spokes and other structural elements. Thus, neighboring doublets cannot slide past each other very far. Instead, the forces exerted by the dynein arms cause the doublets to curve, bending the cilium or flagellum (see Figure 6.25b and c).

Microfilaments (Actin Filaments)

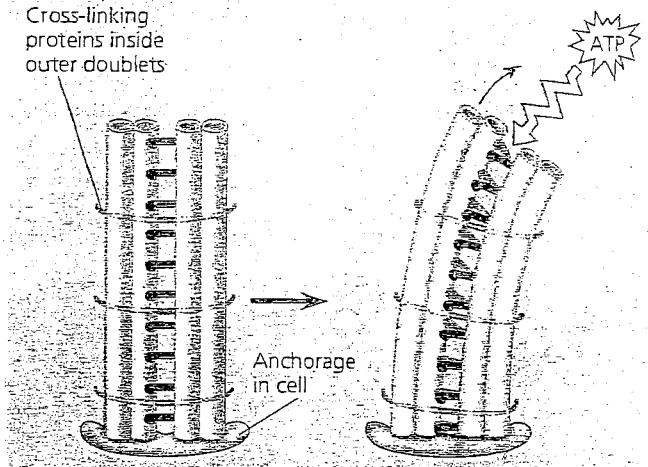
Microfilaments are solid rods about 7 nm in diameter. They are also called actin filaments, because they are built from molecules of **actin**, a globular protein. A microfilament is a twisted double chain of actin subunits (see Table 6.1). Besides occurring as linear filaments, microfilaments can form structural networks, due to the presence of proteins that bind along the side of an actin filament and allow a new filament to extend as a branch. Microfilaments seem to be present in all eukaryotic cells.

In contrast to the compression-resisting role of microtubules, the structural role of microfilaments in the cytoskeleton is to bear tension (pulling forces). The ability of microfilaments to form a three-dimensional network just inside the plasma membrane helps support the cell's shape. This network gives the cortex (outer cytoplasmic layer) of a cell the semisolid consistency of a gel, in contrast with the more fluid (sol) state of the interior cytoplasm. In animal cells specialized for transporting materials across the plasma membrane, such as intestinal cells, bundles of microfilaments make up the core of microvilli, the previously mentioned delicate projections that increase the cell surface area (Figure 6.26).

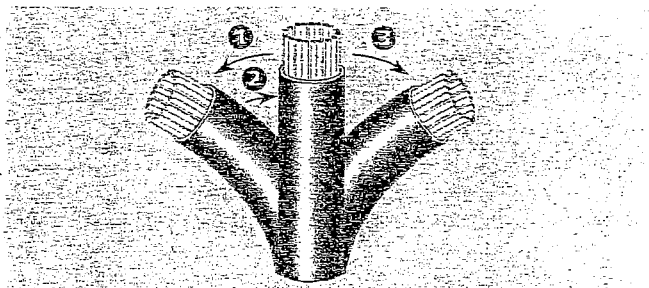
Microfilaments are well known for their role in cell motility, particularly as part of the contractile apparatus of muscle



(a) Dynein "walking." Powered by ATP, the dynein arms of one microtubule doublet grip the adjacent doublet, push it up, release, and then grip again. If the two microtubule doublets were not attached, they would slide relative to each other.

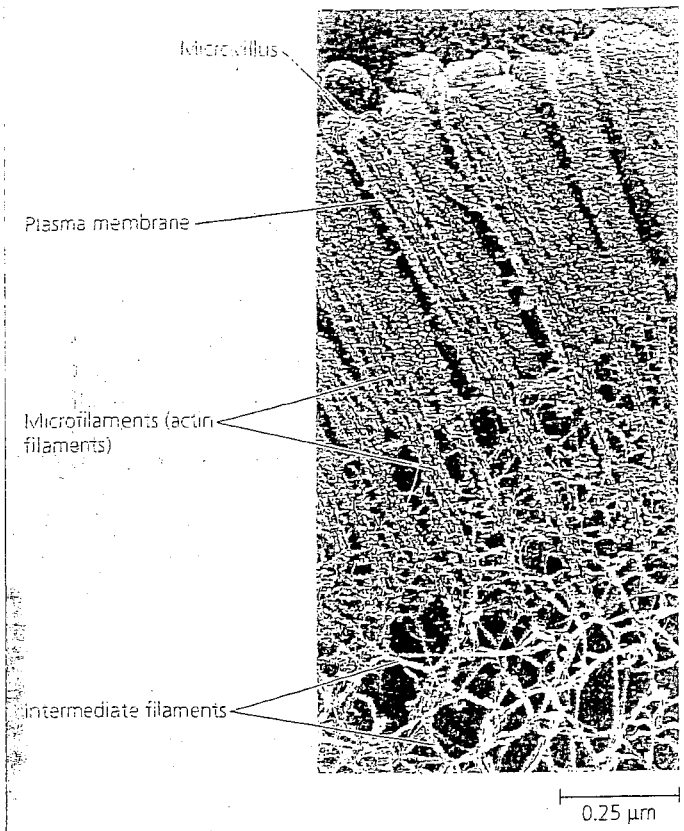


(b) Effect of cross-linking proteins. In a cilium or flagellum, two adjacent doublets cannot slide far because they are physically restrained by proteins, so they bend. (Only two of the nine outer doublets in Figure 6.24b are shown here.)



(c) Wavelike motion. Localized, synchronized activation of many dynein arms probably causes a bend to begin at the base of the cilium or flagellum and move outward toward the tip. Many successive bends, such as the ones shown here to the left and right, result in a wavelike motion. In this diagram, the two central microtubules and the cross-linking proteins are not shown.

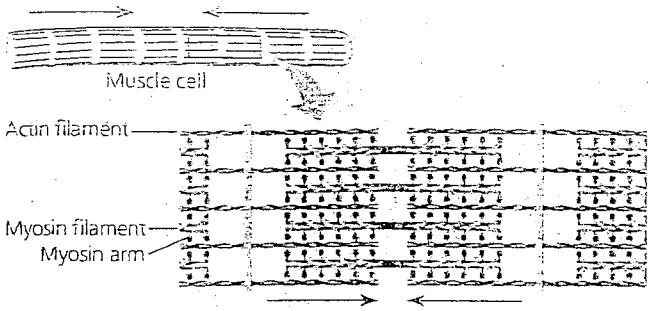
▲ Figure 6.25 How dynein "walking" moves flagella and cilia.



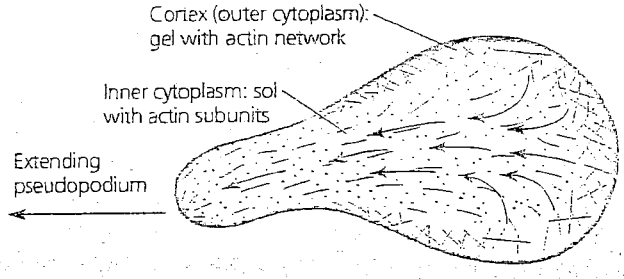
▲ Figure 6.26 **A structural role of microfilaments.** The surface area of this nutrient-absorbing intestinal cell is increased by its many microvilli (singular, microvillus), cellular extensions reinforced by bundles of microfilaments. These actin filaments are anchored to a network of intermediate filaments (TEM).

cells. Thousands of actin filaments are arranged parallel to one another along the length of a muscle cell, interdigitated with thicker filaments made of a protein called myosin (Figure 6.27a). Myosin acts as a motor protein by means of projections (arms) that "walk" along the actin filaments. Contraction of the muscle cell results from the actin and myosin filaments sliding past one another in this way, shortening the cell. In other kinds of cells, actin filaments are associated with myosin in miniature and less elaborate versions of the arrangement in muscle cells. These actin-myosin aggregates are responsible for localized contractions of cells. For example, a contracting belt of microfilaments forms a cleavage furrow that pinches a dividing animal cell into two daughter cells.

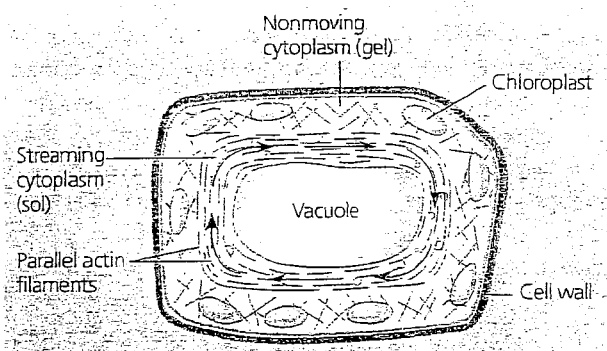
Localized contraction brought about by actin and myosin also plays a role in amoeboid movement (Figure 6.27b), in which a cell, such as an amoeba, for example, crawls along a surface by extending and flowing into cellular extensions called pseudopodia (from the Greek *pseudes*, false, and *pod*, foot). Pseudopodia extend and contract through the reversible assembly of actin subunits into microfilaments and of microfilaments into networks that convert cytoplasm from sol to



(a) **Myosin motors in muscle cell contraction.** The "walking" of myosin arms drives the parallel myosin and actin filaments past each other so that the actin filaments approach each other in the middle (red arrows). This shortens the muscle cell. Muscle contraction involves the shortening of many muscle cells at the same time.



(b) **Amoeboid movement.** Interaction of actin filaments with myosin near the cell's trailing end (at right) squeezes the interior fluid forward (to the left) into the pseudopodium.



(c) **Cytoplasmic streaming in plant cells.** A layer of cytoplasm cycles around the cell, moving over a carpet of parallel actin filaments. Myosin motors attached to organelles in the fluid cytosol may drive the streaming by interacting with the actin.

▲ Figure 6.27 **Microfilaments and motility.** In the three examples shown in this figure, cell nuclei and most other organelles have been omitted for clarity.

gel. According to a widely accepted model, filaments near the cell's trailing end interact with myosin, causing contraction. Like squeezing on a toothpaste tube, this contraction forces the interior fluid into the pseudopodium, where the actin network has been weakened. The pseudopodium extends until

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

In plant cells, both actin-myosin interactions and sol-gel transformations brought about by actin may be involved in cytoplasmic streaming, a circular flow of cytoplasm within cells (Figure 5.27c). This movement, which is especially common in large plant cells, speeds the distribution of materials within the cell.

Intermediate Filaments

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

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

Concept Check

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

For suggested answers, see Appendix A.

Concept 6.4

Extracellular components and connections between cells help coordinate cellular activities

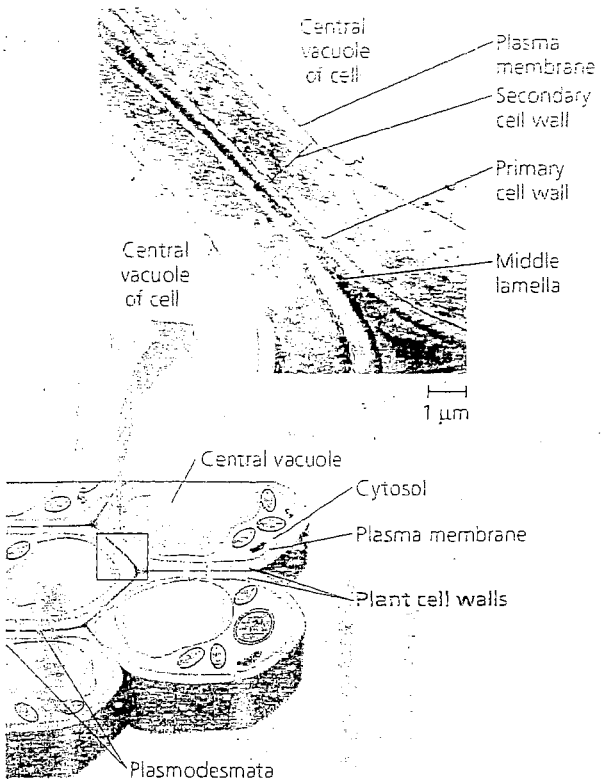
Having crisscrossed the interior of the cell to explore various organelles, we complete our tour of the cell by returning to the surface of this microscopic world, where there are additional structures with important functions. The plasma membrane is usually regarded as the boundary of the living cell,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

Cell Walls of Plants

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

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

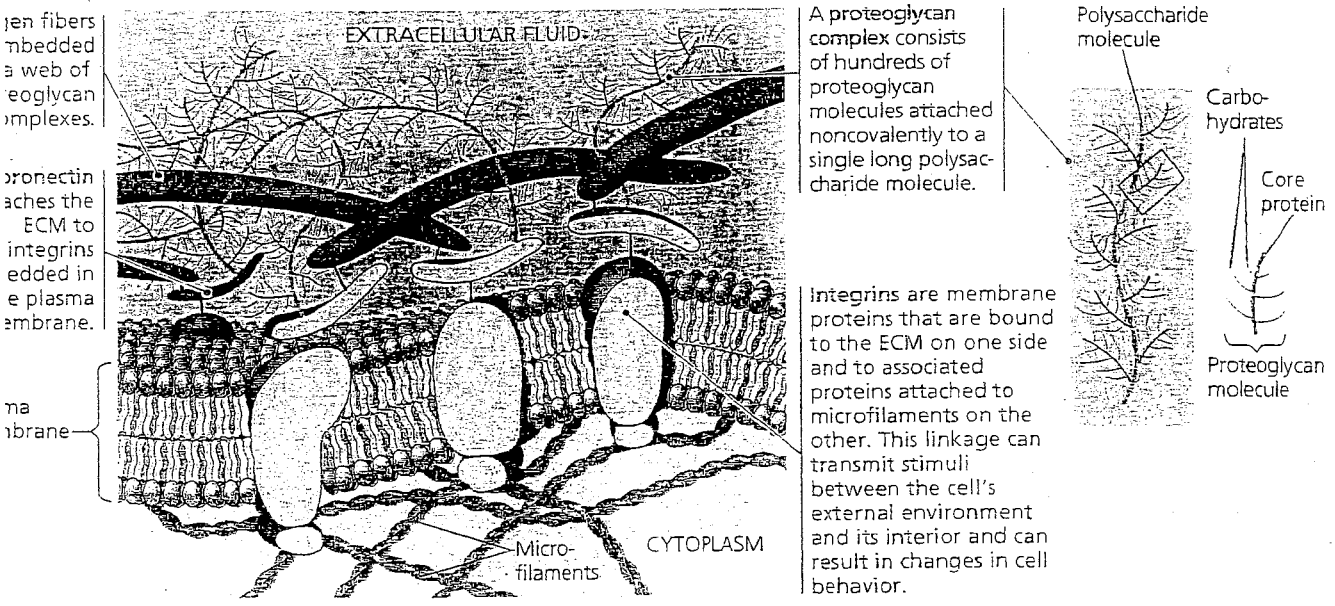
A young plant cell first secretes a relatively thin and flexible wall called the **primary cell wall** (Figure 6.28). Between primary walls of adjacent cells is the **middle lamella**, a thin layer rich in sticky polysaccharides called pectins. The middle lamella glues adjacent cells together (pectin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



ure 6.28 **Plant cell walls.** The orientation drawing shows cells, each with a large vacuole, a nucleus, and several plasts and mitochondria. The transmission electron micrograph shows the cell walls where two cells come together. The yered partition between plant cells consists of adjoining walls ually secreted by the cells.

The Extracellular Matrix (ECM) of Animal Cells

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



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

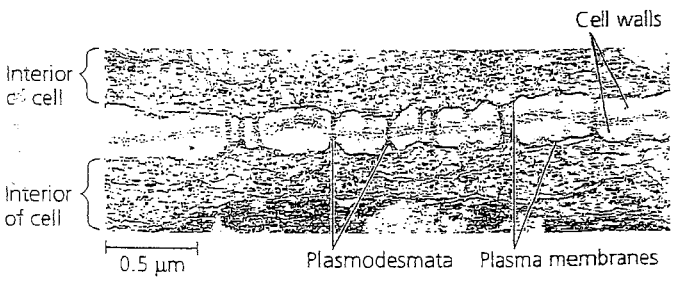
Current research on fibronectin, other ECM molecules, and integrins is revealing the influential role of the extracellular matrix in the lives of cells. By communicating with a cell through integrins, the ECM can regulate a cell's behavior. For example, some cells in a developing embryo migrate along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

Intercellular Junctions

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

Plants: Plasmodesmata

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



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

Animals: Tight Junctions, Desmosomes, and Gap Junctions

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

Concept Check

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

For suggested answers, see Appendix A.

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

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