

CHAPTER 4

Cell Structure

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Introduction

All organisms are composed of cells. The gossamer wing of a butterfly is a thin sheet of cells and so is the glistening outer layer of your eyes. The burger or tomato you eat is composed of cells, and its contents soon become part of your cells. Some organisms consist of a single cell too small to see with the unaided eye. Others, such as humans, are composed of many specialized cells, such as the fibroblast cell shown in the striking fluorescence micrograph on this page. Cells are so much a part of life that we cannot imagine an organism that is not cellular in nature. In this chapter, we take a close look at the internal structure of cells. In chapters 5 to 10, we will focus on cells in action—how they communicate with their environment, grow, and reproduce.

4.1 Cell Theory

Learning Outcomes

1. Discuss the cell theory.
2. Describe the factors that limit cell size.
3. Categorize structural and functional similarities in cells.

Cells are characteristically microscopic in size. Although there are exceptions, a typical eukaryotic cell is 10 to 100 micrometers (μm) (10 to 100 millionths of a meter) in diameter, although most prokaryotic cells are only 1 to 10 μm in diameter.

Because cells are so small, they were not discovered until the invention of the microscope in the 17th century. English natural philosopher Robert Hooke was the first to observe cells in 1665, naming the shapes he saw in cork *cellulae* (Latin, “small rooms”). This is known to us as *cells*. Another early microscopist, Dutch Anton van Leeuwenhoek, first observed living cells, which he termed “animalcules,” or little animals. After these early efforts, a

century and a half passed before biologists fully recognized the importance of cells. In 1838, German botanist Matthias Schleiden stated that all plants “are aggregates of fully individualized, independent, separate beings, namely the cells themselves.” In 1839, German physiologist Theodor Schwann reported that all animal tissues also consist of individual cells. Thus, the cell theory was born.

Cell theory is the unifying foundation of cell biology

The cell theory was proposed to explain the observation that all organisms are composed of cells. It sounds simple, but it is a far-reaching statement about the organization of life.

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

1. All organisms are composed of one or more cells, and the life processes of metabolism and heredity occur within these cells.
2. Cells are the smallest living things, the basic units of organization of all organisms.
3. Cells arise only by division of a previously existing cell.

Although life likely evolved spontaneously in the environment of early Earth, biologists have concluded that no additional cells are originating spontaneously at present. Rather, life on Earth represents a continuous line of descent from those early cells.

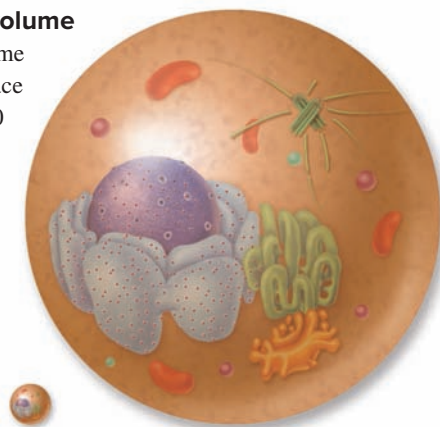
Cell size is limited

Most cells are relatively small for reasons related to the diffusion of substances into and out of them. The rate of diffusion is affected by a number of variables, including (1) surface area available for diffusion, (2) temperature, (3) concentration gradient of diffusing substance, and (4) the distance over which diffusion must occur. As the size of a cell increases, the length of time for diffusion from the outside membrane to the interior of the cell increases as well. Larger cells need to synthesize more macromolecules, have correspondingly higher energy requirements, and produce a greater quantity of waste. Molecules used for energy and biosynthesis must be transported through the membrane. Any metabolic waste produced must be removed, also passing through the membrane. The rate at which this transport occurs depends on both the distance to the membrane and the area of membrane available. For this reason, an organism made up of many relatively small cells has an advantage over one composed of fewer, larger cells.

The advantage of small cell size is readily apparent in terms of the **surface area-to-volume ratio**. As a cell’s size increases, its volume increases much more rapidly than its surface area. For a spherical cell, the surface area is proportional to the square of the radius, whereas the volume is proportional to the cube of the radius. Thus, if the radii of two cells differ by a factor of 10, the larger cell will have 10^2 , or 100 times, the surface area, but 10^3 , or 1000 times, the volume of the smaller cell (figure 4.1).

The cell surface provides the only opportunity for interaction with the environment, because all substances enter and exit a cell via this surface. The membrane surrounding the cell plays a key

Figure 4.1 Surface area-to-volume ratio. As a cell gets larger, its volume increases at a faster rate than its surface area. If the cell radius increases by 10 times, the surface area increases by 100 times, but the volume increases by 1000 times. A cell’s surface area must be large enough to meet the metabolic needs of its volume.



Cell radius (r)	1 unit	10 unit
Surface area ($4\pi r^2$)	12.57 unit ²	1257 unit ²
Volume ($\frac{4}{3}\pi r^3$)	4.189 unit ³	4189 unit ³
Surface Area / Volume	3	0.3

role in controlling cell function. Because small cells have more surface area per unit of volume than large ones, control over cell contents is more effective when cells are relatively small.

Although most cells are small, some quite large cells do exist. These cells have apparently overcome the surface area-to-volume problem by one or more adaptive mechanisms. For example, some cells, such as skeletal muscle cells, have more than one nucleus, allowing genetic information to be spread around a large cell. Some other large cells, such as neurons, are long and skinny, so that any given point within the cell is close to the plasma membrane. This permits diffusion between the inside and outside of the cell to still be rapid.

Microscopes allow visualization of cells and components

Other than egg cells, not many cells are visible to the naked eye (figure 4.2). Most are less than 50 μm in diameter, far smaller than the period at the end of this sentence. So, to visualize cells we need the aid of technology. The development of microscopes and their refinement over the centuries has allowed us to continually explore cells in greater detail.

The resolution problem

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

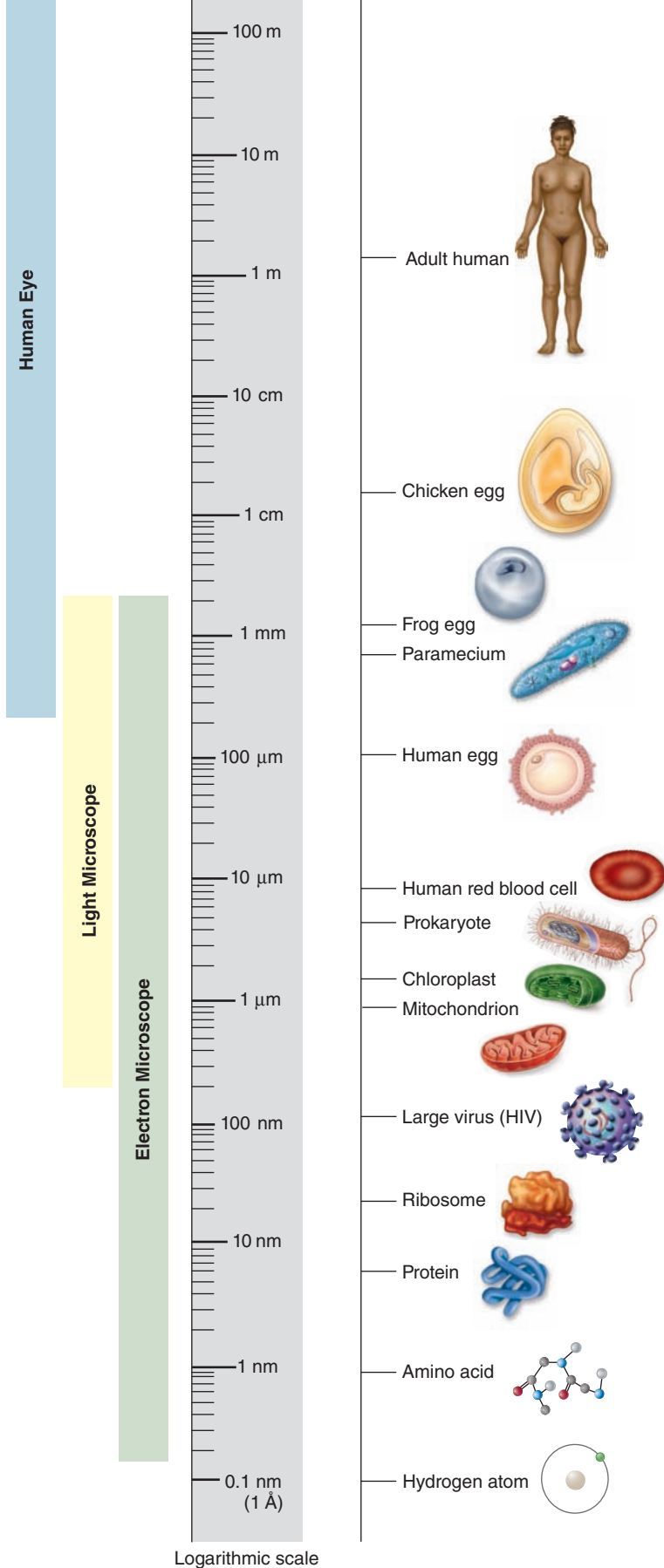


Figure 4.2 The size of cells and their contents. Except for vertebrate eggs, which can typically be seen with the unaided eye, most cells are microscopic in size. Prokaryotic cells are generally 1 to 10 μm across.

$$1 \text{ m} = 10^2 \text{ cm} = 10^3 \text{ mm} = 10^6 \mu\text{m} = 10^9 \text{ nm}$$

Types of microscopes

One way to overcome the limitations of our eyes is to increase magnification so that small objects appear larger. The first microscopists used glass lenses to magnify small cells and cause them to appear larger than the 100- μm limit imposed by the human eye. The glass lens increases focusing power. Because the glass lens makes the object appear closer, the image on the back of the eye is bigger than it would be without the lens.

Modern *light microscopes*, which operate with visible light, use two magnifying lenses (and a variety of correcting lenses) to achieve very high magnification and clarity (table 4.1). The first lens focuses the image of the object on the second lens, which magnifies it again and focuses it on the back of the eye. Microscopes that magnify in stages using several lenses are called *compound microscopes*. They can resolve structures that are separated by at least 200 nanometers (nm).

Light microscopes, even compound ones, are not powerful enough to resolve many of the structures within cells. For example, a cell membrane is only 5 nm thick. Why not just add another magnifying stage to the microscope to increase its resolving power? This doesn't work because when two objects are closer than a few hundred nanometers, the light beams reflecting from the two images start to overlap each other. The only way two light beams can get closer together and still be resolved is if their wavelengths are shorter. One way to avoid overlap is by using a beam of electrons rather than a beam of light. Electrons have a much shorter wavelength, and an *electron microscope*, employing electron beams, has 1000 times the resolving power of a light microscope.

Transmission electron microscopes, so called because the electrons used to visualize the specimens are transmitted through the material, are capable of resolving objects only 0.2 nm apart—which is only twice the diameter of a hydrogen atom!

A second kind of electron microscope, the *scanning electron microscope*, beams electrons onto the surface of the specimen. The electrons reflected back from the surface, together with other electrons that the specimen itself emits as a result of the bombardment, are amplified and transmitted to a screen, where the image can be viewed and photographed. Scanning electron microscopy yields striking three-dimensional images. This technique has improved our understanding of many biological and physical phenomena (table 4.1).

Using stains to view cell structure

Although resolution remains a physical limit, we can improve the images we see by altering the sample. Certain chemical stains increase the contrast between different cellular components. Structures within the cell absorb or exclude the stain differentially, producing contrast that aids resolution.

Stains that bind to specific types of molecules have made these techniques even more powerful. This method uses antibodies that bind, for example, to a particular protein. This process, called *immunohistochemistry*, uses antibodies generated in animals such as rabbits or mice. When these animals are injected with specific proteins, they produce antibodies that bind to the injected protein. The antibodies are then purified and chemically bonded to enzymes, to stains, or to fluorescent molecules. When cells are incubated in a solution containing the antibodies, the antibodies bind to cellular structures that contain the target molecule and can

TABLE 4.1

Microscopes

LIGHT MICROSCOPES

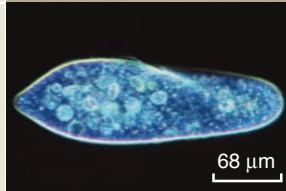
Bright-field microscope:

Light is transmitted through a specimen, giving little contrast. Staining specimens improves contrast but requires that cells be fixed (not alive), which can distort or alter components.



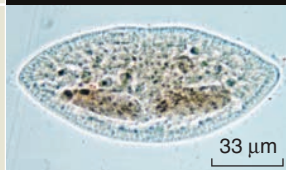
Dark-field microscope:

Light is directed at an angle toward the specimen. A condenser lens transmits only light reflected off the specimen. The field is dark, and the specimen is light against this dark background.



Phase-contrast microscope:

Components of the microscope bring light waves out of phase, which produces differences in contrast and brightness when the light waves recombine.



Differential-interference-contrast microscope:

Polarized light is split into two beams that have slightly different paths through the sample. Combining these two beams produces greater contrast, especially at the edges of structures.



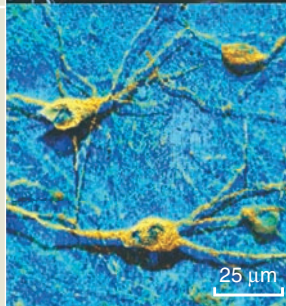
Fluorescence microscope:

Fluorescent stains absorb light at one wavelength, then emit it at another. Filters transmit only the emitted light.



Confocal microscope:

Light from a laser is focused to a point and scanned across the fluorescently stained specimen in two directions. This produces clear images of one plane of the specimen. Other planes of the specimen are excluded to prevent the blurring of the image. Multiple planes can be used to reconstruct a 3-D image.



ELECTRON MICROSCOPES

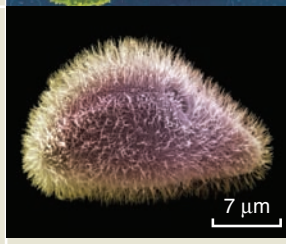
Transmission electron microscope:

A beam of electrons is passed through the specimen. Electrons that pass through are used to expose film. Areas of the specimen that scatter electrons appear dark. False coloring enhances the image.



Scanning electron microscope:

An electron beam is scanned across the surface of the specimen, and electrons are knocked off the surface. Thus, the topography of the specimen determines the contrast and the content of the image. False coloring enhances the image.



be seen with light microscopy. This approach has been used extensively in the analysis of cell structure and function.

All cells share many structural features

The general plan of cellular organization varies between different organisms, but despite these modifications, all cells resemble one another in certain fundamental ways. Before we begin a detailed examination of cell structure, let's first summarize four major features all cells have in common: (1) a nucleoid or nucleus where genetic material is located, (2) cytoplasm, (3) *ribosomes* to synthesize proteins, and (4) a plasma membrane.

Centrally located genetic material

Every cell contains DNA, the hereditary molecule. In **prokaryotes**, the simplest organisms, most of the genetic material lies in a single circular molecule of DNA. It typically resides near the center of the cell in an area called the **nucleoid**. This area is not segregated, however, from the rest of the cell's interior by membranes.

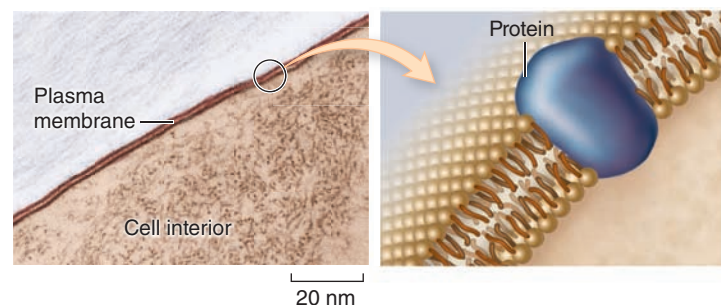
By contrast, the DNA of eukaryotes, which are more complex organisms, is contained in the nucleus, which is surrounded by a double-membrane structure called the **nuclear envelope**. In both types of organisms, the DNA contains the genes that code for the proteins synthesized by the cell. (Details of nucleus structure are described in section 4.3.)

The cytoplasm

A semifluid matrix called the **cytoplasm** fills the interior of the cell. The cytoplasm contains all of the sugars, amino acids, and proteins the cell uses to carry out its everyday activities. Although it is an aqueous medium, cytoplasm is more like Jell-O than water due to the high concentration of proteins and other macromolecules. We call any discrete macromolecular structure in the cytoplasm specialized for a particular function an **organelle**. The part of the cytoplasm that contains organic molecules and ions in solution is called the **cytosol** to distinguish it from the larger organelles suspended in this fluid.

The plasma membrane

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



The proteins of the plasma membrane are generally responsible for a cell's ability to interact with the environment. *Transport proteins* help molecules and ions move across the plasma membrane, either from the environment to the interior of the cell or vice versa. *Receptor proteins* induce changes within the cell when they come in contact with specific molecules in the environment, such as hormones, or with molecules on the surface of neighboring cells. These molecules can function as *markers* that identify the cell as a particular type. This interaction between cell surface molecules is especially important in multicellular organisms, whose cells must be able to recognize one another as they form tissues.

We'll examine the structure and function of cell membranes more thoroughly in chapter 5.

Learning Outcomes Review 4.1

All organisms are single cells or aggregates of cells, and all cells arise from preexisting cells. Cell size is limited primarily by the efficiency of diffusion across the plasma membrane. As a cell becomes larger, its volume increases more quickly than its surface area. Past a certain point, diffusion cannot support the cell's needs. All cells are bounded by a plasma membrane and filled with cytoplasm. The genetic material is found in the central portion of the cell; and in eukaryotic cells, it is contained in a membrane-bounded nucleus.

- Would finding life on Mars change our view of cell theory?

4.2 Prokaryotic Cells

Learning Outcomes

1. Describe the organization of prokaryotic cells.
2. Distinguish between bacterial and archaeal cell types.

When cells were visualized with microscopes, two basic cellular architectures were recognized: eukaryotic and prokaryotic. These terms refer to the presence or absence, respectively, of a membrane-bounded nucleus that contains genetic material. We have already mentioned that in addition to lacking a nucleus, prokaryotic cells do not have an internal membrane system or numerous membrane-bounded organelles.

Prokaryotic cells have relatively simple organization

Prokaryotes are the simplest organisms. Prokaryotic cells are small. They consist of cytoplasm surrounded by a plasma membrane and are encased within a rigid **cell wall**.

They have no distinct interior compartments (figure 4.3). A prokaryotic cell is like a one-room cabin in which eating, sleeping, and watching TV all occur.

Prokaryotes are very important in the ecology of living organisms. Some harvest light by photosynthesis, others break down dead organisms and recycle their components. Still others cause disease or have uses in many important industrial processes. Prokaryotes have two main domains: archaea and bacteria. Chapter 28 covers prokaryotic diversity in more detail.

? **Inquiry question** What modifications would you include if you wanted to make a cell as large as possible?

Although prokaryotic cells do contain organelles like **ribosomes**, which carry out protein synthesis, most lack the membrane-bounded organelles characteristic of eukaryotic cells. It was long thought that prokaryotes also lack the elaborate cytoskeleton found in eukaryotes, but we have now found they have molecules related to both actin and tubulin, which form two of the cytoskeletal elements described in section 4.6. The strength and shape of the cell is determined by the cell wall and not these cytoskeletal elements (figure 4.3). However, cell wall structure is influenced by the cytoskeleton. For instance, the presence of actin like MreB fibers running the length of the cell lead to perpendicular cell-wall fibers that produce a rod-shaped cell. This can be seen when MreB protein is removed, cells become spherical rather than rod-shaped. During cell division, cell-wall deposition is influenced by the tubulin-like FtsZ protein (see chapter 10).

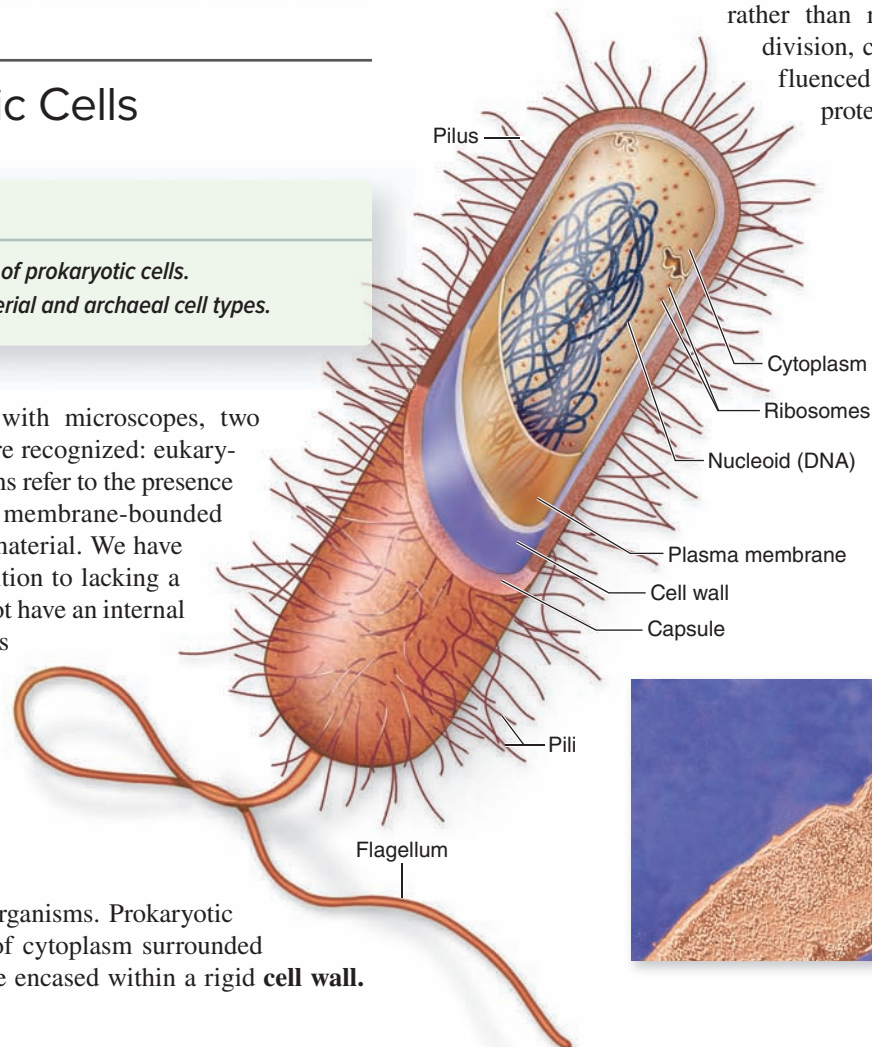
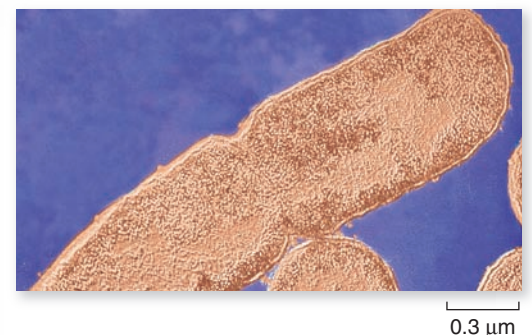


Figure 4.3
Structure of a prokaryotic cell.

Generalized cell organization of a prokaryote. The nucleoid is visible as a dense central region segregated from the cytoplasm. Some prokaryotes have hairlike growths (called pili [singular, *pilus*]) on the outside of the cell.



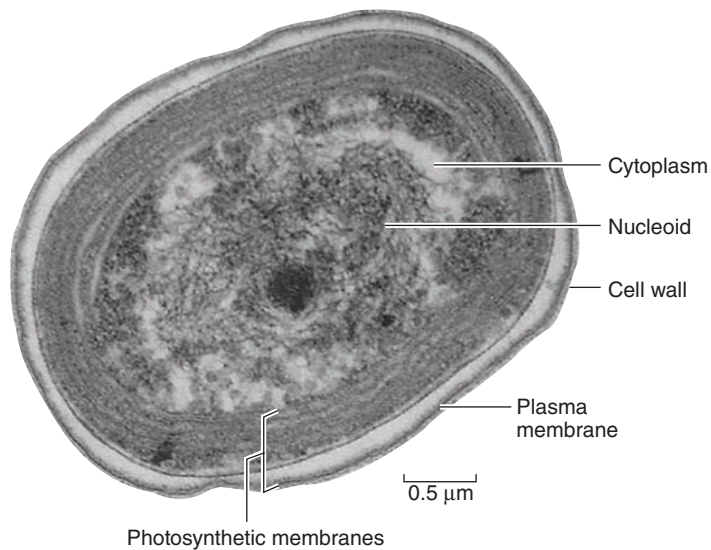


Figure 4.4 Electron micrograph of a photosynthetic bacterial cell. Extensive folded photosynthetic membranes are shown in green in this false colored electron micrograph of a *Prochloron* cell.

The plasma membrane of a prokaryotic cell carries out some of the functions organelles perform in eukaryotic cells. For example, some photosynthetic bacteria, such as the cyanobacterium *Prochloron* (figure 4.4), have an extensively folded plasma membrane, with the folds extending into the cell's interior. These membrane folds contain the bacterial pigments connected with photosynthesis. In eukaryotic plant cells, photosynthetic pigments are found in the inner membrane of the chloroplast.

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

Bacterial cell walls consist of peptidoglycan

Most bacterial cells are encased by a strong **cell wall**. This cell wall is composed of *peptidoglycan*, which consists of a carbohydrate matrix (polymers of sugars) that is cross-linked by short polypeptide units. Details about the structure of this cell wall are discussed in chapter 28. Cell walls protect the cell, maintain its shape, and prevent excessive uptake or loss of water. The exception is the class Mollicutes, which includes the common genus *Mycoplasma*, which lack a cell wall. Plants, fungi, and most protists also have cell walls but with a chemical structure different from peptidoglycan.

The susceptibility of bacteria to antibiotics often depends on the structure of their cell walls. The drugs penicillin and vancomycin, for example, interfere with the ability of bacteria to cross-link the peptides in their peptidoglycan cell wall. Like removing all the nails from a wooden house, this destroys the integrity of the structural matrix, which can no longer prevent water from rushing in and swelling the cell to bursting.

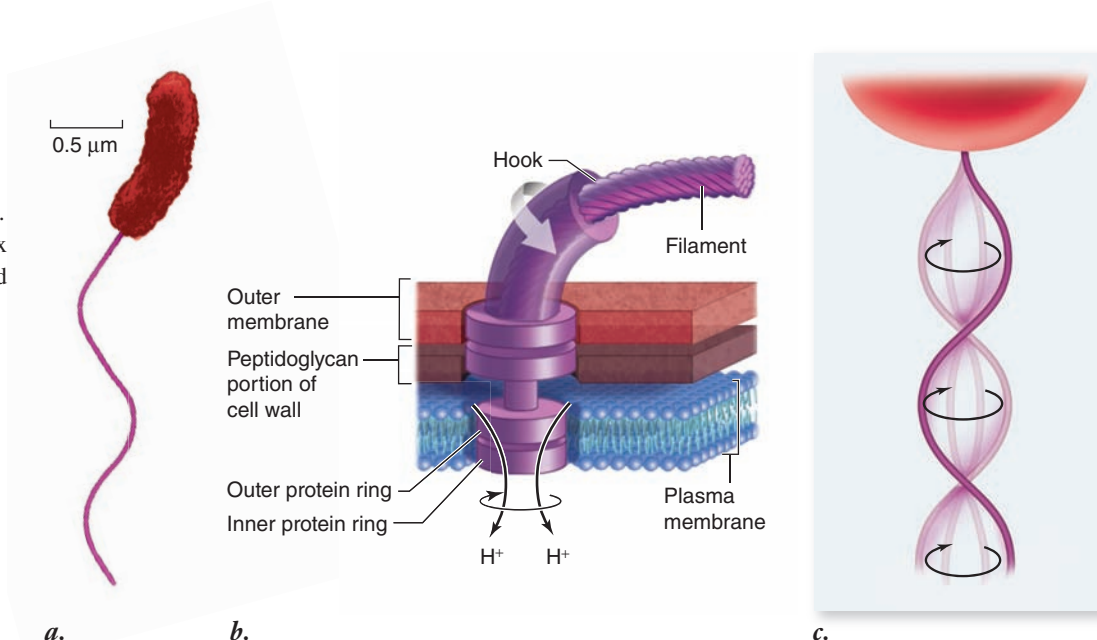
Some bacteria also secrete a jellylike protective capsule of polysaccharide around the cell. Many disease-causing bacteria have such a capsule, which enables them to adhere to teeth, skin, food—or to practically any surface that can support their growth.

Archaea have unusual membrane lipids

We are still learning about the physiology and structure of archaea. Many of these organisms are difficult to culture in the laboratory, and so this group has not yet been studied in detail. More is known about their genetic makeup than about any other feature.

The cell walls of archaea are composed of various chemical compounds, including polysaccharides and proteins, and possibly even inorganic components. A common feature distinguishing archaea from bacteria is the nature of their membrane lipids. The chemical structure of archaeal lipids is distinctly different from that of lipids in bacteria and can include saturated hydrocarbons that are covalently attached to glycerol at both ends, such that their

Figure 4.5 Some prokaryotes move by rotating their flagella. *a.* The photograph shows *Vibrio cholerae*, the microbe that causes the serious disease cholera. *b.* The bacterial flagellum is a complex structure. The motor proteins, powered by a proton gradient, are anchored in the plasma membrane. Two rings are found in the cell wall. The motor proteins cause the entire structure to rotate. *c.* As the flagellum rotates it creates a spiral wave down the structure. This powers the cell forward.



membrane is a monolayer. These features seem to confer greater thermal stability to archaeal membranes, although the trade-off seems to be an inability to alter the degree of saturation of the hydrocarbons—meaning that archaea with this characteristic cannot adapt to changing environmental temperatures.

The cellular machinery that replicates DNA and synthesizes proteins in archaea is more closely related to eukaryotic systems than to bacterial systems. Even though they share a similar overall cellular architecture with prokaryotes, archaea appear to be more closely related on a molecular basis to eukaryotes.

Some prokaryotes move by means of rotating flagella

Flagella (singular, *flagellum*) are long, threadlike structures protruding from the surface of a cell that are used in locomotion. Prokaryotic flagella are protein fibers that extend out from the cell. There may be one or more per cell, or none, depending on the species. Bacteria can swim at speeds of up to 70 cell lengths per second by rotating their flagella like screws (figure 4.5). The rotary motor uses the energy stored in a gradient that transfers protons across the plasma membrane to power the movement of the flagellum. Interestingly, the same principle, in which a proton gradient powers the rotation of a molecule, is used in eukaryotic mitochondria and chloroplasts by an enzyme that synthesizes ATP (see chapters 7 and 8).

Learning Outcomes Review 4.2

Prokaryotes are small cells that lack complex interior organization. The two domains of prokaryotes are archaea and bacteria. The cell wall of bacteria is composed of peptidoglycan, which is not found in archaea. Archaea have cell walls made from a variety of polysaccharides and peptides, as well as membranes containing unusual lipids. Some bacteria move using a rotating flagellum.

- What features do bacteria and archaea share?

4.3 Eukaryotic Cells

Learning Outcomes

1. Compare the organization of eukaryotic and prokaryotic cells.
2. Discuss the role of the nucleus in eukaryotic cells.
3. Describe the role of ribosomes in protein synthesis.

Eukaryotic cells (figures 4.6 and 4.7) are far more complex than prokaryotic cells. The hallmark of the eukaryotic cell is compartmentalization. This is achieved through a combination of an extensive **endomembrane system** that weaves through the cell interior and by numerous *organelles*. These organelles include

membrane-bounded structures that form compartments within which multiple biochemical processes can proceed simultaneously and independently.

Plant cells often have a large, membrane-bounded sac called a **central vacuole**, which stores proteins, pigments, and waste materials. Both plant and animal cells contain **vesicles**—smaller sacs that store and transport a variety of materials. Inside the nucleus, the DNA is wound tightly around proteins and packaged into compact units called **chromosomes**.

All eukaryotic cells are supported by an internal protein scaffold, the **cytoskeleton**. Although the cells of animals and some protists lack cell walls, the cells of fungi, plants, and many protists have strong cell walls composed of cellulose or chitin fibers embedded in a matrix of other polysaccharides and proteins. Through the rest of this chapter, we will examine the internal components of eukaryotic cells in more detail.

The nucleus acts as the information center

The largest and most easily seen organelle within a eukaryotic cell is the **nucleus** (Latin, “kernel” or “nut”), first described by the Scottish botanist Robert Brown in 1831. Nuclei are roughly spherical in shape, and in animal cells, they are typically located in the central region of the cell (figure 4.8a). In some cells, a network of fine cytoplasmic filaments seems to cradle the nucleus in this position.

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

The nuclear envelope

The surface of the nucleus is bounded by *two* phospholipid bilayer membranes, which together make up the **nuclear envelope** (figure 4.8). The outer membrane of the nuclear envelope is continuous with the cytoplasm’s interior membrane system, called the *endoplasmic reticulum* (described in section 4.4).

Scattered over the surface of the nuclear envelope are what appear as shallow depressions in the electron micrograph but are in fact structures called **nuclear pores** (figure 4.8b, c). These pores form 50 to 80 nm apart at locations where the two membrane layers of the nuclear envelope come together. The structure consists of a central framework with eightfold symmetry that is embedded in the nuclear envelope. This is bounded by a cytoplasmic face with eight fibers, and a nuclear face with a complex ring that forms a basket beneath the central ring. The pore allows ions and small molecules to diffuse freely between nucleoplasm and cytoplasm, while controlling the passage of proteins and RNA–protein complexes. Transport across the pore is controlled and consists mainly of the import of proteins that function in the nucleus, and the export to the cytoplasm of RNA and RNA–protein complexes formed in the nucleus.

The inner surface of the nuclear envelope is covered with a network of fibers that make up the nuclear lamina (figure 4.8d). This is composed of intermediate filament fibers called *nuclear lamins*.

Figure 4.6 Structure of an animal cell. In this generalized diagram of an animal cell, the plasma membrane encases the cell, which contains the cytoskeleton and various cell organelles and interior structures suspended in a semifluid matrix called the cytoplasm. Some kinds of animal cells possess fingerlike projections called microvilli. Other types of eukaryotic cells—for example, many protist cells—may possess flagella, which aid in movement, or cilia, which can have many different functions.

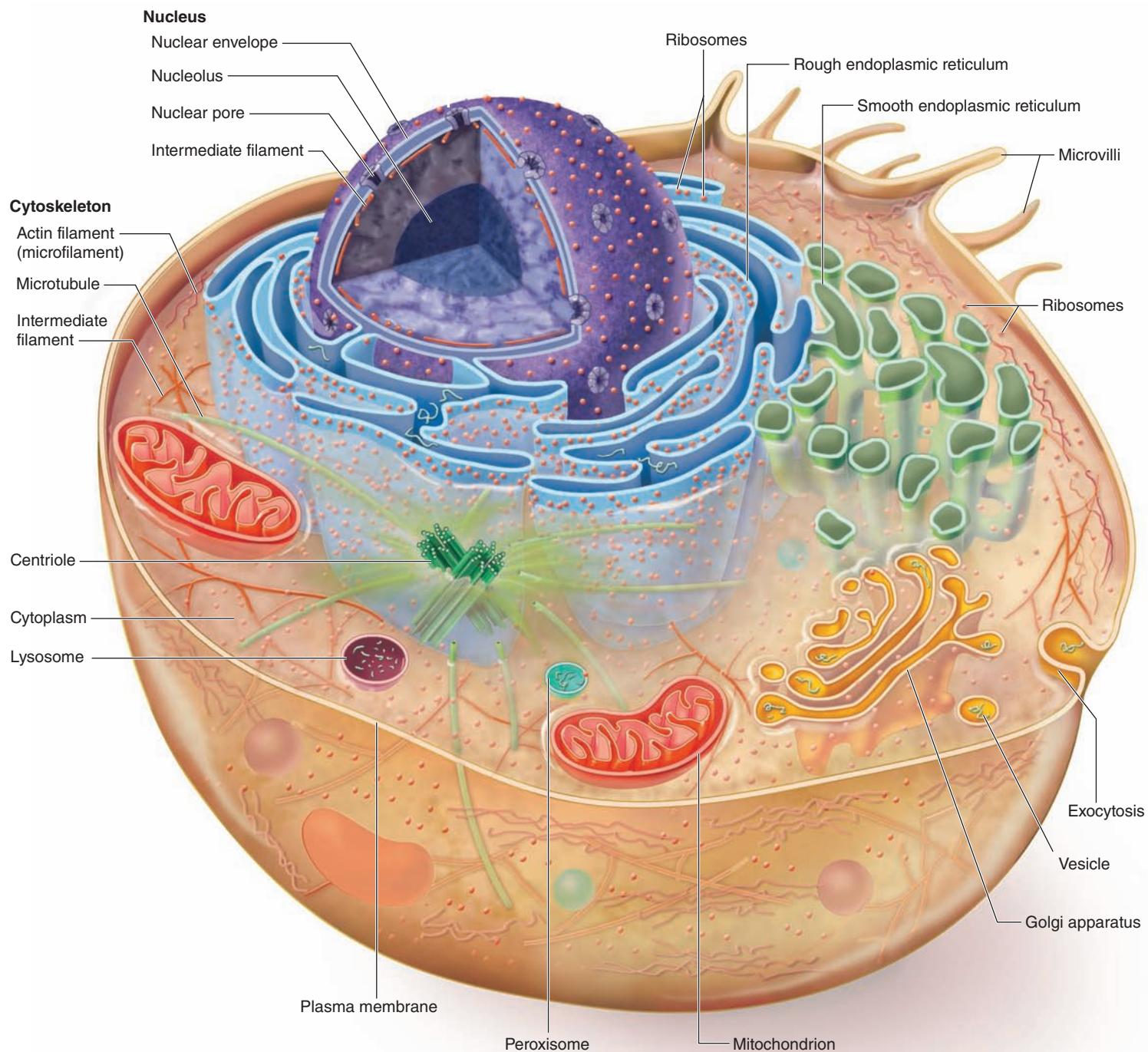


Figure 4.7 Structure of a plant cell. Most mature plant cells contain a large central vacuole, which occupies a major portion of the internal volume of the cell, and organelles called chloroplasts, within which photosynthesis takes place. The cells of plants, fungi, and some protists have cell walls, although the composition of the walls varies among the groups. Plant cells have cytoplasmic connections to one another through openings in the cell wall called plasmodesmata. Flagella occur in sperm of a few plant species, but are otherwise absent from plant and fungal cells. Centrioles are also usually absent.

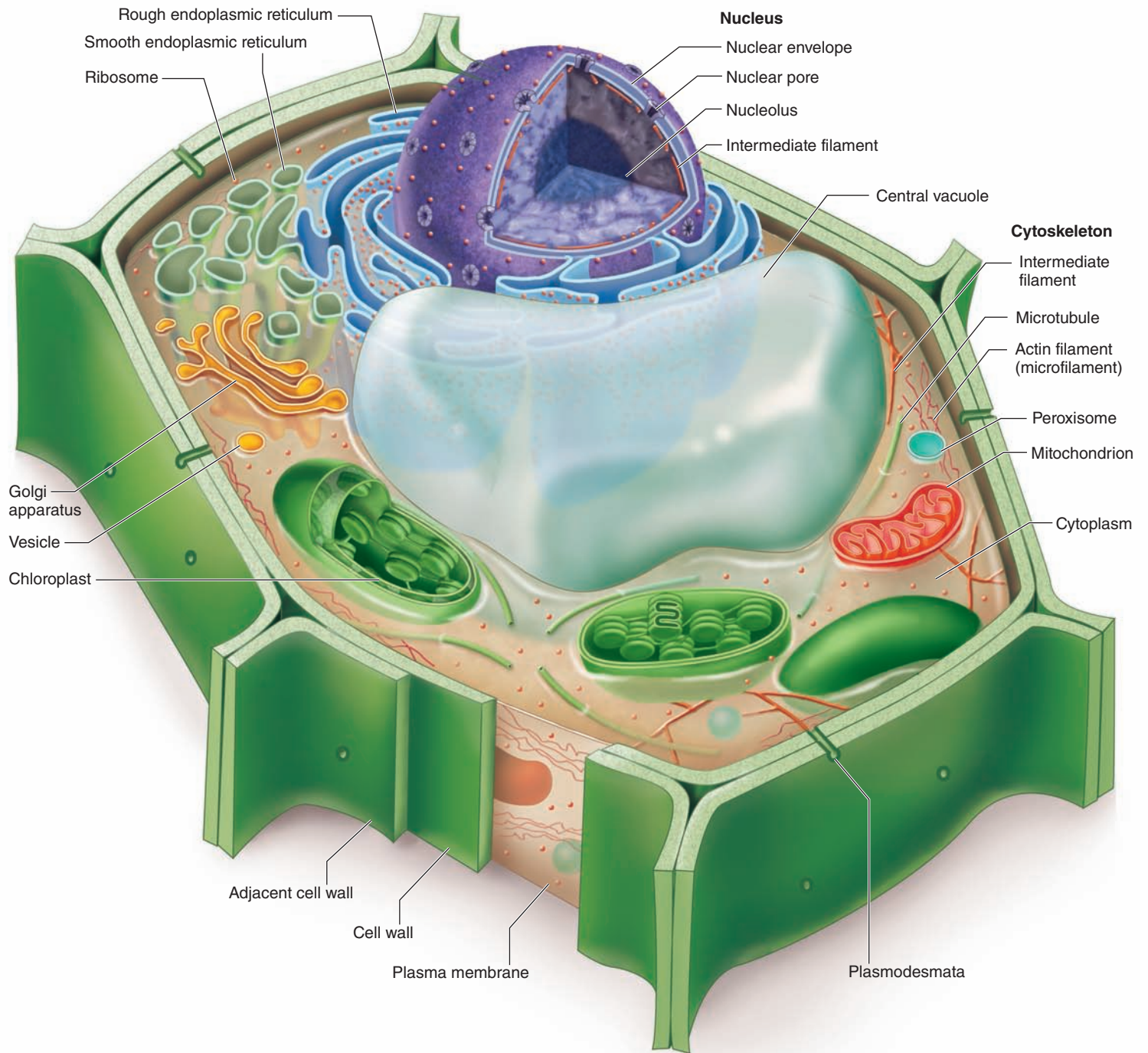
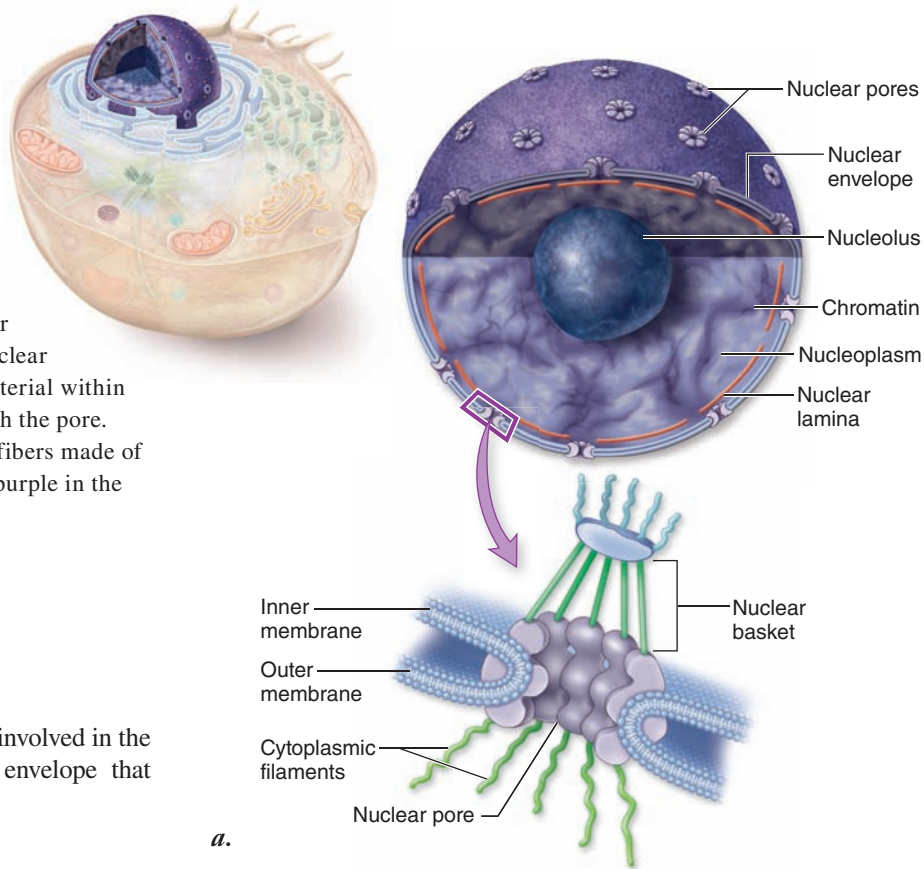


Figure 4.8 The nucleus. *a.* The nucleus is composed of a double membrane called the nuclear envelope, enclosing a fluid-filled interior containing chromatin. The individual nuclear pores extend through the two membrane layers of the envelope.

The close-up of the nuclear pore shows the central hub, cytoplasmic ring with fibers, and nuclear ring with basket. *b.* A freeze-fracture electron micrograph (see figure 5.4) of a cell nucleus, showing many nuclear pores. *c.* A transmission electron micrograph of the nuclear membrane showing a single nuclear pore. The dark material within the pore is protein, which acts to control access through the pore. *d.* The nuclear lamina is visible as a dense network of fibers made of intermediate filaments. The nucleus has been colored purple in the micrographs.



This structure gives the nucleus its shape and is also involved in the deconstruction and reconstruction of the nuclear envelope that accompanies cell division.

Chromatin: DNA packaging

In both prokaryotes and eukaryotes, DNA is the molecule that stores genetic information. In eukaryotes, the DNA is divided into multiple linear chromosomes, which are organized with proteins into a complex structure called **chromatin**. It is becoming clear that the very structure of chromatin affects the function of DNA. Changes in gene expression that do not involve changes in DNA sequence, so-called epigenetic changes, involve alterations in chromatin structure (see chapter 16). Although still not fully understood, this offers an exciting new view of many old ideas.

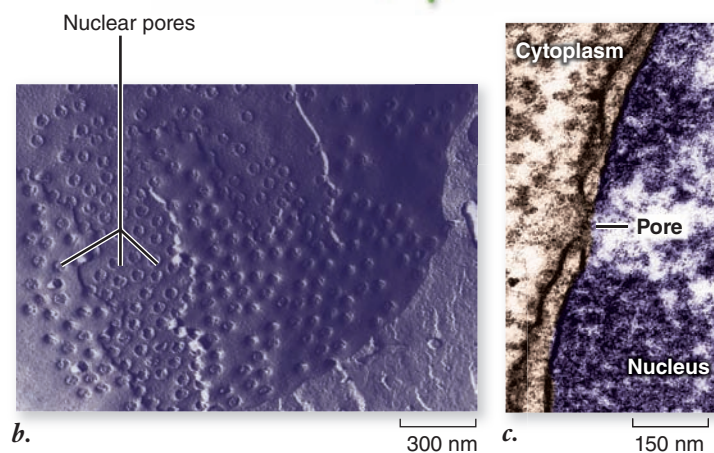
Chromatin is usually in a more extended form that is organized in the nucleus, although we still do not fully understand this organization. When cells divide, the chromatin must be further compacted into a more highly condensed state that forms the X-shaped chromosomes visible in the light microscope.

The nucleolus: Ribosomal subunit manufacturing

Before cells can synthesize proteins in large quantity, they must first construct a large number of ribosomes to carry out this synthesis. Hundreds of copies of the genes encoding the ribosomal RNAs are clustered together on the chromosome, facilitating ribosome construction. By transcribing RNA molecules from this cluster, the cell rapidly generates large numbers of the molecules needed to produce ribosomes.

The clusters of ribosomal RNA genes, the RNAs they produce, and the ribosomal proteins all come together within the nucleus during ribosome production. These ribosomal assembly areas are easily visible within the nucleus as one or more dark-staining regions called nucleoli (singular, *nucleolus*). Nucleoli can be seen under the light microscope even when the chromosomes are uncoiled.

a.

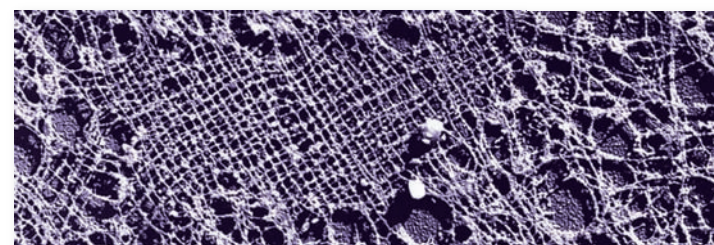


b.

300 nm

c.

150 nm



d.

1 μm

Ribosomes are the cell's protein synthesis machinery

Although the DNA in a cell's nucleus encodes the amino acid sequence of each protein in the cell, the proteins are not assembled there. A simple experiment demonstrates this: If a brief pulse of radioactive amino acid is administered to a cell, the radioactivity shows up associated with newly made protein in the cytoplasm,

4.4 The Endomembrane System

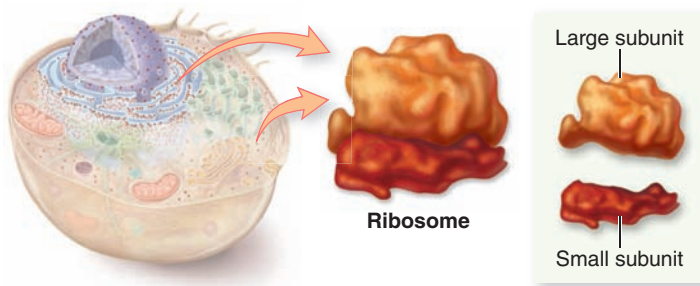


Figure 4.9 A ribosome. Ribosomes consist of a large and a small subunit composed of rRNA and protein. The individual subunits are synthesized in the nucleolus and then move through the nuclear pores to the cytoplasm, where they assemble to translate mRNA. Ribosomes serve as sites of protein synthesis.

not in the nucleus. When investigators first carried out these experiments, they found that protein synthesis is associated with large RNA–protein complexes (called ribosomes) outside the nucleus.

Ribosomes are among the most complex molecular assemblies found in cells. Each ribosome is composed of two subunits (figure 4.9), each of which is composed of a combination of RNA, called **ribosomal RNA (rRNA)**, and proteins. The subunits join to form a functional ribosome only when they are actively synthesizing proteins. This complicated process requires the two other main forms of RNA: **messenger RNA (mRNA)**, which carries coding information from DNA, and **transfer RNA (tRNA)**, which carries amino acids. Ribosomes use the information in mRNA to direct the synthesis of a protein. This process will be described in more detail in chapter 15.

Ribosomes are found either free in the cytoplasm or associated with internal membranes, as described in section 4.4. Free ribosomes synthesize proteins that are found in the cytoplasm, nuclear proteins, mitochondrial proteins, and proteins found in other organelles not derived from the endomembrane system. Membrane-associated ribosomes synthesize membrane proteins, proteins found in the endomembrane system, and proteins destined for export from the cell.

Ribosomes can be thought of as “universal organelles” because they are found in all cell types from all three domains of life. As we build a picture of the minimal essential functions for cellular life, ribosomes will be on the short list. Life is protein-based, and ribosomes are the factories that make proteins.

Learning Outcomes Review 4.3

In contrast to prokaryotic cells, eukaryotic cells exhibit compartmentalization. Eukaryotic cells contain an endomembrane system and organelles that carry out specialized functions. The nucleus, composed of a double membrane connected to the endomembrane system, contains the cell’s genetic information. Material moves between the nucleus and cytoplasm through nuclear pores. Ribosomes translate mRNA, which is transcribed from DNA in the nucleus, into polypeptides that make up proteins. Ribosomes are a universal organelle found in all known cells.

- *Would you expect cells in different organs in complex animals to have the same structure?*

Learning Outcomes

1. *Identify the different parts of the endomembrane system.*
2. *Contrast the different functions of internal membranes and compartments.*
3. *Evaluate the importance of each step in the protein-processing pathway.*

The interior of a eukaryotic cell is packed with membranes that form an elaborate internal, or endomembrane, system. This endomembrane system fills the cell, dividing it into compartments, channeling the passage of molecules through the interior of the cell, and providing surfaces for the synthesis of lipids and some proteins. The presence of these membranes in eukaryotic cells marks one of the fundamental distinctions between eukaryotes and prokaryotes.

The largest of the internal membranes is called the **endoplasmic reticulum (ER)**. The ER is composed of a phospholipid bilayer embedded with proteins. The ER has functional subdivisions, described here, and forms a variety of structures from folded sheets to complex tubular networks (figure 4.10). The ER also may be connected to the cytoskeleton, which can affect

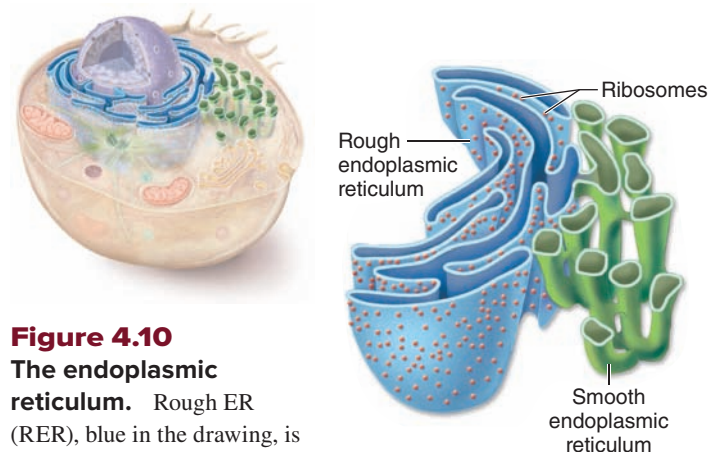
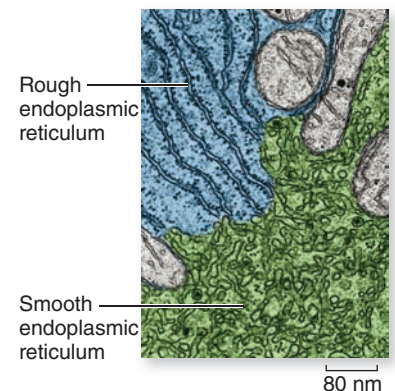


Figure 4.10 The endoplasmic reticulum. Rough ER (RER), blue in the drawing, is composed more of flattened sacs and forms a compartment throughout the cytoplasm. Ribosomes associated with the cytoplasmic face of the RER extrude newly made proteins into the interior, or lumen. The smooth ER (SER), green in the drawing, is a more tubelike structure connected to the RER. The micrograph has been colored to match the drawing.



ER structure and growth. The two largest compartments in eukaryotic cells are the inner region of the ER, called the **cisternal space**, or **lumen**, and the region exterior to it, the cytosol, which is the fluid component of the cytoplasm containing dissolved organic molecules such as proteins and ions.

The rough ER is a site of protein synthesis

The **rough ER (RER)** gets its name from its pebbly surface appearance. The RER is not easily visible with a light microscope, but it can be seen using the electron microscope. It appears to be composed primarily of flattened sacs, the surfaces of which are bumpy with ribosomes (figure 4.10).

The proteins synthesized on the surface of the RER are destined to be exported from the cell, sent to lysosomes or vacuoles (described later in this section), or embedded in the plasma membrane. These proteins enter the cisternal space as a first step in the pathway that will sort proteins to their eventual destinations. This pathway also involves vesicles and the Golgi apparatus. The sequence of the protein being synthesized determines whether the ribosome will become associated with the ER or remain a cytoplasmic ribosome.

In the ER, newly synthesized proteins can be modified by the addition of short-chain carbohydrates to form **glycoproteins**. Those proteins destined for secretion are separated from other products and later packaged into vesicles that move to the Golgi for further modification and packaging for transport to other cellular locations.

The smooth ER has multiple roles

Regions of the ER with relatively few bound ribosomes are referred to as **smooth ER (SER)**. The SER has a variety of structures ranging from a network of tubules, to flattened sacs, to higher order tubular arrays. The membranes of the SER contain many embedded enzymes. Enzymes anchored within the ER are involved in the synthesis of a variety of carbohydrates and lipids. Steroid hormones are synthesized in the SER as well. The majority of membrane lipids are assembled in the SER and then sent to whatever parts of the cell need membrane components. Membrane proteins in the plasma membrane and other cellular membrane are inserted by ribosomes on the RER.

An important function of the SER is to store intracellular Ca^{2+} . This keeps the cytoplasmic level low, allowing Ca^{2+} to be used as a signaling molecule. In muscle cells, for example, Ca^{2+} is used to trigger muscle contraction. In other cells, Ca^{2+} release from SER stores is involved in diverse signaling pathways.

The ratio of SER to RER is not fixed but depends on a cell's function. In multicellular animals such as ourselves, great variation exists in this ratio. Cells that carry out extensive lipid synthesis, such as those in the testes, intestine, and brain, have abundant SER. Cells that synthesize proteins that are secreted, such as antibodies, have much more extensive RER.

Another role of the SER is the modification of foreign substances to make them less toxic. In the liver, the enzymes of the SER carry out this detoxification. This action can include

neutralizing substances that we have taken for a therapeutic reason, such as penicillin. Thus, relatively high doses are prescribed for some drugs to offset our body's efforts to remove them. Liver cells have extensive SER as well as enzymes that can process a variety of substances by chemically modifying them.

The Golgi apparatus sorts and packages proteins

Flattened stacks of membranes form a complex called the **Golgi body**, or **Golgi apparatus** (figure 4.11). These structures are named for Camillo Golgi, the 19th-century Italian physician who first identified them. The individual stacks of membrane are called **cisternae** (Latin, "collecting vessels"), and they vary in number within the Golgi body from 1 or a few in protists, to 20 or more in animal cells and to several hundred in plant cells. In vertebrates individual Golgi are linked to form a Golgi ribbon. They are especially abundant in glandular cells, which manufacture and secrete substances.

The Golgi apparatus functions in the collection, packaging, and distribution of molecules synthesized at one location and used at another within the cell or even outside of it. A Golgi body has a front and a back, with distinctly different membrane compositions at these opposite ends. The front, or receiving end, is called the *cis* face and is usually located near the ER. Materials arrive at the *cis* face in transport vesicles that bud off the ER and exit the

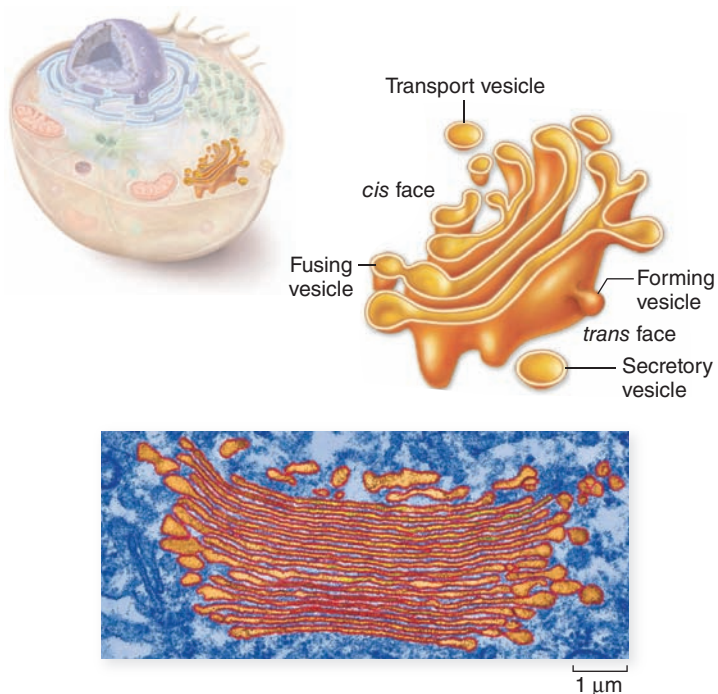


Figure 4.11 The Golgi apparatus. The Golgi apparatus is a smooth, concave, membranous structure. It receives material for processing in transport vesicles on the *cis* face and sends the material packaged in transport or secretory vesicles off the *trans* face. The substance in a vesicle could be for export out of the cell or for distribution to another region within the same cell.

trans face, where they are discharged in secretory vesicles (figure 4.12). How material transits through the Golgi has been a source of much contention. Models include maturation of the individual cisternae from *cis* to *trans*, transport between cisternae by vesicles, and direct tubular connections. Although there is probably transport of material by all of these, it now appears that the primary mechanism is cisternal maturation.

Proteins and lipids manufactured on the rough and smooth ER membranes are transported into the Golgi apparatus and modified as they pass through it. The most common alteration is the addition or modification of short sugar chains, forming glycoproteins and glycolipids. In many instances, enzymes in the Golgi apparatus modify existing glycoproteins and glycolipids made in the ER by cleaving a sugar from a chain or by modifying one or more of the sugars. These are then packaged into small, membrane-bounded vesicles that pinch off from the *trans* face of the Golgi. These vesicles then diffuse to other locations in the cell, distributing the newly synthesized molecules to their appropriate destinations.

Another function of the Golgi apparatus is the synthesis of cell-wall components. Noncellulose polysaccharides that form part of the cell wall of plants are synthesized in the Golgi apparatus and sent to the plasma membrane, where they can be added to the cellulose that is assembled on the exterior of the cell. Other polysaccharides secreted by plants are also synthesized in the Golgi apparatus.

Lysosomes contain digestive enzymes

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

The digestive enzymes in the lysosome are optimally active at acid pH. Lysosomes are activated by fusing with a food vesicle produced by *phagocytosis* (a specific type of endocytosis; see chapter 5) or by fusing with an old or worn-out organelle. The fusion event activates proton pumps in the lysosomal membrane, resulting in a lower internal pH. As the interior pH falls, the arsenal of digestive enzymes contained in the lysosome is activated. This leads to the degradation of macromolecules in the food vesicle or the destruction of the old organelle.

A number of human genetic disorders, collectively called lysosomal storage disorders, affect lysosomes. For example, the genetic abnormality called Tay–Sachs disease is caused by the loss of function of a single lysosomal enzyme (hexosaminidase). This enzyme is necessary to break down a membrane glycolipid found in nerve cells. Accumulation of glycolipid in lysosomes affects nerve cell function, leading to a variety of clinical symptoms such as seizures and muscle rigidity.

In addition to breaking down organelles and other structures within cells, lysosomes eliminate other cells that the cell has

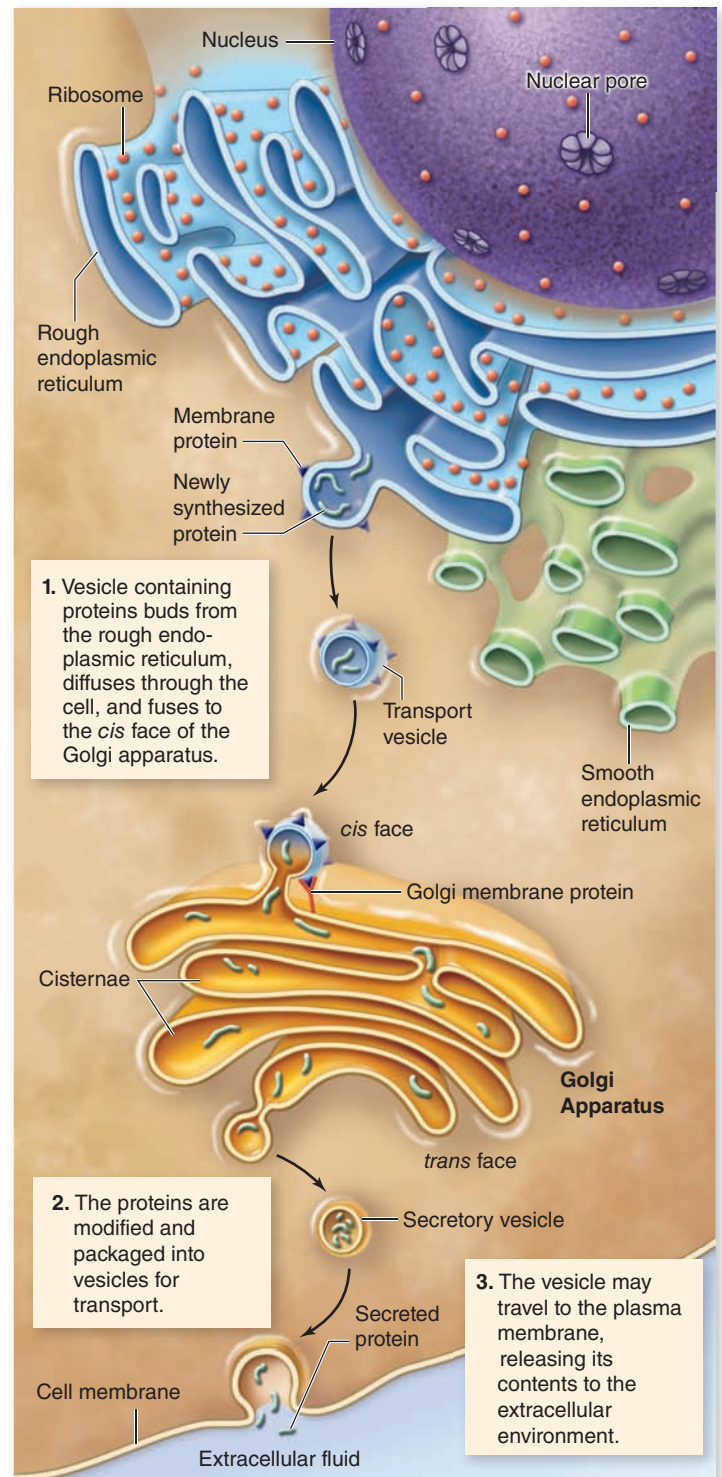


Figure 4.12 Protein transport through the endomembrane system. Proteins synthesized by ribosomes on the RER are translocated into the internal compartment of the ER. These proteins may be used at a distant location within the cell or secreted from the cell. They are transported within vesicles that bud off the RER. These transport vesicles travel to the *cis* face of the Golgi apparatus. There they can be modified and packaged into vesicles that bud off the *trans* face of the Golgi apparatus. Vesicles leaving the *trans* face transport proteins to other locations in the cell, or fuse with the plasma membrane, releasing their contents to the extracellular environment.

engulfed by phagocytosis. When a white blood cell, for example, phagocytizes a passing pathogen, lysosomes fuse with the resulting “food vesicle,” releasing their enzymes into the vesicle and degrading the material within (figure 4.13).

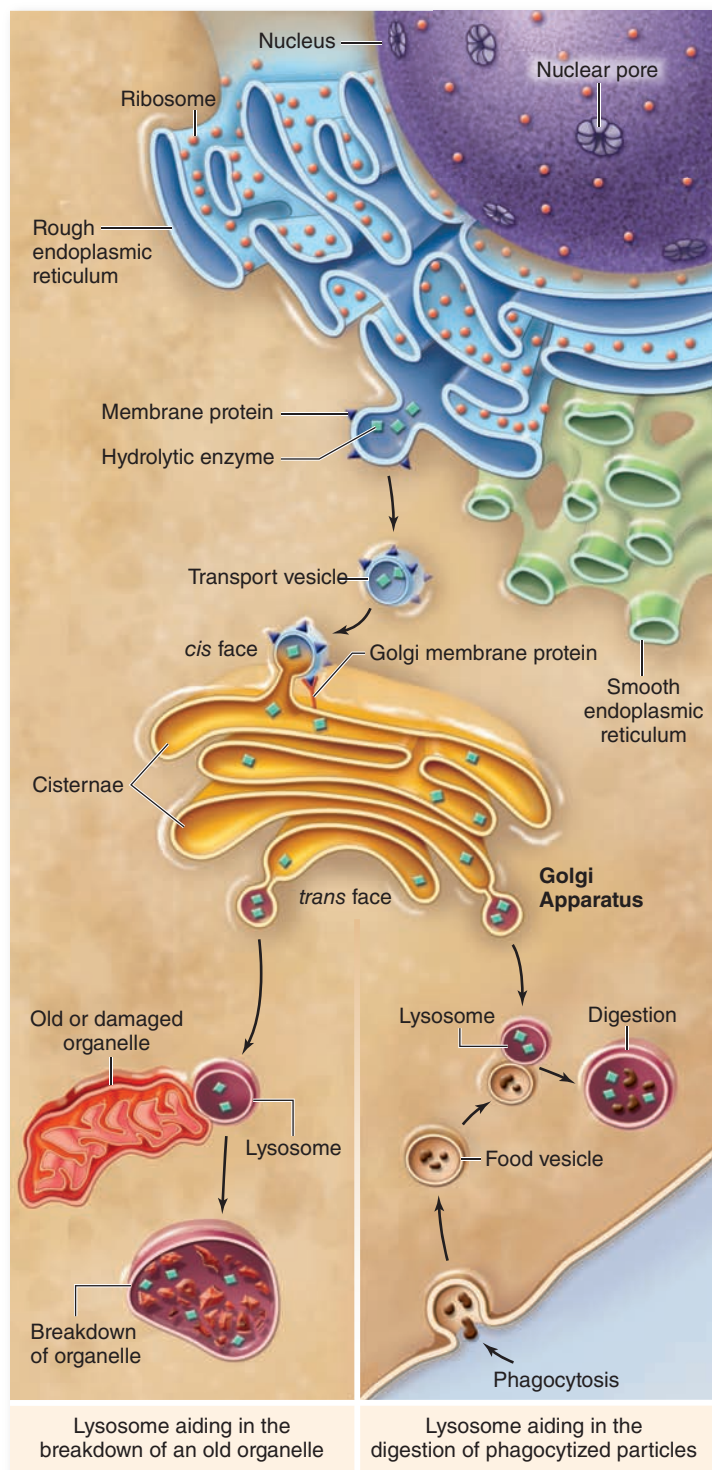


Figure 4.13 Lysosomes. Lysosomes are formed from vesicles budding off the Golgi. They contain hydrolytic enzymes that digest particles or cells taken into the cell by phagocytosis, and break down old organelles.

Microbodies are a diverse category of organelles

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

Peroxisomes: Peroxide utilization

An important type of microbody is the **peroxisome** (figure 4.14), which contains enzymes involved in the oxidation of fatty acids. If these oxidative enzymes were not isolated within microbodies, they would tend to short-circuit the metabolism of the cytoplasm, which often involves adding hydrogen atoms to oxygen. Because many peroxisomal proteins are synthesized by cytoplasmic ribosomes, the organelles themselves were long thought to form by the addition of lipids and proteins, leading to growth. As they grow larger, they divide to produce new peroxisomes. Although division of peroxisomes still appears to occur, it is now clear that peroxisomes can form from the fusion of ER-derived vesicles. These vesicles then import peroxisomal proteins to form a mature peroxisome. Genetic screens have isolated some 32 genes that encode proteins involved in biogenesis and maintenance of peroxisomes. The human genetic diseases called peroxisome biogenesis disorders (PBDs) can be caused by mutations in some of these genes.

Peroxisomes get their name from the hydrogen peroxide produced as a by-product of the activities of oxidative enzymes.

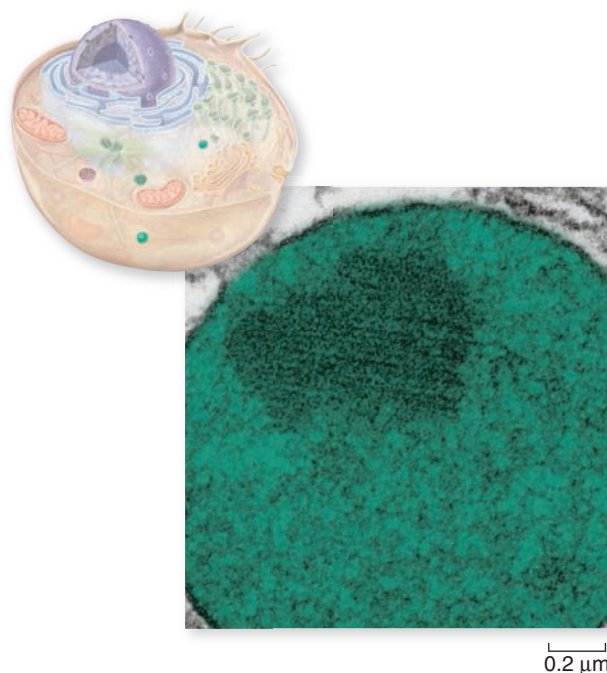


Figure 4.14 A peroxisome. Peroxisomes are spherical organelles that may contain a large crystal structure composed of protein. Peroxisomes contain digestive and detoxifying enzymes that produce hydrogen peroxide as a by-product. A peroxisome has been colored green in the electron micrograph.

Hydrogen peroxide is dangerous to cells because of its violent chemical reactivity. However, peroxisomes also contain the enzyme catalase, which breaks down hydrogen peroxide into its harmless constituents—water and oxygen.

Plants use vacuoles for storage and water balance

Plant cells have specialized membrane-bounded structures called **vacuoles**. The most conspicuous example is the large central vacuole seen in most plant cells (figure 4.15). In fact, *vacuole* actually means blank space, referring to its appearance in the light microscope. The membrane surrounding this vacuole is called the **tonoplast** because it contains channels for water that are used to help the cell maintain its tonicity, or osmotic balance (see osmosis in chapter 5).

For many years biologists assumed that only one type of vacuole existed and that it served multiple functions. The functions assigned to this vacuole included water balance and storage of both useful molecules (such as sugars, ions, and pigments) and waste products. The vacuole was also thought to store enzymes involved in the breakdown of macromolecules and those used in detoxifying foreign substances. Old textbooks of plant physiology referred to vacuoles as the attic of the cell for the variety of substances thought to be stored there.

Studies of tonoplast transporters and the isolation of vacuoles from a variety of cell types have led to a more complex view of vacuoles. These studies have made it clear that different vacuolar types can be found in different cells. These vacuoles are specialized, depending on the function of the cell.

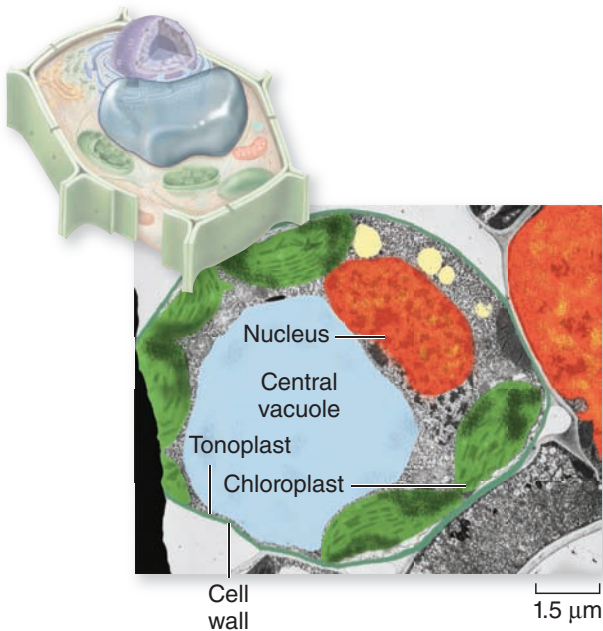


Figure 4.15 The central vacuole. A plant's central vacuole stores dissolved substances and can expand in size to increase the tonicity of a plant cell. Micrograph shown with false color.

The central vacuole is clearly important for a number of roles in all plant cells. The central vacuole and the water channels of the tonoplast maintain the tonicity of the cell, allowing the cell to expand and contract, depending on conditions. The central vacuole is also involved in cell growth by occupying most of the volume of the cell. Plant cells grow by expanding the vacuole, rather than by increasing cytoplasmic volume.

Vacuoles with a variety of functions are also found in some types of fungi and protists. One form is the contractile vacuole, found in some protists, which can pump water and is used to maintain water balance in the cell. Other vacuoles are used for storage or to segregate toxic materials from the rest of the cytoplasm. The number and kind of vacuoles found in a cell depends on the needs of the particular cell type.

Learning Outcomes Review 4.4

The endoplasmic reticulum (ER) is an extensive system of folded membranes that spatially organize the cell's biosynthetic activities. Smooth ER (SER) is the site of lipid and membrane synthesis and is used to store Ca^{2+} . Rough ER (RER) is covered with ribosomes and is a site of protein synthesis. Proteins from the RER are transported by vesicles to the Golgi apparatus where they are modified, packaged, and distributed to their final location. Lysosomes are vesicles that contain digestive enzymes used to degrade materials such as invaders or worn-out components. Peroxisomes carry out oxidative metabolism that generates peroxides. Vacuoles are membrane-bounded structures with roles ranging from storage to cell growth in plants. They are also found in some fungi and protists.

- How do ribosomes on the RER differ from cytoplasmic ribosomes?

4.5 Mitochondria and Chloroplasts: Cellular Generators

Learning Outcomes

1. Describe the structure of mitochondria and chloroplasts.
2. Compare the function of mitochondria and chloroplasts.
3. Explain the probable origin of mitochondria and chloroplasts.

Mitochondria and chloroplasts share structural and functional similarities. Structurally, they are both surrounded by a double membrane, and both contain their own DNA and protein synthesis machinery. Functionally, they are both involved in energy metabolism, as we will explore in detail in chapters 7 and 8 on energy metabolism and photosynthesis.

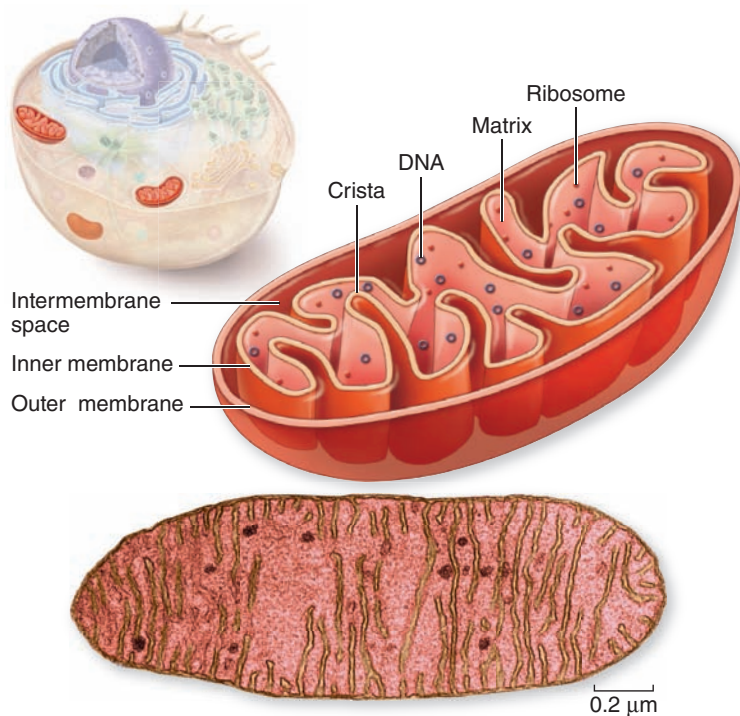


Figure 4.16 Mitochondria. The inner membrane of a mitochondrion is shaped into folds called cristae that greatly increase the surface area for oxidative metabolism. A mitochondrion in cross section and cut lengthwise is shown colored red in the micrograph.

Mitochondria metabolize sugar to generate ATP

Mitochondria (singular, *mitochondrion*) are typically tubular or sausage-shaped organelles about the size of bacteria that are found in all types of eukaryotic cells (figure 4.16). Mitochondria are bounded by two membranes: a smooth outer membrane, and an inner folded membrane with numerous contiguous layers called **cristae** (singular, *crista*).

The cristae partition the mitochondrion into two compartments: a **matrix**, lying inside the inner membrane; and an outer compartment, or **intermembrane space**, lying between the two mitochondrial membranes. On the surface of the inner membrane, and also embedded within it, are proteins that carry out oxidative metabolism, the oxygen-requiring process by which energy in macromolecules is used to produce ATP (see chapter 7).

Mitochondria have their own DNA; this DNA contains several genes that produce proteins essential to the mitochondrion's role in oxidative metabolism. Thus, the mitochondrion, in many respects, acts as a cell within a cell, containing its own genetic information specifying proteins for its unique functions. The mitochondria are not fully autonomous, however, because most of the genes that encode the enzymes used in oxidative metabolism are located in the cell nucleus.

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

Chloroplasts use light to generate ATP and sugars

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

The chloroplast, like the mitochondrion, is surrounded by two membranes (figure 4.17). However, chloroplasts are larger and more complex than mitochondria. In addition to the outer and inner membranes, which lie in close association with each other, chloroplasts have closed compartments of stacked membranes called **grana** (singular, *granum*), which lie inside the inner membrane.

A chloroplast may contain a hundred or more grana, and each granum may contain from a few to several dozen disk-shaped structures called **thylakoids**. On the surface of the thylakoids are the light-capturing photosynthetic pigments, to be discussed in depth in chapter 8. Surrounding the thylakoid is a fluid matrix called the **stroma**. The enzymes used to synthesize glucose during photosynthesis are found in the stroma.

Like mitochondria, chloroplasts contain DNA, but many of the genes that specify chloroplast components are also located in the nucleus. Some of the elements used in photosynthesis,

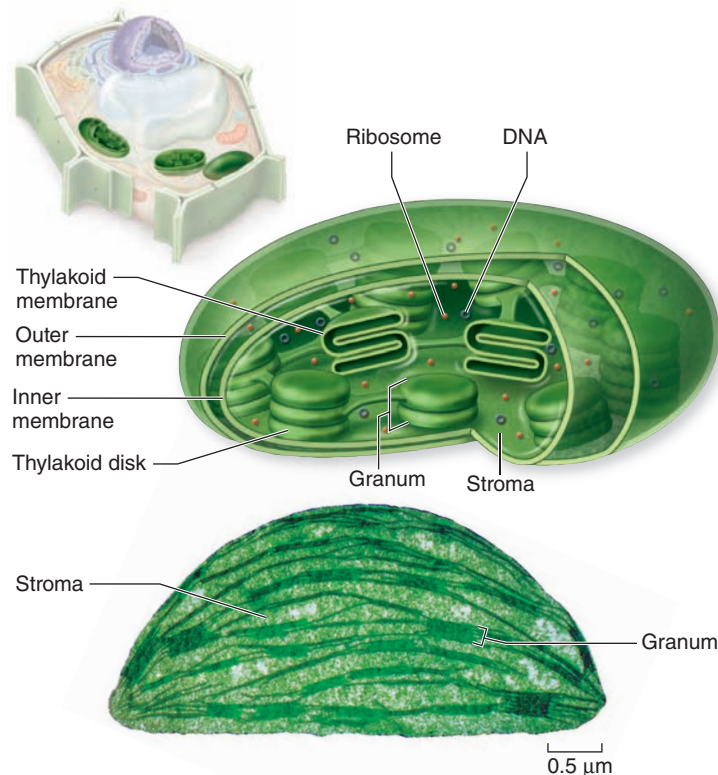


Figure 4.17 Chloroplast structure. The inner membrane of a chloroplast surrounds a membrane system of stacks of closed chlorophyll-containing vesicles called thylakoids, within which photosynthesis occurs. Thylakoids are typically stacked one on top of the other in columns called grana. The chloroplast has been colored green in the micrograph.

including the specific protein components necessary to accomplish the reaction, are synthesized entirely within the chloroplast.

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

? **Inquiry question** Mitochondria and chloroplasts both generate ATP. What structural features do they share?

Mitochondria and chloroplasts arose by endosymbiosis

Symbiosis is a close relationship between organisms of different species that live together. As noted in chapter 29, the theory of

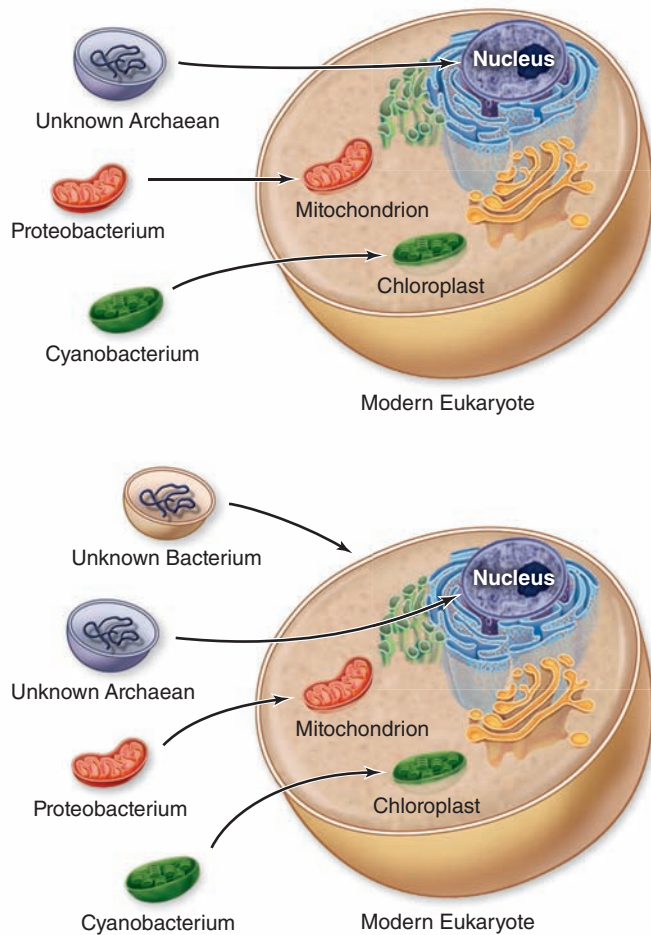


Figure 4.18 Possible origins of eukaryotic cells. Both mitochondria and chloroplasts are thought to have arisen by endosymbiosis when a free-living cell is taken up but not digested. The nature of the engulfing cell is unknown. Two possibilities are (1) the engulfing cell (*top*) is an archaean that gave rise to the nuclear genome and cytoplasmic contents; and (2) the engulfing cell (*bottom*) consists of a nucleus derived from an archaean in a bacterial cell. This could arise by a fusion event or by engulfment of the archaean by the bacterium.

endosymbiosis proposes that some of today's eukaryotic organelles evolved by a symbiosis arising between two cells that were each free-living. One cell, a prokaryote, was engulfed by and became part of another cell, which was the precursor of modern eukaryotes (figure 4.18).

According to the endosymbiont theory, the engulfed prokaryotes provided their hosts with certain advantages associated with their special metabolic abilities. Two key eukaryotic organelles are believed to be the descendants of these endosymbiotic prokaryotes: mitochondria, which are thought to have originated as bacteria capable of carrying out oxidative metabolism, and chloroplasts, which apparently arose from photosynthetic bacteria. This is discussed in detail in chapter 29.

Learning Outcomes Review 4.5

Mitochondria and chloroplasts have similar structures, with an outer membrane and an extensive inner membrane compartment. Both mitochondria and chloroplasts have their own DNA, but both also depend on nuclear genes for some functions. Mitochondria and chloroplasts are both involved in energy conversion: Mitochondria metabolize sugar to produce ATP, whereas chloroplasts harness light energy to produce ATP and synthesize sugars. Endosymbiosis theory proposes that both mitochondria and chloroplasts arose as prokaryotic cells were engulfed by a eukaryotic precursor.

- Many proteins in mitochondria and chloroplasts are encoded by nuclear genes. In light of the endosymbiont hypothesis, how might this come about?

4.6 The Cytoskeleton

Learning Outcomes

1. Contrast the structure and function of different fibers in the cytoskeleton.
2. Illustrate the role of microtubules in intracellular transport.

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

Three types of fibers compose the cytoskeleton

Eukaryotic cells may contain the following three types of cytoskeletal fibers, each formed from a different kind of subunit: (1) actin filaments, sometimes called microfilaments; (2) microtubules; and (3) intermediate filaments.

Actin filaments (microfilaments)

Actin filaments are long fibers about 7 nm in diameter. Each filament is composed of two protein chains loosely twined together like two strands of pearls (figure 4.19). Each “pearl,” or subunit, on the chain is the globular protein **actin**. Actin filaments exhibit polarity—that is, they have plus (+) and minus (–) ends. These

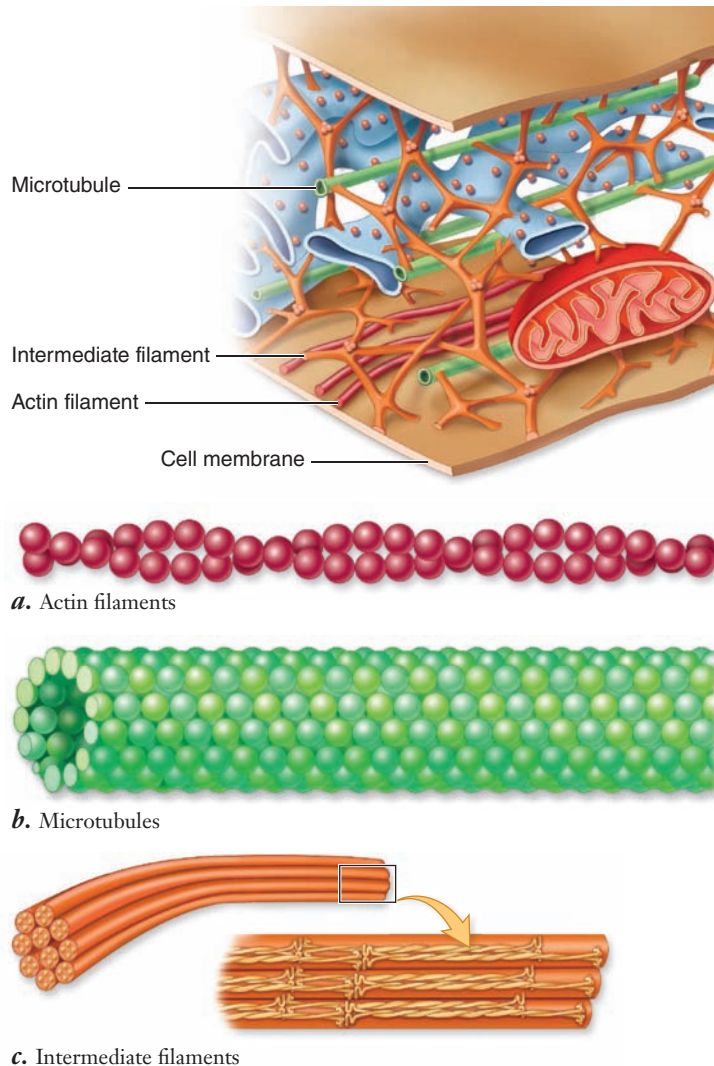


Figure 4.19 Molecules that make up the cytoskeleton.

a. Actin filaments: Actin filaments, also called *microfilaments*, are made of two strands of the globular protein actin twisted together. They are often found in bundles or in a branching network. Actin filaments in many cells are concentrated below the plasma membrane in bundles known as stress fibers, which may have a contractile function. **b. Microtubules:** Microtubules are composed of α - and β -tubulin protein subunits arranged side by side to form a tube. Microtubules are comparatively stiff cytoskeletal elements and have many functions in the cell including intracellular transport and the separation of chromosomes during mitosis. **c. Intermediate filaments:** Intermediate filaments are composed of overlapping staggered tetramers of protein. These tetramers are then bundled into cables. This molecular arrangement allows for a ropelike structure that imparts tremendous mechanical strength to the cell.

designate the direction of growth of the filaments. Actin molecules spontaneously form these filaments, even in a test tube.

Cells regulate the rate of actin polymerization through other proteins that act as switches, turning on polymerization when appropriate. Actin filaments are responsible for cellular movements such as contraction, crawling, “pinching” during division, and formation of cellular extensions.

Microtubules

Microtubules, the largest of the cytoskeletal elements, are hollow tubes about 25 nm in diameter, each composed of a ring of 13 protein protofilaments (figure 4.19). Globular proteins consisting of dimers of α - and β -tubulin subunits polymerize to form the 13 protofilaments. The protofilaments are arrayed side by side around a central core, giving the microtubule its characteristic tube shape.

In many cells, microtubules form from nucleation centers near the center of the cell and radiate toward the periphery. They are in a constant state of flux, continually polymerizing and depolymerizing. The average half-life of a microtubule ranges from as long as 10 minutes in a nondividing animal cell to as short as 20 seconds in a dividing animal cell. The ends of the microtubule are designated as plus (+) (away from the nucleation center) or minus (–) (toward the nucleation center).

Along with facilitating cellular movement, microtubules organize the cytoplasm and are responsible for moving materials within the cell itself, as described shortly.

Intermediate filaments

The most durable element of the cytoskeleton in animal cells is a system of tough, fibrous protein molecules twined together in an overlapping arrangement (figure 4.19). These **intermediate filaments** are characteristically 8 to 10 nm in diameter—between the size of actin filaments and microtubules. Once formed, intermediate filaments are stable and usually do not break down.

Intermediate filaments constitute a mixed group of cytoskeletal fibers. The most common type, composed of protein subunits called *vimentin*, provides structural stability for many kinds of cells. *Keratin*, another class of intermediate filament, is found in epithelial cells (cells that line organs and body cavities) and associated structures such as hair and fingernails. The intermediate filaments of nerve cells are called *neurofilaments*.

Centrosomes are microtubule-organizing centers

Centrioles are barrel-shaped organelles found in the cells of animals and most protists. They occur in pairs, usually located at right angles to each other near the nuclear membranes (figure 4.20). The region surrounding the pair in almost all animal cells is referred to as a *centrosome*. Surrounding the centrioles in the centrosome is the **pericentriolar material**, which contains ring-shaped structures composed of tubulin. The pericentriolar material can nucleate the assembly of microtubules in animal cells. Structures with this function are called *microtubule-organizing centers*. The centrosome is also responsible for the reorganization of microtubules that occurs during cell division. The centrosomes of plants and fungi lack

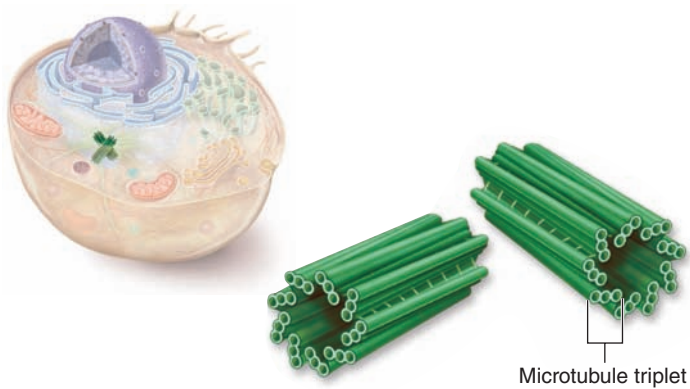


Figure 4.20 Centrioles. Each centriole is composed of nine triplets of microtubules. Centrioles are usually not found in plant cells. In animal cells they help to organize microtubules.

centrioles, but still contain microtubule-organizing centers. You will learn more about the actions of the centrosomes when we describe the process of cell division in chapter 10.

The cytoskeleton helps move materials within cells

Actin filaments and microtubules often orchestrate their activities to affect cellular processes. For example, during cell reproduction (see chapter 10), newly replicated chromosomes move to opposite sides of a dividing cell because they are attached to shortening microtubules. Then, in animal cells, a belt of actin pinches the cell in two by contracting like a purse string.

Muscle cells also use actin filaments, which slide along filaments of the motor protein myosin when a muscle contracts. The fluttering of an eyelash, the flight of an eagle, and the awkward crawling of a baby all depend on these cytoskeletal movements within muscle cells.

Not only is the cytoskeleton responsible for the cell's shape and movement, but it also provides a scaffold that interacts with the ER and other cytoplasmic macromolecules. Enzymes involved in cell metabolism bind to actin filaments, as do ribosomes. By moving and anchoring particular enzymes near one another, the cytoskeleton helps organize the cell's activities.

In both animals and fungi, the ER is associated with both microtubules and actin filaments. In animal cells, if we visualize cellular structures with fluorescent labels, the tubules of the ER align closely with microtubules. This may be involved in the growth and distribution of the ER. In yeast, microfilaments are involved in inheritance of the ER during cell division.

Molecular motors

All eukaryotic cells must move materials from one place to another in the cytoplasm. One way cells do this is by using the channels of the endoplasmic reticulum as an intracellular highway. Material can also be moved using vesicles loaded with cargo that can move along the cytoskeleton like a railroad track. For example, in a nerve cell with an axon that may extend far from the cell body, vesicles can be moved along tracks of microtubules from the cell body to the end of the axon.

Four components are required to move material along microtubules: (1) a vesicle or organelle that is to be transported,

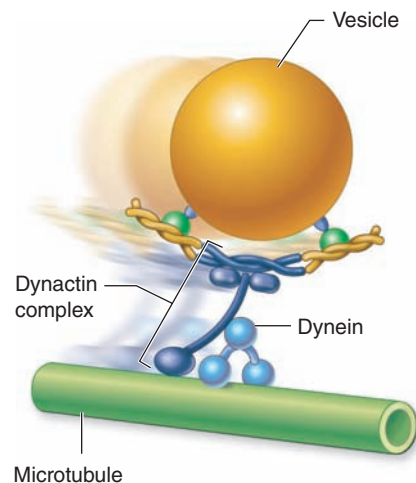


Figure 4.21 Molecular motors.

Vesicles can be transported along microtubules using motor proteins that use ATP to generate force. The vesicles are attached to motor proteins by connector molecules, such as the dynactin complex shown here. The motor protein dynein moves the connected vesicle along microtubules.

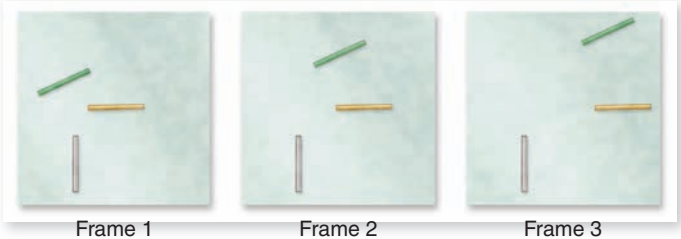
(2) a motor protein that provides the energy-driven motion, (3) a connector molecule that connects the vesicle to the motor molecule, and (4) microtubules on which the vesicle will ride like a train on a rail (figure 4.21).

The direction a vesicle is moved depends on the type of motor protein involved and the fact that microtubules are organized with their plus ends toward the periphery of the cell. In one case, a protein called kinectin binds vesicles to the motor protein *kinesin*. Kinesin uses ATP to power its movement toward the cell periphery, dragging the vesicle with it as it travels along the microtubule toward the plus end (figure 4.22). As nature's tiniest motors, these

SCIENTIFIC THINKING

Hypothesis: *Kinesin molecules can act as molecular motors and move along microtubules using energy from ATP.*

Test: *A microscope slide is covered with purified kinesin. Purified microtubules are added in a buffer containing ATP. The microtubules are monitored under a microscope using a video recorder to capture any movement.*



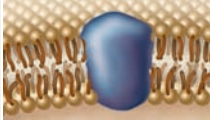
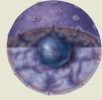
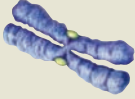

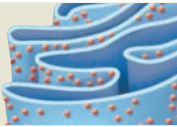


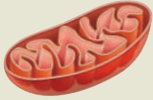



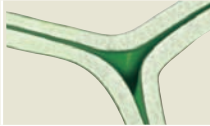
Result: *Over time, the movement of individual microtubules can be observed in the microscope. This is shown schematically in the figure by the movement of specific microtubules shown in color.*

Conclusion: *Kinesin acts as a molecular motor moving along (in this case actually moving) microtubules.*

Further Experiments: *Are there any further controls that are not shown in this experiment? What additional conclusions could be drawn by varying the amount of kinesin sticking to the slide?*

Figure 4.22 Demonstration of kinesin as molecular motor. Microtubules can be observed moving over a slide coated with kinesin.

TABLE 4.2
Eukaryotic Cell Structures and Their Functions

Structure		Description	Function
Plasma membrane		Phospholipid bilayer with embedded proteins	Regulates what passes into and out of cell; cell-to-cell recognition; connection and adhesion; cell communication
Nucleus		Structure (usually spherical) that contains chromosomes and is surrounded by double membrane	Instructions for protein synthesis and cell reproduction; contains genetic information
Chromosomes		Long threads of DNA that form a complex with protein	Contain hereditary information used to direct synthesis of proteins
Nucleolus		Site of genes for rRNA synthesis	Synthesis of rRNA and ribosome assembly
Ribosomes		Small, complex assemblies of protein and RNA, often bound to ER	Sites of protein synthesis
Endoplasmic reticulum (ER)		Network of internal membranes	Intracellular compartment forms transport vesicles; participates in lipid synthesis and synthesis of membrane or secreted proteins
Golgi apparatus		Stacks of flattened vesicles	Packages proteins for export from cell; forms secretory vesicles
Lysosomes		Vesicles derived from Golgi apparatus that contain hydrolytic digestive enzymes	Digest worn-out organelles and cell debris; digest material taken up by endocytosis
Microbodies		Vesicles that are formed from incorporation of lipids and proteins and that contain oxidative and other enzymes	Isolate particular chemical activities from rest of cell
Mitochondria		Bacteria-like elements with double membrane	“Power plants” of the cell; sites of oxidative metabolism
Chloroplasts		Bacteria-like elements with double membrane surrounding a third, thylakoid membrane containing chlorophyll, a photosynthetic pigment	Sites of photosynthesis
Cytoskeleton		Network of protein filaments	Structural support; cell movement; movement of vesicles within cells
Flagella (cilia)		Cellular extensions with 9 + 2 arrangement of pairs of microtubules	Motility or moving fluids over surfaces
Cell wall		Outer layer of cellulose or chitin; or absent	Protection; support

proteins pull the transport vesicles along the microtubular tracks. Another set of vesicle proteins, called the dynactin complex, binds vesicles to the motor protein *dynein* (figure 4.22), which directs movement in the opposite direction along microtubules toward the minus end, inward toward the cell's center. (Dynein is also involved in the movement of eukaryotic flagella, as discussed in section 4.7.) The destination of a particular transport vesicle and its content is thus determined by the nature of the linking protein embedded within the vesicle's membrane.

The major eukaryotic cell structures and their respective functions are summarized in table 4.2.

Learning Outcomes Review 4.6

The three principal fibers of the cytoskeleton are actin filaments (microfilaments), microtubules, and intermediate filaments. These fibers interact to modulate cell shape and permit cell movement. They also act to move materials within the cytoplasm. Material is also moved in large cells using vesicles and molecular motors. The motor proteins move vesicles along tracks of microtubules.

- What advantage does the cytoskeleton give to large eukaryotic cells?

4.7 Extracellular Structures and Cell Movement

Learning Outcomes

1. Describe how cells move.
2. Identify the different cytoskeletal elements involved in cell movement.
3. Classify the elements of extracellular matrix in animal cells.

Essentially all cell motion is tied to the movement of actin filaments, microtubules, or both. Intermediate filaments act as intracellular tendons, preventing excessive stretching of cells. Actin filaments play a major role in determining the shape of cells. Because actin filaments can form and dissolve so readily, they enable some cells to change shape quickly.

Some cells crawl

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

At the leading edge of a crawling cell, actin filaments rapidly polymerize, and their extension forces the edge of the cell forward. This extended region is stabilized when microtubules polymerize

into the newly formed region. Overall forward movement of the cell is then achieved through the action of the protein **myosin**, which is best known for its role in muscle contraction. Myosin motors along the actin filaments contract, pulling the contents of the cell toward the newly extended front edge.

Cells crawl when these steps occur continuously, with a leading edge extending and stabilizing, and then motors contracting to pull the remaining cell contents along. Receptors on the cell surface can detect molecules outside the cell and stimulate extension in specific directions, allowing cells to move toward particular targets.

Flagella and cilia aid movement

In section 4.2, we described the structure of prokaryotic flagella. Eukaryotic cells have a completely different kind of flagellum, consisting of a circle of nine microtubule pairs surrounding two central microtubules. This arrangement is referred to as the **9 + 2 structure** (figure 4.23).

As pairs of microtubules move past each other using arms composed of the motor protein dynein, the eukaryotic flagellum *undulates*, or waves up and down, rather than rotates. When examined carefully, each flagellum proves to be an outward projection of the cell's interior, containing cytoplasm and enclosed by the plasma membrane. The microtubules of the flagellum are derived from a **basal body**, situated just below the point where the flagellum protrudes from the surface of the cell.

The flagellum's complex microtubular apparatus evolved early in the history of eukaryotes. Today the cells of many multicellular and some unicellular eukaryotes no longer possess flagella and are nonmotile. Other structures, called **cilia** (singular, *cilium*), with

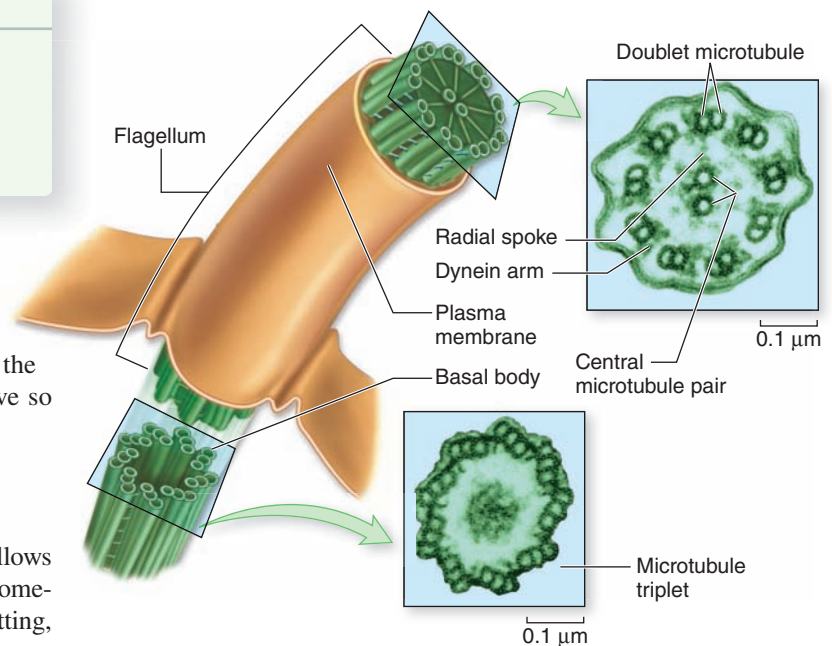
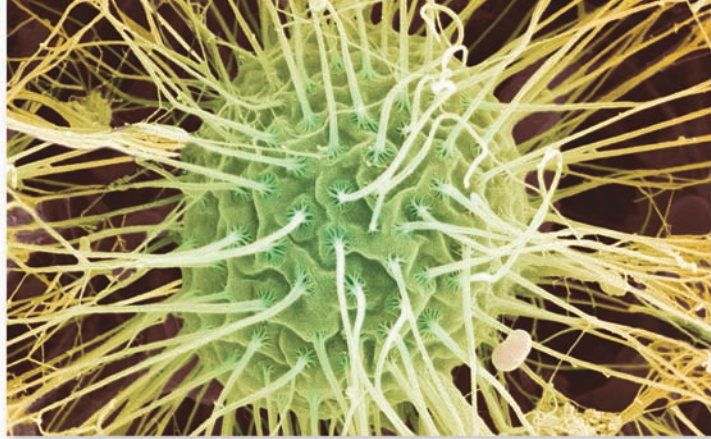
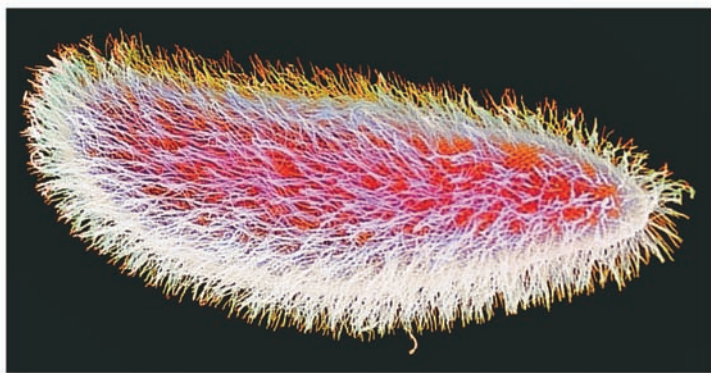


Figure 4.23 Flagella and cilia. A eukaryotic flagellum originates directly from a basal body. The flagellum has two microtubules in its core connected by radial spokes to an outer ring of nine paired microtubules with dynein arms (9 + 2 structure). The basal body consists of nine microtubule triplets connected by short protein segments. The structure of cilia is similar to that of flagella, but cilia are usually shorter.



a.

40 μm



b.

67 μm

Figure 4.24 Flagella and cilia. *a.* A green alga with numerous flagella that allow it to move through the water.

b. Paramecia are covered with many cilia, which beat in unison to move the cell. The cilia can also be used to move fluid into the paramecium's mouth to ingest material.

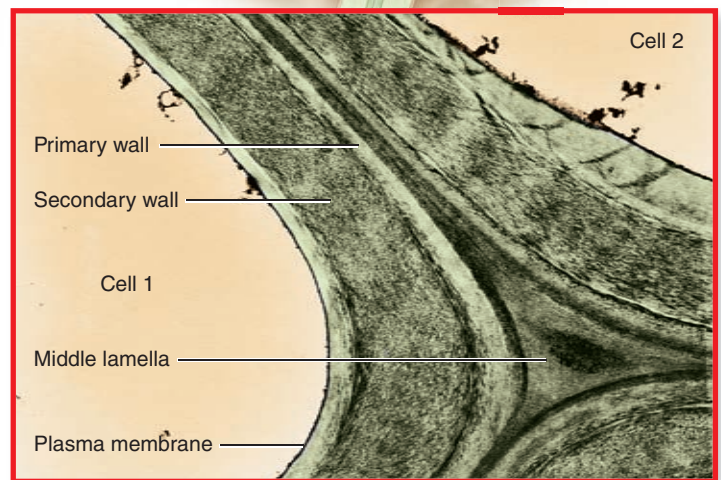
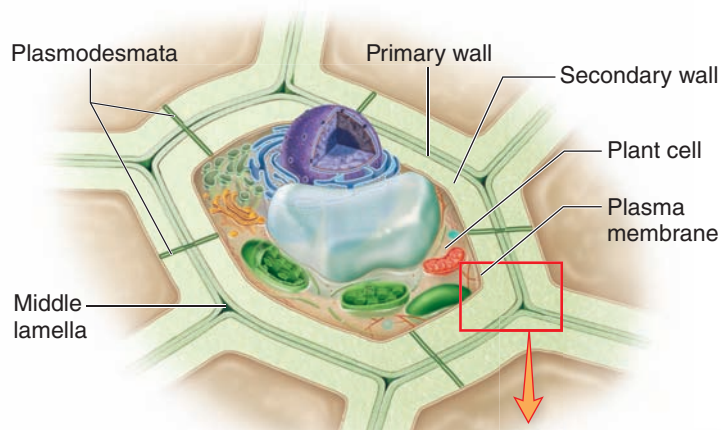
an organization similar to the 9 + 2 arrangement of microtubules can still be found within them. Cilia are short cellular projections that are often organized in rows. They are more numerous than flagella on the cell surface, but have the same internal structure.

In many multicellular organisms, cilia carry out tasks far removed from their original function of propelling cells through water. In several kinds of vertebrate tissues, for example, the beating of rows of cilia move water over the tissue surface. The sensory cells of the vertebrate ear also contain conventional cilia surrounded by actin-based stereocilia; sound waves bend these structures and provide the initial sensory input for hearing. Thus, the 9 + 2 structure of flagella and cilia appears to be a fundamental component of eukaryotic cells (figure 4.24).

Plant cell walls provide protection and support

The cells of plants, fungi, and many types of protists have cell walls, which protect and support the cells. The cell walls of these eukaryotes are chemically and structurally different from prokaryotic cell walls. In plants and protists, the cell walls are composed of fibers of the polysaccharide cellulose, whereas in fungi, the cell walls are composed of chitin.

In plants, **primary walls** are laid down when the cell is still growing. Between the walls of adjacent cells a sticky substance, called the **middle lamella**, glues the cells together (figure 4.25). Some plant cells produce strong **secondary walls**, which are deposited inside the primary walls of fully expanded cells.



0.4 μm

Figure 4.25 Cell walls in plants. Plant cell walls are thick, strong, and rigid. Primary cell walls are laid down when the cell is young. Thicker secondary cell walls may be added later when the cell is fully grown.

Animal cells secrete an extracellular matrix

Animal cells lack the cell walls that encase plants, fungi, and most protists. Instead, animal cells secrete an elaborate mixture of glycoproteins into the space around them, forming the *extracellular matrix (ECM)* (figure 4.26). The fibrous protein collagen, the same protein found in cartilage, tendons, and ligaments may be abundant in the ECM. Strong fibers of collagen and another fibrous protein, elastin, are embedded within a complex web of other glycoproteins, called proteoglycans, that form a protective layer over the cell surface.



Inquiry question The passageways of the human trachea (the path of air flow into and out of the lungs) are known to be lined with ciliated cells. What function could these cilia perform?

The ECM of some cells is attached to the plasma membrane by a third kind of glycoprotein, *fibronectin*. Fibronectin molecules bind not only to ECM glycoproteins but also to proteins called **integrins**. Integrins are an integral part of the plasma membrane, extending into the cytoplasm, where they are attached to the

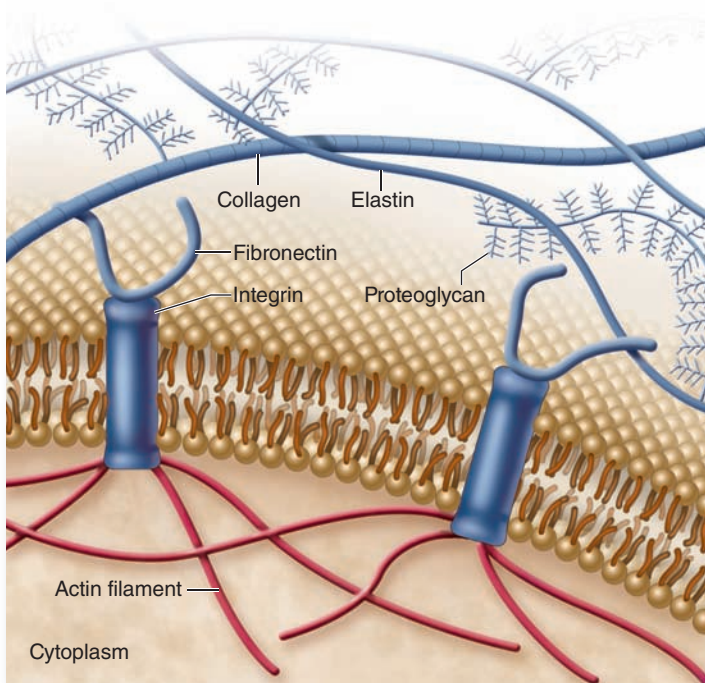


Figure 4.26 The extracellular matrix. Animal cells are surrounded by an extracellular matrix composed of various glycoproteins that give the cells support, strength, and resilience.

microfilaments and intermediate filaments of the cytoskeleton. Linking ECM and cytoskeleton, integrins allow the ECM to influence cell behavior in important ways. They can alter gene expression and cell migration patterns by a combination of mechanical and chemical signaling pathways. In this way, the ECM can help coordinate the behavior of all the cells in a particular tissue.

Table 4.3 compares and reviews the features of three types of cells.

Learning Outcomes Review 4.7

Cell movement involves proteins. These can either be internal in the case of crawling cells that use actin and myosin, or external in the case of cells powered by cilia or flagella. Eukaryotic cilia and flagella are different from prokaryotic flagella because they are composed of bundles of microtubules in a 9 + 2 array. They undulate rather than rotate.

Plant cells have a cellulose-based cell wall. Animal cells lack a cell wall. In animal cells, the cytoskeleton is linked to a web of glycoproteins called the extracellular matrix.

- *What cellular roles are performed by microtubules and microfilaments and not intermediate filaments?*

TABLE 4.3		A Comparison of Prokaryotic, Animal, and Plant Cells		
	Prokaryote	Animal	Plant	
EXTERIOR STRUCTURES				
Cell wall	Present (protein-polysaccharide)	Absent	Present (cellulose)	
Cell membrane	Present	Present	Present	
Flagella/cilia	Flagella may be present	May be present (9 + 2 structure)	Absent except in sperm of a few species (9 + 2 structure)	
INTERIOR STRUCTURES				
Endoplasmic reticulum	Absent	Usually present	Usually present	
Ribosomes	Present	Present	Present	
Microtubules	Absent	Present	Present	
Centrioles	Absent	Present	Absent	
Golgi apparatus	Absent	Present	Present	
Nucleus	Absent	Present	Present	
Mitochondria	Absent	Present	Present	
Chloroplasts	Absent	Absent	Present	
Chromosomes	Single; circle of DNA	Multiple; DNA–protein complex	Multiple; DNA–protein complex	
Lysosomes	Absent	Usually present	Present	
Vacuoles	Absent	Absent or small	Usually a large single vacuole	

4.8 Cell-to-Cell Interactions

Learning Outcomes

1. Differentiate between types of cell junctions.
2. Describe the roles of surface proteins.

A basic feature of multicellular animals is the formation of diverse kinds of *tissue*, such as skin, blood, or muscle, where cells are organized in specific ways. Cells must also be able to communicate with each other and have markers of individual identity. All of these functions—connections between cells, markers of cellular identity, and cell communication—involve membrane proteins and proteins secreted by cells. As an organism develops, the cells acquire their identities by carefully controlling the *expression* of those genes, turning on the specific set of genes that encode the functions of each cell type. Table 4.4 provides a summary of the kinds of connections seen between cells that are explored in this section.

Surface proteins give cells identity

One key set of genes functions to mark the surfaces of cells, identifying them as being of a particular type. When cells make contact, they “read” each other’s cell-surface markers and react accordingly. Cells that are part of the same tissue type recognize each other, and they frequently respond by forming connections between their surfaces to better coordinate their functions.

Glycolipids

Most tissue-specific cell-surface markers are glycolipids—that is, lipids with carbohydrate heads. The glycolipids on the surface of red blood cells are also responsible for the A, B, and O blood types.

MHC proteins

One example of the function of cell-surface markers is the recognition of “self” and “nonself” cells by the immune system. This function is vital for multicellular organisms, which need to defend themselves against invading or malignant cells. The immune system of vertebrates uses a particular set of markers to distinguish self from nonself cells, encoded by genes of the *major histocompatibility complex (MHC)*. Cell recognition in the immune system is covered in chapter 51.



Cell connections mediate cell-to-cell adhesion

The evolution of multicellularity required the acquisition of molecules that can connect cells to each other. It appears that multicellularity arose independently in different lineages, but the types of connections between cells are remarkably conserved, and many of the proteins involved are ancient.

The nature of the physical connections between the cells of a tissue in large measure determines what the tissue is like. Indeed, a tissue’s proper functioning often depends critically on how the individual cells are arranged within it. Just as a house cannot maintain its structure without nails and cement, so a tissue cannot maintain its characteristic architecture without the appropriate cell junctions. Cell junctions can be characterized by both their

TABLE 4.4

Cell-to-Cell Connections and Cell Identity

Type of Connection	Structure	Function	Example
Surface markers	Variable, integral proteins or glycolipids in plasma membrane	Identify the cell	MHC complexes, blood groups, antibodies
Septate junctions Tight junctions	Tightly bound, leakproof, fibrous claudin protein seal that surrounds cell	Hold cells together such that materials pass through but not between the cells	Junctions between epithelial cells in the gut
Adhesive junction (desmosome)	Variant cadherins, desmocollins, bind to intermediate filaments of cytoskeleton	Creates strong flexible connections between cells. Found in vertebrates	Epithelium
Adhesive junction (adherens junction)	Classical cadherins, bind to microfilaments of cytoskeleton	Connects cells together. Oldest form of cell junction, found in all multicellular organisms	Tissues with high mechanical stress, such as the skin
Adhesive junction (hemidesmosome, focal adhesion)	Integrin proteins bind cell to extracellular matrix	Provides attachment to a substrate	Involved in cell movement and important during development
Communicating junction (gap junction)	Six transmembrane connexon/pannexin proteins creating a pore that connects cells	Allows passage of small molecules from cell to cell in a tissue	Excitable tissue such as heart muscle
Communicating junction (plasmodesmata)	Cytoplasmic connections between gaps in adjoining plant cell walls	Communicating junction between plant cells	Plant tissues

visible structure in the microscope, and the proteins involved in the junction.

Adhesive junctions

Adhesive junctions appear to have been the first to evolve. Primitive forms can even be found in sponges, and they are found in all animal species. They mechanically attach the cytoskeleton of a cell to the cytoskeletons of other cells or to the extracellular matrix. These junctions are found in tissues subject to mechanical stress, such as muscle and skin epithelium.

Adherens junctions are based on the protein **cadherin**, which is a Ca^{2+} -dependent adhesion molecule with very wide phylogenetic distribution. Cadherin is a single-pass transmembrane protein with an extracellular domain that can interact with the extracellular domain of a cadherin in an adjacent cell to join the cells together (figure 4.27). Adherens junctions are found in animals ranging from jellyfish to vertebrates. Cadherins found in these junctions are called classical cadherins and are broken down into types I and II. When cells bearing either type I or type II cadherins are mixed, they sort into populations joined by I to I or by II to II interactions. There is some evidence for interactions between type I and type II cadherins, but they are not as strong. On the cytoplasmic side, the cadherins interact indirectly through other proteins with actin to form flexible connections between cells (figure 4.27).

Desmosomes are a cadherin-based junction unique to vertebrates. They contain the cadherins desmocollin and desmoglein, which interact with intermediate filaments of cytoskeletons instead of actin. Desmosomes join adjacent cells (figure 4.28b). These connections support tissues against mechanical stress.

Hemidesmosomes and focal adhesions connect cells to the basal lamina or other ECM. In this case the proteins that interact

with the ECM are called integrins. The integrins are members of a large superfamily of cell-surface receptors that bind to a protein component of the extracellular matrix. At least 20 different integrins exist, each with a differently shaped binding domain. These junctions also connect to the cytoskeleton of cells: actin filaments at focal adhesions and intermediate filaments at hemidesmosomes.

Septate, or Tight, junctions

Septate junctions are found in both invertebrates and vertebrates and form a barrier that can seal off a sheet of cells. The proteins found at these junctions have been given different names in different systems; in *Drosophila*, the proteins include Discs Large and Neurexin. Their wide distribution indicates that they probably evolved soon after or with adherens junctions.

Tight junctions are unique to vertebrates and contain proteins called Claudins because of their ability to occlude or block substances from passing between cells. This form of junction between cells acts as a wall within the tissue, keeping molecules on one side or the other (figure 4.28a).

Creating sheets of cells. The cells that line an animal's digestive tract are organized in a sheet only one cell thick. One surface of the sheet faces the inside of the tract, and the other faces the extracellular space, where blood vessels are located. Tight junctions encircle each cell in the sheet, like a belt cinched around a person's waist. The junctions between neighboring cells are so securely attached that there is no space between them for leakage. Hence, nutrients absorbed from the food in the digestive tract must pass directly through the cells in the sheet to enter the bloodstream because they cannot pass through spaces between cells.

The tight junctions between the cells lining the digestive tract also partition the plasma membranes of these cells into separate compartments. Transport proteins in the membrane facing the inside of the tract carry nutrients from that side to the cytoplasm of the cells. Other proteins, located in the membrane on the opposite side of the sheet, transport those nutrients from the cytoplasm to the extracellular fluid, where they can enter the bloodstream. Tight junctions effectively segregate the proteins on opposite sides of the sheet, preventing them from drifting within the membrane from one side of the sheet to the other. When tight junctions are experimentally disrupted, just this sort of migration occurs.

Communicating junctions

The proteins involved in the junctions previously described can be found in some single-celled organisms as well. The evolution of multicellularity also led to a new form of cellular connection: the *communicating junctions*. These junctions allow communication between cells by diffusion through small openings. Communicating junctions permit small molecules or ions to pass from one cell to the other. In animals, these direct communication channels between cells are called *gap junctions*, and in plants, *plasmodesmata*.

Gap junctions in animals. **Gap junctions** are found in both invertebrates and vertebrates. In invertebrates they are formed by proteins known as pannexins. In vertebrates pannexin-base gap

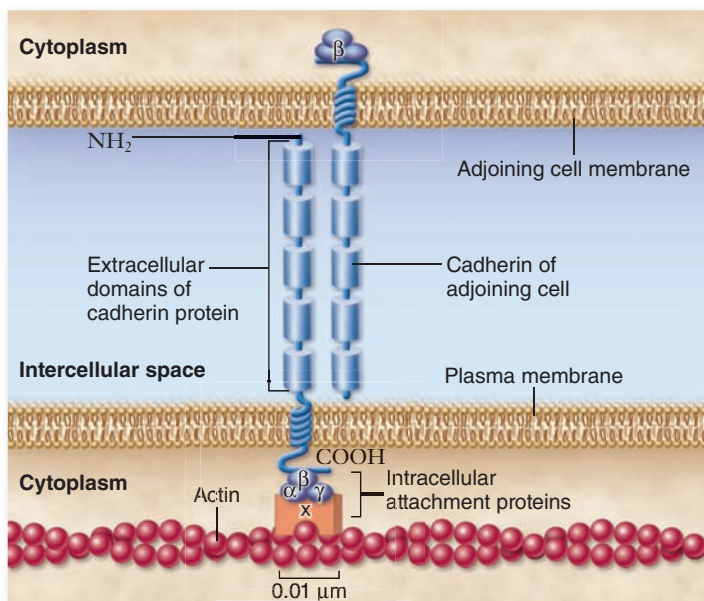


Figure 4.27 A cadherin-mediated junction. The cadherin molecule is anchored to actin in the cytoskeleton and passes through the membrane to interact with the cadherin of an adjoining cell.

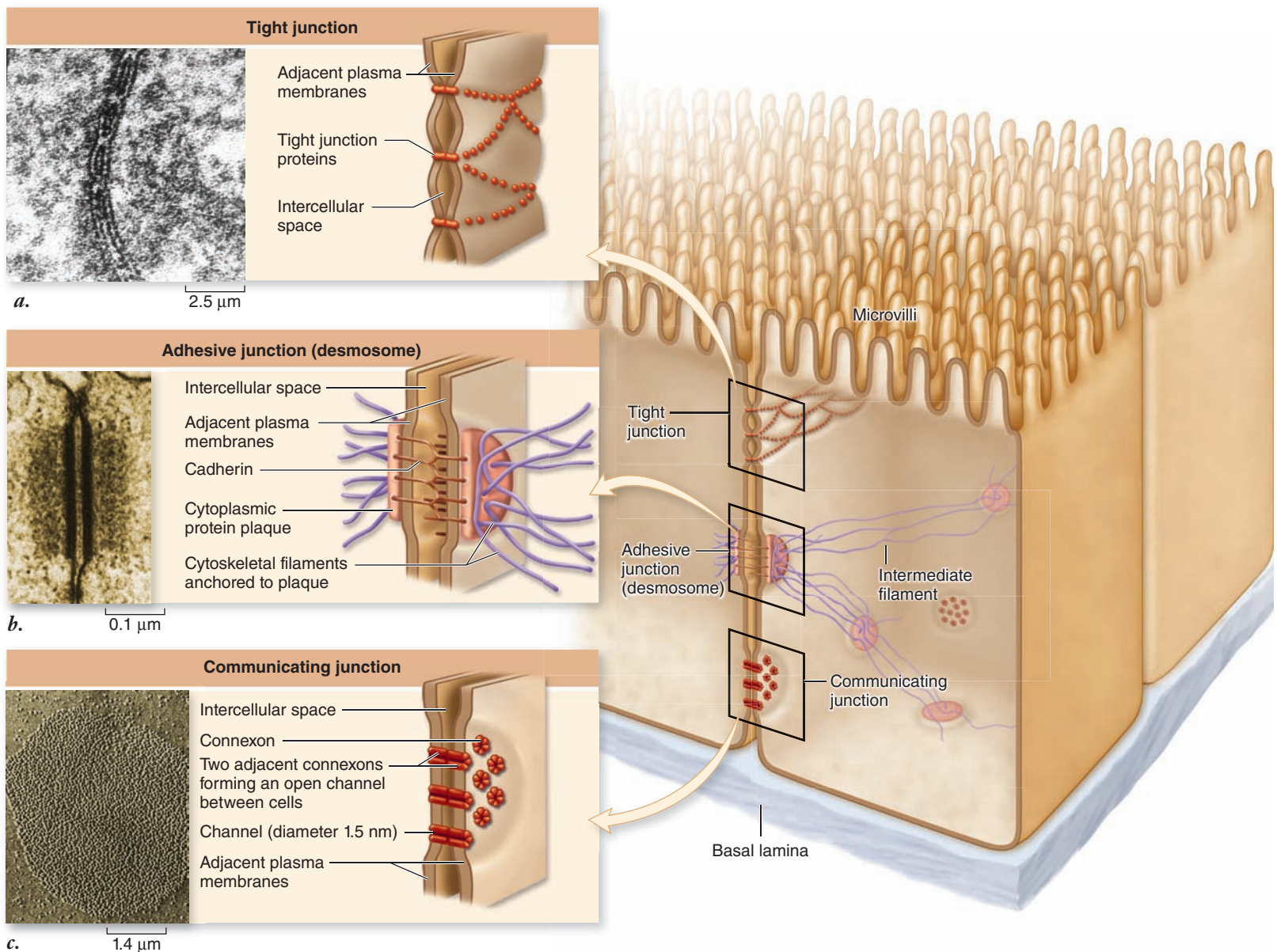


Figure 4.28 Cell junction types in animal epithelium. Here, the diagram of gut epithelial cells on the right illustrates the comparative structures and locations of common cell junctions. The detailed models on the left show the structures of the three major types of cell junctions: (a) tight junction; (b) adhesive junction—the example shown is a desmosome; (c) communicating junction—the example shown is a gap junction.

junctions exist, but there is an additional type based on similar proteins called connexons. In each case, a structure is formed by complexes of six identical transmembrane proteins (figure 4.28c). The proteins are arranged in a circle to create a channel through the plasma membrane that protrudes several nanometers from the cell surface. A gap junction forms when the connexons/pannexins of two cells align perfectly, creating an open channel that spans the plasma membranes of both cells.

Gap junctions provide passageways large enough to permit small substances, such as simple sugars and amino acids, to pass from one cell to the next. Yet the passages are small enough to prevent the passage of larger molecules, such as proteins.

Gap junction channels are dynamic structures that can open or close in response to a variety of factors, including Ca^{2+} and

H^+ ions. This gating serves at least one important function. When a cell is damaged, its plasma membrane often becomes leaky. Ions in high concentrations outside the cell, such as Ca^{2+} , flow into the damaged cell and close its gap junction channels. This isolates the cell and prevents the damage from spreading.

Plasmodesmata in plants. In plants, cell walls separate every cell from all others. Cell–cell junctions occur only at holes or gaps in the walls, where the plasma membranes of adjacent cells can come into contact with one another. Cytoplasmic connections that form across the touching plasma membranes are called **plasmodesmata** (singular, *plasmodesma*) (figure 4.29). The majority of living cells within a higher plant are connected to their neighbors by these junctions.

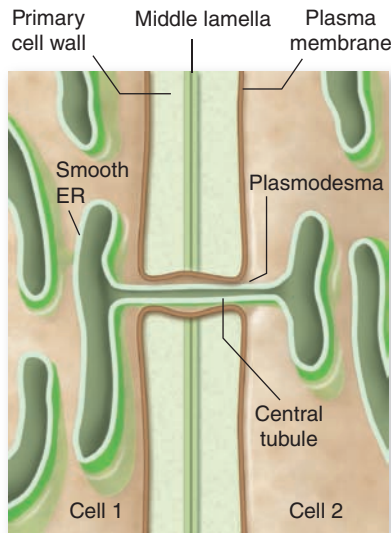


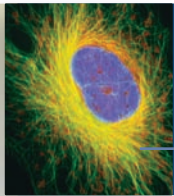
Figure 4.29 Plasmodesmata. Plant cells can communicate through specialized openings in their cell walls, called plasmodesmata, where the cytoplasm of adjoining cells are connected.

Plasmodesmata function much like gap junctions in animal cells, although their structure is more complex. Unlike gap junctions, plasmodesmata are lined with plasma membrane and contain a central tubule that connects the endoplasmic reticulum of the two cells.

Learning Outcomes Review 4.8

The evolution of multicellularity required the acquisition of cell adhesion molecules to connect cells together. Cell connections fall into three basic categories: (1) adhesive junctions provide strength and flexibility; (2) tight, or septate, junctions help to make sheets of cells that form watertight seals; and (3) communicating junctions, including gap junctions in animals and plasmodesmata in plants, allow passage of some materials between cells. Cells in multicellular organisms have distinct identity and connections. Cell identity is conferred by surface glycoproteins, which include the MHC proteins that are important in the immune system.

- How do cell junctions help to form tissues?



Chapter Review

4.1 Cell Theory

Cell theory is the unifying foundation of cell biology.

All organisms are composed of one or more cells. Cells arise only by division of preexisting cells.

Cell size is limited.

Cell size is constrained by the diffusion distance. As cell size increases, diffusion becomes inefficient.

Microscopes allow visualization of cells and components.

Magnification gives better resolution than is possible with the naked eye. Staining with chemicals enhances contrast of structures.

All cells share many structural features.

All cells have centrally located DNA, a semifluid cytoplasm, and an enclosing plasma membrane.

4.2 Prokaryotic Cells (figure 4.3)

Prokaryotic cells have relatively simple organization.

Prokaryotic cells contain DNA and ribosomes, but they lack a nucleus, an internal membrane system, and membrane-bounded organelles. A rigid cell wall surrounds the plasma membrane.

Bacterial cell walls consist of peptidoglycan.

Peptidoglycan is composed of carbohydrate cross-linked with short peptides.

Archaea lack peptidoglycan.

Archaeal cell walls do not contain peptidoglycan, and they have unique plasma membranes.

Some prokaryotes move by means of rotating flagella.

Prokaryotic flagella rotate because of proton transfer across the plasma membrane.

4.3 Eukaryotic Cells (figures 4.6 and 4.7)

Eukaryotic cells have a membrane-bounded nucleus, an endomembrane system, and many different organelles.

The nucleus acts as the information center.

The nucleus is surrounded by an envelope of two phospholipid bilayers; the outer layer is contiguous with the ER. Pores allow exchange of small molecules. The nucleolus is a region of the nucleoplasm where rRNA is transcribed and ribosomes are assembled.

In most prokaryotes, DNA is organized into a single circular chromosome. In eukaryotes, numerous chromosomes are present.

Ribosomes are the cell's protein synthesis machinery.

Ribosomes translate mRNA to produce polypeptides. They are found in all cell types.

4.4 The Endomembrane System

The endoplasmic reticulum (ER) creates channels and passages within the cytoplasm (figure 4.10).

The rough ER is a site of protein synthesis.

The rough ER (RER), studded with ribosomes, synthesizes and modifies proteins and manufactures membranes.

The smooth ER has multiple roles.

The smooth endoplasmic reticulum (SER) lacks ribosomes; it is involved in carbohydrate and lipid synthesis and detoxification.

The Golgi apparatus sorts and packages proteins.

The Golgi apparatus receives vesicles from the ER, modifies and packages macromolecules, and transports them (figure 4.11).

Lysosomes contain digestive enzymes.

Lysosomes break down macromolecules and recycle the components of old organelles (figure 4.13).

Microbodies are a diverse category of organelles.

Plants use vacuoles for storage and water balance.

4.5 Mitochondria and Chloroplasts: Cellular Generators

Mitochondria and chloroplasts have a double-membrane structure, contain their own DNA, and can divide independently.

Mitochondria metabolize sugar to generate ATP.

The inner membrane of mitochondria is extensively folded into layers called cristae. Proteins on the surface and in the inner membrane carry out metabolism to produce ATP (figure 4.16).

Chloroplasts use light to generate ATP and sugars.

Chloroplasts capture light energy via thylakoid membranes arranged in stacks called grana, and use it to synthesize glucose (figure 4.17).

Mitochondria and chloroplasts arose by endosymbiosis.

The endosymbiont theory proposes that mitochondria and chloroplasts were once prokaryotes engulfed by another cell.

4.6 The Cytoskeleton

The cytoskeleton consists of crisscrossed protein fibers that support the shape of the cell and anchor organelles (figure 4.19).

Three types of fibers compose the cytoskeleton.

Actin filaments, or microfilaments, are long, thin polymers involved in cellular movement. Microtubules are hollow structures that move materials within a cell. Intermediate filaments serve a wide variety of functions.

Centrosomes are microtubule-organizing centers.

Centrosomes help assemble the nuclear division apparatus of animal cells (figure 4.20).

The cytoskeleton helps move materials within cells.

Molecular motors move vesicles along microtubules, like a train on a railroad track. Kinesin and dynein are two motor proteins.

4.7 Extracellular Structures and Cell Movement

Some cells crawl.

Cell crawling occurs as actin polymerization forces the cell membrane forward, while myosin pulls the cell body forward.

Flagella and cilia aid movement.

Eukaryotic flagella have a 9 + 2 structure and arise from a basal body. Cilia are shorter and more numerous than flagella.

Plant cell walls provide protection and support.

Plants have cell walls composed of cellulose fibers. The middle lamella, between cell walls, holds adjacent cells together.

Animal cells secrete an extracellular matrix.

Glycoproteins are the main component of the extracellular matrix (ECM) of animal cells.

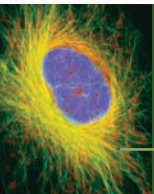
4.8 Cell-to-Cell Interactions (figure 4.28)

Surface proteins give cells identity.

Glycolipids and MHC proteins on cell surfaces help distinguish self from nonself.

Cell connections mediate cell-to-cell adhesion.

Cell junctions include tight junctions, adhesive junctions, and communicating junctions. In animals, gap junctions allow the passage of small molecules between cells. In plants, plasmodesmata penetrate the cell wall and connect cells.



Review Questions

UNDERSTAND

- Which of the following statements is NOT part of the cell theory?
 - All organisms are composed of one or more cells.
 - Cells come from other cells by division.
 - Cells are the smallest living things.
 - Eukaryotic cells have evolved from prokaryotic cells.
- All cells have all of the following except
 - plasma membrane.
 - genetic material.
 - cytoplasm.
 - cell wall.
- Eukaryotic cells are more complex than prokaryotic cells. Which of the following are found only in a eukaryotic cell?
 - Cell wall
 - Plasma membrane
 - Endoplasmic reticulum
 - Ribosomes
- Which of the following are differences between bacteria and archaea?
 - The molecular architecture of their cell walls
 - The type of ribosomes found in each
 - Archaea have an internal membrane system that bacteria lack.
 - Both a and b are correct.
- The cytoskeleton includes
 - microtubules made of actin filaments.
 - microfilaments made of tubulin.
 - intermediate filaments made of twisted fibers of vimentin and keratin.
 - smooth endoplasmic reticulum.
- The smooth endoplasmic reticulum is
 - involved in protein synthesis.
 - a site of protein glycosylation.
 - used to store a variety of ions.
 - the site of lipid and membrane synthesis.

7. Plasmodesmata in plants and gap junctions in animals are functionally similar in that
 - a. each is used to anchor layers of cells.
 - b. they form channels between cells that allow diffusion of small molecules.
 - c. they form tight junctions between cells.
 - d. they are anchored to the extracellular matrix.

APPLY

1. The most important factor that limits the size of a cell is the
 - a. quantity of proteins and organelles a cell can make.
 - b. rate of diffusion of small molecules.
 - c. surface area-to-volume ratio of the cell.
 - d. amount of DNA in the cell.
2. All eukaryotic cells possess each of the following except
 - a. mitochondria.
 - b. cell wall.
 - c. cytoskeleton.
 - d. nucleus.
3. Adherens junctions, which contain cadherin, are found in all animals. Given this, which of the following predictions is most likely?
 - a. Cadherins would not be found in the ancestor to all animals.
 - b. Cadherins would be found in prokaryotes.
 - c. Cadherins would be found in the ancestor to all animals.
 - d. Cadherins would be found in vertebrates but not invertebrates.
4. Different motor proteins like kinesin and myosin are similar in that they can
 - a. interact with microtubules.
 - b. use energy from ATP to produce movement.
 - c. interact with actin.
 - d. do both a and b.
5. The protein sorting pathway involves the following organelles/ compartments in order:
 - a. SER, RER, transport vesicle, Golgi.
 - b. RER, lysosome, Golgi.
 - c. RER, transport vesicle, Golgi, final destination.
 - d. Golgi, transport vesicle, RER, final destination.

6. Chloroplasts and mitochondria have many common features because both
 - a. are present in plant cells.
 - b. arose by endosymbiosis.
 - c. function to oxidize glucose.
 - d. function to produce glucose.
7. Eukaryotic cells are composed of three types of cytoskeletal filaments. How are these three filaments similar?
 - a. They contribute to the shape of the cell.
 - b. They are all made of the same type of protein.
 - c. They are all the same size and shape.
 - d. They are all equally dynamic and flexible.

SYNTHESIZE

1. The smooth endoplasmic reticulum is the site of synthesis of the phospholipids that make up all the membranes of a cell—especially the plasma membrane. Use the diagram of an animal cell (figure 4.6) to trace a pathway that would carry a phospholipid molecule from the SER to the plasma membrane. What endomembrane compartments would the phospholipids travel through? How can a phospholipid molecule move between membrane compartments?
2. Use the information provided in table 4.3 to develop a set of predictions about the properties of mitochondria and chloroplasts if these organelles were once free-living prokaryotic cells. How do your predictions match with the evidence for endosymbiosis?
3. In evolutionary theory, homologous traits are those with a similar structure and function derived from a common ancestor. Analogous traits represent adaptations to a similar environment, but from distantly related organisms. Consider the structure and function of the flagella found on eukaryotic and prokaryotic cells. Are the flagella an example of a homologous or analogous trait? Defend your answer.
4. The protist *Giardia intestinalis* is the organism associated with water-borne diarrheal diseases. *Giardia* is an unusual eukaryote because it seems to lack mitochondria. Provide two possible evolutionary scenarios for this in the context of the endosymbiotic theory.