4

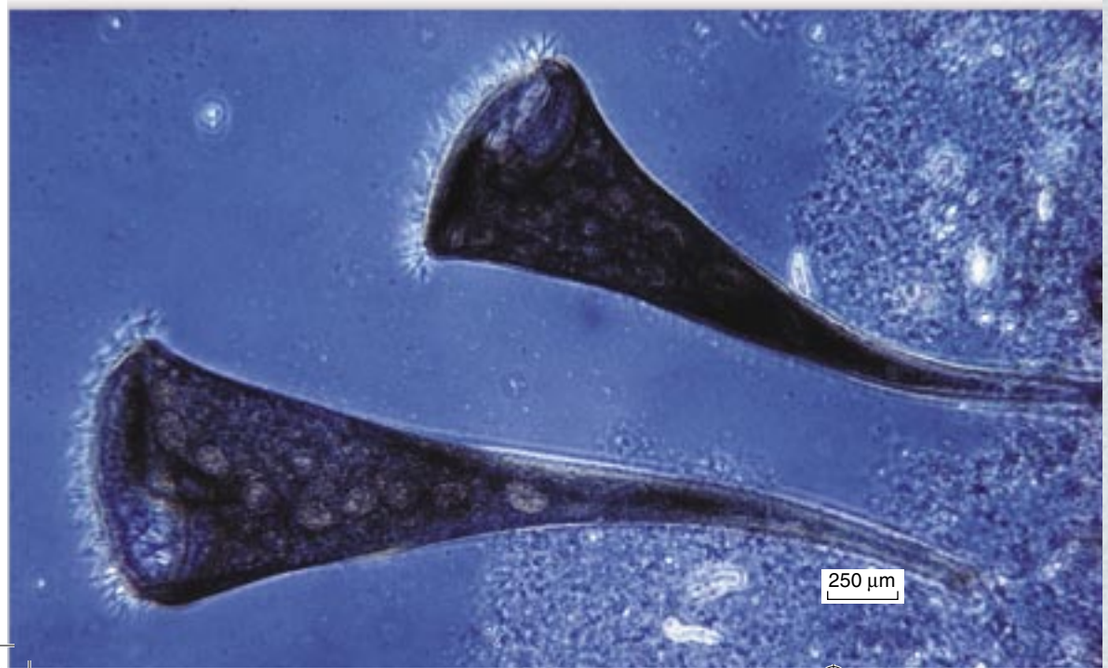
Cell Structure and Function

Cells, the fundamental building blocks of organisms, are so tiny they weren't discovered until the development of the microscope. The Dutch shopkeeper Antonie van Leeuwenhoek (1632–1723) was probably the first person to see cells. After using a magnifying glass to evaluate cloth, he taught himself to grind more powerful lenses and built a microscope. He looked at everything possible including the teeming life in a drop of pond water. Perhaps he even saw the unicellular protist, Stentor, *featured in the accompanying micrograph. Leeuwenhoek's reports of innumerable microscopic "wee beasties and animalcules" were enthusiastically received by the Royal Society of London.*

The English scientist Robert Hooke (1635–1703) was a microscopist who confirmed Leeuwenhoek's observations and was the first to use the word cell. *The tiny chambers he observed in the honeycomb structure of cork reminded him of the rooms, or cells, in a monastery. Naturally, he referred to the boundaries of these chambers as walls. Today, we know that all tissues from the cork of a tree to the nervous tissue of humans are composed of cells.*

A light micrograph does not reveal much cellular detail; a cell's often centrally placed nucleus is the only highly visible structure. The other parts of a cell are largely indistinguishable. Electron microscopy and biochemical analysis of the last century led to the discovery that plant and animal cells contain a variety of organelles, each specialized to perform a particular function. Even the content of organelles is now known. The nucleus may contain numerous chromosomes and thousands of genes!

Micrograph of a freshwater protozoan, *Stentor*.



CONCEPTS

4.1 CELLULAR LEVEL OF ORGANIZATION

The 1830s were exciting times in the history of our knowledge of the cell. In 1831, the English botanist Robert Brown described the nucleus of cells. In 1838, the German botanist Matthais Schleiden stated that all plants are composed of cells. A year later, the German zoologist Theodor Schwann declared that all animals are composed of cells (Fig. 4.1). As a result of their work, the field of cytology (study of cells) began, and we can conclude that a **cell** is the smallest unit of living matter.

In the 1850s, the German physician Rudolph Virchow viewed the human body as a state in which each cell was a citizen. Today, we know that various illnesses of the body, such as diabetes and prostate cancer, are due to a malfunctioning of cells rather than the organ itself. It also means that a cell is the basic unit of function as well as structure in organisms.

Virchow was the first to tell us that cells reproduce and "every cell comes from a preexisting cell." When unicellular organisms reproduce, a single cell divides, and when multicellular organisms grow, many cells divide. Cells are also involved in the sexual reproduction of multicellular organisms. In reality, there is a continuity of cells from generation to generation even back to the very first cell (or cells) in the history of life. Due to countless investigations that began with the work of Virchow, it is evident that cells are capable of self-reproduction.

The **cell theory** is based upon the work of Schleiden, Schwann, and Virchow. It states that (1) all organisms are composed of cells, (2) cells are the basic units of structure and function in organisms, and (3) cells come only from preexisting cells because cells are self-reproducing.

All organisms are made up of cells, and a cell is the structural and functional unit of organs and, ultimately, of organisms. Cells are capable of self-reproduction, and cells come only from preexisting cells.

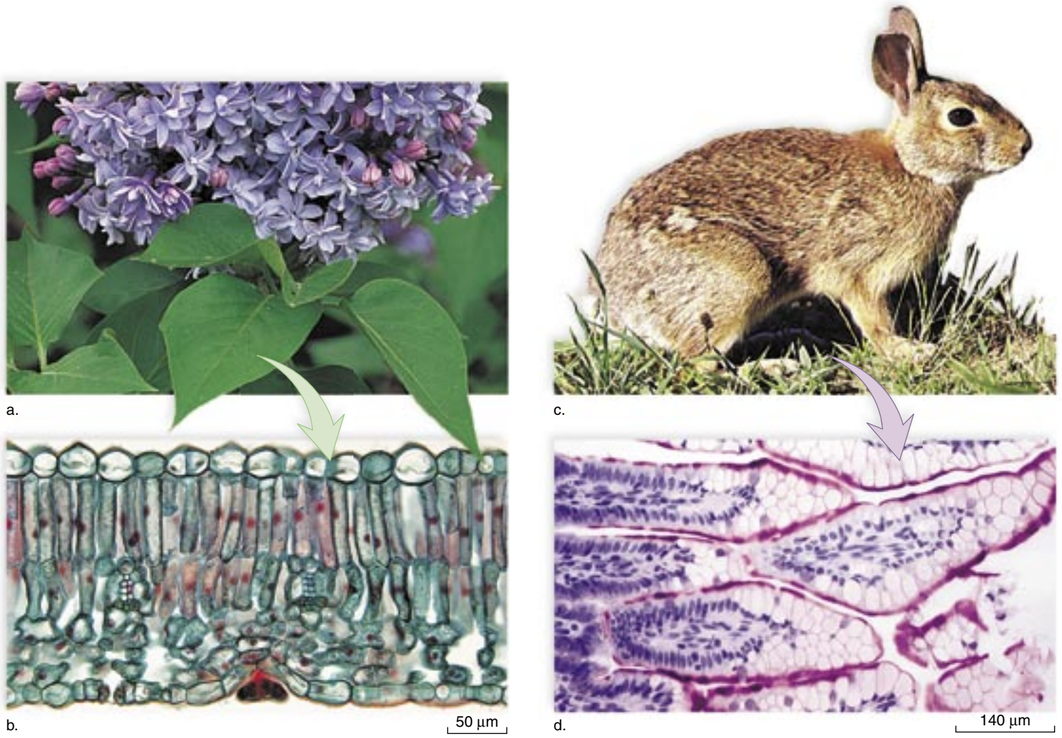


FIGURE 4.1 Organisms and cells.
All organisms, including plants and animals, are composed of cells. This is not readily apparent because a microscope is usually needed to see the cells. **a.** Lilac plant. **b.** Light micrograph of a cross section of a lilac leaf showing many individual cells. **c.** Rabbit. **d.** Light micrograph of a rabbit's intestinal lining showing that it, too, is composed of cells. The dark-staining bodies are nuclei.

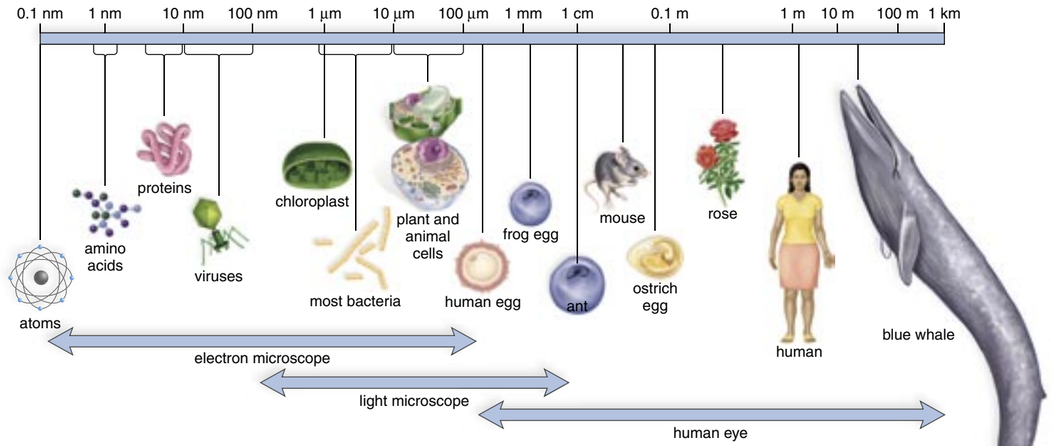


FIGURE 4.2 The sizes of living things and their components.
It takes a microscope to see most cells and lower levels of biological organization. Cells are visible with the light microscope, but not in much detail. An electron microscope is necessary to see organelles in detail and to observe viruses and molecules. In the metric system (see Appendix C), each higher unit is ten times greater than the preceding unit. (1 meter = 10^2 cm = 10^3 mm = 10^6 µm = 10^9 nm.)

Cell Size

Cells are quite small. A frog's egg, at about 1 millimeter (mm) in diameter, is large enough to be seen by the human eye. But most cells are far smaller than 1 mm; some are even as small as 1 micrometer (µm)—one thousandth of a millimeter. Cell inclusions and macromolecules are smaller than a micrometer and are measured in terms of nanometers (nm). Figure 4.2 outlines the visual range of the eye, light microscope, and electron microscope, and the discussion of microscopy in the Science Focus on pages 60 and 61 explains why the electron microscope allows us to see so much more detail than the light microscope does.

Why are cells so small? To answer this question, consider that a cell needs a surface area large enough to allow adequate nutrients to enter and to rid itself of wastes. Small cells, not large cells, are likely to have an adequate surface area for exchanging wastes for nutrients. For example, Figure 4.3 visually demonstrates that cutting a large cube into smaller cubes provides a lot more surface area per volume. The calculations show that a 4-cm cube has a **surface-area-to-volume ratio** of only 1.5:1, whereas a 1-cm cube has a surface-area-to-volume ratio of 6:1.

We would expect, then, that actively metabolizing cells would be small. A chicken's egg is several centimeters in diameter, but the egg is not actively metabolizing. Once the egg is incubated and metabolic activity begins, the egg divides repeatedly without growth. Cell division restores the amount of surface area needed for adequate exchange of materials. Further, cells that specialize in absorption have modifications that greatly increase the surface area per volume of the cell. The columnar epithelial cells along the surface of the intestinal wall have surface foldings called microvilli (sing., microvillus) that increase their surface area. Nerve cells and some large plant cells are long and thin in order to keep the cytoplasm near the plasma membrane.

Total surface area (height × width × number of sides × number of cubes)		
96 cm^2	192 cm^2	384 cm^2
Total volume (height × width × length × number of cubes)		
64 cm^3	64 cm^3	64 cm^3
Surface area: Volume per cube (surface area ÷ volume)		
1.5:1	3:1	6:1

FIGURE 4.3 Surface-area-to-volume relationships.
As cell size decreases from 4 cm^3 to 1 cm^3, the surface-area-to-volume ratio increases.

A cell needs a surface area that can adequately exchange materials with the environment. Surface-area-to-volume considerations require that cells stay small.

science focus

Microscopy Today

Cells were not discovered until the seventeenth century (when the microscope was invented). Since that time, various types of microscopes have been developed for the study of cells and their components.

In the *compound light microscope,* light rays passing through a specimen are brought into focus by a set of glass lenses, and the resulting image is then viewed by the human eye. In the *transmission electron microscope (TEM),* electrons passing through a specimen are brought into focus by a set of magnetic lenses, and the resulting image is projected onto a fluorescent screen or photographic film. In the *scanning electron microscope (SEM),* a narrow beam of electrons is scanned over the surface of the specimen, which is coated with a thin metal layer. The metal gives off secondary electrons that are collected by a detector to produce an image on a television screen. The SEM permits the development of three-dimensional images. Figure 4A shows these three types of microscopic images.

Magnification, Resolution, and Contrast

The magnifying capability of a transmission electron microscope is greater than that of a compound light microscope. A light microscope can magnify objects about a thousand times, but an electron microscope can magnify them hundreds of thousands of times. The difference lies in the means of illumination. The path of light rays and electrons moving through space is wavelike, but the wavelength of electrons is much shorter than the wavelength of light. This difference in wavelength accounts for the electron microscope's greater magnifying capability and its greater resolving power. The greater the resolving power, the greater the detail eventually seen. *Resolution* is the minimum distance between two objects at which they can still be seen, or resolved, as two separate objects. If oil is placed between the sample and the objective lens of the compound light microscope, the resolving power is increased, and if ultraviolet light is used instead of visible light, it is also increased. But typically, a light microscope can resolve down to 0.2 μm, while the transmission electron microscope can resolve down to 0.0002 μm. If the resolving power of the average human eye is set at 1.0, then that of the typical compound light microscope is about 500, and that of the transmission electron microscope is 100,000. This means that this type of electron microscope distinguishes much greater detail (Fig. 4A*b*).

Some microscopes view living specimens, but often specimens are treated prior to observation. Cells are killed, fixed so that they do not decompose, and embedded into a matrix. The matrix strengthens the specimen so that it can be thinly sliced. These sections are often stained with colored dyes (light microscopy) or with electron-dense metals (electron microscopy) to provide contrast. Another way to increase contrast is to use optical methods such as phase contrast and differential interference contrast (Fig. 4B). In addition to optical and electronic methods for contrasting transparent cells, a third very prominent research tool is called *immunofluorescence microscopy,* because it uses fluorescent antibodies to reveal the location of a protein in the cell (see Fig. 4.18). The importance of this method is that the cellular distribution of a single type of protein can be examined.

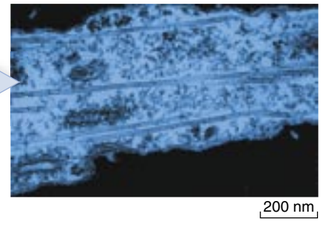
Illumination, Viewing, and Recording

Light rays can be bent (refracted) and brought to focus as they pass through glass lenses, but electrons do not pass through glass. Electrons have a charge that allows them to be brought into focus by magnetic lenses. The human eye uses light to see an object but cannot use electrons for the same purpose. Therefore, electrons leaving the specimen in the electron microscope are directed toward a screen or a photographic plate that is sensitive to their presence. Humans can view the image on the screen or photograph.

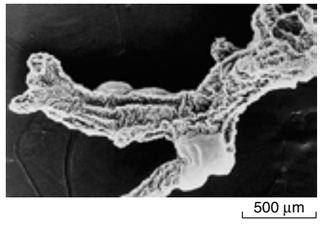
A major advancement in illumination has been the introduction of *confocal microscopy,* which uses a laser beam scanned across the specimen to focus on a single shallow plane within the cell. The microscopist can "optically section" the specimen by focusing up and down, and a series of optical sections can be combined in a computer to create a three-dimensional image, which can be displayed and rotated on the computer screen.

An image from a microscope may be recorded by replacing the human eye with a television camera. The television camera converts the light image into an electronic image, which can be entered into a computer. In *video-enhanced contrast microscopy,* the computer makes the darkest areas of the original image much darker and the lightest areas of the original much lighter. The result is a high-contrast image with deep blacks and bright whites. Even more contrast can be introduced by the computer if shades of gray are replaced by colors.

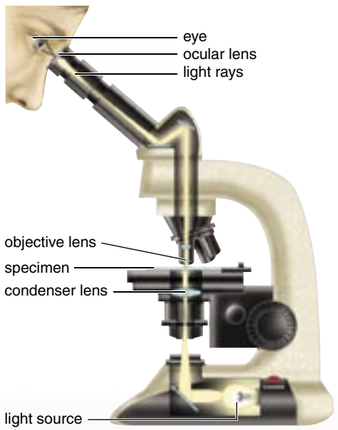
amoeba, light micrograph



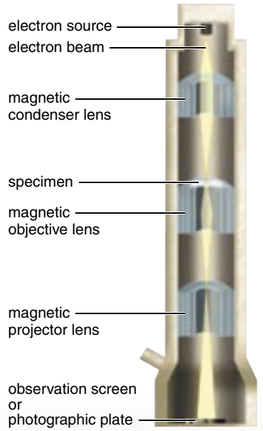
pseudopod segment, transmission electron micrograph



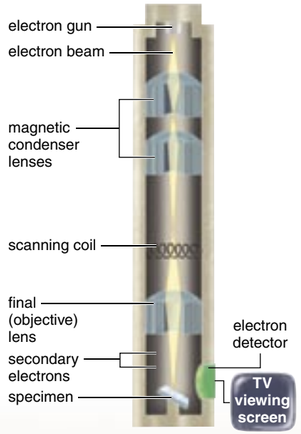
amoeba, scanning electron micrograph



a. Compound light microscope

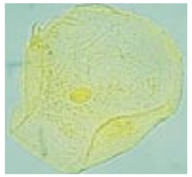


b. Transmission electron microscope

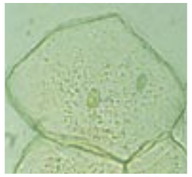


c. Scanning electron microscope

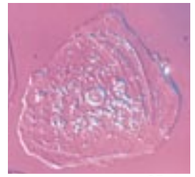
FIGURE 4A Diagram of microscopes with accompanying micrographs of *Amoeba proteus*.
The compound light microscope and the transmission electron microscope provide an internal view of an organism. The scanning electron microscope provides an external view of an organism.



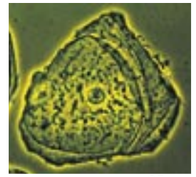
Bright-field. Light passing through the specimen is brought directly into focus. Usually, the low level of contrast within the specimen interferes with viewing all but its largest components.



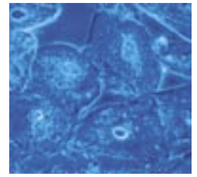
Bright-field (stained). Dyes are used to stain the specimen. Certain components take up the dye more than other components, and therefore contrast is enhanced.



Differential interference contrast. Optical methods are used to enhance density differences within the specimen so that certain regions appear brighter than others. This technique is used to view living cells, chromosomes, and organelle masses.



Phase contrast. Density differences in the specimen cause light rays to come out of "phase." The microscope enhances these phase differences so that some regions of the specimen appear brighter or darker than others. The technique is widely used to observe living cells and organelles.



Dark-field. Light is passed through the specimen at an oblique angle so that the objective lens receives only light diffracted and scattered by the object. This technique is used to view organelles, which appear quite bright against a dark field.

FIGURE 4B Photomicrographs of cheek cells.
Bright-field microscopy is the most common form used with a compound light microscope. Other types of microscopy include differential interference contrast, phase contrast, and dark-field.

4.2 Prokaryotic Cells

Fundamentally, two different types of cells exist. **Prokaryotic cells** [Gk. *pro,* before, and *karyon,* kernel, nucleus] are so named because they lack a membrane-bounded nucleus. The other type of cell, called a **eukaryotic cell,** has a nucleus (see Figs. 4.6 and 4.7). Prokaryotic cells are simpler and much smaller than eukaryotic cells, and they are present in great numbers in the air, in bodies of water, in the soil, and they also live in and on other organisms. Prokaryotes are an extremely successful group of organisms whose evolutionary history dates back to the first cells on Earth.

All prokaryotic cells are structurally simple, and they can be divided into two groups, largely based on nucleic and base sequence differences. These two groups are so biochemically different that they have been placed in separate domains, called domain Bacteria and domain Archaea. Bacteria are well known because they cause some serious diseases, such as tuberculosis, anthrax, tetanus, throat infections, and gonorrhea. But many species of bacteria are important to the environment because they decompose the remains of dead organisms and contribute to ecological cycles. Bacteria also assist humans in another way—we use them to manufacture all sorts of products, from industrial chemicals to foodstuffs and drugs.

The Structure of Bacteria

Bacteria are quite small; an average size is 1.1–1.5 µm wide and 2.0–6.0 µm long. These different shapes are common.

A rod-shaped bacterium is called a **bacillus,** while a spherical-shaped bacterium is a **coccus.** Both of these can occur as pairs or chains, and in addition, cocci can occur as clusters. Some long rods are twisted into spirals, in which case they are **spirilla** if they are rigid or **spirochetes** if they are flexible.

Figure 4.4 shows the generalized structure of a bacterium. This example is a bacillus because of its rod shape. For the sake of discussion, we will divide the organization of bacteria into the cell envelope, the cytoplasm, and the appendages.

Cell Envelope

The **cell envelope** includes the plasma membrane, the cell wall, and the glycocalyx. The **plasma membrane** of a bacterial cell has the same composition as that of a eukaryotic cell—it is a phospholipid bilayer with both embedded and peripheral proteins. The plasma membrane has the important function of regulating the entrance and exit of substances into and out of the cytoplasm. After all, the cytoplasm has a normal composition that needs to be maintained.

The plasma membrane can form internal pouches called mesosomes. **Mesosomes** most likely increase the internal surface area for the attachment of enzymes that are carrying on metabolic activities.

The **cell wall** maintains the shape of the cell even if the cytoplasm should happen to take up an abundance of water. You may recall that the cell wall of a plant cell is strengthened by the presence of cellulose, while the cell wall of a bacterium contains peptidoglycan, a complex molecule containing a unique amino disaccharide and peptide fragments.

The **glycocalyx** is a layer of polysaccharides lying outside the cell wall. When the layer is well organized and not easily washed off, it is called a **capsule.** A slime layer, on the other hand, is not well organized and is easily removed. The glycocalyx aids against drying out and helps bacteria resist a host's immune system. It also helps bacteria attach to almost any surface.

Cytoplasm

The **cytoplasm** is a semifluid solution composed of water and inorganic and organic molecules encased by a plasma membrane. Among the organic molecules are a variety of enzymes, which speed the many types of chemical reactions involved in metabolism.

The DNA of a bacterium is in a single chromosome that coils up and is located in a region called the **nucleoid.** Many bacteria also have an extrachromosomal piece of circular DNA called a **plasmid.** Plasmids are routinely used in biotechnology laboratories as vectors to transport DNA into a bacterium—even human DNA can be put into a bacterium by using a plasmid as a vector. This technology is important in the production of new medicines.

The many proteins specified for by bacterial DNA are synthesized on tiny particles called **ribosomes.** A bacterial cell contains thousands of ribosomes that are smaller than eukaryotic ribosomes. However, bacterial ribosomes still contain RNA and protein in two subunits, as do eukaryotic ribosomes. The **inclusion bodies** found in the cytoplasm are stored granules of various substances. Some are nutrients that can be broken down when needed.

The **cyanobacteria** are bacteria that photosynthesize in the same manner as plants. These organisms live in water, in ditches, on buildings, and on the bark of trees. Their cytoplasm contains extensive internal membranes called **thylakoids** [Gk. *thylakon,* and *eidos,* form] where chlorophyll and other pigments absorb solar energy for the production of carbohydrates. Cyanobacteria are called the blue-green bacteria because some have a pigment that adds a shade of blue to the cell, in addition to the green color of chlorophyll. The cyanobacteria release oxygen as a side product of photosynthesis, and perhaps ancestral cyanobacteria were the first types of organisms on Earth to do so. The addition of oxygen changed the composition of the Earth's atmosphere.

Appendages

The appendages of a bacterium, namely the flagella, fimbriae, and sex pili, are made of protein. Motile bacteria can propel themselves in water by the means of appendages called

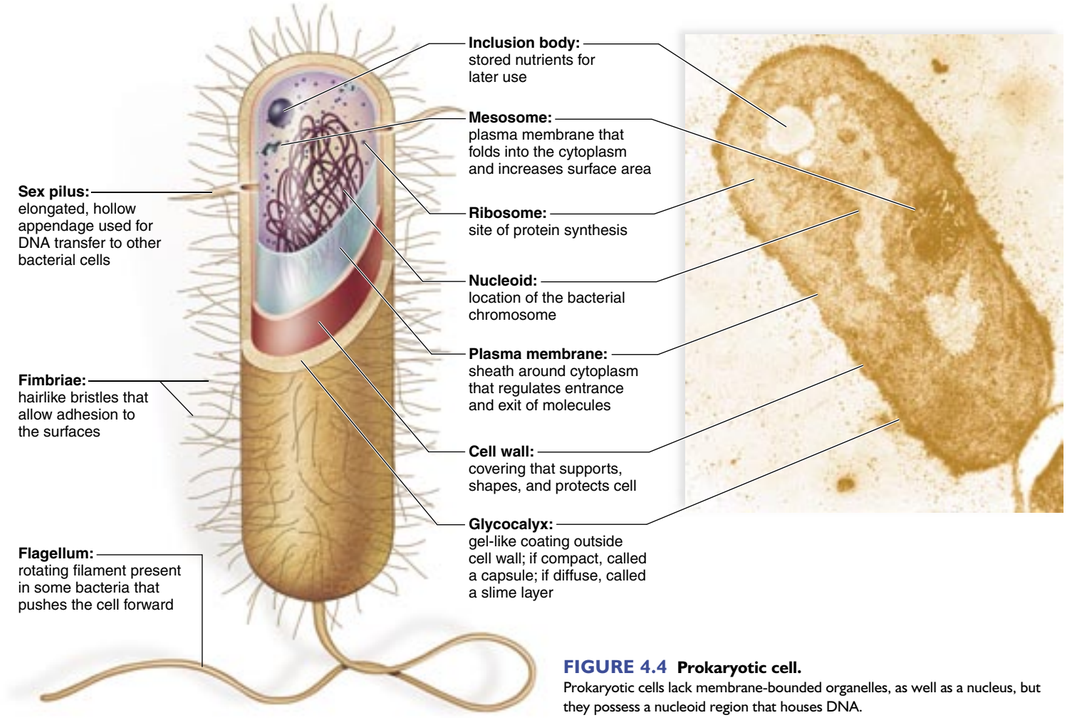


FIGURE 4.4 Prokaryotic cell.
Prokaryotic cells lack membrane-bounded organelles, as well as a nucleus, but they possess a nucleoid region that houses DNA.

flagella (usually 20 nm in diameter and 1–70 nm long). The bacterial flagellum has a filament, a hook, and a basal body. The basal body is a series of rings anchored in the cell wall and membrane. The hook rotates 360° within the basal body, and this motion propels bacteria—the bacterial flagellum does not move back and forth like a whip. Sometimes flagella occur only at the two ends of a cell, and sometimes they are dispersed randomly over the surface. The number and location of flagella are important in distinguishing different types of bacteria.

Fimbriae are small, bristlelike fibers that sprout from the cell surface. They are not involved in locomotion; instead, fimbriae attach bacteria to a surface. **Sex pili** are rigid tubular structures used by bacteria to pass DNA from cell to cell. Bacteria reproduce asexually by binary fission, but they can exchange DNA by way of the sex pili. They can also take up DNA from the external medium or by way of viruses.

The Structure of Archaea

Like bacteria, archaea are prokaryotes. Archaea are more diverse in shape than bacteria because, in addition to the shapes illustrated on page 62, they can be lobed, platelike, or irregular in shape.

The cell wall of archaea does not contain peptidoglycan; it contains polysaccharides and proteins arranged in different ways in various archaea. The membrane lipids are composed of glycerol bonded to hydrocarbons, not fatty acids.

The base sequences of DNA and RNA in archaea match that of eukaryotes better than that of bacteria! Therefore, it is thought that archaea may be more closely related to eukaryotes than to bacteria.

The archaea are well known for living in extreme habitats. They abound in extremely salty and/or hot, aqueous environments. These conditions are thought to resemble the earliest environments on Earth, and archaea may have been the first type of cell to evolve. They are able to adapt to various environments, however and they are even prevalent in the waters off the coast of Antarctica.

Bacteria and archaea are prokaryotic cells. Bacterial cells have these features:

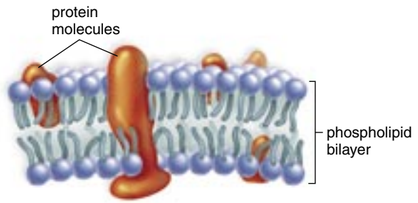
Cell envelope	Glycocalyx Cell wall Plasma membrane
Cytoplasm	Nucleoid Ribosomes Thylakoids (cyanobacteria)
Appendages	Flagella Sex pili Fimbriae

4.3 EUKARYOTIC CELLS

Organisms with eukaryotic cells, namely protists, fungi, plants, and animals, are members of domain Eukarya, the third domain of living things. Unlike prokaryotic cells, eukaryotic cells do have a membrane-bounded **nucleus** [L. *nucleus*, kernel], which houses their DNA. It has been suggested by some scientists that the nucleus evolved as the result of the invagination of the plasma membrane (Fig. 4.5).

Eukaryotic cells are much larger than prokaryotic cells, and therefore they have less surface area per volume than prokaryotic cells (see Fig. 4.2). This difference in surface-area-to-volume ratio is not detrimental to the cells' existence because, unlike prokaryotic cells, eukaryotic cells are compartmentalized. They have small structures called **organelles** that are specialized to perform specific functions.

Eukaryotic cells, like prokaryotic cells, have a plasma membrane that separates the contents of the cell from the environment and regulates the passage of molecules into and out of the cytoplasm. The plasma membrane is a phospholipid bilayer with embedded proteins:



Some eukaryotic cells, notably plant cells, also have an outer boundary called a cell wall. A plant cell wall contains cellulose fibrils and therefore has a different composition than the cell wall of bacteria. A cell wall supports and protects the cell but does not interfere with the movement of molecules across the plasma membrane. The plasmodesmata are channels in a cell wall that allow cytoplasmic strands to extend between adjacent cells.

The Structure of Eukaryotic Cells

Figures 4.6 and 4.7 illustrate cellular anatomy and types of structures and organelles found in animal and plant cells. In this chapter, our discussion of the structures found in eukaryotic cells will be divided into these categories: the nucleus and ribosomes; the organelles of the endomembrane system; the peroxisomes and vacuoles; the energy-related organelles; and the cytoskeleton.

The nucleus communicates with ribosomes in the cytoplasm, and the organelles of the endomembrane system communicate with one another. Each organelle has its own particular set of enzymes and produces its own products, and the products move from one organelle to the other. The products are carried between organelles by little transport vesicles, membranous sacs that enclose the molecules

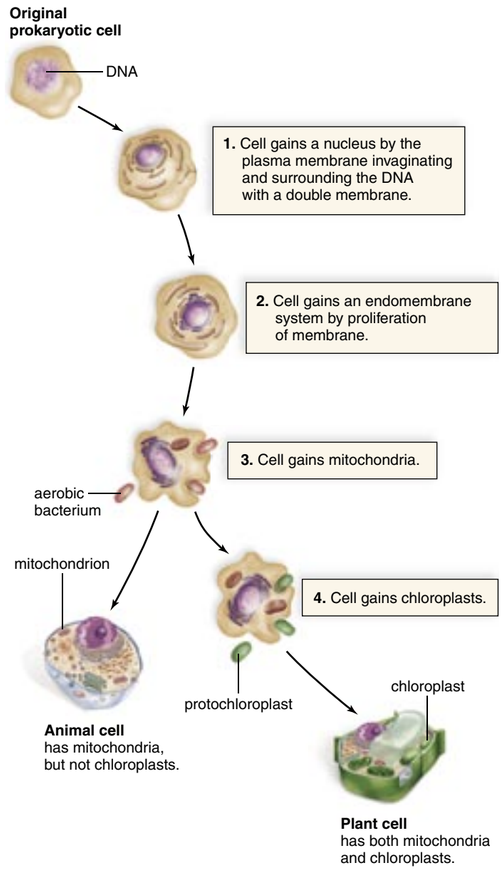


FIGURE 4.5 Origin of organelles.
Invagination of the plasma membrane could have created the nuclear envelope and an endomembrane system. The endosymbiotic hypothesis suggests that mitochondria and chloroplasts could have been independent prokaryotes that took up residence in a eukaryotic cell.

and keep them separate from the cytoplasm. In contrast, the energy-related organelles—the mitochondria in plant and animal cells, and the chloroplasts in plant cells—do not communicate with the other organelles of the cell. Except for importing certain proteins, these organelles are self-sufficient. They even have their own genetic material, and their ribosomes resemble those of prokaryotic cells. This and other evidence suggest that the mitochondria and chloroplasts are derived from prokaryotes that took up residence in an early eukaryotic cell (see Fig. 4.5). Notice that an animal cell has only mitochondria, while a plant cell has both mitochondria and chloroplasts.

science focus

Cell Fractionation and Differential Centrifugation

Modern microscopic techniques can be counted on to reveal the structure and distribution of organelles in a cell. But how do researchers isolate the different types of organelles from a cell so that they can determine their function? Suppose, for example, you wanted to study the function of ribosomes. How would you acquire some ribosomes? First, researchers remove cells from an organism or cell culture and place them in a sugar or salt solution. Then they fractionate (break open) the cells in a homogenizer.

A process called *differential centrifugation* allows researchers to separate the parts of a cell by size and density. A centrifuge works like the spin cycle of a washing machine. Only when the centrifuge spins do cell components come out of suspension and form a sediment. The faster the centrifuge spins, the smaller the components that settle out.

Figure 4C shows that the slowest spin cycle separates out the nuclei, and then progressively faster cycles separate out ever smaller components. In between spins, the fluid portion of the previous cycle must be poured into a clean tube. Why? If you didn't start with a fresh tube, all the different cell parts would pile up in one tube.

By using different salt solutions and different centrifuge speeds, researchers can obtain essentially pure preparations of almost any cell component. Biochemical analysis and manipulation then allow them to determine the function of that component.

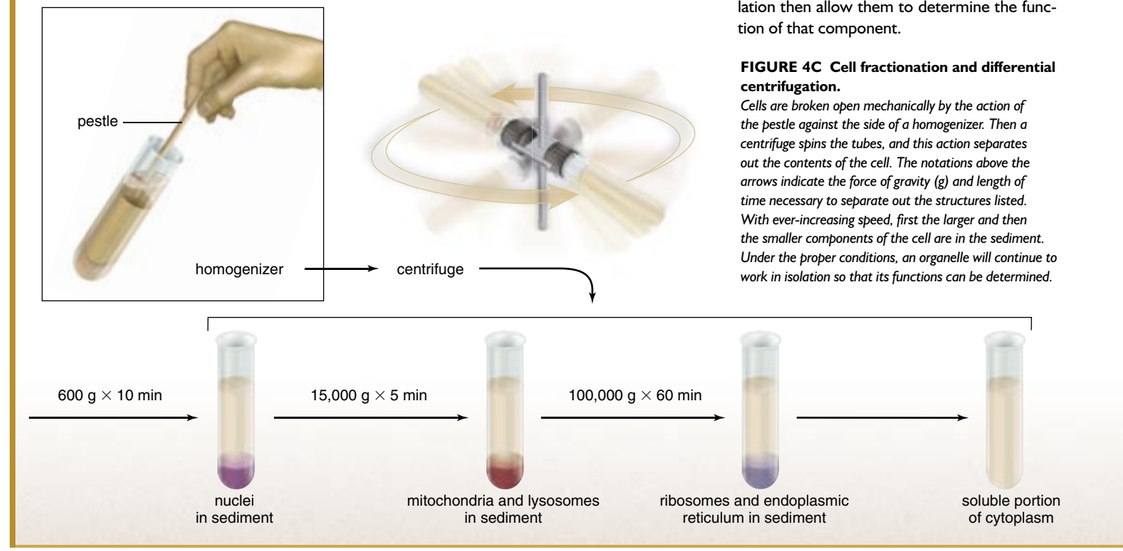


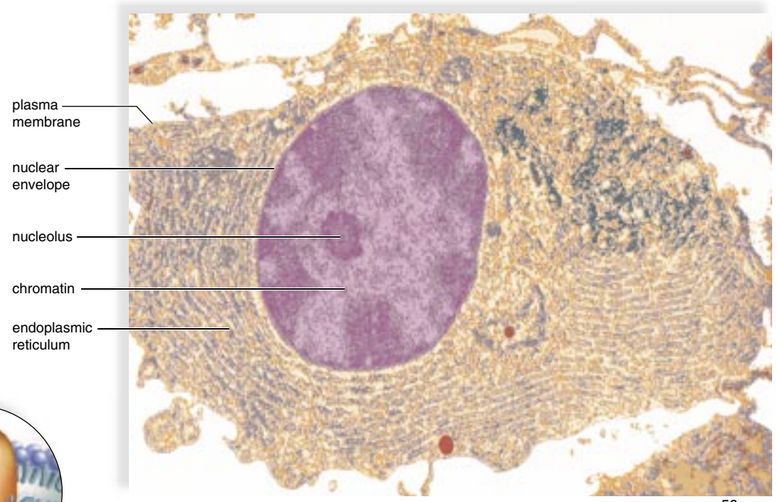
FIGURE 4C Cell fractionation and differential centrifugation.
Cells are broken open mechanically by the action of the pestle against the side of a homogenizer. Then a centrifuge spins the tubes, and this action separates out the contents of the cell. The notations above the arrows indicate the force of gravity (g) and length of time necessary to separate out the structures listed. With ever-increasing speed, first the larger and then the smaller components of the cell are in the sediment. Under the proper conditions, an organelle will continue to work in isolation so that its functions can be determined.

The cytoskeleton is a lattice of protein fibers that maintains the shape of the cell and assists in the movement of organelles. The protein fibers serve as tracks for the transport vesicles that are taking molecules from one organelle to another. In other words, the tracks direct and speed them on their way. The manner in which vesicles and other types of organelles move along these tracks will be discussed in more detail later in the chapter. Without a cytoskeleton, a eukaryotic cell would not have an efficient means of moving organelles and their products within the cell and possibly could not exist.

Each structure in an animal or plant cell (Figs. 4.6 and 4.7) has been given a particular color that will be used for this structure throughout the text.

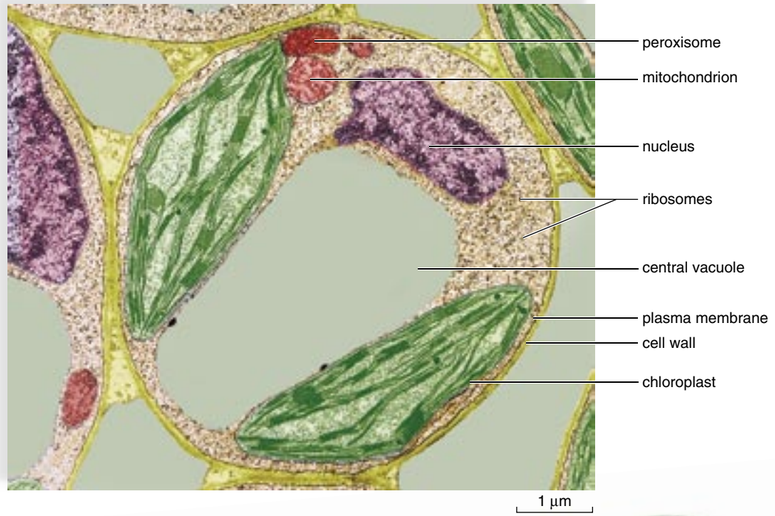
Compartmentalization is seen in eukaryotic cells, and they are larger than prokaryotic cells. We will discuss the nucleus and ribosomes; the organelles of the endomembrane system; the energy-related organelles; and the cytoskeleton. Each of these has a specific structure and function.

FIGURE 4.6
Animal cell anatomy.
Micrograph of liver cell and drawing of a generalized animal cell.



*not in plant cells

FIGURE 4.7
Plant cell anatomy.
False-colored micrograph of a young plant cell and drawing of a generalized plant cell.



*not in animal cells

The Nucleus and Ribosomes

The nucleus is essential to the life of a cell. It contains the genetic information that is passed on from cell to cell and from generation to generation. The ribosomes use this information to carry out protein synthesis.

The Nucleus

The nucleus, which has a diameter of about 5 µm, is a prominent structure in the eukaryotic cell (Fig. 4.8). It generally appears as an oval structure located near the center of most cells. A cell can have more than one nucleus. The nucleus contains **chromatin** [Gk. *chroma,* color, and *teino,* stretch] in a semifluid matrix called the **nucleoplasm.** Chromatin looks grainy, but actually it is a network of strands that condenses and undergoes coiling into rodlike structures called **chromosomes** [Gk. *chroma,* color, and *soma,* body], just before the cell divides. All of the cells of an individual contain the same number of chromosomes, and the mechanics of nuclear division ensure that each daughter cell receives the normal number of chromosomes, except for the egg and sperm, which have half this number. This alone suggested to early investigators that the chromosomes are the carriers of genetic information.

Chromatin, and therefore chromosomes, contains DNA, protein, and some RNA (ribonucleic acid). Genes, composed of DNA, are units of heredity located on the chromosomes.

RNA, of which there are several forms, is produced in the nucleus. A **nucleolus** is a dark region of chromatin where a type of RNA, called ribosomal RNA (rRNA), is produced and where rRNA joins with proteins to form the subunits of ribosomes. Ribosomes are small bodies in the cytoplasm where protein synthesis occurs. Another type of RNA, called messenger RNA (mRNA), acts as an intermediary for DNA and specifies the sequence of amino acids during protein synthesis. Transfer RNA (tRNA) is used in the assembly of amino acids during protein synthesis. The proteins of a cell determine its structure and functions; therefore, the nucleus is the command center for a cell.

The nucleus is separated from the cytoplasm by a double membrane known as the **nuclear envelope.** Even so, the nucleus communicates with the cytoplasm. The nuclear envelope has **nuclear pores** of sufficient size (100 nm) to permit the passage of ribosomal subunits and mRNA out of the nucleus into the cytoplasm and the passage of proteins from the cytoplasm into the nucleus. High-power electron micrographs show that nonmembranous components associated with the pores form a nuclear pore complex.

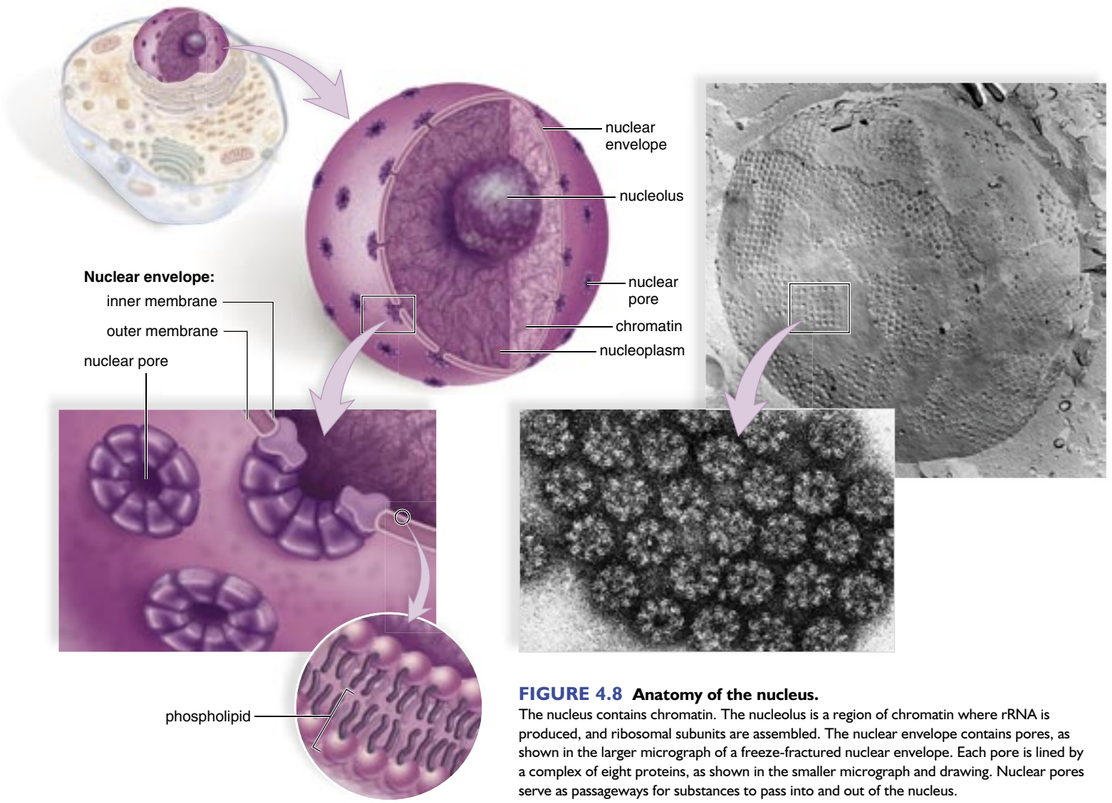


FIGURE 4.8 Anatomy of the nucleus.
The nucleus contains chromatin. The nucleolus is a region of chromatin where rRNA is produced, and ribosomal subunits are assembled. The nuclear envelope contains pores, as shown in the larger micrograph of a freeze-fractured nuclear envelope. Each pore is lined by a complex of eight proteins, as shown in the smaller micrograph and drawing. Nuclear pores serve as passageways for substances to pass into and out of the nucleus.

Ribosomes

Ribosomes are non-membrane-bounded particles where protein synthesis occurs. In eukaryotes, ribosomes are 20 nm by 30 nm, and in prokaryotes they are slightly smaller. In both types of cells, ribosomes are composed of two subunits, one large and one small. Each subunit has its own mix of proteins and rRNA. The number of ribosomes in a cell varies depending on its functions. For example, pancreatic cells and those of other glands have many ribosomes because they produce secretions that contain proteins.

In eukaryotic cells, some ribosomes occur freely within the cytoplasm, either singly or in groups called **polyribosomes,** and others are attached to the endoplasmic reticulum (ER), a membranous system of flattened saccules (small sacs) and tubules, which is discussed more fully on the next page. Ribosomes receive mRNA from the nucleus, and this nucleic acid carries a coded message from DNA indicating the correct sequence of amino acids in a protein. Proteins synthesized by cytoplasmic ribosomes are used in the cytoplasm, and those synthesized by attached ribosomes end up in the ER.

What causes a ribosome to bind to the endoplasmic reticulum? Binding occurs only if the protein being synthesized by a ribosome begins with a signal peptide. The signal peptide binds to a signal recognition particle (SRP), which then binds to an SRP receptor on the endoplasmic reticulum. Once the protein enters the ER, a peptidase cleaves off the signal peptide, and the protein ends up within the lumen (interior) of the ER (Fig. 4.9).

The nucleus is in constant communication with the cytoplasm. The nucleus is the command center of the cell because it contains DNA, the genetic material. DNA, which is located in the chromosomes, specifies the sequence of amino acids in a protein through an intermediary called mRNA. Protein synthesis occurs in the cytoplasm, at the ribosomes, whose subunits are made in the nucleolus. Ribosomes occur singly and in groups (i.e., polyribosomes). Numerous ribosomes become attached to the endoplasmic reticulum.

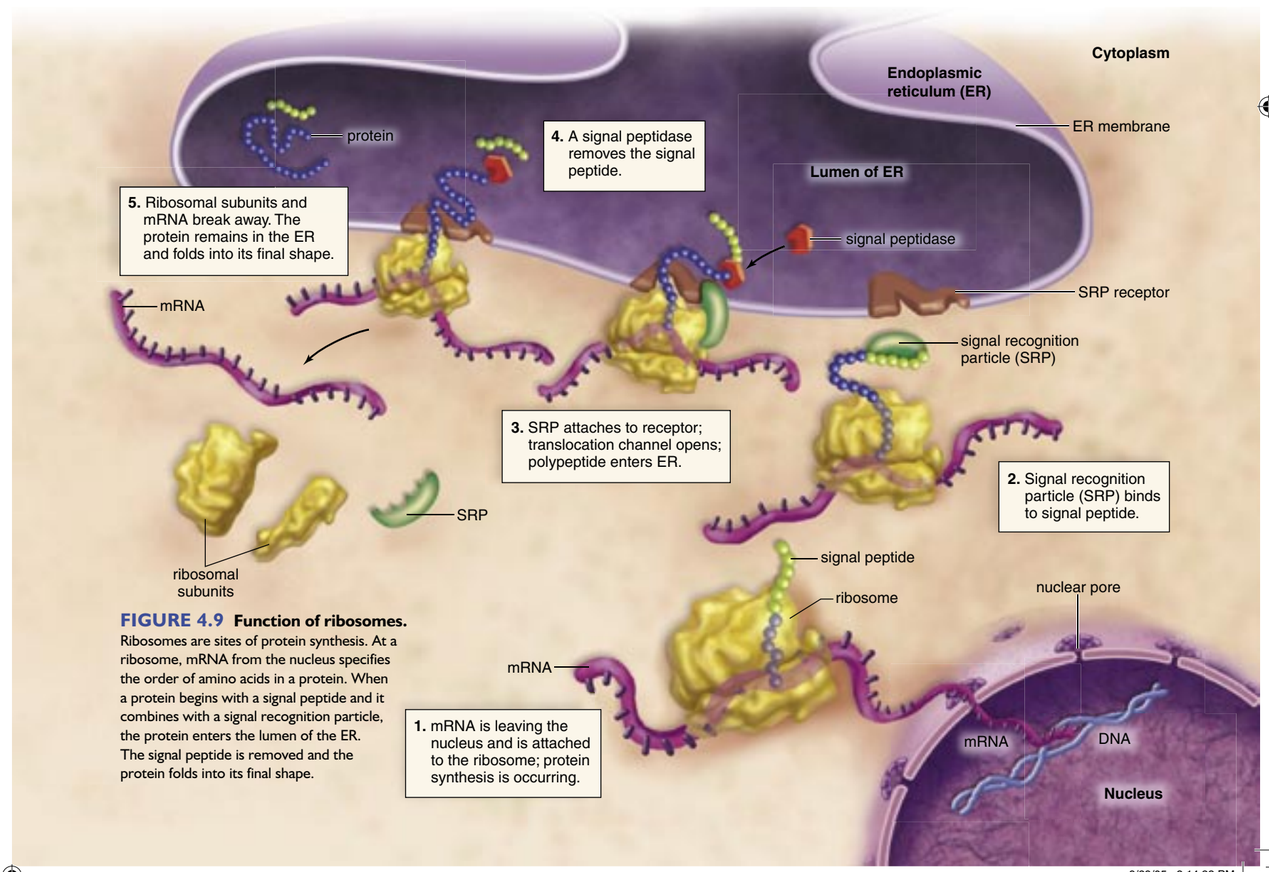


FIGURE 4.9 Function of ribosomes.
Ribosomes are sites of protein synthesis. At a ribosome, mRNA from the nucleus specifies the order of amino acids in a protein. When a protein begins with a signal peptide and it combines with a signal recognition particle, the protein enters the lumen of the ER. The signal peptide is removed and the protein folds into its final shape.

The Endomembrane System

The **endomembrane system** consists of the nuclear envelope, the membranes of the endoplasmic reticulum, the Golgi apparatus, and several types of vesicles. This system compartmentalizes the cell so that particular enzymatic reactions are restricted to specific regions. The vesicles transport molecules from one part of the system to another.

Endoplasmic Reticulum

The **endoplasmic reticulum (ER)** [Gk. *endon,* within; *plasma,* something molded; L. *reticulum,* net], consisting of a complicated system of membranous channels and saccules (flattened vesicles), is physically continuous with the outer membrane of the nuclear envelope (Fig. 4.10). **Rough ER** is studded with ribosomes on the side of the membrane that faces the cytoplasm; therefore, it is correct to say that rough ER synthesizes proteins. It also modifies proteins after they have entered the ER lumen (see Fig. 4.9). Certain ER enzymes add carbohydrate (sugar) chains to proteins, and then these proteins are called glycoproteins. Other proteins assist the folding process that results in the final shape of the protein. The rough ER forms **vesicles** in which large molecules are transported to other parts of the cell. Often these vesicles are on their way to the plasma membrane or the Golgi apparatus.

Smooth ER, which is continuous with rough ER, does not have attached ribosomes. It is more abundant in gland cells, which synthesize lipids, such as phospholipids and steroids. The specific function of smooth ER is dependent on the particular cell. In the testes, it produces testosterone, and in the liver, it helps detoxify drugs. Smooth ER increases in quantity when a person consumes alcohol or takes barbiturates on a regular basis. Regardless of any specialized function, rough and smooth ER also form vesicles that transport molecules to other parts of the cell, notably the Golgi apparatus.

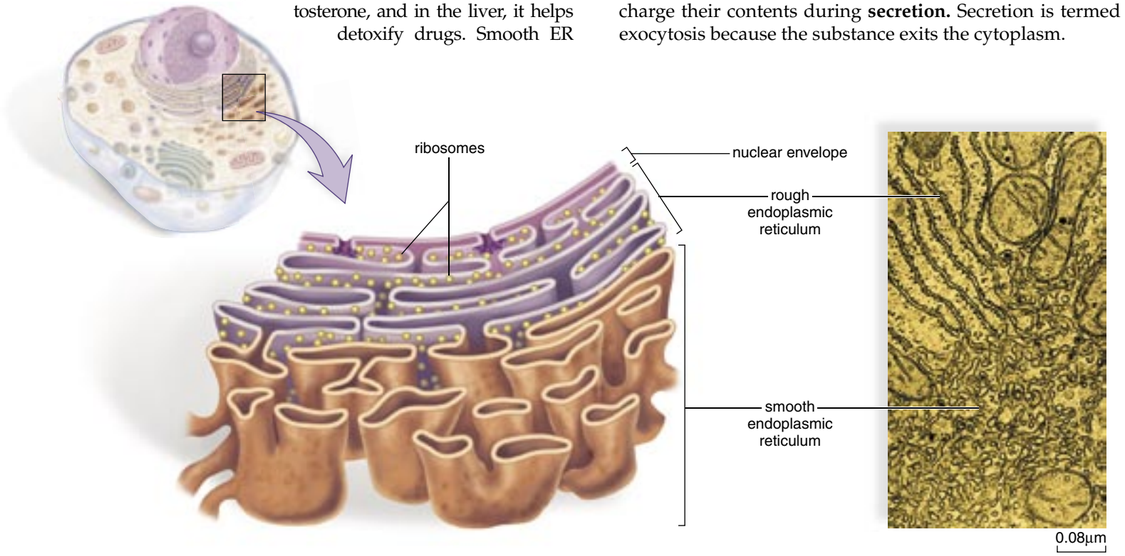


FIGURE 4.10 Endoplasmic reticulum (ER).
Ribosomes are present on rough ER, which consists of flattened saccules, but not on smooth ER, which is more tubular. Proteins are synthesized and modified by rough ER, whereas smooth ER is involved in lipid synthesis, detoxification reactions, and several other possible functions.

The Golgi Apparatus

The **Golgi apparatus** is named for Camillo Golgi, who discovered its presence in cells in 1898. The Golgi apparatus typically consists of a stack of three to twenty slightly curved, flattened saccules whose appearance can be compared to a stack of pancakes (Fig. 4.11). In animal cells, one side of the stack (the cis or inner face) is directed toward the ER, and the other side of the stack (the trans or outer face) is directed toward the plasma membrane. Vesicles can frequently be seen at the edges of the saccules.

Protein-filled vesicles that bud from the rough ER and lipid-filled vesicles that bud from the smooth ER are received by the Golgi apparatus at its inner face. Thereafter, the apparatus alters these substances as they move through its saccules. For example, the Golgi apparatus contains enzymes that modify the carbohydrate chains first attached to proteins in the rough ER. It can change one sugar for another sugar. In some cases, the modified carbohydrate chain serves as a signal molecule that determines the protein's final destination in the cell.

The Golgi apparatus sorts and packages proteins and lipids in vesicles that depart from the outer face. In animal cells, some of these vesicles are lysosomes, which are discussed next. Other vesicles proceed to the plasma membrane, where they become part of the membrane as they discharge their contents during **secretion.** Secretion is termed exocytosis because the substance exits the cytoplasm.

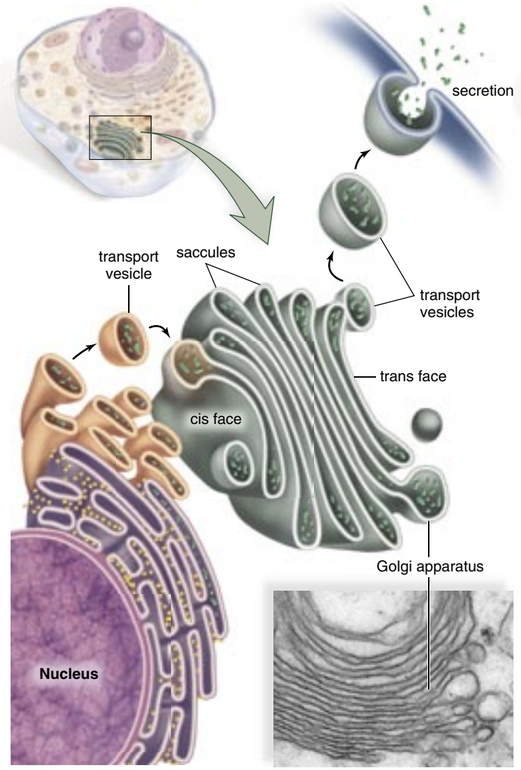


FIGURE 4.11 Golgi apparatus.
The Golgi apparatus is a stack of flattened, curved saccules. It modifies proteins and lipids and packages them in vesicles that distribute these molecules to various locations.

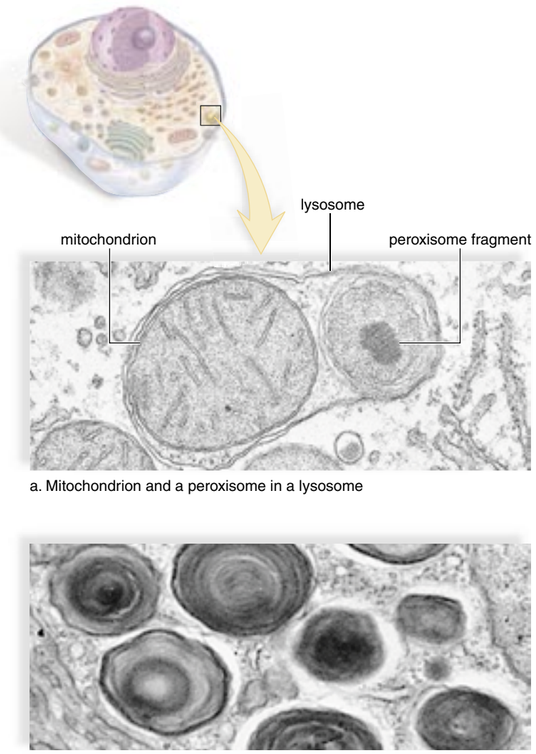


FIGURE 4.12 Lysosomes.
a. Lysosomes, which bud off the Golgi apparatus in cells, are filled with hydrolytic enzymes that digest molecules and parts of the cell. Here a lysosome digests a worn mitochondrion and a peroxisome. **b.** The nerve cells of a person with Tay-Sachs disease are filled with membranous cytoplasmic bodies storing a fat that lysosomes are unable to digest.

Lysosomes

Lysosomes [Gk. *lyo,* loose, and *soma,* body] are membrane-bounded vesicles produced by the Golgi apparatus. They have a very low pH and contain powerful hydrolytic digestive enzymes. Lysosomes are important in recycling cellular material, and destroying nonfunctional organelles and portions of cytoplasm (Fig. 4.12).

Sometimes macromolecules are brought into a cell by vesicle formation at the plasma membrane. When a lysosome fuses with such a vesicle, its contents are digested by lysosomal enzymes into simpler subunits that then enter the cytoplasm. Some white blood cells defend the body by engulfing bacteria that are then enclosed within vesicles. When lysosomes fuse with these vesicles, the bacteria are digested.

A number of human lysosomal storage diseases are due to a missing lysosomal enzyme. In Tay-Sachs disease, the missing enzyme digests a fatty substance that helps insulate nerve cells and increases their efficiency. Because the enzyme is missing, the fatty substance accumulates, literally smothering nerve cells. Affected individuals appear normal at birth but begin to develop neurological problems at four to six months of age. Eventually, the child suffers cerebral degeneration, slow paralysis, blindness, and loss of motor function. Children with Tay-Sachs disease live only about three to four years. In the future, it may be possible to provide the missing enzyme and in that way prevent lysosomal storage diseases.

Lysosomes also participate in **apoptosis,** or programmed cell death, which is a normal part of development. When a tadpole becomes a frog, lysosomes digest away the cells of the tail. The fingers of a human embryo are at first webbed, but they are freed from one another as a result of lysosomal action.

Endomembrane System Summary

We have seen that the endomembrane system is a series of membranous organelles that work together and communicate by means of transport vesicles. The endoplasmic reticulum (ER) and the Golgi apparatus are essentially flattened saccules, and lysosomes are specialized vesicles.

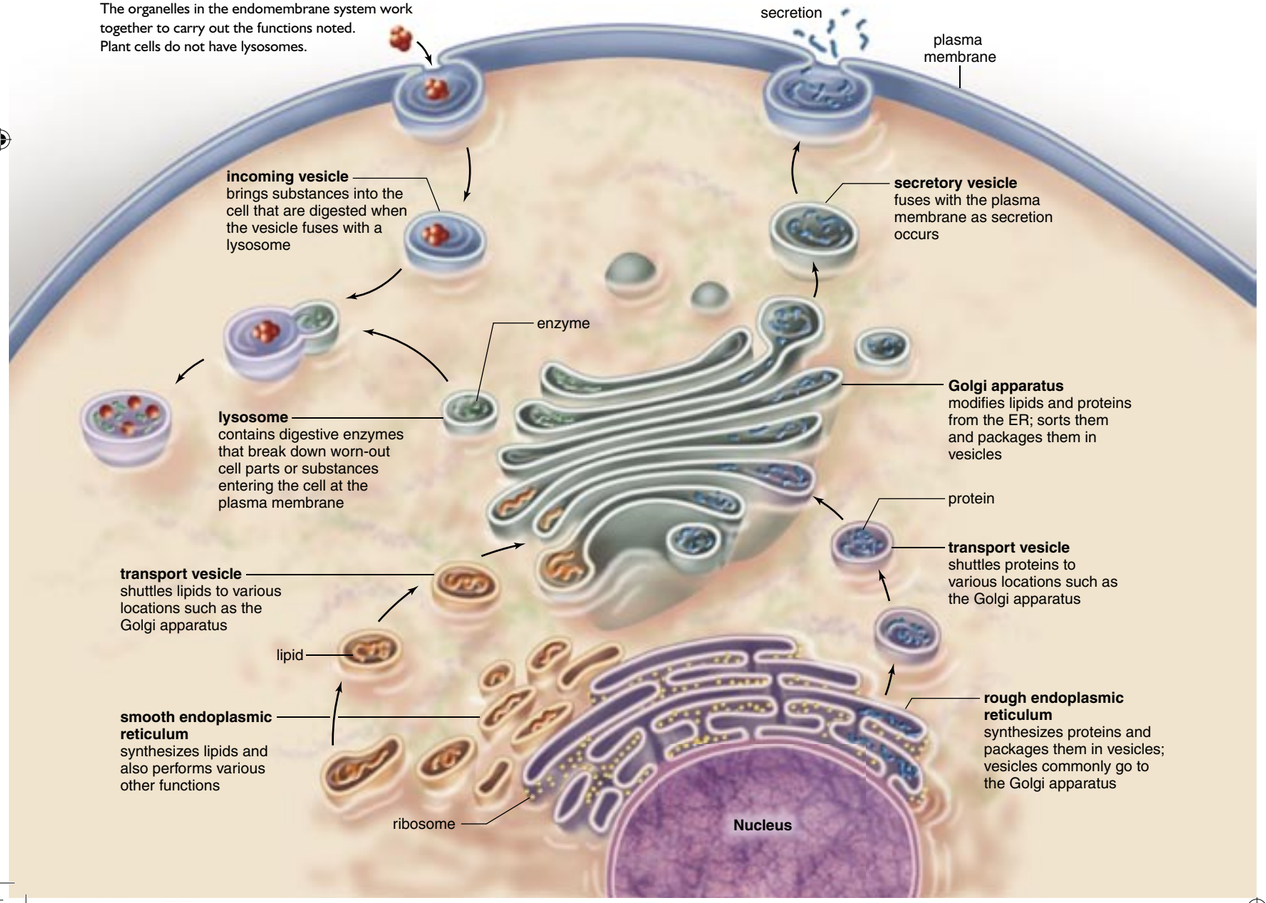
Figure 4.13 shows how the components of the endomembrane system work together. Proteins produced in rough ER and lipids produced in smooth ER are carried in transport vesicles to the Golgi apparatus, where they are further modified before being packaged in vesicles that leave the Golgi. Using signaling sequences, the Golgi apparatus sorts proteins and packages them into vesicles that transport them to various cellular destinations. Secretory vesicles take the proteins to the plasma membrane, where they exit the cell when the vesicles fuse with the membrane. This is called secretion by exocytosis. For example, secretion into ducts occurs when the mammary glands produce milk or the pancreas produces digestive enzymes.

In animal cells, the Golgi apparatus also produces specialized vesicles called lysosomes that contain hydrolytic enzymes. Lysosomes fuse with incoming vesicles from the plasma membrane and digest macromolecules and/or even debris brought into a certain cell. White blood cells are well known for engulfing pathogens (e.g., disease-causing viruses and bacteria) that are then broken down in lysosomes.

The organelles of the endomembrane system are as follows:

Endoplasmic reticulum (ER): series of tubules and saccules
Rough ER: ribosomes are present
Smooth ER: ribosomes are not present
Golgi apparatus: stack of curved saccules
Lysosomes: specialized vesicles
Vesicles: membranous sacs

FIGURE 4.13 Endomembrane system.
The organelles in the endomembrane system work together to carry out the functions noted. Plant cells do not have lysosomes.



Peroxisomes and Vacuoles

Peroxisomes and the vacuoles of cells do not communicate with the organelles of the endomembrane system and therefore are not part of it.

Peroxisomes

Peroxisomes, similar to lysosomes, are membrane-bounded vesicles that enclose enzymes. However, the enzymes in peroxisomes are synthesized by free ribosomes and transported into a peroxisome from the cytoplasm. All peroxisomes contain enzymes whose action results in hydrogen peroxide (H_2O_2).

$$RH_2 + O_2 \longrightarrow R + H_2O_2$$

Hydrogen peroxide, a toxic molecule, is immediately broken down to water and oxygen by another peroxisomal enzyme called catalase. When hydrogen peroxide is applied to a wound, bubbling occurs as peroxisomal enzymes break it down.

The enzymes in a peroxisome depend on the function of a particular cell. However, peroxisomes are especially prevalent in cells that are synthesizing and breaking down lipids. In the liver, some peroxisomes produce bile salts from cholesterol, and others break down fats. In a 1992 movie *Lorenzo's Oil,* the peroxisomes in a boy's cells lack a membrane protein needed to import a specific enzyme from the cytoplasm. As a result, long chain fatty acids accumulate in his brain, and he suffers neurological damage. This disorder is known as adrenoleukodystrophy.

Plant cells also have peroxisomes (Fig. 4.14). In germinating seeds, they oxidize fatty acids into molecules that can be converted to sugars needed by the growing plant. In leaves, peroxisomes can carry out a reaction that is opposite to photosynthesis—the reaction uses up oxygen and releases carbon dioxide.

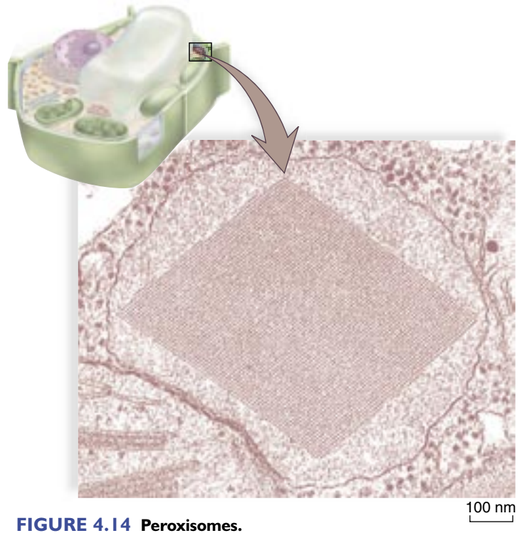


FIGURE 4.14 Peroxisomes.
Peroxisomes contain one or more enzymes that can oxidize various organic substances. Peroxisomes also contain the enzyme catalase, which breaks down hydrogen peroxide (H_2O_2), which builds up after organic substances are oxidized.

Vacuoles

Like vesicles, **vacuoles** are membranous sacs, but vacuoles are larger than vesicles. The vacuoles of some protists are quite specialized; they include contractile vacuoles for ridding the cell of excess water and digestive vacuoles for breaking down nutrients. Vacuoles usually store substances. Plant vacuoles contain not only water, sugars, and salts but also water-soluble pigments and toxic molecules. The pigments are responsible for many of the red, blue, or purple colors of flowers and some leaves. The toxic substances help protect a plant from herbivorous animals.

Plant Cell Central Vacuole. Typically, plant cells have a large **central vacuole** that may take up to 90% of the volume of the cell. The vacuole is filled with a watery fluid called cell sap that gives added support to the cell (Fig. 4.15). Animals must produce more cytoplasm, including organelles, in order to grow, but a plant cell can rapidly increase in size by enlarging its vacuole. Eventually, a plant cell also produces more cytoplasm. The central vacuole maintains hydrostatic pressure or turgor pressure in plant cells.

The central vacuole functions in storage of both nutrients and waste products. A system to excrete wastes never evolved in plants; instead, metabolic waste products are pumped across the vacuole membrane and stored permanently in the central vacuole. As organelles age and become nonfunctional, they fuse with the vacuole, where digestive enzymes break them down. This is a function carried out by lysosomes in animal cells.

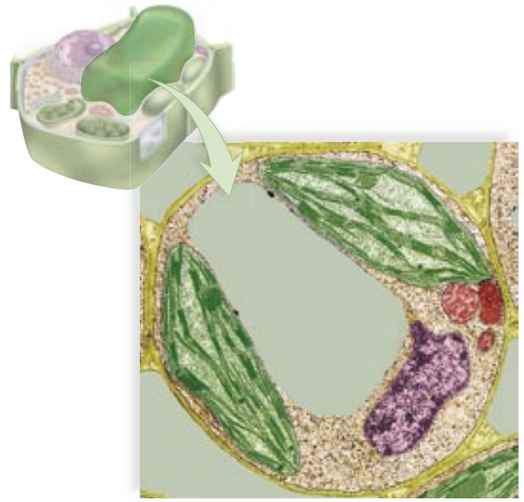


FIGURE 4.15 Plant cell central vacuole.
The large central vacuole of plant cells has numerous functions, from storing molecules to helping the cell increase in size.

Energy-Related Organelles

Life is possible only because a constant input of energy maintains the structure of cells. Chloroplasts and mitochondria are the two eukaryotic membranous organelles that specialize in converting energy to a form that can be used by the cell. **Chloroplasts** use solar energy to synthesize carbohydrates, and carbohydrate-derived products are broken down in **mitochondria** (sing., mitochondrion) to produce ATP molecules. *Photosynthesis,* which usually occurs in chloroplasts [Gk. *chloros,* green, and *plastos,* formed, molded], is the process by which solar energy is converted to chemical energy within carbohydrates. Photosynthesis can be represented by this equation:

$$\text{solar energy} + \text{carbon dioxide} + \text{water} \rightarrow \text{carbohydrate} + \text{oxygen}$$

Plants, algae, and cyanobacteria are capable of carrying on photosynthesis in this manner, but only plants and algae have chloroplasts.

Cellular respiration is the process by which the chemical energy of carbohydrates is converted to that of ATP (adenosine triphosphate). Cellular respiration can be represented by this equation:

$$\text{carbohydrate} + \text{oxygen} \rightarrow \text{carbon dioxide} + \text{water} + \text{energy}$$

Here the word *energy* stands for ATP molecules. When a cell needs energy, ATP supplies it. The energy of ATP is used for synthetic reactions, active transport, and all energy-requiring processes in cells. In eukaryotes, mitochondria are necessary to the process of cellular respiration, which produces ATP.

Chloroplasts

Chloroplasts are a type of **plastid**, plant and algal organelles that are bounded by a double membrane and contain a series of internal membranes and/or vesicles. Plastids have DNA and are produced by division of existing plastids. Chloroplasts contain chlorophyll and carry on photosynthesis, while the other types of plastids have a storage function.

Some algal cells have only one chloroplast, while some plant cells have as many as a hundred. Chloroplasts can be quite large, being twice as wide and as much as five times the length of a mitochondrion. Their structure is shown in Figure 4.16. The double membrane encloses a large space called the **stroma,** which contains **thylakoids,** disklike sacs formed from a third chloroplast membrane. A stack of thylakoids is a **granum.** The lumens of the thylakoids are believed to form a large internal compartment called the thylakoid space. Chlorophyll and the other pigments that capture solar energy are located in the thylakoid membrane, and the enzymes that synthesize carbohydrates are located outside the thylakoid in the fluid of the stroma.

The structure of chloroplasts and the discovery that chloroplasts also have their own DNA and ribosomes support the endosymbiotic hypothesis that chloroplasts are derived from cyanobacteria that entered a eukaryotic cell. It cannot be said too often that, as shown in Figure 4.5, plant and algal cells contain both mitochondria and chloroplasts.

Other Types of Plastids. Other plastids are different from chloroplasts in color, form, and function. **Chromoplasts** contain pigments that result in a yellow, orange, or red color. Chromoplasts are responsible for the color of autumn leaves, fruits, carrots, and some flowers. **Leucoplasts** are generally colorless plastids that synthesize and store starches and oils. A microscopic examination of potato tissue yields a number of leucoplasts.

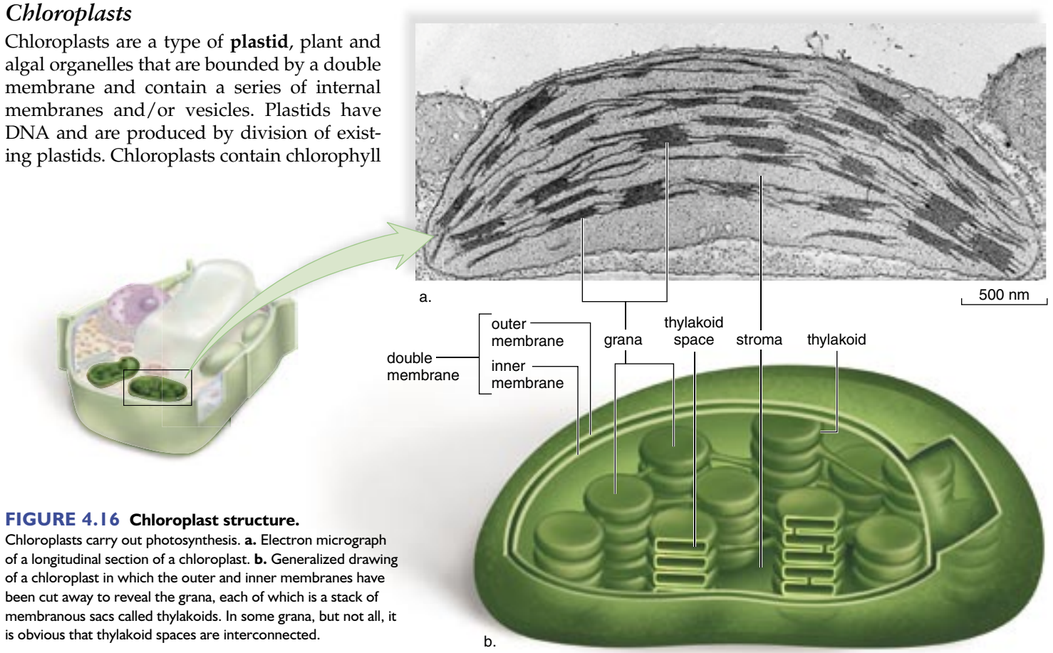


FIGURE 4.16 Chloroplast structure.
Chloroplasts carry out photosynthesis. **a.** Electron micrograph of a longitudinal section of a chloroplast. **b.** Generalized drawing of a chloroplast in which the outer and inner membranes have been cut away to reveal the grana, each of which is a stack of membranous sacs called thylakoids. In some grana, but not all, it is obvious that thylakoid spaces are interconnected.

Mitochondria

Even though mitochondria are smaller than chloroplasts, they can be seen in some cells by using a light microscope. The number of mitochondria can vary in cells depending on their activity. Some cells such as liver cells may have as many as 1,000 mitochondria. We think of mitochondria as having a shape like that shown in Figure 4.17, but actually they often change shape to be longer and thinner or shorter and broader. Mitochondria can form long, moving chains, or they can remain fixed in one location—often where energy is most needed. For example, they are packed between the contractile elements of cardiac cells and wrapped around the interior of a sperm's flagellum.

Mitochondria have two membranes, the outer membrane and the inner membrane. The inner membrane is highly convoluted into **cristae** that project into the matrix. These cristae increase the surface area of the inner membrane so much that in a liver cell they account for about one-third the total membrane in the cell. The inner membrane encloses a **matrix,** which contains mitochondrial DNA and ribosomes. The presence of a double membrane and mitochondrial genes is consistent with the endosymbiotic hypothesis regarding the origin of mitochondria, which was illustrated in Fig. 4.5. This figure suggests that mitochondria are derived from bacteria that took up residence in an early eukaryotic cell.

Mitochondria are often called the powerhouses of the cell because they produce most of the ATP used by the cell through cellular respiration. Cell fractionation and centrifugation, which is described in the Science Focus on page 65, allowed investigators to separate the inner membrane, the outer membrane, and the matrix from each other. Then they discovered that the matrix is a highly concentrated mixture of enzymes that break down carbohydrates and other nutrient molecules. These reactions supply the chemical energy that permits a chain of proteins on the inner membrane to create the conditions that allow ATP synthesis to take place. The entire process, which also involves the cytoplasm, is called cellular respiration because oxygen is used and carbon dioxide is given off, as shown on the previous page.

Mitochondrial Diseases. So far, more than 40 different mitochondrial diseases that affect the brain, muscles, kidneys, heart, liver, eyes, ears, or pancreas have been identified. The common factor among these genetic diseases is that the patient's mitochondria are unable to completely metabolize organic molecules to produce ATP. As a result, toxins accumulate inside the mitochondria and the body. The toxins can be free radicals (sustances that readily form harmful compounds when they react with other molecules), and they damage mitochondria over time. In the United States, between 1,000 and 4,000 children per year are born with a mitochondrial disease. In addition, it is possible that many diseases of aging are due to malfunctioning mitochondria.

Chloroplasts and mitochondria are organelles that transform energy. Chloroplasts capture solar energy and produce carbohydrates. Mitochondria convert the energy within carbohydrates to that of ATP molecules.

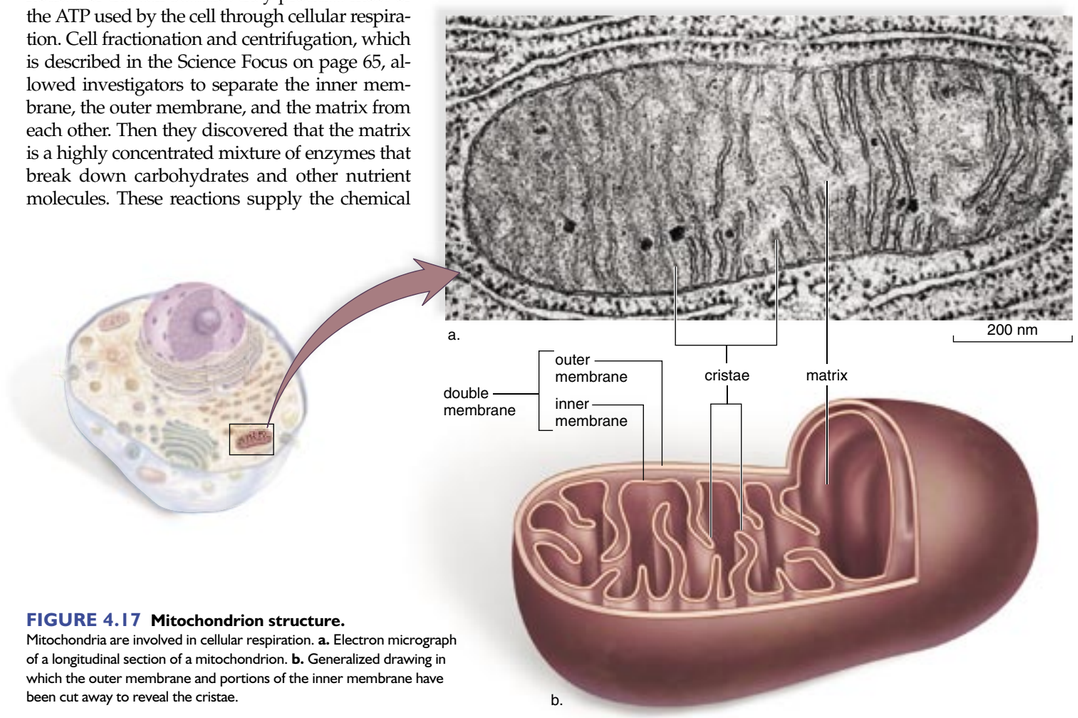


FIGURE 4.17 Mitochondrion structure.
Mitochondria are involved in cellular respiration. **a.** Electron micrograph of a longitudinal section of a mitochondrion. **b.** Generalized drawing in which the outer membrane and portions of the inner membrane have been cut away to reveal the cristae.

The Cytoskeleton

The protein components of the **cytoskeleton** [Gk. *kytos,* cell, and *skeleton,* dried body] interconnect and extend from the nucleus to the plasma membrane in eukaryotic cells. Prior to the 1970s, it was believed that the cytoplasm was an unorganized mixture of organic molecules. Then, high-voltage electron microscopes, which can penetrate thicker specimens, showed instead that the cytoplasm was instead highly organized. The technique of immunofluorescence microscopy identified the makeup of the protein components within the cytoskeletal network (Fig. 4.18).

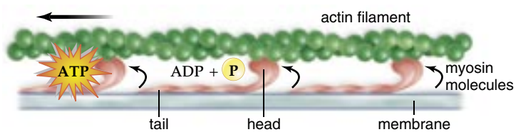
The cytoskeleton contains actin filaments, intermediate filaments, and microtubules, which maintain cell shape and allow the cell and its organelles to move. Therefore, the cytoskeleton is often compared to the bones and muscles of an animal. However, the cytoskeleton is dynamic, especially because its protein components can assemble and disassemble as appropriate. Apparently a number of different mechanisms regulate this process, including protein kinases that phosphorylate proteins. Phosphorylation leads to disassembly, and dephosphorylation causes assembly.

Actin Filaments

Actin filaments (formerly called microfilaments) are long, extremely thin, flexible fibers (about 7 nm in diameter) that occur in bundles or meshlike networks. Each actin filament contains two chains of globular actin monomers twisted about one another in a helical manner.

Actin filaments play a structural role when they form a dense, complex web just under the plasma membrane, to which they are anchored by special proteins. They are also seen in the microvilli that project from intestinal cells, and their presence most likely accounts for the ability of microvilli to alternately shorten and extend into the intestine. In plant cells, actin filaments apparently form the tracks along which chloroplasts circulate in a particular direction; doing so is called cytoplasmic streaming. Also, the presence of a network of actin filaments lying beneath the plasma membrane accounts for the formation of **pseudopods** (false feet), extensions that allow certain cells to move in an amoeboid fashion.

How are actin filaments involved in the movement of the cell and its organelles? They interact with **motor molecules,** which are proteins that can attach, detach, and reattach farther along an actin filament. In the presence of ATP, the motor molecule myosin pulls actin filaments along in this way. Myosin has both a head and a tail. In muscle cells, the tails of several muscle myosin molecules are joined to form a thick filament. In nonmuscle cells, cytoplasmic myosin tails are bound to membranes, but the heads still interact with actin:



During animal cell division, the two new cells form when actin, in conjunction with myosin, pinches off the cells from one another.

Intermediate Filaments

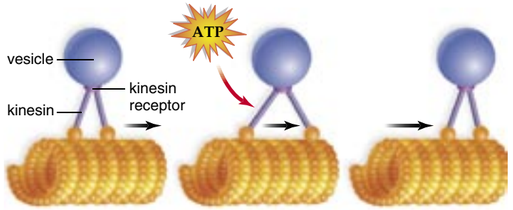
Intermediate filaments (8–11 nm in diameter) are intermediate in size between actin filaments and microtubules. They are a ropelike assembly of fibrous polypeptides, but the specific type varies according to the tissue. Some intermediate filaments support the nuclear envelope, whereas others support the plasma membrane and take part in the formation of cell-to-cell junctions. In the skin, intermediate filaments, made of the protein keratin, give great mechanical strength to skin cells. We now know that intermediate filaments are also highly dynamic and will disassemble when phosphate is added by a kinase.

Microtubules

Microtubules [Gk. *mikros,* small, little; L. *tubus,* pipe] are small, hollow cylinders about 25 nm in diameter and from 0.2–25 μm in length.

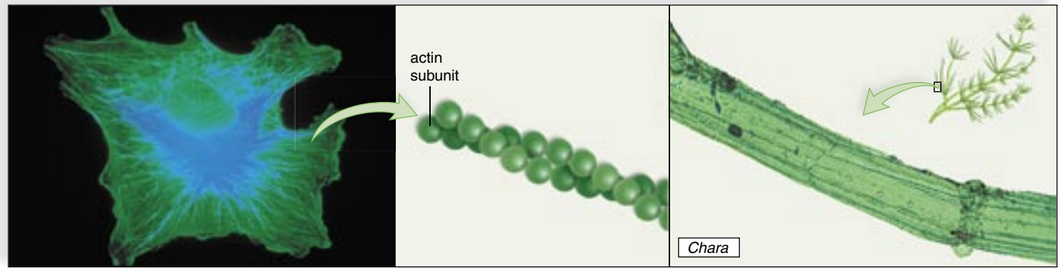
Microtubules are made of a globular protein called tubulin, which is of two types called α and β. There is a slightly different amino acid sequence in α tubulin compared to β tubulin. When assembly occurs, α and β tubulin molecules come together as dimers, and the dimers arrange themselves in rows. Microtubules have 13 rows of tubulin dimers, surrounding what appears in electron micrographs to be an empty central core.

The regulation of microtubule assembly is under the control of a microtubule organizing center (MTOC). In most eukaryotic cells, the main MTOC is in the **centrosome** [Gk. *centrum,* center, and *soma,* body], which lies near the nucleus. Microtubules radiate from the centrosome, helping to maintain the shape of the cell and acting as tracks along which organelles can move. Whereas the motor molecule myosin is associated with actin filaments, the motor molecules kinesin and dynein are associated with microtubules:

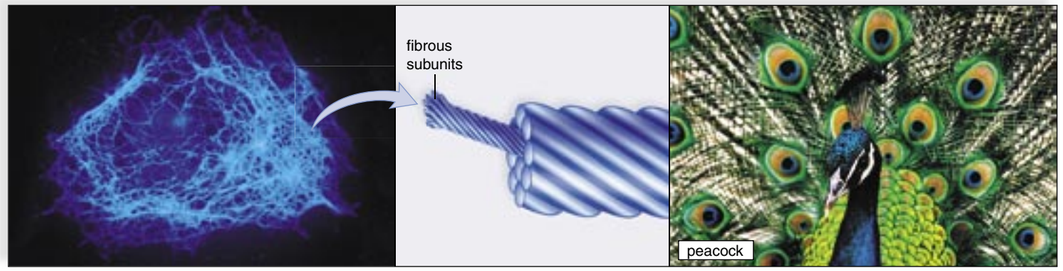


vesicle moves, not microtubule

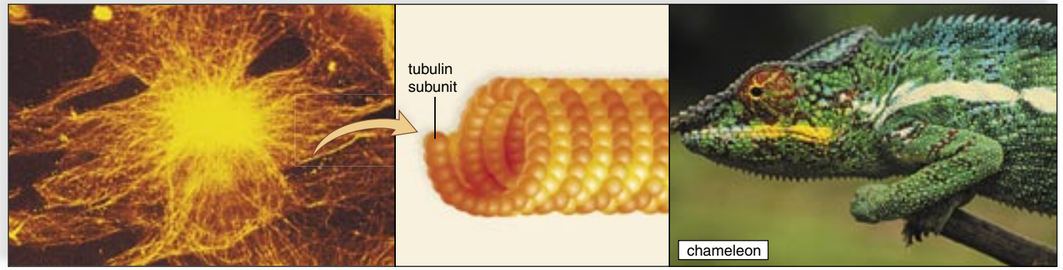
There are different types of kinesin proteins, each specialized to move one kind of vesicle or cellular organelle. Kinesin moves vesicles or organelles in an opposite direction from dynein. Cytoplasmic dynein is closely related to the molecule dynein found in flagella.



a. Actin filaments



b. Intermediate filaments



c. Microtubules

FIGURE 4.18 The cytoskeleton.
The cytoskeleton maintains the shape of the cell and allows its parts to move. Three types of protein components make up the cytoskeleton. They can be detected in cells by using a special fluorescent technique that detects only one type of component at a time. **a.** *Left to right:* Fibroblasts in animal tissue have been treated so that actin filaments can be microscopically detected; the drawing shows that actin filaments are composed of a twisted double chain of actin subunits. The giant cells of the green alga *Chara* rely on actin filaments to move organelles from one end of the cell to another. **b.** *Left to right:* Fibroblasts in an animal tissue have been treated so that intermediate filaments can be microscopically detected; the drawing shows that fibrous proteins account for the ropelike structure of intermediate filaments. A peacock's colorful feathers are strengthened by the presence of intermediate filaments. **c.** *Left to right:* Fibroblasts in an animal tissue have been treated so that microtubules can be microscopically detected; the drawing shows that microtubules are hollow tubes composed of tubulin subunits. The skin cells of a chameleon rely on microtubules to move pigment granules around so that they can take on the color of their environment.

Before a cell divides, microtubules disassemble and then reassemble into a structure called a spindle that distributes chromosomes in an orderly manner. At the end of cell division, the spindle disassembles, and microtubules reassemble once again into their former array. In the arms race between plants and herbivores, plants have evolved various types of poisons that prevent them from being eaten. Colchicine is a plant poison that binds tubulin and blocks the assembly of microtubules.

> The cytoskeleton is an internal skeleton composed of actin filaments, intermediate filaments, and microtubules that maintain the shape of the cell and assist movement of its parts.

Centrioles

Centrioles [Gk. *centrum,* center] are short cylinders with a 9 + 0 pattern of microtubule triplets—that is, a ring having nine sets of triplets with none in the middle. In animal cells and most protists, a centrosome contains two centrioles lying at right angles to each other. A centrosome, as mentioned previously, is the major microtubule-organizing center for the cell. Therefore, it is possible that centrioles are also involved in the process by which microtubules assemble and disassemble.

Before an animal cell divides, the centrioles replicate, and the members of each pair are at right angles to one another (Fig. 4.19). Then each pair becomes part of a separate centrosome. During cell division, the centrosomes move apart and most likely function to organize the mitotic spindle. In any case, each new cell has its own centrosome and pair of centrioles. Plant and fungal cells have the equivalent of a centrosome, but this structure does not contain centrioles, suggesting that centrioles are not necessary to the assembly of cytoplasmic microtubules.

In cells with cilia and flagella, centrioles are believed to give rise to **basal bodies** that direct the organization of microtubules within these structures. In other words, a basal body may do for a cilium or flagellum what the centrosome does for the cell.

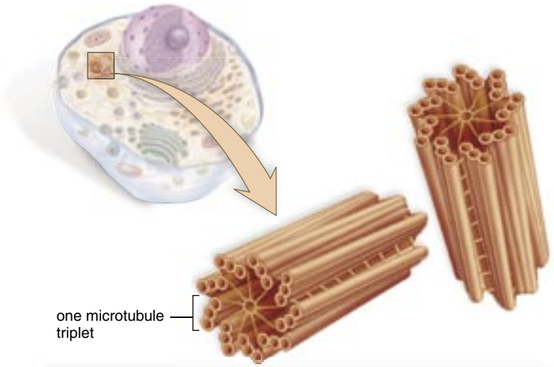


FIGURE 4.19 Centrioles.
In a nondividing animal cell, there is a single pair of centrioles in the centrosome located just outside the nucleus. Just before a cell divides, the centrioles replicate, producing two pairs of centrioles. During cell division, centrioles in their respective centrosomes separate so that each new cell has one centrosome containing one pair of centrioles.

Centrioles, which are short cylinders with a 9 + 0 pattern of microtubule triplets, may give rise to the basal bodies of cilia and flagella.

Cilia and Flagella

Cilia [L. *cilium,* eyelash, hair] and **flagella** [L. *flagello,* whip] are hairlike projections that can move either in an undulating fashion, like a whip, or stiffly, like an oar. Cells that have these organelles are capable of movement. For example, unicellular paramecia move by means of cilia, whereas sperm cells move by means of flagella. The cells that line our upper respiratory tract have cilia that sweep debris trapped within mucus back up into the throat, where it can be swallowed. This action helps keep the lungs clean.

In eukaryotic cells, cilia are much shorter than flagella, but they have a similar construction. Both are membrane-bounded cylinders enclosing a matrix area. In the matrix are nine microtubule doublets arranged in a circle around two central microtubules; this is called the 9 + 2 pattern of microtubules (Fig. 4.20). Cilia and flagella move when the microtubule doublets slide past one another.

As mentioned, each cilium and flagellum has a basal body lying in the cytoplasm at its base. Basal bodies have the same circular arrangement of microtubule triplets as centrioles and are believed to be derived from them. It is possible that basal bodies organize the microtubules within cilia and flagella, but this is not supported by the observation that cilia and flagella grow by the addition of tubulin dimers to their tips.

Cilia and flagella, which have a 9 + 2 pattern of microtubules, are involved in the movement of cells.

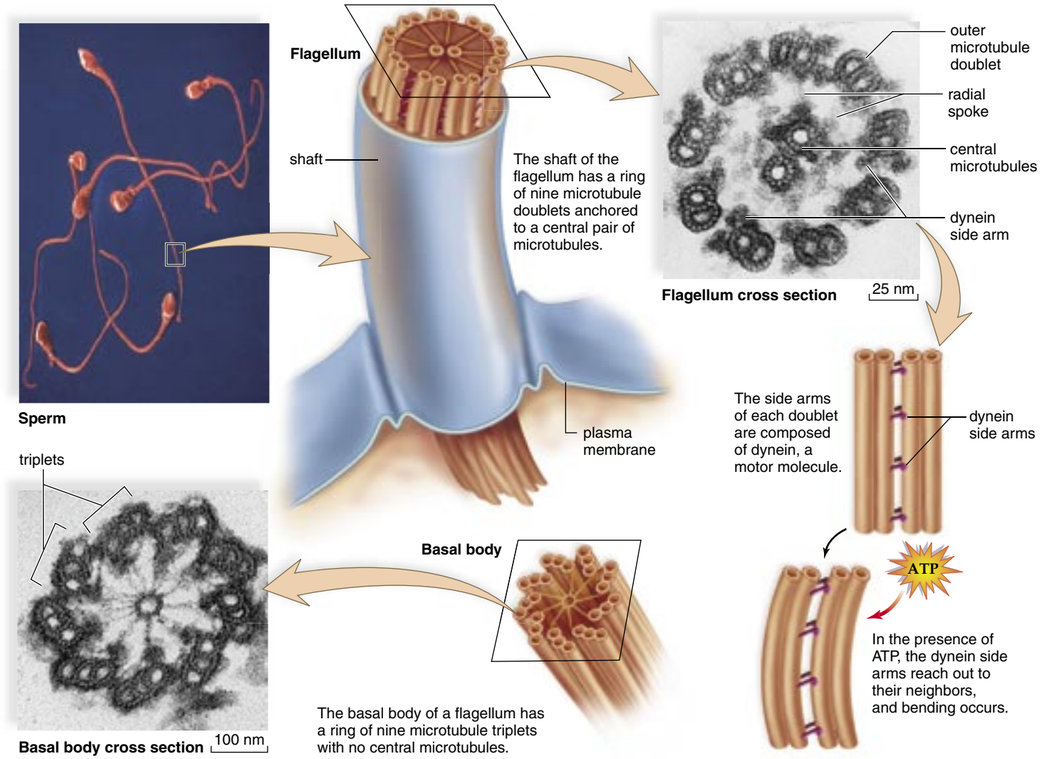


FIGURE 4.20 Structure of a flagellum.
A flagellum has a basal body with a 9 + 0 pattern of microtubule triplets. (Notice the ring of nine triplets, with no central microtubules.) The shaft of the flagellum has a 9 + 2 pattern (a ring of nine microtubule doublets surrounds a central pair of microtubules). Compare the cross section of the basal body to the cross section of the flagellum shaft, and note that in place of the third microtubule, a flagellum's outer doublets have side arms of dynein, a motor molecule. In the presence of ATP, the dynein side arms reach out and attempt to move along their neighboring doublet. Because of the radial spokes connecting the doublets to the central microtubules, bending occurs.

CONNECTING THE CONCEPTS

Cell biology is fundamental to the other fields of biology studied in this text. Many of the organelles of a cell are involved in producing, modifying, and transporting proteins. Each type of cell is characterized by the presence of particular proteins, which are specified by active genes in that cell. The process of protein synthesis makes cell biology directly applicable to the field of genetics, which is the topic of the next part in this text.

Next, we will study the classification of living things, which is dependent on cell type. The organisms in two domains—domain Archaea and domain Bacteria—have prokaryotic cells. The organisms in domain Eukarya—the protists, fungi, plants, and animals—have eukaryotic cells. We will learn that differences in DNA (and RNA) base sequences resulted in recognition of these three domains and that classification based on DNA base sequences are increasingly influencing classification, even down to the species level.

The evolution of life began with the first cell or cells, and we will study how the evolution of the eukaryotic cell led to multicellularity and the forms of life with which we are the most familiar. Without genetic and, consequently, cellular protein changes, adaptations to the environment that resulted in the diversity of life on our planet would never have occurred. In addition to structural differences, DNA sequence data are now helping us trace the relatedness of organisms through time.

Knowledge of the anatomy and physiology of organisms is based on understanding the structure and function of the cells making up different organs. This is never more apparent than in the field of medicine. Almost any human illness can be traced back to malfunctioning cells and metabolic processes that involve cellular enzymes.

This text concludes with ecology, and you might think that cell biology is not pertinent to ecology. However, preservation of organisms within an ecosystem is dependent in part on our knowledge of how the cells of organisms are affected by environmental pollutants. This leads us back to the necessity of understanding the structure and function of cells.

Summary

4.1 CELLULAR LEVEL OF ORGANIZATION

All organisms are composed of cells, the smallest units of living matter. Cells are capable of self-reproduction, and existing cells come only from preexisting cells. Cells are very small and are measured in micrometers. The plasma membrane regulates exchange of materials between the cell and the external environment. Cells must remain small in order to have an adequate amount of surface area to volume.

4.2 PROKARYOTIC CELLS

There are two major groups of prokaryotic cells: the bacteria and the archaea. Prokaryotic cells lack the nucleus of eukaryotic cells. The cell envelope of bacteria includes a plasma membrane, a cell wall, and an outer glycocalyx. The cytoplasm contains ribosomes, inclusion bodies, and a nucleoid that is not bounded by a nuclear envelope. The cytoplasm of cyanobacteria also includes thylakoids. The appendages of a bacterium are the flagella, the fimbriae, and the sex pili.

4.3 EUKARYOTIC CELLS

Eukaryotic cells are much larger than prokaryotic cells, but they are compartmentalized by the presence of organelles, each with a specific structure and function (Table 4.1). The nuclear envelope most likely evolved through invagination of the plasma membrane, but mitochondria and chloroplasts may have arisen when a eukaryotic cell took up bacteria and algae in separate events. Perhaps this accounts for why the mitochondria and chloroplasts function independently. Other membranous organelles are in constant communication by way of transport vesicles.

The nucleus of eukaryotic cells is bounded by a nuclear envelope containing pores. These pores serve as passageways between the cytoplasm and the nucleoplasm. Within the nucleus, chromatin, which contains DNA, undergoes coiling into chromosomes at the time of cell division. The nucleolus is a special region of the chromatin where rRNA is produced and ribosomal subunits are formed.

Ribosomes are organelles that function in protein synthesis. When protein synthesis occurs, mRNA leaves the nucleus with a coded message from DNA that specifies the sequence of amino acids in that protein. After mRNA attaches to a ribosome, it binds to the ER if it has a signal peptide. The signal peptide attaches to a signal recognition particle that, in turn, binds to an SRP receptor on the ER. When completed, the protein enters the lumen of the ER.

The endomembrane system includes the ER (both rough and smooth), the Golgi apparatus, the lysosomes (in animal cells), and transport vesicles. Newly produced proteins are modified in the ER before they are packaged in transport vesicles, many of which go to the Golgi apparatus. The smooth ER has various metabolic functions, depending on the cell type, but it also forms vesicles that carry lipids to different locations, particularly to the Golgi apparatus. The Golgi apparatus modifies, sorts, and repackages proteins. Some proteins are packaged into lysosomes, which carry out intracellular digestion, or into vesicles that fuse with the plasma membrane. Following fusion, secretion occurs.

Cells require a constant input of energy to maintain their structure. Chloroplasts capture the energy of the sun and carry on photosynthesis, which produces carbohydrates. Carbohydrate-derived products are broken down in mitochondria as ATP is produced. This is an oxygen-requiring process called cellular respiration.

The cytoskeleton contains actin filaments, intermediate filaments, and microtubules. These maintain cell shape and allow it and the organelles to move. Actin filaments, the thinnest filaments, interact with the motor molecule myosin in muscle cells to bring about contraction; in other cells, they pinch off daughter cells and have other dynamic functions. Intermediate filaments support the nuclear envelope and the plasma membrane and probably participate in cell-to-cell junctions. Microtubules radiate out from the centrosome and are present in centrioles, cilia, and flagella. They serve as tracks along which vesicles and other organelles move, due to the action of specific motor molecules.

TABLE 4.1

Comparison of Prokaryotic Cells and Eukaryotic Cells

	Prokaryotic Cells	*Eukaryotic Cells*	
		Animal	*Plant*
Size	*Smaller (1–20 μm in diameter)*	*Larger (10–100 μm in diameter)*	
Cell wall	Usually (peptidoglycan)	No	Yes (cellulose)
Plasma membrane	Yes	Yes	Yes
Nucleus	No	Yes	Yes
Nucleolus	No	Yes	Yes
Ribosomes	Yes (smaller)	Yes	Yes
Endoplasmic reticulum	No	Yes	Yes
Golgi apparatus	No	Yes	Yes
Lysosomes	No	Yes	No
Mitochondria	No	Yes	Yes
Chloroplasts	No	No	Yes
Peroxisomes	No	Usually	Usually
Cytoskeleton	No	Yes	Yes
Centrioles	No	Yes	No
9 + 2 cilia or flagella	No	Often	No (in flowering plants) Yes (sperm of bryophytes, ferns, and cycads)

Reviewing the Chapter

1. What are the three basic principles of the cell theory? 58
2. Why is it advantageous for cells to be small? 59
3. Roughly sketch a bacterial (prokaryotic) cell, label its parts, and state a function for each of these. 63
4. How do eukaryotic and prokaryotic cells differ? 64
5. Describe how the nucleus, the chloroplast, and the mitochondrion may have become a part of the eukaryotic cell. 64
6. What does it mean to say that the eukaryotic cell is compartmentalized? 64–65
7. Describe the structure and the function of the nuclear envelope and the nuclear pores. 68
8. Distinguish between the nucleolus, rRNA, and ribosomes. 68–69
9. Name organelles that are a part of the endomembrane system and explain the term. 70
10. Trace the path of a protein from rough ER to the plasma membrane. 72
11. Give the overall equations for photosynthesis and cellular respiration, contrast the two, and tell how they are related. 74
12. Describe the structure and function of chloroplasts and mitochondria. How are these two organelles related to one another? 74–75
13. What are the three components of the cytoskeleton? What are their structures and functions? 76–77
14. Relate the structure of flagella (and cilia) to centrioles, and discuss the function of both. 78–79

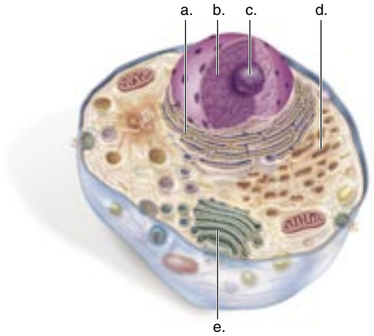
Testing Yourself

Choose the best answer for each question.

1. The small size of cells best correlates with
   a. the fact that they are self-reproducing.
   b. their prokaryotic versus eukaryotic nature.
   c. an adequate surface area for exchange of materials.
   d. the fact that they come in multiple sizes.
   e. All of these are correct.
2. Which of these is not a true comparison of the compound light microscope and the transmission electron microscope?

	LIGHT	**ELECTRON**
a.	Uses light to "view" object	Uses electrons to "view" object
b.	Uses glass lenses for focusing	Uses magnetic lenses for focusing
c.	Specimen must be killed and stained	Specimen may be alive and nonstained
d.	Magnification is not as great	Magnification is greater
e.	Resolution is not as great	Resolution is greater

3. Which of these best distinguishes a prokaryotic cell from a eukaryotic cell?
   a. Prokaryotic cells have a cell wall, but eukaryotic cells never do.
   b. Prokaryotic cells are much larger than eukaryotic cells.
   c. Prokaryotic cells have flagella, but eukaryotic cells do not.
   d. Prokaryotic cells do not have a membrane-bounded nucleus, but eukaryotic cells do have such a nucleus.
   e. Prokaryotic cells have ribosomes, but eukaryotic cells do not have ribosomes.
4. Which of these is not found in the nucleus?
   a. functioning ribosomes
   b. chromatin that condenses to chromosomes
   c. nucleolus that produces rRNA
   d. nucleoplasm instead of cytoplasm
   e. all forms of RNA
5. Vesicles from the ER most likely are on their way to
   a. the rough ER.
   b. the lysosomes.
   c. the Golgi apparatus.
   d. the plant cell vacuole only.
   e. the location suitable to their size.
6. Lysosomes function in
   a. protein synthesis.
   b. processing and packaging.
   c. intracellular digestion.
   d. lipid synthesis.
   e. production of hydrogen peroxide.
7. Mitochondria
   a. are involved in cellular respiration.
   b. break down ATP to release energy for cells.
   c. contain grana and cristae.
   d. are present in animal cells but not plant cells.
   e. All of these are correct.
8. Which organelle releases oxygen?
   a. ribosome
   b. Golgi apparatus
   c. mitochondrion
   d. chloroplast
   e. smooth ER
9. Label these parts of the cell that are involved in protein synthesis and modification. Give a function for each structure.



10. Which of these is not true?
    a. Actin filaments are found in muscle cells.
    b. Microtubules radiate out from the ER.
    c. Intermediate filaments sometimes contain keratin.
    d. Motor molecules use microtubules as tracks.
11. Cilia and flagella
    a. have a 9 + 0 pattern of microtubules.
    b. contain myosin that pulls on actin filaments.
    c. are organized by basal bodies derived from centrioles.
    d. are constructed similarly in prokaryotes and eukaryotes.
    e. Both a and c are correct.
12. Which of the following organelles contains its (their) own DNA, which suggests they were once independent prokaryotes?
    a. Golgi apparatus
    b. mitochondria
    c. chloroplasts
    d. ribosomes
    e. Both b and c are correct.

13. Which organelle most likely originated by invagination of the plasma membrane?
    a. mitochondria
    b. flagella
    c. nucleus
    d. chloroplasts
    e. All of these are correct.
14. Which structures are found in a prokaryotic cell?
    a. cell wall, ribosomes, thylakoids, chromosome
    b. cell wall, plasma membrane, nucleus, flagellum
    c. nucleoid, ribosomes, chloroplasts, capsule
    d. plasmid, ribosomes, enzymes, DNA, mitochondria
    e. chlorophyll, enzymes, Golgi apparatus, plasmids
15. Study the example given in (a) below. Then for each other organelle listed, state another that is structurally and functionally related. Tell why you paired these two organelles.
    a. The nucleus can be paired with nucleoli because nucleoli are found in the nucleus. Nucleoli occur where chromatin is producing rRNA.
    b. mitochondria
    c. centrioles
    d. ER

Thinking Scientifically

1. Protists of the phylum Apicomplexa cause malaria and contribute to infections associated with AIDS. These parasites are unusual because they contain plastids. (Chloroplasts are a type of plastid.) Scientists have discovered that an antibiotic that inhibits prokaryotic enzymes will kill the parasite because it is effective against the plastids contained in the cell. What can be concluded about the plastids?
2. In a cell biology laboratory, students are examining sections of plant cells. Some students report seeing the nucleus; others do not. Some students see a large vacuole; others see a small vacuole. Some see evidence of an extensive endoplasmic reticulum; others see almost none. How can these observations be explained if the students are looking at the same cells?

Bioethical Issue: Stem Cells

Embryonic stem cells are cells from young embryos that divide indefinitely. They are of interest to researchers because they are undifferentiated and have the ability to develop into a variety of cell types, including brain, heart, bone, muscle, and skin cells. They can help researchers to understand how cells change as they mature. In addition, they offer the hope of curing cell-based diseases such as diabetes, Parkinson disease, and heart disease. Embryonic stem cell research involves the destruction of human embryos. Opponents of this research argue that embryos should not be destroyed because they have the same rights as all human beings. Proponents counter that the embryos used for research are excess embryos from in vitro fertilization procedures, and they would be destroyed anyway. Therefore, they should be used to alleviate human suffering. Do you think that human embryos should be used for stem cell research?

Understanding the Terms

actin filament 76
apoptosis 71
bacillus 62
basal body 78
capsule 62
cell 58
cell envelope (of prokaryotes) 62
cell theory 58
cell wall 62
central vacuole (of plant cell) 73
centriole 78
centrosome 76
chloroplast 74
chromatin 68
chromoplast 74
chromosome 68
cilium 78
coccus 62
cristae 75
cyanobacteria 62
cytoplasm 62
cytoskeleton 76
endomembrane system 70
endoplasmic reticulum (ER) 70
eukaryotic cell 62
fimbriae 63
flagellum (pl., flagella) 62, 78
glycocalyx 62
Golgi apparatus 70
granum 74
inclusion body 62
intermediate filament 76
leucoplast 74
lysosome 71
matrix 75
mesosome 62
microtubule 76
mitochondrion 74
motor molecule 76
nuclear envelope 68
nuclear pore 68
nucleoid 62
nucleolus 68
nucleoplasm 68
nucleus 64
organelle 64
peroxisome 73
plasma membrane 62
plasmid 62
plastid 74
polyribosome 69
prokaryotic cell 62
pseudopod 76
ribosome 62, 69
rough ER 70
secretion 70
sex pili 63
smooth ER 70
spirillum 62
spirochete 62
stroma 74
surface-area-to-volume ratio 59
thylakoid 62, 74
vacuole 73
vesicle 70

Match the terms to these definitions:

a. _____ Organelle, consisting of saccules and vesicles, that processes, packages, and distributes molecules about or from the cell.
b. _____ Especially active in lipid metabolism; always produces H_2O_2.
c. _____ Dark-staining, spherical body in the cell nucleus that produces ribosomal subunits.
d. _____ Internal framework of the cell, consisting of microtubules, actin filaments, and intermediate filaments.
e. _____ Allows prokaryotic cells to attach to other cells.

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