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microscope, *fascinated by the sight of her own cells. She had obtained the cells by gently scraping them from the inner lining of her mouth, smearing them onto a microscope slide, and then staining them with blue dye. Laurel noticed that each cell contained a darker blue spot. She remembered from biology lecture that this region is known as the nucleus, and it is especially important because it contains instructions in the form of DNA for all the cell's functions. As Laurel carefully sketched one of the cells, she realized that each cell had a distinct boundary that separated it from its surroundings. This, she determined, must be*

the plasma membrane.

Laurel looked through the

Laurel then observed numerous smaller blue dots all over her cheek cells. Adjusting her microscope to a higher magnification, she viewed the dots again, wondering if they, too, might be cells of some kind. Laurel checked with her lab instructor, who said that the little dots were indeed cells. In fact, they were various types of bacteria that live in everyone's mouth.

This chapter is an introduction to the study of cells. As we will see, all life on Earth consists of cells, which come in an astounding variety of shapes, sizes, and arrangements. Laurel's body is made up of trillions of cells, many with specialized functions, but all working together to keep her alive and healthy. The bacteria thriving in the environment of Laurel's mouth are tiny, single-celled organisms. They are smaller than any of Laurel's own cells, and yet they are also capable of carrying out a versatile range of life activities.

Cell Structure and Function

C h a p t e r C o n c e p t s

3.1 The Cellular Level of Organization

- What do we call the small structures in eukaryotic cells that carry out **specific functions? 46**
- What does the cell theory state? 46
- What limits the size of a cell? 46
- What boundary is common to all cells? 47
- What instruments would a scientist use to study and view small cells? 46

3.2 Prokaryotic Cells

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3.3 Eukaryotic Cells

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- What structure is responsible for protein synthesis? 54
- What membranous system within eukaryotic cells is involved in the **production, modification, transport, storage, secretion, and/or digestion of macromolecules? 54–56**
- What energy transformation structures are present in plant and **animal cells? What does each structure produce? 57–58**
- What is the composition of the cytoskeleton, and what is its function? 59–62
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3.4 Origin and Evolution of the Eukaryotic Cell

■ What theory suggests how eukaryotic cells arose? 63

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3.1 The Cellular Level of Organization

The cell marks the boundary between the nonliving and the living. The molecules that serve as food for a cell and the macromolecules that make up a cell are not alive, and yet the cell is alive. The cell is the structural and functional unit of an organism, the smallest structure capable of performing all the functions necessary for life. Thus, the answer to what life is must lie within the cell, because the smallest living organisms are unicellular, while larger organisms are multicellular—that is, composed of many cells.

Cells can be classified as either prokaryotic or eukaryotic. Prokaryotic cells do not contain the membraneenclosed structures found in eukaryotic cells. Therefore, eukaryotic cells are thought to have evolved from prokaryotic cells (see Section 3.4). Prokaryotic cells are exemplified by the bacteria.

The diversity of cells is illustrated by the many types in the human body, such as muscle cells and nerve cells. But despite a variety of forms and functions, human cells contain the same components. The basic components that are common to all eukaryotic cells, regardless of their specializations, are the subject of this chapter. Viewing these components requires a microscope. The Science Focus on page 53 introduces you to the microscopes most used today to study cells. Electron microscopy and biochemical analyses have revealed that eukaryotic cells actually contain tiny, specialized structures called **organelles.** Each organelle performs specific cellular functions.

Today, we are accustomed to thinking of living things as being constructed of cells. But the word cell didn't enter biology until the seventeenth century. Antonie van Leeuwenhoek of Holland is now famous for making his own microscopes and observing all sorts of tiny things that no one had seen before. Robert Hooke, an Englishman, confirmed Leeuwenhoek's observations and was the first to use the term "cell." The tiny chambers he observed in the honeycomb structure of cork reminded him of the rooms, or cells, in a monastery.

Over 150 years later—in the 1830s—the German microscopist Matthias Schleiden stated that plants are composed of cells; his counterpart, Theodor Schwann, stated that animals are also made up of living units called cells. This was quite a feat, because aside from their own exhausting examination of tissues, both had to take into consideration the studies of many other microscopists. Rudolf Virchow, another German microscopist, later came to the conclusion that cells don't suddenly appear; rather, they come from preexisting cells. Think about how we reproduce. The sperm fertilizes an egg and a human being develops from a resulting cell, called a zygote.

The **cell theory** states that all organisms are made up of basic living units called cells, and that all cells come only from previously existing cells. Today, the cell theory is a basic theory of biology.

The cell theory states the following:

- All organisms are composed of one or more cells.
- Cells are the basic living unit of structure and
- **function in organisms.** ■ All cells come only from other cells.

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 3.1 outlines the visual range of the eye, light microscope, and electron microscope, and the discussion of microscopy in the Science Focus explains why the electron microscope allows us to see so much more detail than the light microscope does.

The fact that cells are so small is a great advantage for multicelluar organisms. Nutrients, such as glucose and oxygen, enter a cell, and wastes, such as carbon dioxide, exit a cell at its surface; therefore, the amount of surface area affects the ability to get material into and out of the cell. A large cell requires more nutrients and produces more wastes than a small cell. But, as cells get larger in volume, the proportionate amount of surface area actually decreases. For example, for a cube-shaped cell, the volume increases by the cube of the sides (height \times width \times depth), while the surface area increases by the square of the sides and number of sides (height \times width \times 6). If a cell doubles in size, its surface area only increases fourfold while its volume increases eightfold. Therefore, small cells, not large cells, are likely to have an adequate surface area for exchanging nutrients and wastes. As Figure 3.2 demonstrates, cutting a large cube into smaller cubes provides a lot more surface area per volume.

Most actively metabolizing cells are small. The frog's egg is not actively metabolizing. But once the egg is fertilized and metabolic activity begins, the egg divides repeatedly without growth. These cell divisions restore the amount of surface area needed for adequate exchange of materials. Further, cells that specialize in absorption have modifications that greatly increase their surface-area-tovolume ratio. For example, the columnar epithelial cells along the surface of the intestinal wall have surface foldings called microvilli (sing., microvillus) that increase their surface area.

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Figure 3.1 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 μ m = 10^9 nm.)

Plasma Membrane and Cytoplasm

All cells are surrounded by a **plasma membrane** that consists of a phospholipid bilayer in which some protein molecules are embedded:

One 4-cm cube Eight 2-cm cubes Sixty-four 1-cm cubes

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Figure 3.2 Surface-area-to-volume relationships. All three have the same volume, but the group on the right has four times the surface area.

3.2 Prokaryotic Cells

Cells can be classified by the presence or absence of a nucleus. **Prokaryotic cells** lack a membrane-bounded nucleus. The domains Archaea and Bacteria consist of prokaryotic cells. Prokaryotes generally exist as unicellular organisms (single cells) or as simple strings and clusters. Many people think of germs when they hear the word bacteria, but not all bacteria cause disease. In fact, most bacteria are beneficial and are essential for other living organisms' survival.

Figure 3.3 illustrates the main features of bacterial anatomy. The **cell wall,** located outside of the plasma membrane, contains peptidoglycan, a complex molecule that is unique to bacteria and composed of chains of disaccharides joined by peptide chains. The cell wall protects the bacteria. Some antibiotics, such as penicillin, interfere with the synthesis of

The plasma membrane is a living boundary that separates the living contents of the cell from the nonliving surrounding environment. Inside the cell is a semifluid medium called the **cytoplasm.** The cytoplasm is composed of water, salts, and dissolved organic molecules. The plasma membrane regulates the entrance and exit of molecules into and out of the cytoplasm.

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

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Flagellum: rotating filament present in some bacteria that pushes the cell forward

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covering that supports, shapes, and protects cell

Capsule: gel-like coating outside cell wall

Figure 3.3 Prokaryotic cell.

Prokaryotic cells lack a nucleus and other membrane-bounded organelles, but they possess a nucleoid region that houses DNA.

peptidoglycan. In some bacteria, the cell wall is further surrounded by a **capsule** and/or a gelatinous sheath called a **slime layer.** Some bacteria have long, very thin appendages called flagella (sing., **flagellum**), which are composed of subunits of the protein flagellin. The flagella rotate like propellers, allowing the bacterium to move rapidly in a fluid medium. Some bacteria also have **fimbriae,** which are short appendages that help them attach to an appropriate surface. The capsule and fimbriae often give pathogenic bacteria increased ability to cause disease.

Prokaryotes have a single chromosome (loop of DNA and associated proteins) located within a region of the cytoplasm called the **nucleoid.** The nucleoid is not bounded by a membrane. Many prokaryotes also have small accessory rings of DNA called **plasmids.** The cytoplasm has thousands of **ribosomes** for the synthesis of proteins. The ribosomes of prokaryotic organisms are smaller and structurally different from those of eukaryotic cells, which makes ribosomes a good target for antibacterial drugs. In addition, the photosynthetic cyanobacteria have light-sensitive pigments, usually within the membranes of flattened disks called **thylakoids.**

Although prokaryotes are structurally simple, they are much more metabolically diverse than eukaryotes. Many of them can synthesize all their structural components from very simple, even inorganic molecules. Indeed, humans exploit the metabolic capability of bacteria by using them to produce a wide variety of chemicals and products. Prokaryotes have also adapted to living in almost every environment on Earth. In particular, archaea have been found living under conditions that would not support any other form of life—for example, in water at temperatures above boiling. Archaeal membranes have unique membrane-spanning lipids that help them survive in extremes of heat, pH, and salinity. Table 3.1 compares the major structures of prokaryotes (archaea and bacteria) with those of eukaryotes.

3.3 Eukaryotic Cells

Eukaryotic cells are structurally very complex. The principal distinguishing feature of eukaryotic cells is the presence of a nucleus, which separates the chromosomes (DNA) from the cytoplasm of the cell. In addition, eukaryotic cells possess a variety of other organelles, many of which are surrounded by membranes. Animals, plants, fungi, and protists are all composed of eukaryotic cells.

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Cell Walls

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Some eukaryotic cells have a permeable but protective cell wall, in addition to a plasma membrane. Many plant cells have both a primary and a secondary cell wall. A main constituent of a primary cell wall is cellulose molecules. Cellulose molecules form fibrils that lie at right angles to one another for added strength. The secondary cell wall, if present, forms inside the primary cell wall. Such secondary cell walls contain lignin, a substance that makes them even stronger than primary cell walls. The cell walls of some fungi are composed of cellulose and chitin, the same type of polysaccharide found in the exoskeleton of insects. Algae, members of the kingdom Protista, contain cell walls composed of cellulose.

Organelles of Animal and Plant Cells

Originally the term organelle referred to only membranous structures, but we will use it to include any well-defined subcellular structure (Table 3.2). Just as all the assembly lines of a factory operate at the same time, so all the organelles of a cell function simultaneously. Raw materials enter a factory where different departments turn them into various products. In the same way, the cell takes in chemicals, and then the organelles process them.

Both animal cells (Fig. 3.4) and plant cells (Fig. 3.5) contain mitochondria, but only plant cells have chloroplasts. Only animal cells have centrioles. In the illustrations throughout this text, note that each of the organelles has an assigned color.

The Nucleus

The **nucleus**, which has a diameter of about $5 \mu m$, is a prominent structure in the eukaryotic cell. The nucleus is of primary importance because it stores the genetic material, DNA, which governs the characteristics of the cell and its metabolic functioning. Every cell in an individual contains the same DNA, but in each cell type, certain genes are turned on and certain others are turned off. Activated DNA, with RNA acting as an intermediary, specifies the sequence of amino acids when a protein is synthesized. The proteins of a cell determine its structure and the functions it can perform.

** Plant cells only. ** Animal cells only.*

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Figure 3.5 Plant cell anatomy.

plant cell and drawing of a generalized plant cell. See Table 3.2 for a description of these structures, along with a listing

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When you look at the nucleus, even in an electron micrograph, you cannot see a DNA molecule. You can see **chromatin,** which consists of DNA and associated proteins (Fig. 3.6). Chromatin looks grainy, but actually it is a threadlike material that undergoes coiling to form rodlike structures, called **chromosomes** during the initial stages of cell division. Chromatin is immersed in a semifluid medium called the **nucleoplasm.** A difference in pH between the nucleoplasm and the cytoplasm suggests that the nucleoplasm has a different composition.

Most likely, too, when you look at an electron micrograph of a nucleus, you will see one or more regions that look darker than the rest of the chromatin. These are nucleoli (sing., **nucleolus**), where another type of RNA, called ribosomal RNA (rRNA), is produced and where rRNA joins with proteins to form the subunits of ribosomes described in the next section.

The nucleus is separated from the cytoplasm by a double membrane known as the **nuclear envelope,** which is continuous with the endoplasmic reticulum (also discussed next). The nuclear envelope has **nuclear pores** of sufficient size (100 nm) to permit proteins to pass into the nucleus and ribosomal subunits to pass out.

The structural features of the nucleus include:

Nucleolus: Chromatin and ribosomal subunits Nuclear envelope: Double membrane with pores

Figure 3.6 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. Nuclear pores serve as passageways for substances to pass into and out of the nucleus.

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Microscopy Today

Today, scientists use two types of microscopes: light microscopes and electron microscopes. Figure 3A depicts one type of light microscope and two types of electron microscopes, along with micrographs obtained with each one.

The most commonly used light microscope is the compound light microscope. "Compound" refers to the presence of more than one lens. In a compound light microscope, light rays pass through a specimen such as a blood smear, a tissue section, or even living cells. The light rays are brought to a focus by a set of glass lenses and the resulting image is then viewed. Specimens are often stained to provide viewing contrast.

In an electron microscope, electrons rather than light rays are brought to focus by a set of magnetic lenses, and the resulting image is projected onto a viewing screen or photographic film. Electron microscopes produce images of much higher magnification than may be obtained with even the best compound light microscope. The ability to distinguish two points as separate points (resolution) is much greater with electron microscopes. The greater resolving power is due to the fact that electrons travel at a much shorter wavelength than do light rays. Live specimens however cannot be viewed and must be dried out. Two commonly used types of electron microscopes are transmission and scanning.

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A transmission electron microscope (a TEM) may magnify an object's image over 100,000 times, compared to approximately 1,000 times with a compound light microscope. Also, a TEM has a much greater ability to make out detail. Much of our knowledge of the internal structures of cells comes from with a TEM.

The magnifying and resolving powers of a typical scanning electron microscope a (SEM) are not as great as with a TEM although they are still greater than those of a compound light microscope. A SEM provides a striking threedimensional view of the surface of an object.

A picture obtained using a compound light microscope is sometimes called a photomicrograph, and a picture resulting from the use of an electron microscope is called a transmission or scanning electron micrograph, depending on the type of microscope used. Color may be added to electron micrographs, such as those in Figure 3A, using a computer.

Discussion Questions

- 1. What distortions or artifacts might be seen in electron microscopy when viewing a dried, nonliving specimen?
- 2. What happens to an image if the magnification is increased without increasing the resolution?
- 3. Why are electron micrographs always in black and white (or artificially colored)?

Figure 3A Diagram of microscopes with accompanying micrographs. 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.

amoeba, light micrograph, stained with dye mitochondrion, TEM, artificially colored dinoflagellate, SEM, artificially colored

a. Compound light microscope

b. Transmission electron microscope

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c. Scanning electron microscope

Ribosomes

Ribosomes are composed of two subunits, called "large" and "small" because of their sizes relative to each other. Each subunit is a complex of unique ribosomal RNA (rRNA) and protein molecules. Ribosomes can be found individually in the cytoplasm, as well as in groups called **polyribosomes** (several ribosomes associated simultaneously with a single mRNA molecule). Ribosomes can also be found attached to the endoplasmic reticulum, a membranous system of saccules and channels discussed in the next section. Proteins synthesized at ribosomes attached to the endoplasmic reticulum have a different destination from that of proteins synthesized at ribosomes free in the cytoplasm.

Ribosomes are small organelles where protein synthesis occurs. Ribosomes occur in the cytoplasm, both singly and in groups (i.e., polyribosomes). Numerous ribosomes are also attached to the endoplasmic reticulum.

The Endomembrane System

The endomembrane system consists of the nuclear envelope, the endoplasmic reticulum, the Golgi apparatus, and several **vesicles** (tiny membranous sacs). This system compartmentalizes the cell so that particular enzymatic reactions are restricted to specific regions. Organelles that make up the endomembrane system are connected either directly or by transport vesicles.

The Endoplasmic Reticulum

The **endoplasmic reticulum (ER),** a complicated system of membranous channels and saccules (flattened vesicles), is physically continuous with the outer membrane of the nuclear envelope. Rough ER is studded with ribosomes on the side of the membrane that faces the cytoplasm (Fig. 3.7). Here, proteins are synthesized and enter the ER interior, where processing and modification begin.

Proper folding, processing, and transport of proteins are critical to the functioning of the cell. For example, in cystic fibrosis a mutated plasma membrane channel protein is retained in the endoplasmic reticulum because it is folded incorrectly. Without this protein in its correct location, the cell is unable to regulate the transport of the chloride ion, resulting in the various symptoms of the disease.

Smooth ER, which is continuous with rough ER, does not have attached ribosomes. Smooth ER synthesizes the phospholipids that occur in membranes and performs various other functions depending on the particular cell. In the testes, it produces testosterone, and in the liver, it helps detoxify drugs. Regardless of any specialized function, smooth ER also forms vesicles in which products are transported to the Golgi apparatus.

ER is involved in protein synthesis (rough ER) and various other processes, such as lipid synthesis (smooth ER). Vesicles transport products from the ER to the Golgi apparatus.

Figure 3.7 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 consists of a stack of three to twenty slightly curved saccules whose appearance can be compared to a stack of pancakes (Fig. 3.8). The Golgi apparatus is referred to as the post office of the cell because it collects, sorts, packages, and distributes materials such as proteins and lipids. In animal cells, one side of the stack (the inner face) is directed toward the ER, and the other side of the stack (the outer face) is directed toward the plasma membrane. Vesicles can frequently be seen at the edges of the saccules.

The Golgi apparatus receives proteins and also lipidfilled vesicles that bud from the ER. These molecules then move through the Golgi from the inner face to the outer face. How this occurs is still being debated. According to the maturation saccule model, the vesicles fuse to form an inner face saccule, which matures as it gradually becomes

a saccule at the outer face. According to the stationary saccule model, the molecules move through stable saccules from the inner face to the outer face by shuttle vesicles. It is likely that both models apply, depending on the organism and the type of cell.

During their passage through the Golgi apparatus, proteins and lipids can be modified before they are repackaged in secretory vesicles. Secretory vesicles proceed to the plasma membrane, where they discharge their contents. This action is termed **secretion**.

The Golgi apparatus is also involved in the formation of lysosomes, vesicles that contain proteins and remain within the cell. How does the Golgi apparatus direct traffic—in other words, what makes it direct the flow of proteins to different destinations? It now seems that proteins made at the rough ER have specific molecular tags that serve as "zip codes" to tell the Golgi apparatus whether they belong inside the cell in some membrane-bounded organelle or in a secretory vesicle.

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Lysosomes

Lysosomes are membrane-bounded vesicles produced by the Golgi apparatus. Lysosomes contain hydrolytic digestive enzymes.

Sometimes macromolecules are brought into a cell by vesicle formation at the plasma membrane (Fig. 3.8). 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 pathogens via vesicle formation. When lysosomes fuse with these vesicles, the bacteria are digested. Even parts of a cell are digested by its own lysosomes (called autodigestion). For example, the finger webbing found in the human embryo is later dissolved by lysosomes so that the fingers are separated.

Lysosomes contain many enzymes for digesting all sorts of molecules. Occasionally, a child inherits the inability to make a lysosomal enzyme, and therefore has a lysosomal storage disease. For example, in Tay Sachs disease, the cells that surround nerve cells cannot break down a particular lipid, which then accumulates inside lysosomes and affects the nervous system. At about six months, the infant can no longer see and, then, gradually loses hearing and even the ability to move. Death follows at about three years of age.

The endomembrane system consists of the endoplasmic reticulum, Golgi apparatus, lysosomes, and transport vesicles.

Vacuoles

A **vacuole** is a large membranous sac. A vacuole is larger than a vesicle. Although animal cells have vacuoles, they are much more prominent in plant cells. Typically, plant cells have a large central vacuole so filled with a watery fluid that it gives added support to the cell (see Fig. 3.5).

Vacuoles store substances. Plant vacuoles contain not only water, sugars, and salts but also 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. The vacuoles present in unicellular protozoans are quite specialized; they include contractile vacuoles for ridding the cell of excess water and digestive vacuoles for breaking down nutrients.

Vacuoles are larger than vesicles. Plants typically have a large central vacuole for storage of various molecules.

Figure 3.9 Peroxisomes.

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

Peroxisomes

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Peroxisomes, similar to lysosomes, are membrane-bounded vesicles that enclose enzymes (Fig. 3.9). However, the enzymes in peroxisomes are synthesized by cytoplasmic ribosomes and transported into a peroxisome by carrier proteins. Typically, peroxisomes contain enzymes whose action results in hydrogen peroxide (H_2O_2) , a toxic molecule:

> $RH_2 + O_2 \longrightarrow R + H_2O_2$ $(R = remainder of molecule)$

Hydrogen peroxide is immediately broken down to water and oxygen by another peroxisomal enzyme called catalase.

The enzymes present in a peroxisome depend on the function of the cell. Peroxisomes are especially prevalent in cells that are synthesizing and breaking down fats. In the liver, some peroxisomes break down fats and others produce bile salts from cholesterol. In the movie *Lorenzo's Oil,* Lorenzo's cells lacked a carrier protein to transport an enzyme into peroxisomes. As a result, long-chain fatty acids accumulated in his brain and he suffered from neurological damage.

Plant cells also have peroxisomes. 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.

Typically, the enzymes in peroxisomes break down molecules and as a result produce hydrogen peroxide molecules.

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Energy-Related Organelles

Life is possible only because of a constant input of energy. Organisms use this energy for maintenance and growth. Chloroplasts and mitochondria are the two eukaryotic membranous organelles that specialize in converting energy to a form the cell can use. **Chloroplasts** use solar energy to synthesize carbohydrates, and carbohydrate-derived products are broken

This diagram shows that chemicals recycle between chloroplasts and mitochondria, but energy flows from the sun through these organelles to ATP. When cells use ATP as an energy source, energy dissipates as heat. Life could not exist without a constant input of solar energy.

Only plants, algae, and cyanobacteria are capable of carrying on photosynthesis in this manner:

solar energy + carbon dioxide + water \longrightarrow carbohydrate + oxygen

Plants and algae have chloroplasts (Fig. 3.10), while cyanobacteria carry on photosynthesis within independent thylakoids. Solar energy is the ultimate source of energy for cells because nearly all organisms, either directly or indirectly, use the carbohydrates produced by photosynthesizers as an energy source.

All organisms carry on cellular respiration, the process by which the chemical energy of carbohydrates is converted to that of ATP (adenosine triphosphate), the common energy carrier in cells. All organisms, except bacteria, complete the process of cellular respiration in mitochondria. Cellular respiration can be represented by this equation:

carbohydrate + oxygen \longrightarrow carbon dioxide + water + energy

Here, *energy* is in the form of ATP molecules. When a cell needs energy, ATP supplies it. The energy of ATP is used for all energy-requiring processes in cells.

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Chloroplasts

Plant and algal cells contain chloroplasts, the organelles that allow them to produce their own organic food. Chloroplasts are about $4-6 \mu m$ in diameter and $1-5 \mu m$ in length; they belong to a group of organelles known as plastids. Among the plastids are also the *amyloplasts,* common in roots, which store starch, and the *chromoplasts,* common in leaves, which contain red and orange pigments. A chloroplast is green, of course, because it contains the green pigment chlorophyll.

A chloroplast is bounded by two membranes that enclose a fluid-filled space called the **stroma** (Fig. 3.10). A membrane system within the stroma is organized into interconnected flattened sacs called thylakoids. In certain regions, the thylakoids are stacked up in structures called grana (sing., **granum**). There can be hundreds of grana within a single chloroplast (Fig. 3.10). Chlorophyll, which is located within the thylakoid membranes of grana, captures the solar energy needed to enable chloroplasts to produce carbohydrates. The stroma also contains DNA, ribosomes, and enzymes that synthesize carbohydrates from carbon dioxide and water.

Mitochondria

All eukaryotic cells, including those of plants and algae, contain mitochondria. This means that plant cells contain both chloroplasts and mitochondria. Mitochondria are usually $0.5-1.0 \mu m$ in diameter and $2-5 \mu m$ in length.

Mitochondria, like chloroplasts, are bounded by a double membrane (Fig. 3.11). In mitochondria, the inner fluid-filled space is called the **matrix.** The matrix contains DNA, ribosomes, and enzymes that break down carbohydrate products, releasing energy to be used for ATP production.

The inner membrane of a mitochondrion invaginates to form **cristae.** Cristae provide a much greater surface area to accommodate the protein complexes and other participants that produce ATP.

Mitochondria and chloroplasts are able to make some proteins, encoded by their own genes—but other proteins, encoded by nuclear genes, are imported from the cytoplasm.

In humans, all mitochondria come from the maternal line through the egg. The father's sperm does not contribute any mitochondria to the offspring. Mutations in the mitochondrial DNA usually affect high-energy-demand tissues such as the eye, brain, central nervous system, and muscles.

Chloroplasts and mitochondria are membranous organelles with structures that lend themselves to the energy occuring within them.

The Cytoskeleton

The protein components of the **cytoskeleton** interconnect and extend from the nucleus to the plasma membrane in eukaryotic cells. Prior to the 1970s, scientists believed that the cytoplasm was an unorganized mixture of organic molecules. Then, high-voltage electron micro-

scopes, which can penetrate thicker specimens, showed instead that the cytoplasm is highly organized. The technique of immunofluorescence microscopy identified the makeup of the protein components within the cytoskeletal network (Fig. 3.12).

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c. Microtubules

Figure 3.12 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 identified 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. Human hair is 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.

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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 add phosphates to 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. 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 and perform a structural role in the cell. 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 skin cells, intermediate filaments, made of the protein keratin, give great mechanical strength. We now know that intermediate filaments are also highly dynamic and will disassemble when phosphate is added by a kinase.

Microtubules

Microtubules are small, hollow cylinders about 25 nm in diameter and 0.2 -25 μ m in length.

Microtubules are made of the globular protein tubulin, which is of two types, called α and β . 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 controlled by a microtubule organizing center (MTOC). In most eukaryotic cells, the main MTOC is in the **centrosome,** 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

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.

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.

SECOND PASS

Figure 3.13 Centrioles.

In a nondividing animal cell, a single pair of centrioles lies 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

Centrioles 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 (Fig. 3.13). In animal cells, a centrosome contains two centrioles lying at right angles to each other. The centrosome is the major microtubule organizing center for the cell, and centrioles may be involved in the process of microtubule assembly and disassembly.

Before an animal cell divides, the centrioles replicate such that the members of each pair are again at right angles to one another (Fig. 3.13). Then, each pair becomes part of a separate centrosome. During cell division, the centrosomes move apart and may function to organize the mitotic spindle. Plant cells have the equivalent of a centrosome, but it does not contain centrioles, suggesting that centrioles are not necessary to the assembly of cytoplasmic microtubules.

Centrioles, which are short cylinders with a 9+**0 pattern of microtubule triplets, may be involved in microtubule formation.**

Cilia and Flagella

Cilia and flagella 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 organisms called paramecia move by means of cilia, whereas sperm cells move by means of flagella. In the human body, 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 or ejected. 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. Therefore, they have a 9+2 pattern of microtubules. Cilia and flagella move when the microtubule doublets slide past one another (Fig. 3.14).

Cilia and flagella, which have a 9+**2 pattern of microtubules, enable some cells to move.**

Visual Focus

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Cilia

 \bigoplus

Figure 3.14 Structure of a flagellum or cilium.

The shaft of a flagellum (or cilium) contains microtubule doublets whose side arms are motor molecules that cause the projection to move. Sperm have flagella. Without the ability of sperm to move to the egg, human reproduction would not be possible. Cilia cover the surface of the cells of the respiratory system where they beat upward to remove foreign matter.

3.4 Origin and Evolution of the Eukaryotic Cell

The fossil record, which is based on the remains of ancient life, suggests that the first cells were prokaryotes. Therefore, scientists believe that eukaryotic cells evolved from prokaryotic cells. Both bacteria and archaea are candidates, but biochemical data suggest that eukaryotes are more closely related to the archaea. The eukaryotic cell probably evolved from a prokaryotic cell in stages. Invagination of the plasma membrane might explain the origin of the nuclear envelope and such organelles as the endoplasmic reticulum and the Golgi apparatus. Some believe that the other organelles could also have arisen in this manner.

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Another, more interesting hypothesis of organelles has been put forth. Observations in the laboratory indicate that an amoeba infected with bacteria can become dependent upon them. Some investigators believe mitochondria and chloroplasts are derived from prokaryotes that were taken up by a much larger cell (Fig. 3.15). Perhaps mitochondria were originally aerobic heterotrophic bacteria, and chloroplasts were originally cyanobacteria. The eukaryotic host cell would have benefited from an ability to utilize oxygen or synthesize organic food when, by chance, the prokaryote was taken up and not destroyed. After the prokaryote entered the host cell, the two would have begun living together cooperatively. This proposal is known as the **endosymbiotic theory** (*endo*-, in; *symbiosis,* living together) some of the evidence supporting this hypothesis is as follows:

- **1.** Mitochondria and chloroplasts are similar to bacteria in size and in structure.
- **2.** Both organelles are bounded by a double membrane—the outer membrane may be derived from the engulfing vesicle, and the inner one may be derived from the plasma membrane of the original prokaryote.
- **3.** Mitochondria and chloroplasts contain a limited amount of genetic material and divide by splitting. Their DNA (deoxyribonucleic acid) is a circular loop like that of prokaryotes.
- **4.** Although most of the proteins within mitochondria and chloroplasts are now produced by the eukaryotic host, they do have their own ribosomes and they do produce some proteins. Their ribosomes resemble those of prokaryotes.
- **5.** The RNA (ribonucleic acid) base sequence of the ribosomes in chloroplasts and mitochondria also suggests a prokaryotic origin of these organelles.

It is also just possible that the flagella of eukaryotes are derived from an elongated bacterium with a flagellum that became attached to a host cell. However, the flagella of eukaryotes are constructed differently than those of modern bacteria.

Figure 3.15 Origin of organelles.

Invagination of the plasma membrane could have created the nuclear envelope and an endomembrane system. The endosymbiotic theory suggests that mitochondria and chloroplasts were once independent prokaryotes that took up residence in a eukaryotic cell.

According to the endosymbiotic theory, heterotrophic bacteria became mitochondria, and cyanobacteria became chloroplasts after being taken up by precursors to modernday eukaryotic cells.

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Bioethical Focus

Therapeutic and Reproductive Cloning

Cloning refers to the production of identical copies, whether of a particular molecule, a type of cell, or an entire organism. Cloning of particular molecules through biotechnology has become fairly commonplace. Insulin, vaccines, and other pharmaceuticals are currently produced in this manner. However, two types of cloning associated with humans raise several difficult bioethical questions: therapeutic cloning and reproductive cloning.

Therapeutic cloning involves genetically manipulating human cells and then cloning those cells in culture. The intent is to eventually provide a source of "good" or "cured" cells for a diseased or injured person. For example, the ability to alter specific genes and selectively produce a given tissue type offers strong promise for the treatment of conditions such as Parkinson disease and Alzheimer disease. Scientists would like to use embryonic stem cells as the starting material for therapeutic cloning, and

currently the best sources of such cells are early (approximately one week old) human embryos. Some of these embryos are a byproduct of in vitro fertilization attempts, while others come from abortions.

Embryonic stem cells are unspecialized cells that can be cultivated in the laboratory and, in theory, coaxed with the addition of particular chemical signals to develop into any one of the many cell types in the human body. Currently, much of this work is in the developmental stage, and thus cloned cells are used primarily for research purposes. Those opposed to the use of embryonic stem cells have suggested that other possible sources of stem cells be pursued, including stored newborn umbilical cord cells and adult stem cells.

Reproductive cloning does not currently have much support in our society. In humans, this type of cloning would involve producing another human being with the exact genetic material of an existing person.

This type of cloning has been successful with other animals, including some endangered species and household cats, but currently the United States and 19 European nations have a moratorium on the cloning of humans.

Form Your Own Opinion

- 1. Should scientists be allowed to use early human embryos as a source of stem cells?
- 2. With in vitro fertilization, extra embryos are produced that are frozen, and ultimately destroyed. Is there a problem with using these embryos for research if they would be destroyed anyway?
- 3. What could be the advantages of cloning animals, such as endangered species?
- 4. Can you think of any good reasons to lift the moratorium on human reproductive cloning?

Summarizing the Concepts

3.1 The Cellular Level of Organization

All organisms are composed of cells, the smallest units of living matter. Cells are capable of self-reproduction, and new cells come only from preexisting cells. Cells must remain small in order to have an adequate ratio of surface-area-to-volume for exchange of molecules with the environment. All cells contain a plasma membrane made up of phospholipids that separates the inside of the cell from the outside and regulates the import and export of molecules. The inside of the cell is filled with a fluid called cytoplasm.

3.2 Prokaryotic Cells

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Prokaryotic cells do not have a nucleus, but they do have a nucleoid that is not bounded by a nuclear envelope. They also lack most of the other organelles that compartmentalize eukaryotic cells. Prokaryotic cells, as exemplified by the bacteria and archaea, are structurally less complex than eukaryotic cells but metabolically very diverse.

3.3 Eukaryotic Cells

The nucleus of eukaryotic cells, which include animal, plant, fungi, and protist cells, is bounded by a nuclear envelope containing pores. These pores serve as passageways between the cytoplasm and the nucleoplasm. Within the nucleus, the chromatin is a complex of DNA and protein. In dividing cells, the DNA is found in separate structures called chromosomes. The nucleolus is a special region of the chromatin where rRNA is produced and where proteins from the cytoplasm gather to form ribosomal subunits.

Ribosomes are organelles that function in protein synthesis. They can be bound to the endoplasmic reticulum (ER) or can exist within the cytoplasm singly or in groups called polyribosomes.

The endomembrane system includes the ER, the Golgi apparatus, the lysosomes, and other types of vesicles and vacuoles. The endomembrane system compartmentalizes the cell. The rough endoplasmic reticulum (RER) is covered with ribosomes and is involved in the folding, modification, and transport of proteins. The smooth ER has various metabolic functions depending on the cell type, but it also forms vesicles that carry products to the Golgi apparatus. The Golgi apparatus processes proteins and repackages them into lysosomes, which carry out intracellular digestion, or into vesicles for transport to the plasma membrane or other organelles. Vacuoles are large storage sacs, and vesicles are smaller ones. The large single plant cell vacuole not only stores substances but also lends support to the plant cell.

Peroxisomes contain enzymes that oxidize molecules by producing hydrogen peroxide, which is subsequently broken down.

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. Carbohydratederived products are broken down in mitochondria at the same time 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 the cell and its 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. Microtubules radiate out from the centrosome and are present in centrioles, cilia, and flagella. In the cytoplasm they serve as tracks along which vesicles and other organelles move due to the action of specific motor molecules.

3.4 Origin and Evolution of the Eukaryotic Cell

The first cells were probably prokaryotic cells. Eukaryotic cells most likely arose from prokaryotic cells in stages. Biochemical data suggest that eukaryotic cells are closer evolutionarily to the archaea than to the bacteria. The nuclear envelope, most likely, evolved through invagination of the plasma membrane, but mitochondria and chloroplasts may have arisen through endosymbiotic events.

Testing Yourself

Choose the best answer for each question.

1. Proteins are produced

- c. in the golgi apparatus. d. None of these are correct.
- 2. Which is associated with DNA?
	- a. chromatin b. chromosome
	- c. nucleus d. All of these are correct.
- 3. Cell walls are found in _______ and contain _____
	- a. animals, chitin b. animals, cellulose
	- c. plants, chitin d. plants, cellulose
- 4. Which structure is characteristic of prokaryotic cells?
	- a. nucleus b. mitochondria
	- c. nucleoid d. All of these are correct.
- 5. Eukaryotic cells are associated with _____, and prokaryotic cells are associated with the
	- a. chloroplasts, nucleus
	- b. chloroplasts, chloroplasts
	- c. individual thylakoids, chloroplasts
	- d. chloroplasts, individual thylakoids

For questions 6–9, match the statements to the terms in the key.

Key:

- a. chloroplasts b. lysosomes
	- c. vacuoles d. nucleus
- 6. All eukaryotic cells
- 7. Photosynthetic site
- 8. Store water
- 9. Contain enzymes for digestion
- 10. The Golgi apparatus can be found in _____ cells.
	- a. animal b. plant
	- c. bacterial d. Both a and b are correct.
- 11. _____ are (is) produced by the smooth ER.
	- a. Proteins b. DNA
	- c. Lipids d. Ribosomes
- 12. Mitochondria and chloroplasts contain _____ and are able to synthesize _____.
	- a. RNA, fatty acids b. DNA, proteins
	- c. DNA, fatty acids d. cholesterol, fatty acids
- 13. Which of these are involved in the movement of structures inside a cell? a. actin b. microtubules
	-
-
-
-
-
- - -
- *the key.*

Key:

- a. movement of cell b. transport of proteins
- c. photosynthesis d. ribosome formation
-
- 16. Chloroplasts
- 17. Flagella
-
-
-
- 21. Which of these sequences depicts a hypothesized
	- evolutionary scenario?
	- a. cyanobacteria \rightarrow mitochondria
	- b. Golgi \rightarrow mitochondria
	- c. mitochondria \rightarrow cyanobacteria
	- d. cyanobacteria \rightarrow chloroplast
- 22. Vacuoles are most prominent in
	- a. animal cells. b. plant cells.
	- c. Both a and b are correct. d. Neither a nor b is correct.
- 23. A " $9 + 2$ " formation refers to
	-
	- a. cilia. b. flagella.
	- c. centrioles. d. Both a and b are correct.
- 24. The products of photosynthesis are
	- a. carbohydrates and oxygen. b. carbon dioxide and water.
	- c. oxygen and water. d. carbohydrates and water.
- 25. Label these parts of the cell that are involved in protein synthesis and modification. Give a function for each structure.

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- c. centrioles d. All of these are correct.
- 14. Lysosomes function in _____
- a. protein synthesis. b. processing and packaging.
	- c. intracellular digestion. d. lipid synthesis.
	- e. All of these are correct.
- 15. Which of these could you see with a light microscope?
	- a. atom b. amino acid
	- c. proteins d. None of these are correct.
- *For questions 16–20, match the structure to the function in*
-

-
- e. folds and processes proteins
-
-
- 18. Golgi apparatus
- 19. Rough ER
- 20. Nucleolus

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- 26. The cell theory states:
	- a. Cells form as organelles and molecules become grouped together in an organized manner.
	- b. The normal functioning of an organism does not depend on its individual cells.
	- c. The cell is the basic unit of life.
	- d. Only eukaryotic organisms are made of cells.
- 27. The small size of cells is best correlated 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. their vast versatility.
	- e. All of these are correct.
- 28. Mitochondria
	- a. are involved in cellular respiration.
	- b. break down ATP to release energy for cells.
	- c. contain grana and cristae.
	- d. have a convoluted outer membrane.
	- e. All of these are correct.
- 29. Which of these compounds is broken down during cellular respiration?

- e. Both c and d are correct.
- 30. Which of the following is not one of the three components of the cytoskeleton?
	- a. flagella b. actin filaments
	- c. microtubules d. intermediate filaments
-
- 31. Which of the following structures would be found in both plant and animal cells?
	- a. centrioles
	- b. chloroplasts
	- c. cell wall
	- d. mitochondria
	- e. All of these are found in both types of cells.

Understanding the Terms

capsule 49 cell theory 46 cell wall 47 centriole 61 centrosome 60 chloroplast 57 chromatin 50 chromosome 53 cilia (pl., cilia) 61 cristae 58 cytoplasm 47 cytoskeleton 59 endoplasmic reticulum (ER) 54 endosymbiotic theory 63 eukaryotic cell 50

fimbriae 49

flagellum (pl., flagella) 49 Golgi apparatus 55 granum (pl., grana) 58 lysosome 56 matrix 58 mitochondrion 57 motor molecule 60 nuclear envelope 53 nuclear pore 53 nucleoid 49 nucleolus (pl., nucleoli) 53 nucleoplasm 53 nucleus 50 organelle 46 peroxisome 56

plasma membrane 47 plasmid 49 polyribosome 54 prokaryotic cell 47 ribosome 49 secretion 55

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slime layer 49 stroma 58 thylakoid 49 vacuole 56 vesicle 54

Match the terms to these definitions:

System of membranous saccules and channels in the cytoplasm, often with attached ribosomes.

Thinking Critically

- 1. At the beginning of this chapter, you met Laurel, who was examining cells scraped from the inside of her mouth, placed on a slide, and stained with blue dye. What type of microscope was Laurel most likely using to look at her cells? What was the purpose of the dye?
- 2. In the 1958 movie *The Blob,* a giant, single-celled alien creeps and oozes around, attacking and devouring helpless humans. Why couldn't there be a real single-celled organism as large as the Blob?
- 3. A red blood cell circulating in your bloodstream has no nucleus. It had one, but it ejected it during the maturation process. Is the mature red blood cell a prokaryotic cell or a eukaryotic cell? What characteristics, apart from a nucleus, would help you distinguish between a prokaryotic cell and a eukaryotic cell?
- 4. Calculate the surface-area-to-volume ratio of a 1 mm cube and a 2 mm cube. Which has the smaller ratio?
- 5. Some of the proteins in the mitochondria are encoded by mitochondrial DNA, while others are encoded by nuclear DNA. If the mitochondria were once free-living prokaryotic cells, how would you explain this?

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