UNIT 2

Cell Structure and Function

Unit Opener Copy and Image to Come
Inside the Cell

KEY CONCEPTS

■ The structure of cell components is closely correlated with their function.

■ Inside cells, materials are transported to their destinations with the help of molecular “zip codes.”

■ Cells are dynamic. Thousands of chemical reactions occur each second within cells; molecules constantly enter and exit across the plasma membrane; cell products are shipped along protein fibers; and elements of the cell’s internal skeleton grow and shrink.

In Chapter 1 you were introduced to the cell theory, which states that all organisms consist of cells and that all cells are derived from preexisting cells. Since this theory was initially developed and tested in the 1850s and 1860s, an enormous body of research has confirmed that the cell is the fundamental structural and functional unit of life. Life on Earth is cellular.

In a very real sense, then, understanding how an organism works is a matter of understanding how cells are structured and how they function. To drive this point home, recall from Chapter 1 that many eukaryotic organisms and virtually all bacteria and archaea are unicellular. In number of individuals present, unicellular organisms dominate life on Earth. For researchers who study these species, understanding the cell is synonymous with understanding the organism as a whole. Even in plants, animals, and other multicellular eukaryotes, complex behavior originates at the level of the cell. For example, your ability to read this page begins with changes in light-sensitive molecules located in cells at the back of your eyes. When these molecules change shape, they trigger changes in the membranes of nerve cells that connect your eyes to your brain. To understand complex processes such as vision, then, researchers often begin by studying the structure and function of the individual cells involved—the parts that make up the whole.

Chapter 6 introduced an essential part of the cell: the plasma membrane. Thanks to the selective permeability of phospholipid bilayers and the activity of membrane transport proteins, this structure creates an internal environment that is different from conditions outside the cell. Our task now is to explore the structures that are found inside the membrane and analyze what they do. We’ll focus on several particularly dynamic structures and processes and introduce some of the experimental approaches that biologists use to...
understand them. Let’s begin by surveying the basic types of cells, cell structures, and cell processes that biologists have documented to date.

### 7.1 What’s Inside the Cell?

In Chapter 1 you read about the two fundamental types of cells observed in nature. Recall that eukaryotic cells have a membrane-bound compartment called a nucleus, while prokaryotic cells do not. In terms of morphology (“form”), then, species fall into the two broad categories: (1) prokaryotes and (2) eukaryotes. But in terms of phylogeny, or evolutionary history, organisms fall into the three broad groups called (1) Bacteria, (2) Archaea, and (3) Eukarya. Members of the Bacteria and Archaea are prokaryotic; members of the Eukarya—including algae, fungi, plants, and animals—are eukaryotic.

In the late seventeenth century, biologists began studying the structure of cells with microscopes. Over time, improvements in optics and cell preparation techniques allowed researchers to catalogue the structures reviewed in this section. When electron microscopes became widely available in the 1950s, investigators described the internal anatomy of these structures in more detail. More recent advances in microscopy have allowed investigators to videotape certain types of cell processes in living cells.

What have anatomical studies based on microscopy revealed? Let’s look first at the general anatomy of prokaryotic cells and eukaryotic cells, and then consider how the structures that have been identified help cells function.

### Prokaryotic Cells

**Figure 7.1** shows the general structure of a prokaryotic cell. For most bacterial and archaeal species, the plasma membrane encloses a single compartment—meaning that the cell has few or no substructures delimited by internal membranes. Closer examination reveals a series of intricate structures, however. Let’s take a look at a typical prokaryotic cell, starting at the outside and working in.

As Chapter 6 pointed out, the cell membrane, or plasma membrane, consists of a phospholipid bilayer and proteins that either span the bilayer or attach to one side. Inside the membrane, the contents of a cell are collectively termed the cytoplasm (“cell-formed”). Because the cytoplasm contains a high concentration of solutes, in most habitats it is hypertonic relative to the surrounding environment. When this is the case, water enters the cell via osmosis and makes the cell’s volume expand. In virtually all bacteria and archaea, this pressure is resisted by a stiff cell wall. Bacterial and archaeal cell walls are a tough, fibrous layer that surrounds the plasma membrane. In many species the cell wall is made of a carbohydrate-protein complex called peptidoglycan or related substances (**Figure 7.2**). The pressure of the plasma membrane against the cell wall is about the same as the pressure in an automobile tire. The cell wall protects the organism and gives it shape and rigidity. In addition, many
bacteria have an additional protective layer outside the cell wall that consists of lipids with polysaccharides attached. Lipid molecules that contain carbohydrate groups are termed glycolipids.

In the cytoplasm of a prokaryotic cell, the most prominent structure is the chromosome. The prokaryotic chromosome consists of a large DNA molecule associated with a small number of proteins. In most species there is a single, circular chromosome, but other species have several circular chromosomes, and a few species—including the bacterium that causes Lyme disease—have one to several linear chromosomes. In prokaryotes and all other organisms, the sequence of nitrogenous bases in DNA acts as a code that contains the genetic, or heredity, information. Stated another way, the primary structure of DNA contains the instructions for making the proteins and other molecules needed by the cell. A gene is a segment of DNA that contains the information for building an RNA molecule or a polypeptide. Genes are components of chromosomes.

Prokaryotic chromosomes are found in a localized area of the cell called the nucleoid. The genetic material is not separated from the rest of the cytoplasm by a membrane, however. In the well-studied bacterium Escherichia coli, the circular chromosome is 500 times longer than the cell itself. This situation is typical in prokaryotes. To fit into the cell, the DNA double helix coils on itself with the aid of enzymes to form the highly compact, "supercoiled" structure shown in Figure 7.3. Supercoiled regions of DNA resemble a rubber band that has been held at either end and then twisted.

Depending on the species and population being considered, prokaryotic cells may also contain one to about a hundred small, usually circular, supercoiled DNA molecules called plasmids. Plasmids contain genes but are physically independent of the main, cellular chromosome. In most cases the genes carried by plasmids are not required under normal conditions; instead they help cells adapt to unusual circumstances, such as the sudden presence of a poison in the environment. As a result, plasmids can be considered auxiliary genetic elements. They are copied independently of the main chromosome and are passed along to daughter cells when the parent cell divides. Certain plasmid genes also allow a copy of the entire plasmid to be transferred from one cell to another. As a result, plasmids can spread through a population or even be passed between species. Plasmids have been studied intensively because some carry genes that confer resistance to antibiotics. One recently characterized plasmid carries genes that provide resistance to seven distinct antibiotics.

Two other prominent cell structures found in prokaryotes are ribosomes, which manufacture proteins, and flagella (singular: flagellum), which power movement. Ribosomes are observed in all prokaryotic cells and are found throughout the cytoplasm. Bacterial ribosomes are complex structures consisting of a total of three distinct RNA molecules and over 50 different proteins. These molecular components are organized into two major structural elements, called the large subunit and small subunit (Figure 7.4). It is not unusual for a single cell to contain 10,000 ribosomes. Both ribosomes and prokaryotic flagella lack a membrane. Not all bacterial species have flagella, however. When present they are usually few in number and are located on the surface of the cell. Over 40 different proteins are involved in building and controlling bacterial flagella. At top speed, flagellar movement can drive a bacterial cell through water at 60 cell lengths per second. In contrast, the cheetah qualifies as the fastest land animal but can sprint at a mere 25 body lengths per second.
Prokaryotes lack a nucleus, but it is not correct to say that no membrane-bound structures ever occur inside these cells. Many species contain membrane-bound storage containers, and extensive internal membranes occur in bacteria and archaia that perform photosynthesis. The photosynthetic membranes arise as invaginations of the plasma membrane. As the plasma membrane folds in, either vesicles pinch off or the types of flattened stacks shown in Figure 7.5 form. The internal parts of this membrane contain the enzymes and pigment molecules required to convert the kinetic energy in sunlight into chemical energy in the form of sugar.

In addition, recent research indicates that at least one bacterial species has an internal compartment that qualifies as an organelle (“little organ”). An organelle is a membrane-bound compartment in the cytoplasm that contains enzymes specialized for a particular function. The bacterial organelle that was just discovered has proton pumps in its membrane and an acidic environment inside, where calcium ions ($Ca^{2+}$) are stored.

Recent research has also shown that bacteria and archaea contain long, thin fibers that serve a structural role in the cell. All bacterial species, for example, contain fibers made from the protein FtsZ. These filaments are essential for cell division to take place. Some species also have protein filaments that help maintain cell shape. Protein filaments such as these form the basis of the cytoskeleton (“cell skeleton”).

Even though internal membranes and some cytoskeletal components are found in prokaryotic cells, their extent pales in comparison with that in eukaryotes. When typical prokaryotic and eukaryotic cells are compared side by side, three outstanding differences jump out: (1) Eukaryotic cells are usually much larger; (2) they contain extensive amounts of internal membrane; and (3) they feature a diverse and dynamic cytoskeleton.

Eukaryotic Cells

The lineage called Eukarya includes forms ranging from unicellular species to 100-meter-tall redwoods. Brown algae, red algae, fungi, amoebae, and slime molds are all eukaryotic, as are green plants and animals.

The first thing that strikes biologists about eukaryotic cells is how much larger they are on average than bacteria and archaia. Most eukaryotic cells range from about 5 to 100 \( \mu \text{m} \) in diameter, while most prokaryotic cells vary between 1 and 10 \( \mu \text{m} \) in diameter. A micrograph of an average eukaryotic cell, at the same scale as the bacterial cell in Figure 7.5, would fill this page. This difference in size inspired the hypothesis that when eukaryotes first evolved, they made their living by ingesting bacterial and archaeal cells whole. Stated another way, the evolution of large cell size is thought to have made it possible for eukaryotic cells to act as predators—organisms that kill and consume other organisms. Hundreds of eukaryotic species alive today still make their living by surrounding and taking in whole bacterial and archaeal cells.

The evolution of large cells has a downside, however. Ions and small molecules such as adenosine triphosphate (ATP), amino acids, and nucleotides cannot diffuse across a large volume quickly. If ATP is used up on one side of a large cell, ATP from the other side of the cell would take a long time to diffuse to that location. Prokaryotic cells are small enough that ions and small molecules arrive where they are needed via diffusion. In fact, the size of prokaryotic cells is probably limited by the distance that molecules must diffuse or be transported inside the cell.

How do eukaryotic cells solve the diffusion problem? The answer lies in the numerous organelles observed in eukaryotic cells. In effect, the huge volume inside a eukaryotic cell is compartmentalized into a large number of bacterium-sized parts. Because eukaryotic cells are subdivided, the molecules required for specific chemical reactions are often located within a given compartment and do not need to diffuse long distances to be useful. But solving the diffusion problem is not the only advantage conferred by organelles:

- **Compartmentalization of the cell allows incompatible chemical reactions to be separated.** For example, new fatty acids are synthesized in one organelle while excess or damaged fatty acids are degraded and recycled in a different organelle.
- **Compartmentalization increases the efficiency of chemical reactions.** First, the substrates required for particular reactions can be localized and maintained at high concentration within organelles. Second, groups of enzymes that work together can be clustered on internal membranes instead of floating free in the cytoplasm. Clustering these molecules increases the speed and efficiency of the reactions, because reactants have shorter distances over which to diffuse or be transported.

Based on their morphological differences, prokaryotic cells can be compared to small machine shops while eukaryotic cells
On average, prokaryotes are about 10 times smaller than eukaryotic cells in diameter and about 1000 times smaller than eukaryotic cells in volume.

FIGURE 7.6 Animal and Plant Cells
Generalized or "typical" (a) animal and (b) plant cells. (Compare with the prokaryotic cell, shown at true relative size at bottom left.)

QUESTION Which organelles are unique to animal cells, and which organelles are unique to plant cells? Which are common to both?
resemble sprawling industrial complexes. The organelles and other structures found in eukaryotes are analogous to highly specialized buildings that act as factories, power stations, warehouses, transportation corridors, and administrative centers. Figure 7.6 shows how organelles are arranged in a typical animal cell and plant cell. What are these structures, and what do they do?

The Nucleus The nucleus is among the largest organelles and is highly organized (Figure 7.7). It is enclosed by a unique structure—a complex double membrane called the nuclear envelope, which is studded with openings called nuclear pores. The inside surface of the nuclear envelope is associated with fibrous proteins that form a lattice-like sheet called the nuclear lamina. The nuclear lamina stiffens the envelope and helps organize the chromosomes. Each chromosome occupies a distinct area inside the nucleus and is attached to the nuclear lamina and the inner surface of the nuclear envelope in at least one location. In eukaryotes, chromosomes are linear and consist of DNA that is tightly complexed with a series of ball-shaped histone proteins, forming a structure called chromatin. Some sections of each chromosome are condensed into a highly compact, supercoiled structure called heterochromatin; other sections are unwound into long, filamentous strands called euchromatin. The nucleus also includes a distinctive region called the nucleolus, where the RNA molecules found in ribosomes are manufactured and the large and small ribosomal subunits are assembled. Section 7.2 discusses the structure and function of the nucleus, and particularly the nuclear envelope, in more detail.

Ribosomes In eukaryotes, the cytoplasm consists of everything inside the plasma membrane excluding the nucleus; the fluid portion of the cytoplasm is called the cytosol. Many of the cell’s millions of ribosomes are scattered throughout the cytosol. The ribosomes shown in Figure 7.8 are comprised of two subunits, one small and one large. Each subunit is comprised of several different proteins and one large RNA molecule. In eukaryotes the large subunit also contains two small RNA molecules. (In prokaryotes the large subunit has just one small and one large RNA molecule.) Neither ribosomal subunit is enclosed by a membrane. When the two subunits come together, they form a complex molecular machine that synthesizes proteins.

Rough Endoplasmic Reticulum In addition to the ribosomes found free in the cytosol, many ribosomes are associated with membranes. More specifically, hundreds of thousands of ribosomes are attached to a network of membrane-bound sacs and tubules called the rough endoplasmic reticulum, or rough ER. Translated literally, endoplasmic reticulum means “inside-formed network.” Notice in Figure 7.6 that the ER is continuous with the outer membrane of the nuclear envelope. From there, the layers of sacs extend into the cytoplasm.
The ribosomes associated with the rough ER are responsible for synthesizing proteins that will be inserted into the plasma membrane, secreted to the cell exterior, or shipped to an organelle called the lysosome. As they are being manufactured by ribosomes, these proteins move to the interior of the sac-like component of the rough ER (Figure 7.9). The interior of any sac-like structure in a cell or body is called the lumen. In the lumen of the rough ER, newly manufactured proteins undergo folding and other types of processing.

The proteins produced in the rough ER have a variety of functions. Some carry messages to other cells; some act as membrane transport proteins or pumps; others are enzymes. The common theme is that rough ER products are destined for transport to a distant destination—often to the surface of the cell or beyond.

Golgi Apparatus In many cases, the products of the rough ER pass through the Golgi apparatus before they reach their final destination. The Golgi apparatus consists of flattened, membranous sacs called cisternae (singular: cisternum), which are stacked on top of one another (Figure 7.10). The organelle also has a distinct polarity, or sidedness. The cis (“this side”) surface is closest to the rough ER and nucleus, and the trans (“across”) surface is oriented toward the plasma membrane. The cis side receives products from the rough ER, and the trans side ships them out toward the cell surface. In between, within the cisternae, the rough ER’s products are processed and packaged for delivery. Micrographs often show “bubbles” on either side of the Golgi stack. These are membrane-bound vesicles that carry proteins or other products to and from the organelle. Section 7.3 analyzes the intracellular movement of products in more detail.

Smooth Endoplasmic Reticulum Not all of the ER is associated with transport of material to Golgi sacs, and not all ER has ribosomes attached. While parts of the ER that contain ribosomes look dotted and rough in electron micrographs, the portions of the organelle that are free of ribosomes appear smooth and even. Appropriately enough, these parts of the ER are called smooth endoplasmic reticulum or smooth ER (Figure 7.11). The smooth ER membrane contains enzymes that are required for reactions involving lipids. Depending on the type of cell, these enzymes may be involved in synthesizing specialized types of lipids needed by the organism or in breaking down hydrophobic molecules that are poisonous to the cell. Smooth ER is the manufacturing site for phospholipids required for the plasma membrane, and smooth ER also functions as a reservoir for calcium ions ($Ca^{2+}$) that act as a signal inside the cell.

The structure of endoplasmic reticulum correlates closely with its function. Rough ER has ribosomes and functions primarily as a protein-manufacturing center; smooth ER lacks ribosomes and functions primarily as a lipid-processing center.
Together with the Golgi apparatus and lysosomes, the endoplasmic reticulum forms the endomembrane system. The endomembrane (“inner-membrane”) system is the primary center for protein and lipid synthesis in eukaryotic cells.

**Peroxisomes** Peroxisomes are globular organelles that are found in virtually all eukaryotic cells (Figure 7.12). They have a single membrane and grow and divide independently of other organelles. Although different types of cells from the same individual may have distinct types of peroxisomes, these organelles are united by a common function: Peroxisomes are centers for oxidation reactions. In many cases the products of these reactions include hydrogen peroxide ($\text{H}_2\text{O}_2$), which is highly corrosive. If hydrogen peroxide escaped from the peroxisome, the $\text{H}_2\text{O}_2$ would quickly damage organelle membranes and the plasma membrane. This is rare, however. Inside the peroxisome, the enzyme catalase quickly converts hydrogen peroxide to water and oxygen.

The various types of peroxisomes that exist contain different suites of enzymes. As a result, each is specialized for oxidizing particular compounds. For example, the peroxisomes in your liver cells contain enzymes that oxidize an array of toxins, including the ethanol in alcoholic beverages. The products of these oxidation reactions are usually harmless and are either excreted from the body or used in other reactions. Other peroxisomes contain enzymes that catalyze the oxidation of fatty acids. These reactions result largely in the production of a molecule called acetyl CoA, which is used for the synthesis of fatty acids in the cell. In plant leaves, specialized peroxisomes called glyoxisomes are packed with enzymes that convert one of the products of photosynthesis into a sugar that can be used to produce energy for the cell. Seeds do not perform photosynthesis, so they lack this type of peroxisome. Instead, they have peroxisomes with enzymes that oxidize fatty acids to yield glucose. The glucose is then used by the young plant as it begins to grow. In each case, there is a clear connection between structure and function: The enzymes found inside the peroxisome make a specialized set of oxidation reactions possible.

**Lysosomes** The major structures involved in solid-waste processing and materials storage in the cell are called lysosomes. The size and shape of these organelles vary widely, and in the cells of plants, fungi, and certain other groups they are referred to as vacuoles. In animal cells, lysosomes function as digestive centers (Figure 7.13). The organelle’s interior, or lumen, is acidic and has a single membrane.
because a proton pump in the lysosome membrane imports enough hydrogen ions to maintain a pH of 5.0. This organelle also contains about 40 different enzymes. Each of these proteins is specialized for breaking up a different type of macromolecule—proteins, nucleic acids, lipids, or carbohydrates—into its component monomers. These digestive enzymes are collectively called acid hydrolases because they hydrolyze macromolecules most efficiently at pH 5.0. In the cytosol, where the pH is about 7.2, these enzymes are less active.

**Figure 7.14** illustrates three ways that materials are delivered to lysosomes in animal cells:

1. **When phagocytosis (“eat-cell-act”)** occurs, the plasma membrane of a cell surrounds a smaller cell or a food particle and engulfs it. The resulting structure is delivered to a lysosome, where it is taken in and digested.

2. **During autophagy (“same-eating”),** damaged organelles are surrounded by a membrane and delivered to a lysosome. There the components are digested and recycled.

3. **Materials can also find their way into lysosomes as a result of receptor-mediated endocytosis.** This process begins when macromolecules outside the cell bind to membrane proteins that act as receptors. More than 25 distinct receptors have now been characterized, each specialized for responding to a different macromolecule. Once binding occurs, the plasma membrane folds in and pinches off to form a membrane-bound vesicle called an early endosome (“inside-body”). Early endosomes undergo a series of processing steps that include the receipt of digestive enzymes from the Golgi apparatus and the activation of proton pumps that gradually lower their pH. In this way, early endosomes undergo a gradual maturation process that may lead to the formation of a late endosome and eventually a fully functioning lysosome.

Regardless of whether materials are delivered to lysosomes via phagocytosis, autophagy, or receptor-mediated endocytosis, the result is similar: molecules are hydrolyzed. The amino acids, nucleotides, sugars, and other molecules that result from acid hydrolysis leave the lysosome via transport proteins in the organelle’s membrane. Once in the cytoplasm, they can be reused.

It is important to note, however, that not all of the materials that are surrounded by membrane and taken into a cell end up in lysosomes. Endocytosis (“inside-cell-act”) refers to any pinching off of the plasma membrane that results in the uptake of material from outside the cell. Endocytosis can occur in three ways: (1) phagocytosis, (2) receptor-mediated endocytosis, and (3) pinocytosis (“drink-cell-act”). Pinocytosis brings fluid into the cytoplasm via tiny vesicles that form from invaginations of the plasma membrane. The fluid inside these vesicles is not transported to lysosomes, but is used elsewhere in the cell. In addition, most of the macromolecules that collect in early endosomes are selectively removed and used long before the structure becomes a lysosome.

Compared with the lysosomes of animal cells, the vacuoles of plant and fungal cells are large—sometimes taking up as much as 80 percent of a plant cell’s volume (**Figure 7.15**). Although some vacuoles contain enzymes that are specialized for digestion, most of the vacuoles observed in plant and fungal cells are storage centers. **Figure 7.15** shows a vacuole with a scale bar of 1 µm.
cells act as storage depots. In many cases, the stored material is water, which maintains the cell’s normal volume, or ions such as potassium ($K^+$) and chloride ($Cl^-$). But inside seeds, cells may contain a large vacuole filled with proteins. When germination occurs, enzymes begin digesting these proteins to provide amino acids for the growing individual. In cells that make up flower petals or fruits, vacuoles are filled with colorful pigments. Elsewhere in the plant, vacuoles may be packed with noxious compounds that protect leaves and stems from being eaten by predators. The type of chemical involved varies by species, ranging from bitter-tasting tannins to toxins such as nicotine, morphine, caffeine, or cocaine.

Mitochondria The chemical energy required to build all of these organelles and do other types of work comes from adenosine triphosphate (ATP), most of which is produced in the cell’s mitochondria (singular: mitochondrion). As Figure 7.16 shows, each mitochondrion has two membranes. The outer membrane defines the organelle’s surface, while the inner membrane contacts a series of sac-like cristae. The solution inside the inner membrane is called the mitochondrial matrix. In eukaryotes, most of the enzymes and molecular machines responsible for providing chemical energy in the form of ATP from food molecules are embedded in the membranes of the cristae or suspended in the matrix. Depending on the type of cell, from 50 to more than a million mitochondria may be present.

Each mitochondrion contains its own small chromosome, independent of the main chromosomes in the nucleus. Mitochondrial DNA is a component of a circular and supercoiled chromosome that is similar in structure to bacterial chromosomes. Mitochondria also manufacture their own ribosomes. Like most organelles, mitochondria can grow and divide independently of nuclear division and cell division.

Chloroplasts Most algal and plant cells possess an organelle called the chloroplast, in which sunlight is converted to chemical energy during photosynthesis. The chloroplast has a double membrane around its exterior, analogous to the structure of a mitochondrion (Figure 7.17). Instead of featuring sac-like cristae that connect to the inner membrane, though, the interior of the chloroplast is dominated by hundreds of membrane-bound, flattened vesicles called thylakoids, which are independent of the inner membrane. Thylakoids are stacked like pancakes into piles called grana (singular: granum). Many of the pigments, enzymes, and molecular machines responsible for converting light energy into carbohydrates are embedded in the thylakoid membranes. Certain critical enzymes and substrates, however, are found outside the thylakoids in the region called the stroma.

The number of chloroplasts per cell varies from none to several dozen. Like mitochondria, each chloroplast contains a circular chromosome. Chloroplast DNA is independent of the main
genetic material inside the nucleus. Chloroplasts also grow and divide independently of nuclear division and cell division.

Cytoskeleton  The final major structural feature that is common to all eukaryotic cells is an extensive system of protein fibers called the cytoskeleton. As we’ll see in Section 7.4, the cytoskeleton contains several distinct types of proteins and fibers and has an array of functions. In addition to giving the cell its shape, cytoskeletal proteins are involved in moving the cell itself and in moving materials within the cell.

The Cell Wall In fungi, algae, and plants, cells possess an outer cell wall in addition to their plasma membrane (Figure 7.18). Animals, amoebae, and other groups lack this feature. Although the composition of the cell wall varies among species and even between types of cells in the same individual, the general plan is similar: Rods or fibers composed of a carbohydrate run through a stiff matrix made of other polysaccharides and proteins. In addition, some plant cells produce a secondary cell wall that features a particularly tough molecule called lignin. Lignin forms a branching, cagelike network that is almost impossible for enzymes to attack. The combination of cellulose fibers and lignin in secondary cell walls makes up most of the material we call wood.

How Does Cell Structure Correlate with Function? The preceding discussion emphasized how the structure of each organelle fits with its role in the cell. As Table 7.1 indicates, an organelle’s membrane and its complement of enzymes correlate closely with its function. The same connection between structure and function occurs at the level of the entire cell. Inside an individual plant or animal, cells are specialized for certain tasks and have a structure that correlates with those tasks. For example, the muscle cells in your upper leg are extremely long, tube-shaped structures. They are filled with protein fibers that slide past one another as the entire muscle flexes or extends. It is this sliding motion that allows your muscles to contract or extend as you run. Muscle cells are also jam packed with mitochondria, which produce the ATP required for the sliding motion to occur. In contrast, nearby fat cells are rounded, globular structures. They consist of little more than a plasma membrane, a nucleus, and a fat droplet. Neither cell bears a close resemblance to the generalized animal cell pictured in Figure 7.6a.

To drive home the correlation between the overall structure and function of a cell, examine the transmission electron micrographs in Figure 7.19. The animal cell in Figure 7.19a is from the pancreas and is specialized for the manufacture and export of digestive enzymes. It is packed with rough ER and

![Figure 7.18](image1.png)

**FIGURE 7.18** Cell Walls Protect Plants and Fungi
Plants have cell walls that contain cellulose; in fungi the major structural component of the cell wall is chitin.

![Figure 7.19](image2.png)

**FIGURE 7.19** Cell Structure Correlates with Function
EXERCISE In each cell, label ribosomes, rough ER, chloroplasts, the nucleus, smooth ER, mitochondria, vacuole, plasma membrane, and cell wall if they are visible.
TABLE 7.1 A Summary of Cell Components

<table>
<thead>
<tr>
<th>Structure</th>
<th>Membrane</th>
<th>Components</th>
<th>Function</th>
</tr>
</thead>
<tbody>
<tr>
<td>Nucleus</td>
<td>Double (“envelope”); openings called nuclear pores</td>
<td>Chromosomes, Nucleolus, Nuclear lamina</td>
<td>Genetic information, Assembly of ribosome subunits, Structural support</td>
</tr>
<tr>
<td>Ribosomes</td>
<td>None</td>
<td>Large/small subunits, Complex of RNA and proteins</td>
<td>Protein synthesis</td>
</tr>
<tr>
<td>Endomembrane system</td>
<td>None</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Rough ER</td>
<td>Single; contains receptors for entry of selected proteins</td>
<td>Network of branching sacs, Ribosomes associated</td>
<td>Protein synthesis and processing</td>
</tr>
<tr>
<td>Golgi apparatus</td>
<td>Single; contains receptors for products of rough ER</td>
<td>Stack of flattened cisternae</td>
<td>Processing of proteins</td>
</tr>
<tr>
<td>Smooth ER</td>
<td>Single; contains enzymes for synthesizing phospholipids</td>
<td>Network of branching sacs, Enzymes for synthesizing lipids</td>
<td>Lipid synthesis</td>
</tr>
<tr>
<td>Peroxisomes</td>
<td>Single; contains transporters for selected macromolecules</td>
<td>Enzymes that catalyze oxidation reactions, Catalase (processes peroxide)</td>
<td>Processing of fatty acids</td>
</tr>
<tr>
<td>Lysosomes</td>
<td>Single; contains proton pumps</td>
<td>Acid hydrolases (catalyze hydrolysis reactions)</td>
<td>Digestion and recycling</td>
</tr>
<tr>
<td>Vacuoles</td>
<td>Single; contains transporters for selected molecules</td>
<td>Varies—pigments, oils, carbohydrates, water, or toxins</td>
<td>Varies—coloration; storage of oils, carbohydrates, water, or toxins</td>
</tr>
<tr>
<td>Mitochondria</td>
<td>Double; outer contains enzymes for processing pyruvate; inner contains enzymes for ATP production</td>
<td>Enzymes that catalyze oxidation-reduction reactions, ATP synthesis</td>
<td>ATP production</td>
</tr>
<tr>
<td>Chloroplasts</td>
<td>Double, plus membrane-bound sacs in interior</td>
<td>Pigments, Enzymes that catalyze oxidation-reduction reactions</td>
<td>Production of ATP and sugars via photosynthesis</td>
</tr>
<tr>
<td>Cytoskeleton</td>
<td>None</td>
<td>Actin filaments, Intermediate filaments, Microtubules</td>
<td>Structural support, Movement of materials, In some species: movement of whole cell</td>
</tr>
<tr>
<td>Plasma membrane</td>
<td>Single; contains transport and receptor proteins</td>
<td>Phospholipid bilayer with transport and receptor proteins</td>
<td>Selective permeability—maintains intracellular environment</td>
</tr>
<tr>
<td>Cell wall</td>
<td>None</td>
<td>Carbohydrate fibers running through carbohydrate or protein matrix</td>
<td>Protection, structural support</td>
</tr>
</tbody>
</table>

Golgi, which make this function possible. The animal cell in Figure 7.19b is from the testis and synthesizes the lipid-soluble signaling molecule called testosterone. This cell is dominated by smooth ER, where lipid processing takes place. The plant cell in Figure 7.19c is from the leaf of a potato and is specialized for absorbing light and manufacturing sugars; the cell in Figure 7.19d is from a potato tuber (part of an underground stem) and functions as a starch storage container. The leaf cell contains hundreds of chloroplasts, while the tuber cell has a prominent storage vacuole filled with carbohydrate. In each case, the type of organelles in each cell and their size and number correlate with the cell’s specialized function.

The Dynamic Cell

Biologists describe the structure and function of organelles and cells by a combination of tools and approaches. Light microscopes and transmission electron microscopes have allowed researchers to see cells at increasingly high magnification. Microscopy allowed biologists to characterize the basic size and shape of organelles and where they occurred in the cell; a technique called differential centrifugation made it possible to isolate particular cell components and analyze their chemical composition. As Box 7.1 (page 140) explains, differential centrifugation is based on breaking cells apart to create a complex mixture and then separating components in a centrifuge. The individual parts of the cell can then be purified and studied in detail.

Although these techniques have led to an increasingly sophisticated understanding of how cells work, they have a limitation. Transmission electron microscopy is based on a fixed “snapshot” of the cell that is to be observed, and differential centrifugation is based on splitting cells apart to create a complex mixture and then separating components in a centrifuge. The information gleaned from these techniques can make cells seem somewhat static. In reality, cells are dynamic.
For decades, the centrifuge was among the most common tools used by biologists who study life at the level of molecules and cells. It was vital to early studies of organelles and other cell structures because it can separate cell components efficiently. A centrifuge accomplishes this by spinning cells in a solution that allows molecules and other cell components to separate according to their density or size and shape.

The first step in preparing a cell sample for centrifugation is to release the organelles and cell components by breaking the cells apart. This can be done by putting them in a hypotonic solution, by exposing them to ultrasonic vibration, by treating cells with a detergent, or by grinding them up. Each of these methods breaks apart plasma membranes and releases the contents of the cells.

The pieces of plasma membrane broken up by these techniques quickly resell to form small vesicles, often trapping cell components inside. The solution that results from the homogenization step is a mixture of these vesicles, free-floating macromolecules released from the cells, and organelles. A solution such as this is called a cell extract or cell homogenate.

When a cell homogenate is placed in a centrifuge tube and spun at high speed, the components that are in solution tend to move outward, along the dashed line in Figure 7.20a. The effect is similar to a merry-go-round, which seems to push you outward in a straight line away from the spinning platform. In response to this outward-directed force, the solution containing the cell homogenate exerts a centripetal (“center-seeking”) force that pushes the homogenate away from the bottom of the tube. Larger, denser molecules or particles resist this inward force more readily than do smaller, less dense ones and so reach the bottom of the centrifuge tube faster.

To separate the components of a cell extract, researchers often perform a series of centrifuge runs. Steps 1 and 2 of Figure 7.20b illustrate how an initial treatment at low speed causes larger, heavier parts of the homogenate to move below smaller, lighter parts. The material that collects at the bottom of the tube

is called the pellet, and the solution and solutes left behind comprise the supernatant (“above swimming”). The supernatant is placed in a fresh tube and centrifuged at increasingly higher speeds and longer durations. Each centrifuge run continues to separate cell components based on their size and density.

To accomplish even finer separation of macromolecules or organelles, researchers frequently follow up with centrifugation at extremely high speeds. One strategy is based on filling the centrifuge tube with a series of sucrose solutions of increasing density. The density gradient allows cell components to separate on the basis of small differences in size and shape. When the centrifuge run is complete, each cell component comprises a distinct band of material in the tube. A researcher can then collect the material in each band for further study.
The amount of chemical activity and the speed of molecular movement inside cells is nothing short of fantastic. Bacterial ribosomes add up to 20 amino acids per second to a growing polypeptide, and eukaryotic ribosomes typically add two per second. Given that there are about 15,000 ribosomes in each bacterium and possibly a million in an average eukaryotic cell, hundreds or even thousands of new protein molecules can be finished each second in every cell. In the same amount of time, a typical cell in your body uses an average of 10 million ATP molecules and synthesizes just as many. It’s not unusual for a cellular enzyme to catalyze 25,000 or more reactions per second; most cells contain hundreds or thousands of enzymes. A minute is more than enough time for each membrane phospholipid in your body to travel the breadth of the organelle or cell where it resides. The hundreds of trillions of mitochondria inside you are completely replaced about every 10 days, for as long as you live. The plasma membrane is fluid, and its composition is constantly changing.

Because humans are such large organisms, it is impossible for us to imagine what life is really like inside a cell. At the scale of a ribosome or an organelle or a cell, gravity is inconsequential. Instead, electrostatic attractions between molecules and the kinetic energy of motion are the dominant forces. At this level, events take nanoseconds, and speeds are measured in micrometers per second. Contemporary methods for studying cells, including those featured in Box 7.2, capture this dynamism by tracking how organelles and molecules move and interact over time.

The rest of this chapter focuses on this theme of cellular dynamism and movement. To begin, let’s look at how molecules move into and out of the cell’s control center—the nucleus. Then we’ll consider how proteins move from ribosomes into the lumen of the rough ER and then to the Golgi apparatus and beyond. The chapter closes by analyzing how cytoskeletal elements help transport cargo inside the cell or move the cell itself.

**BOX 7.2 Techniques for Studying the Dynamic Cell**

Contemporary methods for studying cells allow researchers to see specific molecules moving inside living cells. One of the most popular techniques for tagging molecules of interest relies on a fluorescent molecule called green fluorescent protein, or GFP. GFP is naturally synthesized in jellyfish that fluoresce, or emit light. By affixing GFP molecules to another protein and then inserting it into a cell, investigators can follow its fate over time and even videotape its movement. For example, recent studies have used GFP to tag proteins that are secreted from the cell. Control experiments show that GFP does not affect the behavior of these proteins. Researchers then videotaped the GFP-tagged protein’s transport from the rough ER through the Golgi apparatus and out to the plasma membrane. This is cell biology; the movie.

To produce extremely high resolution still images of proteins that are tagged with GFP or other fluorescing tags, researchers often rely on confocal microscopy. This technique is based on mounting live cells on a microscope slide and then focusing a beam of ultraviolet light at a specific depth within the specimen. The fluorescing tag emits visible light in response. A detector for this light is then set up at exactly the position where the emitted light comes into focus. The result is a sharp image of a precise plane in the cell being studied (Figure 7.21).

(a) Conventional fluorescence image  
(b) Confocal fluorescence image

**FIGURE 7.21 Confocal Microscopy Provides Sharp Images of Living Cells**
The same living cells from the intestine of a mouse at the same magnification. (a) The conventional image is blurred, because it results from light emitted by the entire group of cells. (b) The confocal image is sharp, because it results from light emitted at a single plane inside the cells.
7.2 The Nuclear Envelope: Transport Into and Out of the Nucleus

The nucleus is the information center of eukaryotic cells. It is a corporate headquarters, design center, and library all rolled into one. Appropriately enough, its interior is highly organized. The organelle’s overall shape and structure are defined by the mesh-like nuclear lamina, which also helps anchor each chromosome. The remainder of each chromosome occupies a well-defined region in the nucleus, and specific centers exist where the genetic information in DNA is decoded and processed. At these locations, large suites of enzymes interact to produce RNA messages from specific genes at specific times. Meanwhile, the nucleolus functions as the site of ribosome synthesis.

Consistent with its role as information repository and processing center, the nucleus is separated from the rest of the cell by the nuclear envelope. Biologists began to understand exactly how the nuclear envelope is structured when electron microscopy became available in the 1950s. As Figure 7.22a shows, the nuclear envelope has two membranes, each consisting of a lipid bilayer. The inner membrane and the outer membrane are separated by a space that is continuous with the lumen of the endoplasmic reticulum. Later, electron micrographs showed that the envelope contains thousands of openings called nuclear pores (Figure 7.22b). Because these pores extend through both inner and outer nuclear membranes, they connect the inside of the nucleus with the cytoplasm. The pore itself consists of over 50 different proteins. These molecules form an elaborate structure called the nuclear pore complex (Figure 7.22c).

A series of experiments in the early 1960s showed that molecules travel into and out of the nucleus through the nuclear pore complexes. The initial studies were based on injecting tiny gold particles into cells and then preparing them for electron microscopy. In electron micrographs, gold particles show up as black dots. One or two minutes after injection, the micrographs showed that most of the gold particles were in the cytoplasm. A few, however, were closely associated with nuclear pores. Ten minutes after injection, particles were inside the nucleus as well as in the cytoplasm. These data supported the hypothesis that the pores function as the doors to the nucleus. Follow-up work confirmed that the nuclear pore complex is the only gate between the cytoplasm and the nucleus and that only certain molecules go in and out. Passage through the nuclear pore is selective.

What substances traverse nuclear pores? DNA clearly does not—it never leaves the nucleus. But information coded in DNA is used to synthesize RNA inside the nucleus. Several distinctive types of RNA molecules are produced, each distinguished by size and function. For example, most ribosomal RNAs are manufactured in the nucleolus, where they bind to proteins to form completed ribosomal subunits. Messenger RNAs, in contrast, carry the information required to manufacture proteins out to the cytoplasm, where protein synthesis takes place. To perform their function, all of the various types of RNA move out of the nucleus. Traffic in the other direction is also impressive.
triposphates that act as building blocks for DNA and RNA must enter the nucleus, as do the proteins responsible for copying DNA, synthesizing RNAs, extending the nuclear lamina, assembling ribosomes, or building chromosomes (Figure 7.23). To summarize, ribosomal subunits and various types of RNAs exit the nucleus; proteins that are needed inside enter it. In a typical cell, over 500 molecules pass through each of the 3000–4000 nuclear pores every second. The traffic is intense. How is it regulated and directed?

How Are Molecules Imported into the Nucleus?

The first experiments on how molecules move through the nuclear pore focused on proteins that are produced by viruses. Viruses are parasites that use the cell’s machinery to make copies of themselves. When a virus infects a cell, certain of its proteins enter the nucleus. Investigators noticed that if a particular amino acid in one of these proteins happens to be altered, the viral protein is no longer able to pass through the nuclear pore. This simple-sounding observation led to a key hypothesis: Proteins that are synthesized by ribosomes in the cytosol but are headed for the nucleus contain a “zip code”—a molecular address tag that marks them for transport through the nuclear pore complex. The idea was that viral proteins enter the nucleus if they have the same address tag as normal cellular proteins have. This zip code came to be called the nuclear localization signal (NLS).

A series of experiments on a protein called nucleoplasmin helped researchers better understand the nature of this signal. Nucleoplasmin plays an important role in the assembly of chromosomes and happens to have a distinctive structure: It consists of a globular protein core surrounded by a series of extended protein “tails.” When researchers labeled nucleoplasmin with a radioactive atom and injected it into the cytoplasm of living cells, they found that the radioactive signal quickly ended up in the nucleus.

Figure 7.24 outlines how the nuclear localization signal in nucleoplasmin was found. Researchers began by using enzymes called proteases to separate the core sections of nucleoplasmin from the tails. After separating the two components, the researchers labeled each part with radioactive atoms and injected them into the cytoplasm of different cells. When they

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**Question:** Where is the “Send to nucleus” zip code in the nucleoplasmin protein?

**Hypothesis:** The “Send to nucleus” zip code is in either the tail region or the core region of the nucleoplasmin protein.

**Null hypothesis:** The zip code is not on the nucleoplasmin protein itself, or there is no zip code.

**Experimental setup:**

1. Use protease to cleave tails off of nucleoplasmin protein core.
2. Attach radioactive label.
3. Inject labeled protein fragments into cytoplasm of cell.
4. Wait, then locate labeled fragments ....

**Prediction:**

**Prediction of null hypothesis:**

**Results:**

Tail fragments located in nucleus  
Core fragments still located in cytoplasm

**Conclusion:**

Figure 7.24 Where is the “Send to Nucleus” Zip Code in the Nucleoplasmin Protein?  
EXERCISE Without looking at the text, fill in the predictions and conclusion(s) in this experiment.
examined the experimental cells with the electron microscope, they found that tail fragments were transported to the nucleus. Core fragments, in contrast, remained in the cytoplasm. These data suggested that the zip code must be somewhere in the tail part of the protein.

By analyzing different stretches of the tail section, the biologists eventually found a 17-amino-acid-long section that had to be present to direct proteins to the nucleus. The biologists therefore concluded that instead of consisting of five numbers, the NLS zip code consisted of 17 specific amino acids in the tail.

Follow-up work confirmed that other proteins bound for the nucleus have similar localization signals, and that these signals interact with proteins called importins. Figure 7.25 summarizes the current model for how nuclear import takes place. Several different molecules are involved: the protein being transported, an importin, ATP, guanosine diphosphate (GDP) or guanosine triphosphate (GTP), and a protein called Ran. GTP is similar in structure to ATP and has high potential energy. If you think of the protein as cargo, the importin as a delivery truck, and ATP as gas, then Ran is the unloading crew and GTP is their supervisor. More specifically, data suggest that when an importin in the cytoplasm binds to a molecule that has a nuclear localization signal, the importin/cargo complex enters the nucleus along with Ran that has GDP bound to it. The movement of the cargo requires ATP. Inside, an enzyme exchanges the GDP for GTP. When this reaction occurs, Ran’s conformation changes. It binds to the importin/cargo complex, causing the cargo molecule to drop off. Ran then escorts the importin back out to the cytoplasm. There the import sequence starts anew.

Work on nuclear import carries two general messages:

1. Movement is highly regulated. Although small molecules can diffuse freely into and out of the nuclear pore complex, larger molecules can enter only if they contain a nuclear localization signal.

2. Movement of large molecules is an energy-demanding, active process.

Do the same general principles hold when RNAs and other materials move out of the nucleus?

How Are Molecules Exported from the Nucleus?

After several decades’ worth of experiments, biologists have come to a satisfying conclusion: Export of ribosome subunits, proteins, and other materials from the nucleus is almost exactly the reverse of import. In almost all cases, Ran and GTP are involved, as are shuttle proteins called exportins. Further, proteins that leave the nucleus have a specific zip code—a nuclear export signal. Distinct types of exportins are specialized for binding to the different types of materials and ferrying them to the cytoplasm. The Ran molecules and exportins responsible for nuclear export cycle back and forth, into and out of the nucleus, just as they do during import. Like nuclear import, nuclear export is both highly regulated and energy demanding.

Currently, biologists are focused on understanding how Ran interacts with proteins inside the nuclear pore complex as cargo moves in and out. Investigators are also trying to unravel how traffic is regulated to avoid backups and head-on collisions. The goal is to understand the precise physical mechanisms responsible for moving cargo into and out of the nuclear pore complex.

**Figure 7.25 An Importin, Ran, and GDP Are Required to Import Proteins into the Nucleus**

Importin, Ran, and GDP are recycled to the cytoplasm after they deliver cargo to the nucleus.
7.3 The Endomembrane System: Manufacturing and Shipping Proteins

The nuclear membrane is not the only place in cells where cargo moves in a regulated and energy-demanding fashion. For example, Chapter 6 highlighted how specific ions and molecules are pumped into and out of cells or transported across the plasma membrane by specialized membrane proteins. In addition, proteins that are synthesized by ribosomes in the cytosol but are used inside mitochondria or chloroplasts contain special signal sequences, analogous to the nuclear localization signal, that target the proteins for transport to these organelles.

Perhaps the most intricate of all manufacturing and shipping systems, however, involves proteins that are synthesized in the rough ER and move to the Golgi apparatus for processing, and from there travel to the cell surface or other destinations. The idea that materials might move through the endomembrane system in an orderly way was inspired by a simple observation. According to electron micrographs, cells that secrete digestive enzymes, hormones, or other types of products have particularly large amounts of rough ER and Golgi. This correlation led to the idea that these cells have a “secretory pathway” that starts in the rough ER and ends with products leaving the cell (Figure 7.26). How does this hypothesized pathway work?

George Palade and colleagues did pioneering research on the secretory pathway with an experimental approach known as a pulse-chase experiment. The strategy is based on providing experimental cells with a large concentration of a labeled molecule for a short time. For example, if a cell receives a large amount of labeled amino acid for a short time, virtually all of the proteins synthesized during that interval will be labeled. This “pulse” of labeled molecule is followed by a chase—large amounts of an unlabeled version of the same molecule, provided for a long time. If the chase consists of unlabeled amino acid, then the proteins synthesized during the chase period will not be labeled. The general idea is to mark a population of molecules at a particular interval and then follow their fate over time. This approach is analogous to adding a small amount of dye to a stream and then following the movement of the dye molecules.

In testing the secretory pathway hypothesis, Palade’s team focused on pancreatic cells that were growing in culture, or in vitro. These cells are specialized for secreting digestive enzymes into the small intestine and are packed with rough ER and Golgi. The basic experimental approach was to supply the cells with a 3-minute pulse of the amino acid leucine, labeled with a radioactive atom, followed by a long chase with nonradioactive leucine. Because the radioactive leucine was incorporated into all proteins being produced during the pulse, it labeled them. Then the researchers

1The term in vitro is Latin for “in glass.” Experiments that are performed outside living cells are done in vitro. The term in vivo, in contrast, is Latin for “in life.” Experiments performed with living organisms are done in vivo.

WEB TUTORIAL 7.2
A Pulse-Chase Experiment

FIGURE 7.26 The Secretory Pathway
Hypothesis
The secretory pathway hypothesis proposes that proteins intended for secretion from the cell are synthesized and processed in a highly prescribed set of steps.
prepared a sample of the cells for electron microscopy and autoradiography (see Chapter 4). When they examined cells immediately after the pulse, they found the newly synthesized proteins inside the rough ER (Figure 7.27a). Seven minutes later, most of the labeled proteins were in a Golgi apparatus or inside structures called secretory vesicles on the trans side of a Golgi apparatus (Figure 7.27b). After 80 minutes, most labeled proteins were in secretory vesicles or actually outside the cell (Figure 7.27c).

These results were consistent with the hypotheses that a secretory pathway exists and that the rough ER and Golgi apparatus function as an integrated endomembrane system. Clearly, proteins produced in the rough ER don’t float around the cytoplasm aimlessly or drift randomly from organelle to organelle. Instead, traffic through the endomembrane system is highly organized and directed. Now let’s break the system down and examine four of the steps in more detail. The ribosomes in rough ER are bound to the outside of the membrane. How do the proteins that they manufacture get into the lumen of the ER? How do they move from the ER to the Golgi apparatus? Once they’re inside the Golgi, what happens to them? And finally, how do the finished proteins get to their destination? Let’s consider each question in turn.

**Entering the Endomembrane System: The Signal Hypothesis**

How do proteins enter the endomembrane system? The signal hypothesis, proposed by Günter Blobel and colleagues, predicted that proteins bound for the endomembrane system have a signal analogous to the nuclear localization signal. The idea was that these proteins are synthesized by ribosomes that are attached to the outside of the ER and that the first few amino acids in the growing polypeptide act as a signal that brings the protein into the lumen of the ER.

This hypothesis received important support when researchers made a puzzling observation: When proteins that are normally synthesized in the rough ER are manufactured by naked ribosomes in vitro—with no ER present—they are 20 amino acids longer than usual. Blobel seized on these data. He claimed that the 20 amino acids are the “Send to ER” signal and that the signal is removed inside the organelle. His group went on to identify the exact sequence of amino acids in the ER signal sequence.

More recent work has documented the mechanisms responsible for receiving the send-to-ER signal and inserting the protein into the rough ER (Figure 7.28). The action begins when a ribosome synthesizes the ER signal sequence, which then binds to a signal recognition particle (SRP) in the cytosol. An SRP is a complex of RNA and protein that acts as a receptor for the ER signal sequence. The ribosome + signal sequence + SRP complex then attaches to an SRP receptor in the ER membrane itself. You can think of the SRP as a key that is activated by an ER signal sequence. The receptor in the ER membrane is the lock. Once the lock and key connect, the rest of the protein is synthesized, and then the signal sequence is removed. The finished polypeptide has one of two fates: (1) proteins that will eventually be shipped to an organelle or secreted from the cell enter the lumen of the rough ER; or (2) membrane proteins that remain in the rough ER membrane as they are being manufactured.

Once proteins are inside the rough ER or inserted into its membrane, they fold into their three-dimensional shape with
The Signal Hypothesis Explains How Proteins Destined for Secretion Enter the Endomembrane System

According to the signal hypothesis, proteins destined for secretion contain a short stretch of amino acids that interact with a signal recognition particle (SRP) in the cytoplasm. This interaction allows the protein to enter the ER.

1. Signal sequence is synthesized by ribosome.
2. Signal sequence binds to signal recognition particle (SRP).
4. Protein synthesis continues. Protein enters ER. SRP is released.
5. Protein synthesis is complete. Signal sequence is removed.

FIGURE 7.28 The Signal Hypothesis Explains How Proteins Destined for Secretion Enter the Endomembrane System

Getting from the ER to the Golgi

How do proteins travel from the ER to the Golgi apparatus? Palade’s group thought they had the answer, based on data from the pulse-chase experiments that first confirmed the existence of the endomembrane system. When labeled proteins appeared in a region between the rough ER and the Golgi apparatus, they appeared to be inside small membrane-bound structures. Based on these observations, the biologists suggested that proteins are transported between the two organelles in vesicles. The idea was that vesicles bud off of the ER, move away, fuse with the membrane on the cis face of the Golgi apparatus, and dump their contents inside.

This hypothesis was supported when other researchers used differential centrifugation to isolate and characterize the vesicles that contained labeled proteins. Using this approach, investigators have established that distinctive types of vesicles carry proteins from the rough ER to the Golgi apparatus and from layer to layer within the Golgi apparatus.

What Happens Inside the Golgi Apparatus?

Recall from Section 7.1 that the Golgi apparatus consists of a stack of flattened vesicles called cisternae, and that cargo enters one side of the structure and exits the other. It is still not clear, however, exactly how material moves through the stack. There is strong evidence that at least some molecules move among the
cisternae inside vesicles. But other data suggest that the cister-
nae themselves mature and change over time, meaning that new

cisternae are created at the cis face and old cisternae break

apart at the trans face. If so, then cisternae would have to
change in composition and activity over time. Figure 7.30 illus-

trates these two hypotheses. Is each cisterna static except for
occasional additions or subtractions via vesicle delivery and
shipment, or is the entire structure dynamic? The answer is not
yet known, and the dichotomy is not necessarily absolute—
both processes may occur to some degree.

Although the structure of the Golgi apparatus is still
somewhat uncertain, its function is not. By separating indi-

gual cisternae and analyzing their contents, researchers
have found that each cisterna contains a different suite of en-

zymes that catalyze glycosylation reactions. As a result, pro-

teins undergo further modification as they move from one

cisterna to the next. Some proteins have sugar groups that
are phosphorylated in a vesicle near the cis face. Later, the

carbohydrate group that was added in the rough ER is re-
moved. In other cisternae, various types of carbohydrate
chains are attached that may protect the protein or help it att-
tach to surfaces.

How Are Products Shipped from the Golgi?
The rough ER and Golgi apparatus are like an assembly line.
Some of the products stay in the endomembrane system itself, re-
placing worn-out molecules. But if proteins are processed to the
end of the line, they will be sent to one of several destinations, in-
cluding lysosomes, the plasma membrane, or the outside of the

cell. How are these finished products put into the right shipping
containers, and how are the different containers addressed?

Studies on enzymes that are shipped to lysosomes have pro-
vided some answers to both questions. A key finding was that
lysosome-bound proteins have a phosphate group attached to a
specific sugar subunit on their surface, forming the compound
mannose-6-phosphate. If mannose-6-phosphate is removed from
these proteins, they are not transported to a lysosome. This is
strong evidence that the phosphorylated sugar serves as a zip
code, analogous to the nuclear localization and rough ER signals
analyzed earlier. More specifically, data indicate that mannose-6-
phosphate binds to a protein in membranes of certain vesicles.
These vesicles, in turn, have proteins on their surface that interact
specifically with proteins in the lysosomal membranes. In this
way, the presence of mannose-6-phosphate targets proteins for
vesicles that deliver their contents to lysosomes.

**Figure 7.30 Two Hypotheses for How Materials Move through the Golgi Apparatus**

**QUESTION** Are these hypotheses mutually exclusive? Explain your answer.
2. Proteins are sorted in the Golgi when they bind to different receptors.

3. Transport vesicles bud off the trans face of the Golgi and travel to their destinations.

4. Proteins on vesicle surface interact with receptors at destination.

5. Vesicle delivers contents.

**Figure 7.31** In the Golgi Apparatus, Proteins Are Sorted into Vesicles That Are Targeted to a Destination

Summary of the current model for how proteins are sorted into distinct vesicles in the Golgi apparatus and how these vesicles are then targeted to their correct destination.

**CHECK YOUR UNDERSTANDING**

Ions, ATP, amino acids, and other small molecules diffuse randomly throughout the cell, but the transport of proteins and other large molecules is energy demanding and tightly regulated. Proteins must have the appropriate molecular zip code to enter or leave the nucleus, enter the lumen of the rough ER, or become incorporated into vesicles destined for lysosomes or the plasma membrane. In many cases, proteins and other types of cargo are shipped in vesicles that contain molecular zip codes on their surface. You should be able to (1) propose a hypothesis for how proteins are targeted to chloroplasts, and (2) outline an experiment that would test your hypothesis.

**7.4 The Dynamic Cytoskeleton**

Based on early observations with light microscopes, biologists viewed the cytoplasm of eukaryotic cells as a fluid-filled space devoid of structure. As microscopy improved, however, researchers realized that the cytoplasm contains an extremely dense and complex network of fibers. This cytoskeleton helps maintain cell shape by providing structural support. It's
important to recognize, though, that the cytoskeleton is not a static structure like the scaffolding used at construction sites. The fibrous proteins that make up the cytoskeleton move and change to change the cell’s shape, to move materials from place to place, and to move the entire structure. Like the rest of the cell, the cytoskeleton is dynamic.

As Figure 7.32 shows, there are several distinct types of cytoskeletal elements: actin filaments (also known as microfilaments), intermediate filaments, and microtubules. Each of these elements has a distinct size, structure, and function. Let’s look at each one in turn.

### Actin Filaments
Actin filaments are sometimes referred to as microfilaments because they are the cytoskeletal element with the smallest diameter. As Figure 7.32 indicates, actin filaments are long, fibrous structures made of a globular protein called actin. In animal cells, actin is often the most abundant of all proteins—typically it represents 5–10 percent of the total protein in the cell. Each of your liver cells contains about half a billion of these molecules.

Actin filaments form when individual actin molecules polymerize. The completed structure resembles two strands that coil around each other. Because each actin monomer in the strand is asymmetrical, the structure as a whole has a distinct polarity. The two ends of an actin filament are different and are referred to as plus and minus ends. Actin filaments tend to grow at the plus end, because polymerization occurs fastest there.

**Figure 7.33a** shows a fluorescence micrograph of the actin filaments in a mammalian kidney cell. Note that groups of actin filaments are organized into long bundles or dense networks and that actin filaments are particularly abundant just under the plasma membrane. Whether they are arranged in parallel as part of bundles or crisscrossed in networks, individual actin filaments are linked to one another by other proteins. In combination, the bundles and networks of actin filaments help stiffen the cell and define its shape.

Although actin filaments are an important part of the cell’s structural support, it would be a mistake to think that they are static. Instead, actin filaments grow and shrink as actin subunits are added or subtracted from each end of the structure. This phenomenon is called treadmilling, because the dynamics of the fibers resemble those of a treadmill.

In addition, many cells have actin filaments that interact with the specialized protein myosin. When ATP that is bound to myosin is hydrolyzed to ADP, the “head” region of the myosin molecule binds to actin and moves. The movement of this protein causes the actin filament to slide (Figure 7.34a). As Figure 7.34b shows, the (ATP-powered) interaction between actin and myosin is the basis for an array of cell movements:

- Cell crawling occurs in amoebae, slime molds, and certain types of human cells. Cell crawling is based on three processes: a directional extension of actin filaments that pushes the plasma membrane into bulges called pseudopodia (“false-feet”), adherence to a solid substrate, and a myosin-driven contraction of actin filaments at the cell’s other end. In com-

<table>
<thead>
<tr>
<th>Actin Filaments (Microfilaments)</th>
<th>Intermediate Filaments</th>
<th>Microtubules</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Protein subunits</strong></td>
<td>Actin</td>
<td>Keratin, vimentin, lamin, others</td>
</tr>
<tr>
<td><strong>Structure</strong></td>
<td>Strands in double helix</td>
<td>Fibers wound into thicker cables</td>
</tr>
</tbody>
</table>
| **Functions** | • maintain cell shape by resisting tension (pull)  
• motility via muscle contraction or cell crawling  
• cell division in animals  
• movement of organelles and cytoplasm in plants, fungi, and animals | • maintain cell shape by resisting tension (pull)  
• anchor nucleus and some other organelles | • maintain cell shape by resisting compression (push)  
• motility via flagella or cilia  
• move chromosomes during cell division  
• formation of cell plate during plant cell division  
• move organelles  
• growth of plant cell walls |
bination, the three events result in directed movement by whole cells.

- **Cytokinesis** ("cell-moving") is the process of cell division in animals. For these cells to divide in two, actin filaments that are arranged in a ring under the plasma membrane must slide past one another. Because they are connected to the plasma membrane, the movement of the actin fibers pinches the cell in two.
- **Cytoplasmic streaming** is the directed flow of cytosol and organelles around plant and fungal cells. The movement occurs along actin filaments and is powered by myosin.

In addition, extension of actin filaments is responsible for the expansion of long, thin fungal cells into soil or rotting wood. The same mechanism causes structures called pollen tubes to grow toward the egg cells of plants, so sperm can be delivered prior to fertilization.

### Intermediate Filaments

Unlike actin filaments and microtubules, intermediate filaments (Figure 7.33b) are defined by size rather than composition. Many types of intermediate filaments exist, each consisting of a different protein. In many cases, different types of cells in the same organism contain different types of intermediate filaments. This is in stark contrast to actin filaments and microtubules, which are made from the same protein subunits in all eukaryotic cells. In addition, intermediate filaments are not polar; instead, each end of these filaments is identical. As a result, intermediate filaments do not treadmill, and they are not

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**FIGURE 7.33 How Are Cytoskeletal Elements Distributed in the Cell?**

To make these micrographs, researchers attached a fluorescent compound to (a) actin, the protein subunit of actin filaments, to (b) a protein found in intermediate filaments, and to (c) tubulin dimers.

**FIGURE 7.34 Many Cellular Movements Are Based on Actin-Myosin Interactions**

(a) When the "head" region of the myosin protein binds to ATP or ADP, myosin attaches to actin and changes shape. The movement causes the actin filament to slide. (b) Actin-myosin interactions can move cells, divide cells, and move organelles and cytoplasm.

---

(a) Actin and myosin interact to cause movement.

(b) Actin-myosin interactions produce several types of movement.
involved in directed movement driven by myosin or related proteins. Intermediate filaments serve a purely structural role in eukaryotic cells.

The intermediate filaments that you are most familiar with belong to a family of molecules called the keratins. The cells that make up your skin and that line surfaces inside your body contain about 20 types of keratin. The presence of these intermediate filaments provides the mechanical strength required for these cells to resist pressure and abrasion. Skin cells secrete another 10 distinct forms of keratin. Depending on the location of the skin cell and keratins involved, the secreted filaments form fingernails, toenails, or hair.

Nuclear lamins, which make up the nuclear lamina layer introduced in Section 7.1, also qualify as intermediate filaments. These fibers form a dense mesh under the nuclear envelope. Recall that in addition to giving the nucleus its shape, they anchor the chromosomes. They are also involved in the breakup and reassembly of the nuclear envelope when cells divide. Some intermediate filaments project from the nucleus through the cytoplasm to the plasma membrane, where they are linked to intermediate filaments that run parallel to the cell surface. In this way, intermediate filaments form a flexible skeleton that helps shape the cell surface and hold the nucleus in place.

**Microtubules**

Microtubules are composed of the proteins α-tubulin and β-tubulin and are the largest cytoskeletal components in terms of diameter (Figure 7.33c). Molecules of α-tubulin and β-tubulin bind to form dimers (“two-parts”), compounds formed by the joining of two monomers. Tubulin dimers then polymerize to form the large, hollow tube called a microtubule. Because each end of a tubulin dimer is different, each end of a microtubule has a distinct polarity. Like actin filaments, microtubules are dynamic and more likely to grow from one end than they are from the other. Microtubules grow and shrink in length as tubulin dimers are added or subtracted.

Microtubules are similar to actin filaments in function as well as structure. Both cytoskeletal elements provide structural support, and both are involved in cell division. Although microtubules are not involved in the physical division of the cell, they are essential for the directed movement of chromosomes to each of the two resulting cells. In animals and fungi, the microtubules involved in chromosome movement emanate from a structure called the centrosome. Distinctive structures called centrioles are found inside centrosomes (Figure 7.35). Centrioles may help organize microtubules; however, they are not essential for cell division to occur. In plants and many other eukaryotes, a region called the microtubule organizing center performs the same function as the centrosome.

Microtubules are involved in many other types of cellular movement as well. For the remainder of this chapter, we’ll focus on how microtubules function in moving materials inside cells and in moving the entire cell.

**Figure 7.35 Centrosomes Are A Type of Microtubule Organizing Center**

Microtubules emanate from microtubule organizing centers, which in animals are called centrosomes. The centrioles inside a centrosome are made of microtubules.

**Studying Vesicle Transport** Materials are transported to a wide array of destinations inside cells. To study how this movement happens, Ronald Vale and colleagues focused on a cell called the giant axon that is found in squid. The giant axon is an extremely large nerve cell that runs the length of a squid’s body. If the animal is disturbed, the cell signals muscles to contract so the individual can jet away to safety.

The researchers decided to study this particular cell for three reasons. First, the giant axon is so large that it is relatively easy to see and manipulate. Second, signaling molecules are synthesized in the cell’s ER and then transported in vesicles down the length of the cell. As a result, a large amount of cargo moves a long distance. Third, the researchers found that if they gently squeeze the cytoplasm out of the cell, vesicle transport still occurs in the cytoplasmic material.

In short, the squid giant axon provided a cell-free system that could be observed and manipulated efficiently. What did the biologists find out?

**Microtubules Act as “Railroad Tracks”** To watch vesicle transport in action, researchers mounted a video camera to a microscope. As Figure 7.36 shows, this technique allowed them to document that vesicle transport occurred along a filamentous track. A simple experiment convinced the group that this movement was an energy-dependent process. If they depleted the amount of ATP in the cytoplasm, vesicle transport stopped.

To identify the type of filament involved, the biologists measured the diameter of the tracks and analyzed their chemical composition. Both types of data indicated that the tracks consisted of microtubules. Microtubules also appear to be required for movement of materials elsewhere in the cell. If experimental cells are treated with a drug that disrupts microtubules, the movement of vesicles from the rough ER to the Golgi apparatus is impaired.

The general message of these experiments is that transport vesicles move through the cell along microtubules. How? Do the tracks themselves move, like a conveyor belt, or are vesicles carried along on some sort of molecular truck?
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Microtubule tracks

(a) Micrograph image  (b) Video image
(at higher magnification)

Vesicles

FIGURE 7.36 Vesicles Move along Microtubule Tracks
Transport vesicles moving along microtubules. The images are of extruded cytoplasm from a squid giant axon. (a) An electron micrograph that allowed researchers to measure the diameter of the filaments and confirm that they are microtubules. (b) A slightly fuzzy but higher-magnification videomicroscope image, in which researchers actually watched vesicles move.

A Motor Protein Generates Motile Forces
To study the way vesicles move along microtubules, Vale’s group set out to tear the squid axon’s transport system apart and then put it back together. To begin, they assembled microtubule fibers from purified α-tubulin and β-tubulin. Then they used differential centrifugation to isolate transport vesicles. But when they mixed purified microtubules and vesicles with ATP, no transport occurred.

Something had been left out—but what?
To find the missing element or elements, the researchers purified one subcellular part after another, using differential centrifugation, and added it to the microtubule + vesicle + ATP system. Through trial and error, they found something that triggered movement. After further purification steps, the researchers finally succeeded in isolating a protein that generated vesicle movement. They named the molecule kinesin, from the Greek word kinein (“to move”). Like myosin, kinesin is a motor protein that converts chemical energy in ATP into mechanical work, just as a car’s motor converts chemical energy in gasoline.

Biologists began to understand how kinesin works when X-ray diffraction studies similar to those that revealed the helical nature of DNA revealed the three-dimensional structure of kinesin. As Figure 7.37a shows, the protein consists of two intertwined polypeptide chains. It has three major regions: a head section with two globular pieces, a tail, and a stalk that connects the head and tail. Follow-up studies confirmed that the two globular components of the head bind to the microtubule. The tail region binds to the transport vesicle. The kinesin molecule is like a delivery person who carries transport vesicles along microtubule tracks. Cells contain a number of different kinesin proteins, each specialized for carrying a different type of vesicle.

How does kinesin move? More detailed studies of this protein’s structure indicated that each of the globular components of the molecule’s head has a site for binding ATP as well as a site that binds to the microtubule. To pull these observations together, biologists propose that kinesin transports vesicles by “walking” along a microtubule. The idea is that each part of the head region undergoes a conformational change when it binds ATP. As Chapter 3 showed, these types of shape changes often alter the activity of a protein. As Figure 7.37b shows, the ATP-dependent conformational change in kinesin results in a step forward. As each head...
alternately binds and hydrolyzes ATP, the protein and its cargo move down the microtubule track.

In short, kinesins move molecular cargo to destinations throughout the cell. They are not the only type of motor protein active inside cells, however. Recall that myosin causes actin filaments to slide, resulting in the movement of cells or cytoplasm. Dynein is also involved in the movement of organelles along tracks made of actin. And a third motor protein, dynein, powers the transport of certain organelles as well as swimming movements that move the entire cell. Let’s take a closer look at how cells swim.

Cilia and Flagella: Moving the Entire Cell
Flagella are long hairlike projections from the cell surface that function in movement. Flagella are found in many bacteria and eukaryotes. The structure of flagella is completely different in the two groups, however. Bacterial flagella are made of a protein called flagellin; eukaryotic flagella are constructed from microtubules (tubulin). Bacterial flagella move the cell by rotating like a ship’s propeller; eukaryotic flagella move the cell by undulating. Eukaryotic flagella are surrounded by plasma membrane; bacterial flagella are not. Based on these observations, biologists conclude that the two structures evolved independently—even though their function is similar.

To understand how cells move, we’ll focus on eukaryotic flagella. Eukaryotic flagella are closely related to structures called cilia (singular: cilium), which are short filamentous projections that are also found in some eukaryotic cells. Unicellular eukaryotes may have either flagella or cilia, while some multicellular organisms have both. In humans, for example, the cells that line the respiratory tract have cilia; sperm cells have flagella.

Flagella are generally longer than cilia, and cells typically have just one or two flagella but many cilia (Figure 7.38). But when researchers examined the two structures with the electron microscope, they found that their underlying organization is identical.

How Are Cilia and Flagella Constructed? In the 1950s, anatomical studies established that both cilia and flagella have a characteristic “9 + 2” arrangement of microtubules. As Figure 7.39a shows, nine microtubule pairs, or doublets, surround two central microtubules. The doublets, consisting of one complete and one incomplete microtubule, are arranged around the periphery of the structure. The entire 9 + 2 structure is called the axoneme (“axle-thread”). The axoneme attaches to the cell at a structure called the basal body. The basal body is derived from the centrioles found inside the centrosome. The basal body has a “9 + 0” arrangement of microtubules and plays a central role in the growth of the axoneme.

As electron microscopy improved, biologists gained a more detailed view of the structure. As the sketch in Figure 7.39b illustrates, spoke-like structures connect each doublet to the central pair of microtubules. In addition, molecular bridges connect the nine doublets to one another. Finally, each of the doublets has a set of arms that project toward an adjacent doublet. Microtubules are complex. How do their components interact to generate motion?

FIGURE 7.38 Cilia and Flagella Differ in Length and Number
Cilia are relatively short and large in number; flagella are relatively long and few in number.

FIGURE 7.39 The Structure of Cilia and Flagella
(a) Transmission electron micrograph of a cross section through an axoneme. (b) The major structural elements in cilia and flagella. The microtubules are connected by bridges and spokes, and the entire structure is surrounded by the plasma membrane. EXERCISE Label the “9 + 2” arrangement of microtubules.
A Motor Protein in the Axoneme  In the 1960s Ian Gibbons began studying the cilia of a common unicellular eukaryote called Tetrahymena, which lives in pond water. Gibbons found that by using a detergent to remove the plasma membrane that surrounds cilia and then subjecting the resulting solution to differential centrifugation, he could isolate axonemes. Further, the isolated structures would beat if Gibbons supplied them with ATP. These results confirmed that the beating of cilia is an energy-demanding process. They also provided Gibbons with a cell-free system for exploring the molecular mechanism of movement.

In an early experiment with isolated axonemes, Gibbons treated the structures with a molecule that affects the ability of proteins to bind to one another. The axonemes that resulted from this treatment could not bend or use ATP. When Gibbons examined them in the electron microscope, he found that the arms had fallen off. This observation led to the hypothesis that the arms are required for movement. Follow-up work showed that the arms are made of a large protein that Gibbons named dynein (from the Greek word dyne, meaning “force”).

Like myosin and kinesin, dynein is a motor protein. Structural and chemical studies have shown that dynein undergoes a conformational change when a phosphate group from ATP attaches to it. More specifically, the end of a dynein molecule changes shape when it is phosphorylated. This shape change moves the molecule along the nearby microtubule. When the protein reattaches, it has succeeded in walking up the microtubule. This walking motion allows the microtubule doublets to slide past one another. But because each of the nine doublets in the axoneme is connected to the central pair of microtubules by a spoke, and because all of the doublets are connected to each other by molecular bridges, the sliding motion is constrained. So if dynein arms on just one side of the axoneme walk while those on the other side are at rest, the result of the constrained, localized movement is bending (Figure 7.40). The result of the bending of cilia or flagella is a swimming motion.

Scaled for size, flagellar-powered swimming can be rapid. In terms of the number of body or cell lengths traveled per second, a sperm cell from a bull moves faster than a human world-record-holder does when swimming freestyle. At the level of the cell, life is fast paced.

CHECK YOUR UNDERSTANDING

Each component of the cytoskeleton has a unique structure and set of functions. In addition to providing structural support, actin filaments and microtubules work in conjunction with motor proteins to move the cell or materials inside the cell. Intermediate filaments provide structural support. Most elements of the cytoskeleton are dynamic—they grow and shrink over time. You should be able to predict what will happen when experimental cells are treated with drugs that inhibit formation of each type of cytoskeletal filament.

FIGURE 7.40 How Do Flagella Bend?
Researchers attached a pair of gold beads to a flagellum and photographed its movement over a short time sequence. As the flagellum bends and beats back and forth, the sperm cell swims forward. When dynein arms walk along the microtubule doublets on one side of a flagellum, the structure bends.
The structure of cell components is closely correlated with their function. Because all organisms consist of cells, many questions in biology can be answered by understanding the structure and function of cells and cell components. There are two basic cellular designs: prokaryotic and eukaryotic. Eukaryotic cells are usually much larger and more structurally complex than prokaryotic cells. Prokaryotic cells consist of a single membrane-bound compartment in which nearly all cellular functions occur. Eukaryotic cells contain numerous membrane-bound compartments called organelles. Organelles allow eukaryotic cells to compartmentalize functions and grow to a large size.

Eukaryotic organelles are specialized for carrying out different functions, and their structure is often correlated closely with their function. Mitochondria and chloroplasts have extensive internal membrane systems, where the enzyme machines responsible for ATP generation and photosynthesis reside. Rough ER is named for the ribosomes that attach to it. Ribosomes are protein-making machines, and rough ER is a site for protein synthesis and processing.
Questions

Content Review

1. Which of the following best describe the nuclear envelope?
   a. It is continuous with the endomembrane system.
   b. It is continuous with the nucleolus.
   c. It is continuous with the plasma membrane.
   d. It contains a single membrane and nuclear pores.

2. What is a nuclear localization signal?
   a. A stretch of amino acids that directs proteins from the nucleus to the ER.
   b. A molecule that is attached to nuclear proteins so that they are retained inside the nucleus.
   c. A signal built into a protein that directs it to the nucleus.
   d. A component of the nuclear pore complex.

3. Which of the following is not true of secreted proteins?
   a. They are synthesized in ribosomes.
   b. They are transported through the endomembrane system in membrane-bound transport organelles.
   c. They are transported from the Golgi apparatus to the ER.
   d. They contain a signal sequence that directs them into the ER.

4. To find the nuclear localization signal in the protein nucleoplasm, researchers separated the molecule's core and tail segments, labeled both with a radioactive atom, and injected them into the cytoplasm.

Why did the researchers conclude that the signal is in the tail region of the protein?
   a. The protein reassembled and folded into its normal shape spontaneously.
   b. Only the tail segments appeared in the nucleus.
   c. With a confocal microscope, tail segments were clearly visible in the nucleus.
   d. The tail and head segments appeared together in the nucleus.

5. Molecular zip codes direct molecules to particular destinations in the cell. How are these signals read?
   a. They bind to receptor proteins.
   b. They enter transport vesicles.
   c. They bind to motor proteins.
   d. They are glycosylated by enzymes in the Golgi apparatus.

6. The number and size of organelles in a cell correlates with that cell's function. Propose a function for cells that contain extensive rough ER.
   a. Rapid cell division in growing bones or muscle tissues.
   b. Production and processing of fatty acids and other lipids.
   c. Movement via cell crawling.
   d. Production of proteins that are secreted from the cell.
Conceptual Review

1. Compare and contrast the structure of a generalized plant cell, animal cell, and prokaryotic cell. Which features are common to all cells? Which are specific to certain lineages?

2. Draw a diagram that traces the movement of a secreted protein from its site of synthesis to the outside of a eukaryotic cell. Identify all of the organelles that the protein passes through, and indicate the direction of movement.

3. Describe how a motor protein such as kinesin can move a transport vesicle down a microtubule track. Include all necessary steps and components.

4. Describe the logic of a pulse-chase experiment. How was this approach used to document the pattern of protein transport through the endomembrane system?

5. Briefly describe how researchers use centrifugation to isolate particular cell components for further study.

6. Compare and contrast the structure and function of actin filaments, intermediate filaments, and microtubules. Why is it misleading to refer to the cytoskeleton as “scaffolding”?

Group Discussion Problems

1. In addition to delivering cellular products to specific organelles, eukaryotic cells can take up material from the outside and transport it to specific organelles. For example, specialized cells of the human immune system ingest bacteria and viruses and then deliver them to lysosomes for degradation. Suggest a hypothesis for how this material is tagged and directed to lysosomes. How would you test this hypothesis?

2. The leading hypothesis to explain the origin of the nuclear envelope is that a deep infolding of the plasma membrane occurred in an ancient prokaryote. Draw a diagram that illustrates this infolding hypothesis. Does your model explain the existence of the structure’s inner and outer membranes? Explain.

3. Propose a function for cells that contain (a) a large number of lysosomes, (b) a particularly extensive cell wall, and (c) many peroxisomes.

4. Suggest a hypothesis or a series of hypotheses to explain why bacteria, archaea, algae, and plants have cell walls. Suppose that mutant individuals from each group lacked a cell wall. How could you use these individuals to test your idea(s)?