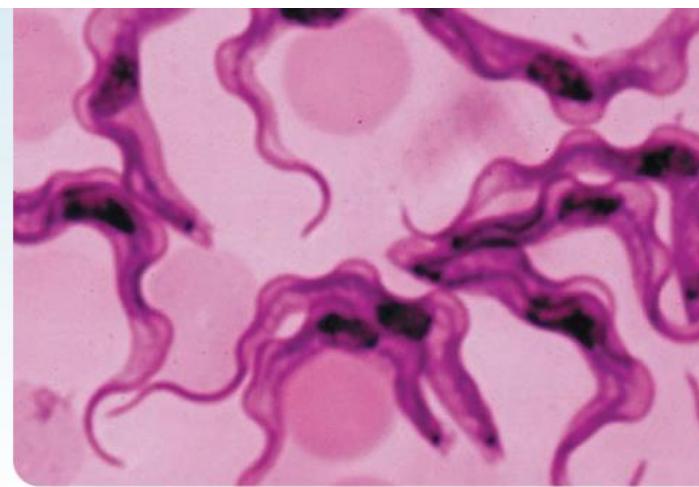


4

Eucaryotic Cell Structure and Function



Often we emphasize prokaryotes and viruses, but eucaryotic microorganisms also have major impacts on human welfare. For example, the protozoan parasite *Trypanosoma brucei gambiense* is a cause of African sleeping sickness. The organism invades the nervous system and the victim frequently dies after suffering several years from symptoms such as weakness, headache, apathy, emaciation, sleepiness, and coma.

PREVIEW

- Eucaryotic cells differ most obviously from prokaryotic cells in having a variety of complex membranous organelles in the cytoplasmic matrix and the majority of their genetic material within membrane-delimited nuclei. Each organelle has a distinctive structure directly related to specific functions.
- A cytoskeleton composed of microtubules, microfilaments, and intermediate filaments helps give eucaryotic cells shape; the cytoskeleton is also involved in cell movements, intracellular transport, and reproduction.
- When eucaryotes reproduce, genetic material is distributed between cells by the highly organized, complex processes called mitosis and meiosis.
- Despite great differences between eucaryotes and prokaryotes with respect to such things as morphology, they are similar on the biochemical level.

Chapter 4 focuses on eucaryotic cell structure and its relationship to cell function. Because many valuable studies on eucaryotic cell ultrastructure have used organisms other than microorganisms, some work on nonmicrobial cells is presented. At the end of the chapter, prokaryotic and eucaryotic cells are compared in some depth.

4.1 AN OVERVIEW OF EUKARYOTIC CELL STRUCTURE

The most obvious difference between eucaryotic and prokaryotic cells is in their use of membranes. Eucaryotic cells have membrane-delimited nuclei, and membranes also play a prominent part in the structure of many other organelles (figures 4.2 and 4.3). **Organelles** are intracellular structures that perform specific functions in cells analogous to the functions of organs in the body. The name organelle (little organ) was coined because biologists saw a parallel between the relationship of organelles to a cell and that of organs to the whole body. It is not satisfactory to define organelles as membrane-bound structures because this would exclude such components as ribosomes and bacterial flagella. A comparison of figures 4.2 and 4.3 with figures 3.4 and 3.13a shows how structurally complex the eucaryotic cell is. This complexity is due chiefly to the use of internal membranes for several purposes. The partitioning of the eucaryotic cell interior by membranes makes possible the placement of different biochemical and physiological functions in separate compartments so that they can more easily take place simultaneously under independent control and proper coordination. Large membrane surfaces

In chapter 3 considerable attention is devoted to prokaryotic cell structure and function because prokaryotes are immensely important in microbiology and have occupied a large portion of microbiologists' attention in the past. Nevertheless, protists and fungi also are microorganisms and have been extensively studied. These eucaryotes often are extraordinarily complex, interesting in their own right, and prominent members of ecosystems (figure 4.1). In addition, many protists and fungi are important model organisms, as well as being exceptionally useful in industrial microbiology. A number of protists and fungi are also major human pathogens; one only need think of candidiasis, malaria, or African sleeping sickness to appreciate the significance of eucaryotes in medical microbiology. So although this text emphasizes prokaryotes, eucaryotic microorganisms also demand attention and are briefly discussed in this chapter.

The key to every biological problem must finally be sought in the cell.

—E. B. Wilson

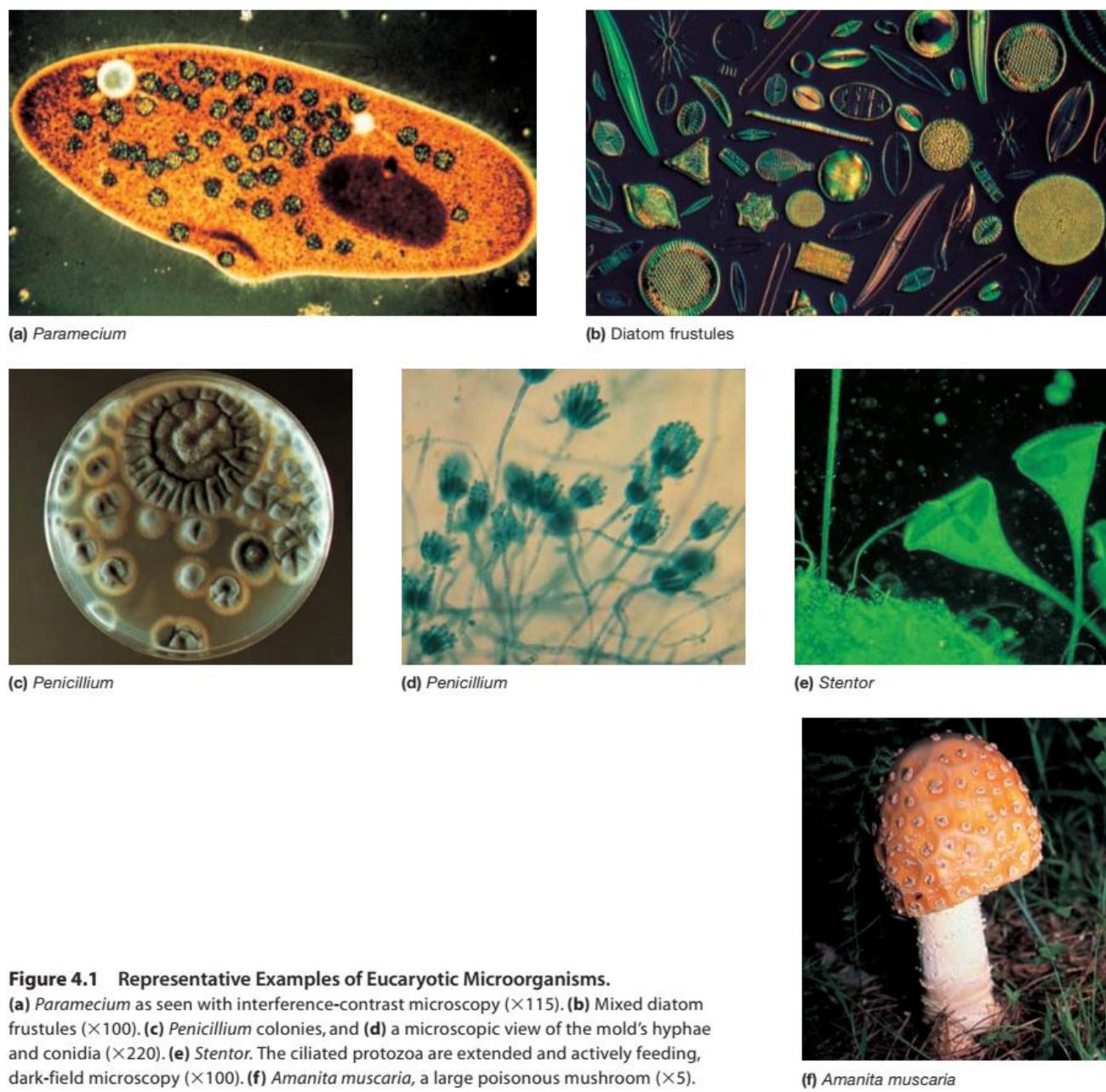


Figure 4.1 Representative Examples of Eucaryotic Microorganisms.
(a) *Paramecium* as seen with interference-contrast microscopy ($\times 115$). **(b)** Mixed diatom frustules ($\times 100$). **(c)** *Penicillium* colonies, and **(d)** a microscopic view of the mold's hyphae and conidia ($\times 220$). **(e)** *Stentor*. The ciliated protozoa are extended and actively feeding, dark-field microscopy ($\times 100$). **(f)** *Amanita muscaria*, a large poisonous mushroom ($\times 5$).

make possible greater respiratory and photosynthetic activity because these processes are located exclusively in membranes. The intracytoplasmic membrane complex also serves as a transport system to move materials between different cell locations. Thus abundant membrane systems probably are necessary in eucaryotic cells because of their large volume and the need for adequate regulation, metabolic activity, and transport.

Figures 4.2 and 4.3 illustrate most of the organelles to be discussed here. **Table 4.1** briefly summarizes the functions of the

major eucaryotic organelles. Our detailed discussion of eucaryotic cell structure begins with the eucaryotic membrane. We then proceed to organelles within the cytoplasm, and finally to components outside the membrane.

1. What is an organelle?
2. Why is the compartmentalization of the cell interior advantageous to eucaryotic cells?

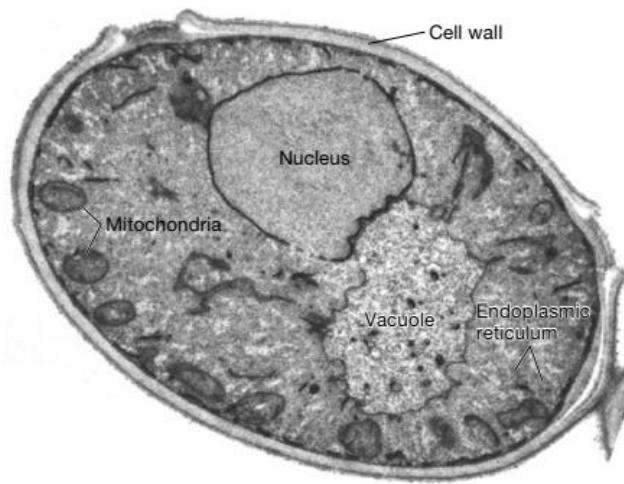


Figure 4.2 Eucaryotic Cell Ultrastructure. The yeast *Saccharomyces* ($\times 7,200$). Note the nucleus, mitochondrion, vacuole, endoplasmic reticulum, and cell wall.

4.2 THE PLASMA MEMBRANE AND MEMBRANE STRUCTURE

As discussed in chapter 3, the fluid mosaic model of membrane structure is based largely on studies of eucaryotic membranes. In eucaryotes, the major membrane lipids are phosphoglycerides, sphingolipids, and cholesterol (figure 4.4). The distribution of these lipids is asymmetric. Lipids in the outer monolayer differ from those of the inner monolayer. Although most lipids in individual monolayers mix freely with each other, there are microdomains that differ in lipid and protein composition. One such microdomain is the **lipid raft**, which is enriched in cholesterol and lipids with many saturated fatty acids including some sphingolipids. The lipid raft spans the membrane bilayer, and lipids in the adjacent monolayers interact. These lipid rafts appear to participate in a variety of cellular processes (e.g., cell movement and signal transduction). They also may be involved in the entrance of some viruses into their host cells and the assembly of some viruses before they are released from their host cells.

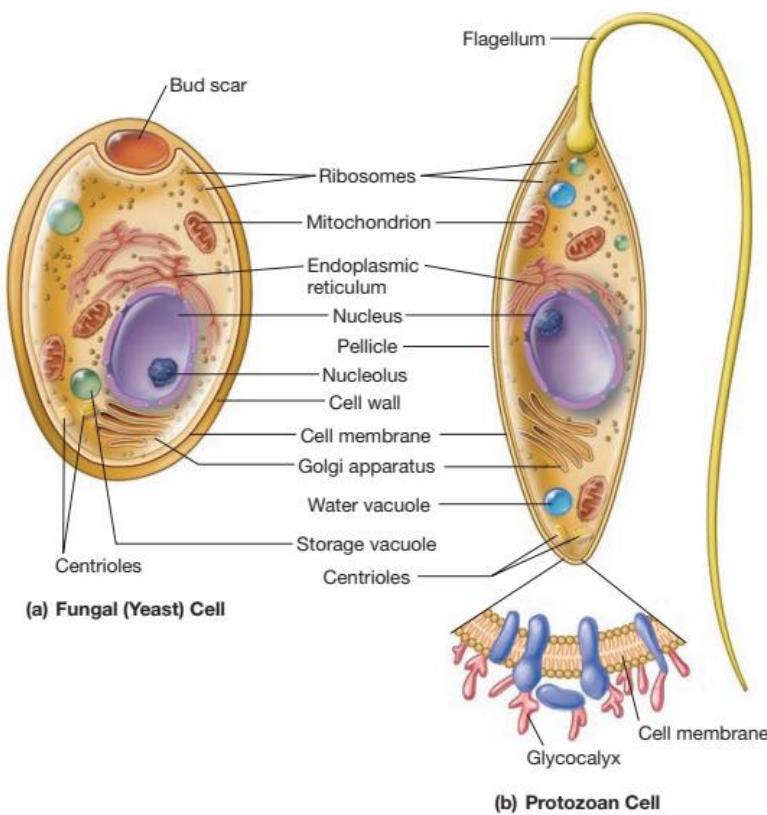


Figure 4.3 The Structure of Two Representative Eucaryotic Cells. Illustrations of a yeast cell (fungus) (a) and the flagellated protozoan *Peranema* (b).

Table 4.1 Functions of Eucaryotic Organelles	
Plasma membrane	Mechanical cell boundary, selectively permeable barrier with transport systems, mediates cell-cell interactions and adhesion to surfaces, secretion
Cytoplasmic matrix	Environment for other organelles, location of many metabolic processes
Microfilaments, intermediate filaments, and microtubules	Cell structure and movements, form the cytoskeleton
Endoplasmic reticulum	Transport of materials, protein and lipid synthesis
Ribosomes	Protein synthesis
Golgi apparatus	Packaging and secretion of materials for various purposes, lysosome formation
Lysosomes	Intracellular digestion
Mitochondria	Energy production through use of the tricarboxylic acid cycle, electron transport, oxidative phosphorylation, and other pathways
Chloroplasts	Photosynthesis—trapping light energy and formation of carbohydrate from CO ₂ and water
Nucleus	Repository for genetic information, control center for cell
Nucleolus	Ribosomal RNA synthesis, ribosome construction
Cell wall and pellicle	Strengthen and give shape to the cell
Cilia and flagella	Cell movement
Vacuole	Temporary storage and transport, digestion (food vacuoles), water balance (contractile vacuole)

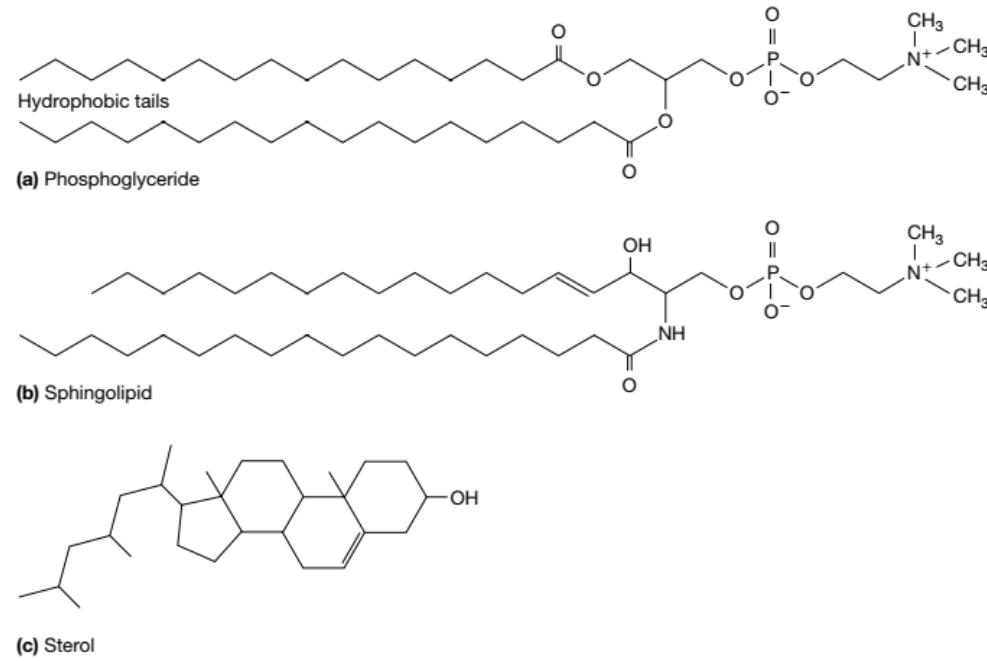


Figure 4.4 Examples of Eucaryotic Membrane Lipids. (a) Phosphatidylcholine, a phosphoglyceride. (b) Sphingomyelin, a sphingolipid. (c) Cholesterol, a sterol.

4.3 THE CYTOPLASMIC MATRIX, MICROFILAMENTS, INTERMEDIATE FILAMENTS, AND MICROTUBULES

The many organelles of eucaryotic cells lie in the **cytoplasmic matrix**. The matrix is one of the most important and complex parts of the cell. It is the “environment” of the organelles and the location of many important biochemical processes. Several physical changes seen in cells—viscosity changes, cytoplasmic streaming, and others—also are due to matrix activity.

A major component of the cytoplasmic matrix is a vast network of interconnected filaments called the **cytoskeleton**. The cytoskeleton plays a role in both cell shape and movement. Three types of filaments form the cytoskeleton: microfilaments, microtubules, and intermediate filaments (**figure 4.5**). **Microfilaments** are minute protein filaments, 4 to 7 nm in diameter, that may be either scattered within the cytoplasmic matrix or organized into networks and parallel arrays. Microfilaments are composed of an actin protein that is similar to the actin contractile protein of muscle tissue. Microfilaments are involved in cell motion and shape changes such as the motion of pigment granules, amoeboid movement, and protoplasmic streaming in slime molds. Interestingly, some pathogens use the actin proteins of their eucaryotic hosts to move rapidly

through the host cell and to propel themselves into new host cells (**Disease 4.1: Getting Around**). **Protist classification: Eumycetozoa and Stramenopiles** (section 25.6)

Microtubules are shaped like thin cylinders about 25 nm in diameter. They are complex structures constructed of two spherical protein subunits— α -tubulin and β -tubulin. The two proteins are the same molecular weight and differ only slightly in terms of their amino acid sequence and tertiary structure. Each tubulin is approximately 4 to 5 nm in diameter. These subunits are assembled in a helical arrangement to form a cylinder with an average of 13 subunits in one turn or circumference (figure 4.5).

Microtubules serve at least three purposes: (1) they help maintain cell shape, (2) are involved with microfilaments in cell movements, and (3) participate in intracellular transport processes. Microtubules are found in long, thin cell structures requiring support such as the axopodia (long, slender, rigid pseudopodia) of protists (figure 4.6). Microtubules also are present in structures that participate in cell or organelle movements—the mitotic spindle, cilia, and flagella.

Intermediate filaments are heterogeneous elements of the cytoskeleton. They are about 10 nm in diameter and are assembled from a group of proteins that can be divided into several classes. Intermediate filaments having different functions are assembled from one or more of these classes of proteins. The role

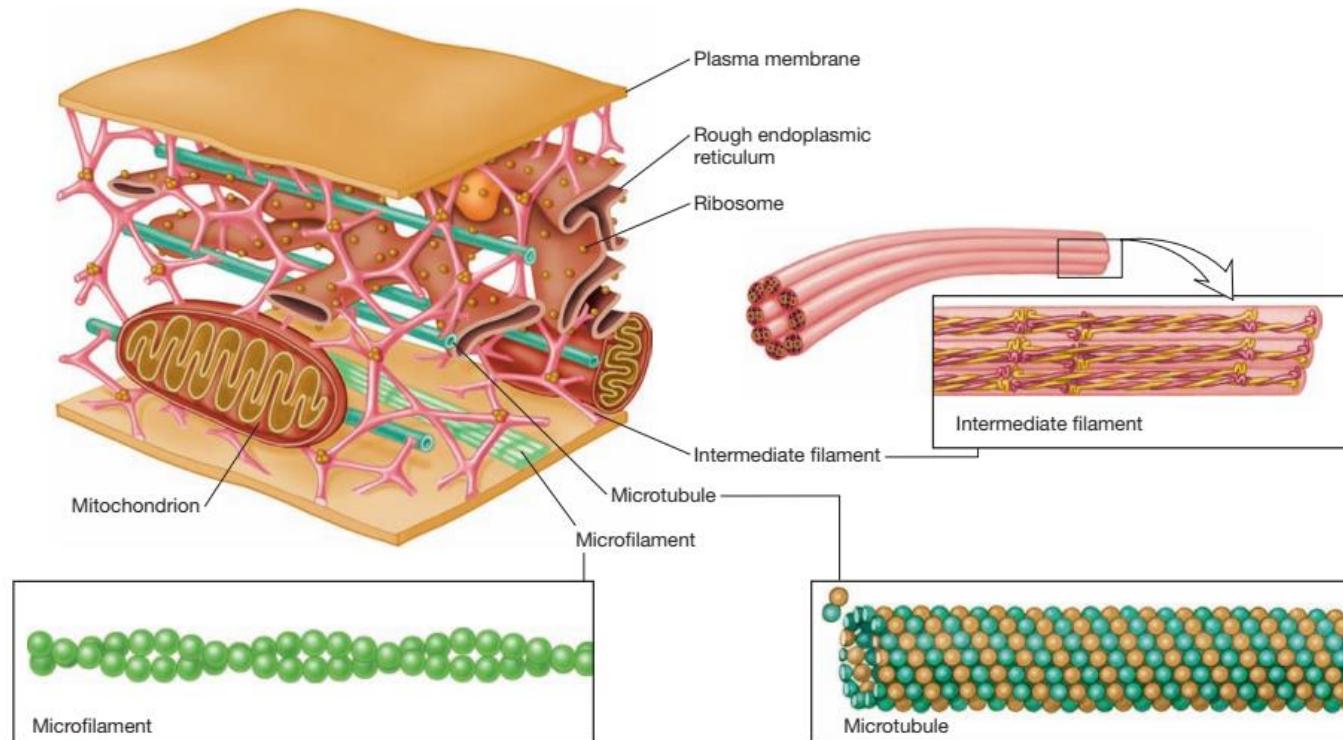


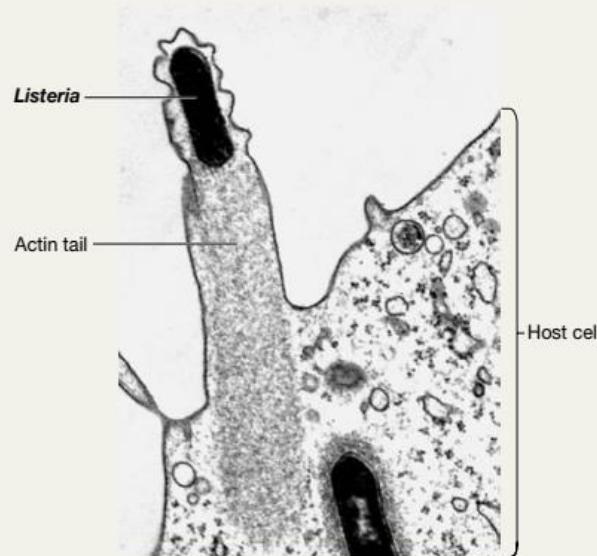
Figure 4.5 The Eucaryotic Cytoplasmic Matrix and Cytoskeleton. The cytoplasmic matrix of eucaryotic cells contains many important organelles. The cytoskeleton helps form a framework within which the organelles lie. The cytoskeleton is composed of three elements: microfilaments, microtubules, and intermediate filaments.



Disease

4.1 Getting Around

Listeria monocytogenes is a gram-positive, rod-shaped bacterium responsible for the disease listeriosis. Listeriosis is a food-borne infection that is usually mild but can cause serious disease (meningitis, sepsis, and stillbirth) in immunocompromised individuals and pregnant women. *L. monocytogenes* is an intracellular pathogen that has a number of important virulence factors. One virulence factor is the protein ActA, which the bacterium releases after entering a host cell. ActA causes actin proteins to polymerize into filaments that form a tail at one end of the bacterium (see **Box figure**). As more and more of the actin proteins are polymerized, the growing tail pushes the bacterium through the host cell at rates up to 11 $\mu\text{m}/\text{minute}$. The bacterium can even be propelled through the cell surface and into neighboring cells.



Listeria Motility and Actin Filaments. A *Listeria* cell is propelled through the cell surface by a bundle of actin filaments.

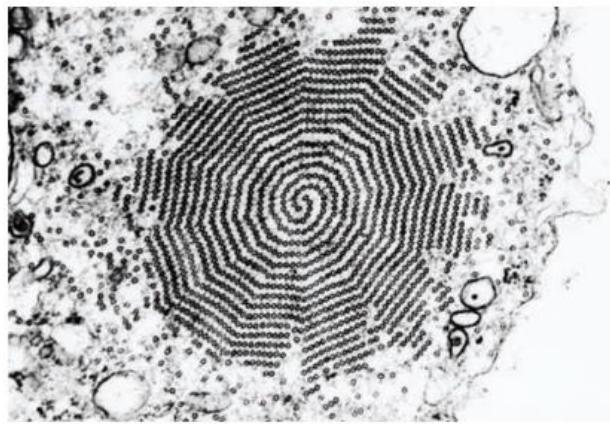


Figure 4.6 Cytoplasmic Microtubules. Electron micrograph of a transverse section through the axopodium of a protist known as a heliozoan ($\times 48,000$). Note the parallel array of microtubules organized in a spiral pattern.

of intermediate filaments, if any, in eucaryotic microorganisms is unclear. Thus far, they have been identified and studied only in animals: some intermediate filaments have been shown to form the nuclear lamina, a structure that provides support for the nuclear envelope (see p. 91); and other intermediate filaments help link cells together to form tissues.

1. Compare the membranes of *Eucarya*, *Bacteria*, and *Archaea*. How are they similar? How do they differ?
2. What are lipid rafts? What roles do they play in eucaryotic cells?
3. Define cytoplasmic matrix, microfilament, microtubule, and tubulin. Discuss the roles of microfilaments, intermediate filaments, and microtubules.
4. Describe the cytoskeleton. What are its functions?

4.4 ORGANELLES OF THE BIOSYNTHETIC-SECRETORY AND ENDOCYTIC PATHWAYS

In addition to the cytoskeleton, the cytoplasmic matrix is permeated with an intricate complex of membranous organelles and vesicles that move materials into the cell from the outside (endocytic pathway), and from the inside of the cell out, as well as from location to location within the cell (biosynthetic-secretory pathway). In this section, some of these organelles are described. This is followed by a summary of how the organelles function in the biosynthetic-secretory and endocytic pathways.

The Endoplasmic Reticulum

The **endoplasmic reticulum (ER)** (figure 4.3 and **figure 4.7**) is an irregular network of branching and fusing membranous tubules, around 40 to 70 nm in diameter, and many flattened sacs called **cisternae** (s., **cisterna**). The nature of the ER varies with

the functional and physiological status of the cell. In cells synthesizing a great deal of protein for purposes such as secretion, a large part of the ER is studded on its outer surface with ribosomes and is called **rough endoplasmic reticulum (RER)**. Other cells, such as those producing large quantities of lipids, have ER that lacks ribosomes. This is **smooth ER (SER)**.

The endoplasmic reticulum has many important functions. Not only does it transport proteins, lipids, and other materials

through the cell, it is also involved in the synthesis of many of the materials it transports. Lipids and proteins are synthesized by ER-associated enzymes and ribosomes. Polypeptide chains synthesized on RER-bound ribosomes may be inserted either into the ER membrane or into its lumen for transport elsewhere. The ER is also a major site of cell membrane synthesis.

The Golgi Apparatus

The **Golgi apparatus** is composed of flattened, saclike cisternae stacked on each other (figure 4.8). These membranes, like the smooth ER, lack bound ribosomes. There are usually around 4 to 8 cisternae in a stack, although there may be many more. Each is 15 to 20 nm thick and separated from other cisternae by 20 to 30 nm. A complex network of tubules and vesicles (20 to 100 nm in diameter) is located at the edges of the cisternae. The stack of cisternae has a definite polarity because there are two faces that are quite different from one another. The sacs on the **cis** or forming face often are associated with the ER and differ from the sacs on the **trans** or maturing face in thickness, enzyme content, and degree of vesicle formation.

The Golgi apparatus is present in most eukaryotic cells, but many fungi and ciliate protozoa lack a well-formed structure. Sometimes the Golgi consists of a single stack of cisternae; however, many cells may contain up to 20, and sometimes more, separate stacks. These stacks of cisternae, often called **dictyosomes**, can be clustered in one region or scattered about the cell.

The Golgi apparatus packages materials and prepares them for secretion, the exact nature of its role varying with the organism. For instance, the surface scales of some flagellated photosynthetic and radiolarian protists appear to be constructed within the Golgi apparatus and then transported to the surface in vesicles. The Golgi often participates in the development of cell membranes

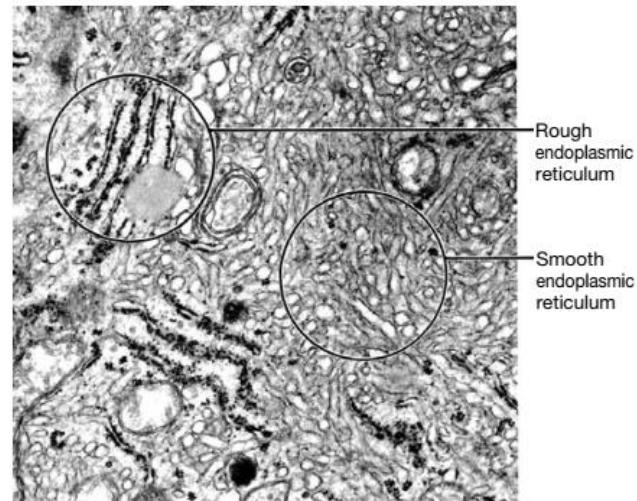
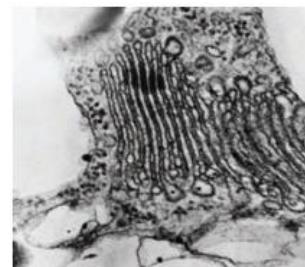
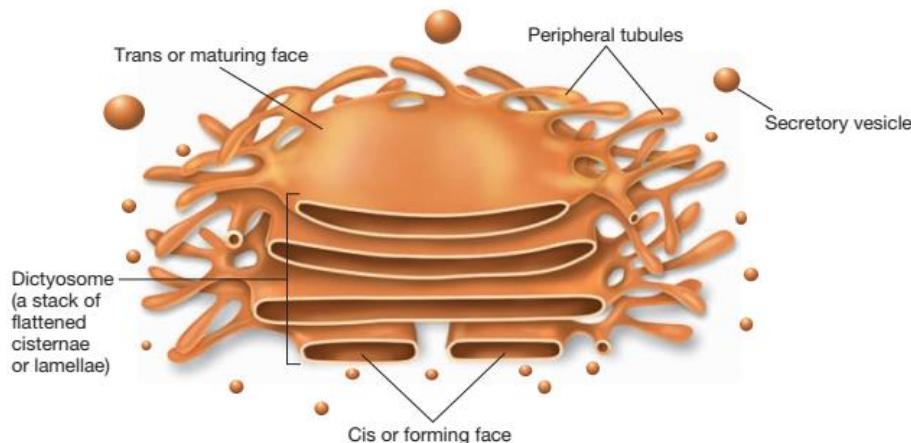


Figure 4.7 The Endoplasmic Reticulum. A transmission electron micrograph of the corpus luteum in a human ovary showing structural variations in eukaryotic endoplasmic reticulum. Note the presence of both rough endoplasmic reticulum lined with ribosomes and smooth endoplasmic reticulum without ribosomes ($\times 26,500$).



(a)



(b)

Figure 4.8 Golgi Apparatus Structure. Golgi apparatus of *Euglena gracilis*. Cisternal stacks are shown in the electron micrograph ($\times 165,000$) in (a) and diagrammatically in (b).

and in the packaging of cell products. The growth of some fungal hyphae occurs when Golgi vesicles contribute their contents to the wall at the hyphal tip. [The protists \(chapter 25\)](#)

Lysosomes

Lysosomes, or structures very much like them, are found in most eucaryotic organisms, including protists, fungi, plants, and animals. Lysosomes are roughly spherical and enclosed in a single membrane; they average about 500 nm in diameter, but range from 50 nm to several μm in size. They are involved in intracellular digestion and contain the enzymes needed to digest all types of macromolecules. These enzymes, called **hydrolases**, catalyze the hydrolysis of molecules and function best under slightly acidic conditions (usually around pH 3.5 to 5.0). Lysosomes maintain an acidic environment by pumping protons into their interior.

The Biosynthetic-Secretory Pathway

The **biosynthetic-secretory pathway** is used to move materials to lysosomes as well as from the inside of the cell to either the cell membrane or cell exterior. The process is complex and not fully understood. The movement of proteins is of particular importance and is the focus of this discussion.

Proteins destined for the cell membrane, lysosomes, or secretion are synthesized by ribosomes attached to the rough endoplasmic reticulum (RER) (figure 4.7). These proteins have sequences of amino acids that target them to the lumen of the RER through which they move until released in small vesicles that bud from the ER. As the proteins pass through the ER, they are often modified by the addition of sugars—a process known as **glycosylation**.

The vesicles released from the ER travel to the cis face of the Golgi apparatus (figure 4.8). A popular model of the biosynthetic-secretory pathway posits that these vesicles fuse to form the cis face of the Golgi. The proteins then proceed to the trans face of the Golgi by a process called cisternal maturation. As the proteins proceed from the cis to trans side, they are further modified. Some of these modifications target the proteins for their final location. For instance, lysosomal proteins are modified by the addition of phosphates to their mannose sugars.

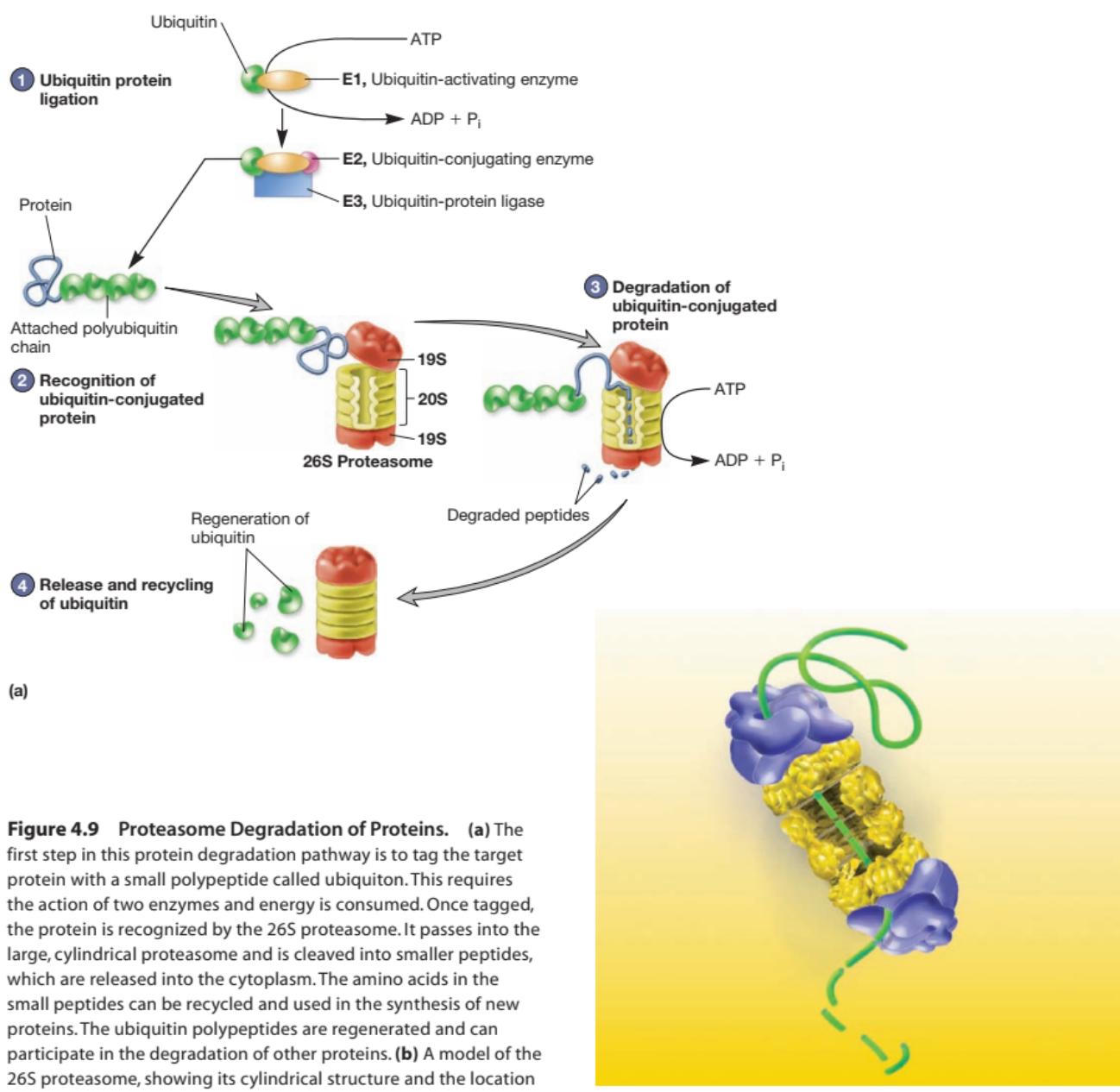
Transport vesicles are released from the trans face of the Golgi. Some deliver their contents to lysosomes. Others deliver proteins and other materials to the cell membrane. Two types of vesicles transport materials to the cell membrane. One type constitutively delivers proteins in an unregulated manner, releasing them to the outside of the cell as the transport vesicle fuses with the plasma membrane. Other vesicles, called secretory vesicles, are found only in multicellular eucaryotes, where they are observed in secretory cells such as mast cells and other cells of the immune system. Secretory vesicles store the proteins to be released until the cell receives an appropriate signal. Once received, the secretory vesicles move to the plasma membrane, fuse with it, and release their contents to the cell exterior. [Cells, tissues, and organs of the immune system \(section 31.2\)](#)

One interesting and important feature of the biosynthetic-secretory pathway is its quality-assurance mechanism. Proteins that fail to fold or have misfolded are not transported to their intended destination. Instead they are secreted into the cytosol, where they are targeted for destruction by the attachment of several small ubiquitin polypeptides as detailed in [figure 4.9](#). **Ubiquitin** marks the protein for degradation, which is accomplished by a huge, cylindrical complex called a **26S proteasome**. The protein is broken down to smaller peptides in an ATP-dependent process as the ubiquitins are released. The proteasome also is involved in producing peptides for antigen presentation during many immunological responses described in chapter 31.

The Endocytic Pathway

Endocytosis is used to bring materials into the cell from the outside. During endocytosis a cell takes up solutes or particles by enclosing them in vesicles pinched off from the plasma membrane. In most cases, these materials are delivered to a lysosome where they are digested. Endocytosis occurs regularly in all cells as a mechanism for recycling molecules in the membrane. In addition, some cells have specialized **endocytic pathways** that allow them to concentrate materials outside the cell before bringing them in. Others use endocytic pathways as a feeding mechanism. Many viruses and other intracellular pathogens use endocytic pathways to enter host cells.

Numerous types of endocytosis have been described. **Phagocytosis** involves the use of protrusions from the cell surface to surround and engulf particulates. It is carried out by certain immune system cells and many eucaryotic microbes. The endocytic vesicles formed by phagocytosis are called **phagosomes** ([figure 4.10](#)). Other types of endocytosis also involve invagination of the plasma membrane. As the membrane invaginates, it encloses liquid, soluble matter, and, in some cases, particulates in the resulting endocytic vesicle. One example of endocytosis by invagination is **clathrin-dependent endocytosis**. Clathrin-dependent endocytosis begins with coated pits, which are specialized membrane regions coated with the protein **clathrin** on the cytoplasmic side. The endocytic vesicles formed when these regions invaginate are called coated vesicles. Coated pits have receptors on their extracellular side that specifically bind macromolecules, concentrating them before they are endocytosed. Therefore this endocytic mechanism is referred to as **receptor-mediated endocytosis**. Clathrin-dependent endocytosis is used to ingest such things as hormones, growth factors, iron, and cholesterol. Another example of endocytosis by invagination is **caveolae-dependent endocytosis**. **Caveolae** ("little caves") are tiny, flask-shaped invaginations of the plasma membrane (about 50 to 80 nm in diameter) that are enriched in cholesterol and the membrane protein **caveolin**. The vesicles formed when caveolae pinch off are called **caveolar vesicles**. Caveolae-dependent endocytosis has been implicated in signal transduction, transport of small molecules such as folic acid, as well as transport of macromolecules. There is evidence that toxins such as cholera toxin enter their target cells via caveolae. Caveolae also appear to be used by many viruses, bacteria, and protozoa to enter host cells.



With the exception of caveolar vesicles, all other endocytic vesicles eventually deliver their contents to lysosomes. However, the route used varies. **Coated vesicles** fuse with small organelles containing lysosomal enzymes. These organelles are called **early endosomes** (figure 4.10). Early endosomes mature into late endosomes, which fuse with transport vesicles from the Golgi delivering additional lysosomal enzymes. **Late endosomes** eventually become lysosomes. The development of endosomes into lysosomes is not well understood. It appears that maturation in-

volves the movement of the organelles to a more central location in the cell and the selective retrieval of membrane proteins. Phagosomes take a slightly different route to lysosomes; they fuse with late endosomes rather than early endosomes (figure 4.10).

Materials for digestion can also be delivered to lysosomes by another route that does not involve endocytosis. Cells selectively digest and recycle cytoplasmic components (including organelles such as mitochondria) by a process called **autophagy**. It is believed that the cell components to be digested are surrounded by

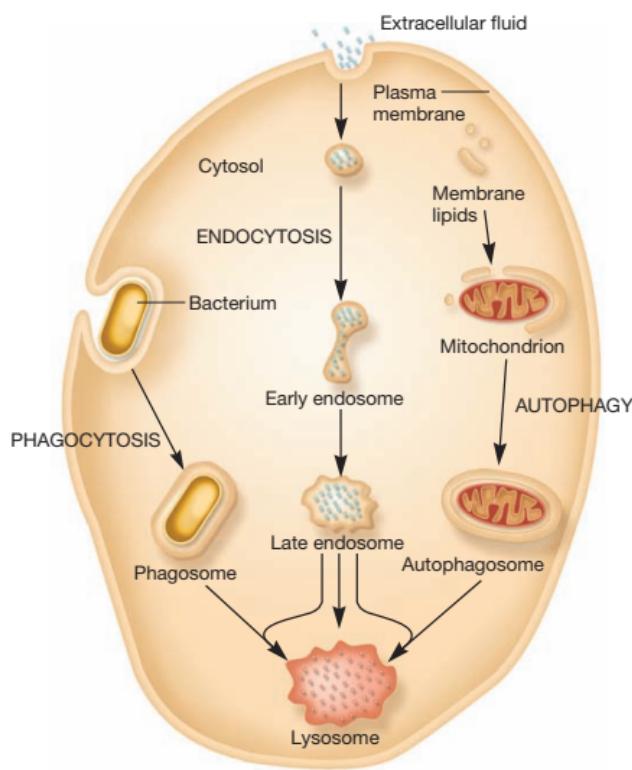


Figure 4.10 The Endocytic Pathway. Materials ingested by endocytic processes (except caveolae-dependent endocytosis) are delivered to lysosomes. The pathway to lysosomes differs, depending on the type of endocytosis. In addition, cell components are recycled when autophagosomes deliver them to lysosomes for digestion. This process is called autophagy.

a double membrane, as shown in figure 4.10. The source of the membrane is unknown, but it has been suggested that a portion of the ER is used. The resulting **autophagosome** fuses with a late endosome in a manner similar to that seen for phagosomes.

No matter the route taken, digestion occurs once the lysosome is formed. Amazingly, the lysosome accomplishes this without releasing its digestive enzymes into the cytoplasmic matrix. As the contents of the lysosome are digested, small products of digestion leave the lysosome, where they are used as nutrients or for other purposes. The resulting lysosome containing undigested material is often called a **residual body**. In some cases, the residual body can release its contents to the cell exterior by a process called lysosome secretion.

- How do the rough and smooth endoplasmic reticulum differ from one another in terms of structure and function? List the processes in which the ER is involved.
- Describe the structure of a Golgi apparatus in words and with a diagram. How do the cis and trans faces of the Golgi apparatus differ? List the major Golgi apparatus functions discussed in the text.

- What is a proteasome? Why is it important to the proper functioning of the endoplasmic reticulum?
- What are lysosomes? How do they participate in intracellular digestion?
- Describe the biosynthetic-secretory pathway. To what destinations does this pathway deliver proteins and other materials?
- Define endocytosis. Describe the endocytic pathway and the three routes that deliver materials to lysosomes for digestion. Which type of endocytosis does not deliver ingested material to lysosomes?
- Define autophagy, autophagosome, phagosome, phagocytosis, and residual body.
- Caveolae-mediated endocytosis is used by a number of pathogens to enter their host cells. Why might this route of entry be advantageous to the pathogens that use it?

4.5 EUKARYOTIC RIBOSOMES

The eukaryotic ribosome (i.e., one not found in mitochondria and chloroplasts) is larger than the prokaryotic 70S ribosome. It is a dimer of a 60S and a 40S subunit, about 22 nm in diameter, and has a sedimentation coefficient of 80S and a molecular weight of 4 million. Eukaryotic ribosomes can be either associated with the endoplasmic reticulum or free in the cytoplasmic matrix. When bound to the endoplasmic reticulum to form rough ER, they are attached through their 60S subunits.

Both free and ER-bound ribosomes synthesize proteins. Proteins made on the ribosomes of the RER are often secreted or are inserted into the ER membrane as integral membrane proteins. Free ribosomes are the sites of synthesis for nonsecretory and nonmembrane proteins. Some proteins synthesized by free ribosomes are inserted into organelles such as the nucleus, mitochondrion, and chloroplast. As discussed in chapters 3 and 11, molecular chaperones aid the proper folding of proteins after synthesis. They also assist the transport of proteins into eukaryotic organelles such as mitochondria.

- Describe the structure of the eukaryotic 80S ribosome and contrast it with the prokaryotic ribosome.
- How do free ribosomes and those bound to the ER differ in function?

4.6 MITOCHONDRIA

Found in most eukaryotic cells, **mitochondria** (s., **mitochondrion**) frequently are called the “powerhouses” of the cell (figure 4.11). Tricarboxylic acid cycle activity and the generation of ATP by electron transport and oxidative phosphorylation take place here. In the transmission electron microscope, mitochondria usually are cylindrical structures and measure approximately 0.3 to 1.0 μm by 5 to 10 μm . (In other words, they are about the same size as prokaryotic cells.) Although some cells possess 1,000 or more mitochondria, others, including some yeasts, unicellular algae, and trypanosome protozoa, have a single, giant, tubular mitochondrion twisted into a continuous net-

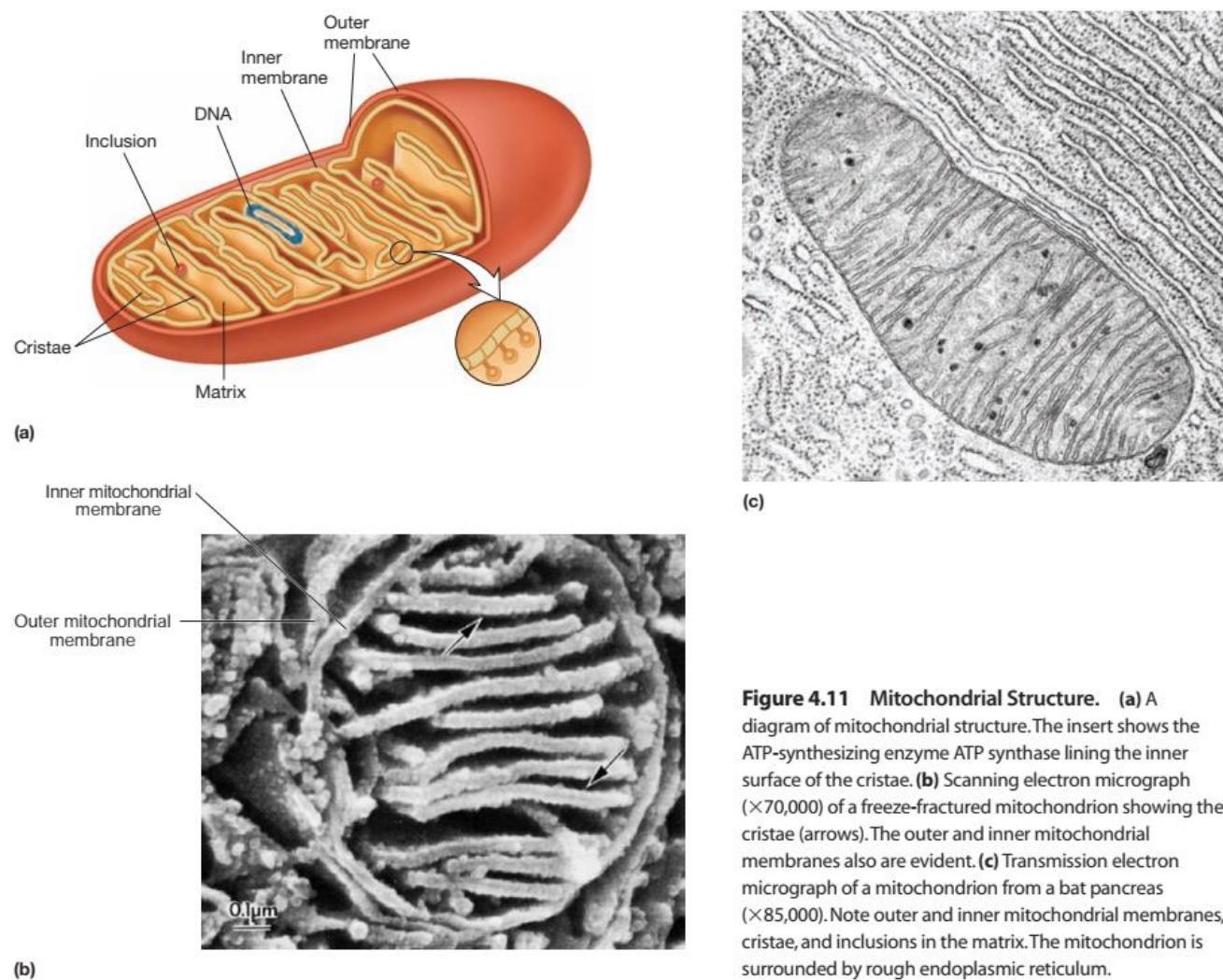


Figure 4.11 Mitochondrial Structure. (a) A diagram of mitochondrial structure. The insert shows the ATP-synthesizing enzyme ATP synthase lining the inner surface of the cristae. (b) Scanning electron micrograph ($\times 70,000$) of a freeze-fractured mitochondrion showing the cristae (arrows). The outer and inner mitochondrial membranes also are evident. (c) Transmission electron micrograph of a mitochondrion from a bat pancreas ($\times 85,000$). Note outer and inner mitochondrial membranes, cristae, and inclusions in the matrix. The mitochondrion is surrounded by rough endoplasmic reticulum.

work permeating the cytoplasm (figure 4.12). [The tricarboxylic acid cycle \(section 9.4\)](#); [Electron transport and oxidative phosphorylation \(section 9.5\)](#)

The mitochondrion is bounded by two membranes, an outer mitochondrial membrane separated from an inner mitochondrial membrane by a 6 to 8 nm intermembrane space (figure 4.11). The outer mitochondrial membrane contains porins and thus is similar to the outer membrane of gram-negative bacteria. The inner membrane has special infoldings called **cristae** (s., **crista**), which greatly increase its surface area. The shape of cristae differs in mitochondria from various species. Fungi have platelike (lamellar) cristae, whereas euglenoid flagellates may have cristae shaped like disks. Tubular cristae are found in a variety of eukaryotes; however, amoebae can possess mitochondria with cristae in the shape of vesicles (figure 4.13). The inner membrane encloses the mitochondrial matrix, a dense matrix containing ribosomes, DNA, and often large calcium phosphate granules. Mitochondrial ribosomes are smaller than cytoplasmic

ribosomes and resemble those of bacteria in several ways, including their size and subunit composition. In many organisms, mitochondrial DNA is a closed circle, like bacterial DNA. However, in some protists, mitochondrial DNA is linear.

Each mitochondrial compartment is different from the others in chemical and enzymatic composition. The outer and inner mitochondrial membranes, for example, possess different lipids. Enzymes and electron carriers involved in electron transport and oxidative phosphorylation (the formation of ATP as a consequence of electron transport) are located only in the inner membrane. The enzymes of the tricarboxylic acid cycle and catabolism of fatty acids are located in the matrix. [Lipid catabolism \(section 9.9\)](#)

The mitochondrion uses its DNA and ribosomes to synthesize some of its own proteins. In fact, mutations in mitochondrial DNA often lead to serious diseases in humans. Most mitochondrial proteins, however, are manufactured under the direction of

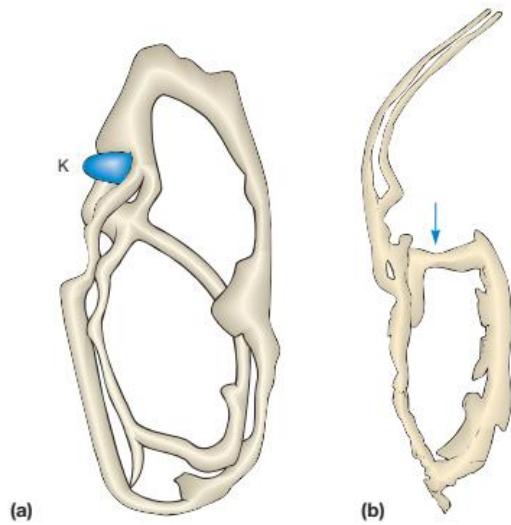


Figure 4.12 Trypanosome Mitochondria. The giant mitochondria from trypanosomes. (a) *Cryptosoma fasciculata* mitochondrion with kinetoplast, K. The kinetoplast contains DNA that codes for mitochondrial RNA and protein. (b) *Trypanosoma cruzi* mitochondrion with arrow indicating position of kinetoplast.

the nucleus. Mitochondria reproduce by binary fission. Because mitochondria resemble bacteria to some extent, it is thought that they arose from symbiotic associations between bacteria and larger cells (**Microbial Diversity & Ecology 4.2**). **Microbial evolution: Endosymbiotic origin of mitochondria and chloroplasts** (section 19.1)

4.7 CHLOROPLASTS

Plastids are cytoplasmic organelles of photosynthetic protists and plants that often possess pigments such as chlorophylls and carotenoids, and are the sites of synthesis and storage of food reserves. The most important type of plastid is the chloroplast. **Chloroplasts** contain chlorophyll and use light energy to convert CO₂ and water to carbohydrates and O₂. That is, they are the site of photosynthesis.

Although chloroplasts are quite variable in size and shape, they share many structural features. Most often they are oval with dimensions of 2 to 4 μm by 5 to 10 μm , but some algae possess one huge chloroplast that fills much of the cell. Like mitochondria, chloroplasts are encompassed by two membranes (figure 4.14). A matrix, the **stroma**, lies within the inner membrane. It contains DNA, ribosomes, lipid droplets, starch granules, and a complex internal membrane system whose most prominent components are flattened, membrane-delimited sacs, the **thylakoids**. Clusters of two or more thylakoids are dispersed within the stroma of most algal chloroplasts (figures 4.14 and 4.24b). In some photosynthetic protists, several disklike thylakoids are stacked on each other like coins to form **grana** (s., **granum**).

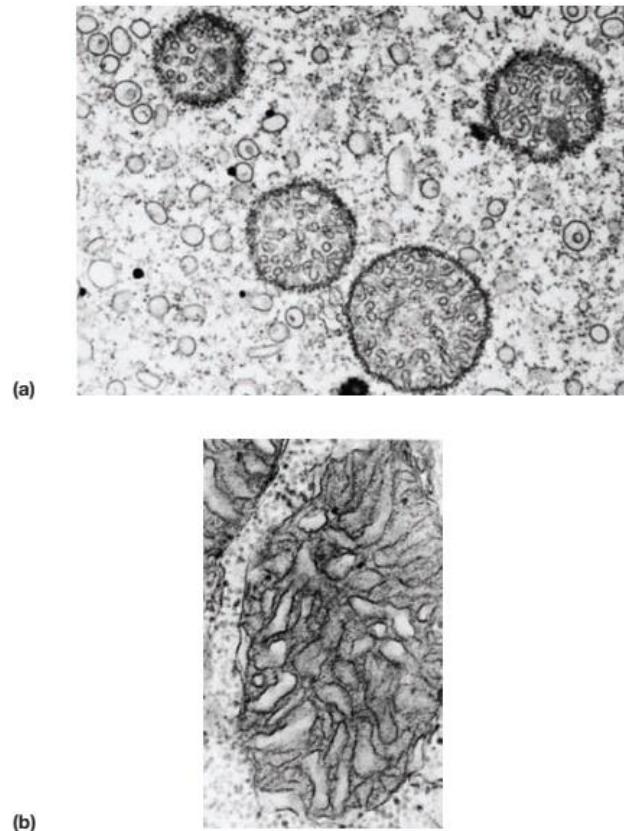


Figure 4.13 Mitochondrial Cristae. Mitochondria with a variety of cristae shapes. (a) Mitochondria from the slime mold *Schizoplasmodiopsis micropunctata*. Note the tubular cristae ($\times 49,500$). (b) The protist *Actinosphaerium* with vesicular cristae ($\times 75,000$).

Photosynthetic reactions are separated structurally in the chloroplast just as electron transport and the tricarboxylic acid cycle are in the mitochondrion. The trapping of light energy to generate ATP, NADPH, and O₂ is referred to as the **light reactions**. These reactions are located in the thylakoid membranes, where chlorophyll and electron transport components are also found. The ATP and NADPH formed by the light reactions are used to form carbohydrates from CO₂ and water in the **dark reactions**. The dark reactions take place in the stroma. **Phototrophy** (section 9.12)

The chloroplasts of many algae contain a **pyrenoid** (figure 4.24b), a dense region of protein surrounded by starch or another polysaccharide. Pyrenoids participate in polysaccharide synthesis.

1. Describe in detail the structure of mitochondria and chloroplasts. Where are the different components of these organelles' energy-trapping systems located?
2. Define plastid, dark reactions, light reactions, and pyrenoid.



Microbial Diversity & Ecology

4.2

The Origin of the Eucaryotic Cell

The profound differences between eucaryotic and prokaryotic cells have stimulated much discussion about how the more complex eucaryotic cell arose. Some biologists believe the original “protoeucaryote” was a large, aerobic archaeon or bacterium that formed mitochondria, chloroplasts, and nuclei when its plasma membrane invaginated and enclosed genetic material in a double membrane. The organelles could then evolve independently. It also is possible that a large cyanobacterium lost its cell wall and became phagocytic. Subsequently, primitive chloroplasts, mitochondria, and nuclei would be formed by the fusion of thylakoids and endoplasmic reticulum cisternae to enclose specific areas of cytoplasm.

By far the most popular theory for the origin of eucaryotic cells is the **endosymbiotic theory**. In brief, it is supposed that the ancestral prokaryotic cell, which may have been an archaeon, lost its cell wall and gained the ability to obtain nutrients by phagocytosing other prokaryotes. When photosynthetic cyanobacteria arose, the environment slowly became oxic. If an anaerobic, amoeboid, phagocytic prokaryote—possibly already possessing a developed nucleus—engulfed an aerobic bacterial cell and established a permanent symbiotic relationship with it, the host would be better adapted to its increasingly oxic environment. The endosymbiotic aerobic bacterium eventually would develop into the mitochondrion. Similarly, symbiotic associations with cyanobacteria could

lead to the formation of chloroplasts and photosynthetic eucaryotes. Some have speculated that cilia and flagella might have arisen from the attachment of spirochete bacteria (see chapter 21) to the surface of eucaryotic cells, much as spirochetes attach themselves to the surface of the motile protozoan *Myxotricha paradoxa* that grows in the digestive tract of termites.

There is evidence to support the endosymbiotic theory. Both mitochondria and chloroplasts resemble bacteria in size and appearance, contain DNA in the form of a closed circle like that of bacteria, and reproduce semiautonomously. Mitochondrial and chloroplast ribosomes resemble prokaryotic ribosomes more closely than those in the eucaryotic cytoplasmic matrix. The sequences of the chloroplast and mitochondrial genes for ribosomal RNA and transfer RNA are more similar to bacterial gene sequences than to those of eucaryotic rRNA and tRNA nuclear genes. Finally, there are symbiotic associations that appear to be bacterial endosymbioses in which distinctive prokaryotic characteristics are being lost. For example, the protozoan flagellate *Cyanophora paradoxa* has photosynthetic organelles called cyanellae with a structure similar to that of cyanobacteria and the remains of peptidoglycan in their walls. Their DNA is much smaller than that of cyanobacteria and resembles chloroplast DNA. The endosymbiotic theory is discussed in more detail in chapter 19.

- 3. What is the role of mitochondrial DNA?
- 4. What features of chloroplasts and mitochondria support the endosymbiotic theory of their evolution?

4.8 THE NUCLEUS AND CELL DIVISION

The **nucleus** is by far the most visually prominent organelle in eucaryotic cells. It was discovered early in the study of cell structure and was shown by Robert Brown in 1831 to be a constant feature of eucaryotic cells. The nucleus is the repository for the cell's genetic information and is its control center.

Nuclear Structure

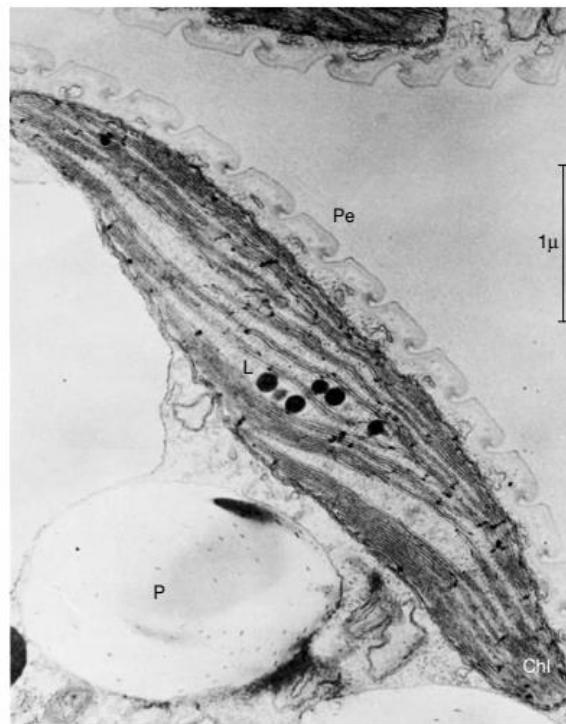
Nuclei are membrane-delimited spherical bodies about 5 to 7 μm in diameter (figures 4.2 and 4.24b). Dense fibrous material called **chromatin** can be seen within the nucleoplasm of the nucleus of a stained cell. This is the DNA-containing part of the nucleus. In nondividing cells, chromatin is dispersed, but it condenses during cell division to become visible as **chromosomes**. Some chromatin, the **euchromatin**, is loosely organized and contains those genes that are actively expressed. In contrast, **heterochromatin** is coiled more tightly, appears darker in the electron microscope, and is not genetically active most of the time.

The nucleus is bounded by the **nuclear envelope** (figures 4.2 and 4.24b), a complex structure consisting of inner and outer membranes separated by a 15 to 75 nm perinuclear space. The envelope is continuous with the ER at several points and its outer membrane is covered with ribosomes. A network of intermediate filaments, called the nuclear lamina, is observed in animal cells. It lies against the inner surface of the envelope and supports it. Chromatin usually is associated with the inner membrane.

Many **nuclear pores** penetrate the envelope (figure 4.15), and each pore is formed by a fusion of the outer and inner membranes. Pores are about 70 nm in diameter and collectively occupy about 10 to 25% of the nuclear surface. A complex ringlike arrangement of granular and fibrous material called the annulus is located at the edge of each pore.

The nuclear pores serve as a transport route between the nucleus and surrounding cytoplasm. Particles have been observed moving into the nucleus through the pores. Although the function of the annulus is not understood, it may either regulate or aid the movement of material through the pores. Substances also move directly through the nuclear envelope by unknown mechanisms.

Often the most noticeable structure within the nucleus is the **nucleolus** (figure 4.16). A nucleus may contain from one to many nucleoli. Although the nucleolus is not membrane-enclosed, it is a complex organelle with separate granular and fibrillar regions.



(a)

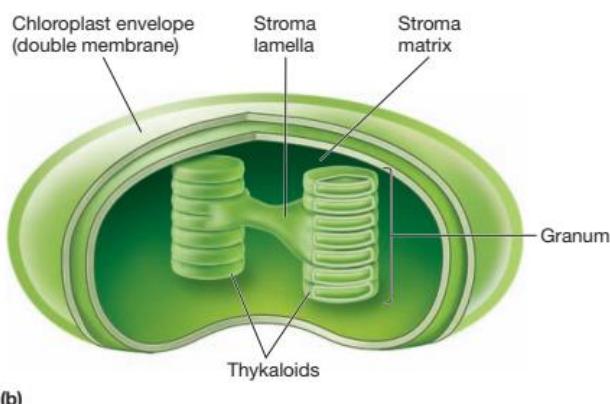


Figure 4.14 Chloroplast Structure. (a) The chloroplast (Chl), of the euglenoid flagellate *Colacium cyclopicum*. The chloroplast is bounded by a double membrane and has its thylakoids in groups of three or more. A paramylon granule (P), lipid droplets (L), and the pellicular strips (Pe) can be seen ($\times 40,000$). (b) A diagram of chloroplast structure.

It is present in nondividing cells, but frequently disappears during mitosis. After mitosis the nucleolus reforms around the nucleolar organizer, a particular part of a specific chromosome.

The nucleolus plays a major role in ribosome synthesis. The nucleolar organizer DNA directs the production of ribosomal



Figure 4.15 The Nucleus. A freeze-etch preparation of the conidium of the fungus *Geotrichum candidum* ($\times 44,600$). Note the large, convex nuclear surface with nuclear pores scattered over it.

RNA (rRNA). This RNA is synthesized in a single long piece that is cut to form the final rRNA molecules. The processed rRNAs next combine with ribosomal proteins (which have been synthesized in the cytoplasmic matrix) to form partially completed ribosomal subunits. The granules seen in the nucleolus are probably these subunits. Immature ribosomal subunits then leave the nucleus, presumably by way of the nuclear envelope pores, and mature in the cytoplasm.

Mitosis and Meiosis

When a eucaryotic microorganism reproduces asexually, its genetic material must be duplicated and then separated so that each new nucleus possesses a complete set of chromosomes. This process of nuclear division and chromosome distribution in eucaryotic cells is called **mitosis**. Mitosis actually occupies only a small portion of a microorganism's life as can be seen by examining the **cell cycle** (figure 4.17). The cell cycle is the total sequence of events in the growth-division cycle between the end of one division and the end of the next. Cell growth takes place in the **interphase**, that portion of the cycle between periods of mitosis. Interphase is composed of three parts. The **G₁ period** (gap 1 period) is a time of active synthesis of RNA, ribosomes, and other cytoplasmic constituents accompanied by considerable cell growth. This is followed by the **S period** (synthesis period) in which DNA is replicated and doubles in quantity. Finally, there is a second gap, the **G₂ period**, when the cell prepares for mitosis, the **M period**, by activities such as the synthesis of special division proteins. The total length of the cycle differs considerably between microorganisms, usually due to variations in the length of G₁.

Mitotic events are summarized in figure 4.17. During mitosis, the genetic material duplicated during the S period is distributed

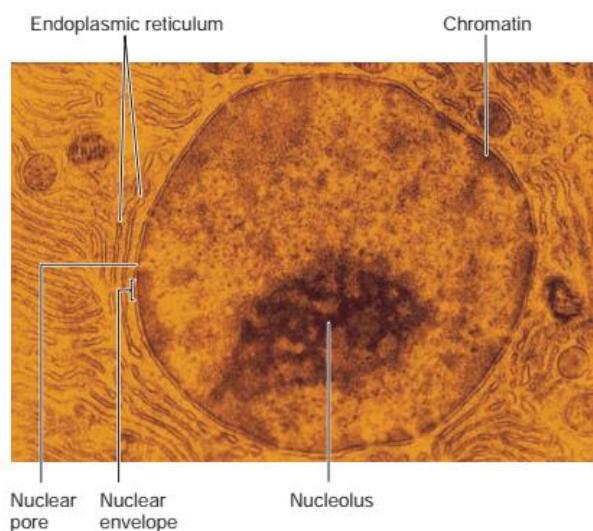


Figure 4.16 The Nucleolus. The nucleolus is a prominent feature of the nucleus. It functions in rRNA synthesis and the assembly of ribosomal subunits. Chromatin, nuclear pores, and the nuclear envelope are also visible in this electron micrograph of an interphase nucleus.

equally to the two new nuclei by cytoskeletal elements so that each has a full set of genes. There are four phases in mitosis. In **prophase**, the chromosomes—each with two chromatids—become visible and move toward the equator of the cell. The mitotic spindle forms, the nucleolus disappears, and the nuclear envelope begins to dissolve. The chromosomes are arranged in the center of the spindle during **metaphase** and the nuclear envelope disappears. During **anaphase** the chromatids in each chromosome separate and move toward the opposite poles of the spindle (figure 4.18). Finally during **telophase**, the chromatids become less visible, the nucleolus reappears, and a nuclear envelope reassembles around each set of chromatids to form two new nuclei. The resulting progeny cells have the same number of chromosomes as the parent. Thus after mitosis, a diploid organism will remain diploid.

Mitosis in some eukaryotic microorganisms can differ from that pictured in figure 4.17. For example, the nuclear envelope does not disappear in many fungi and some protists. Frequently cytokinesis, the division of the parental cell's cytoplasm to form new cells, begins during anaphase and finishes by the end of telophase. However, mitosis can take place without cytokinesis to generate multinucleate or coenocytic cells.

Many microorganisms have a sexual phase in their life cycles (figure 4.19). In this phase, they must reduce their chromosome number by half, from the diploid state to the haploid or 1N (a single copy of each chromosome). Haploid cells may immediately act as gametes and fuse to reform diploid organisms or may form gametes only after a considerable delay (figure 4.19). The process

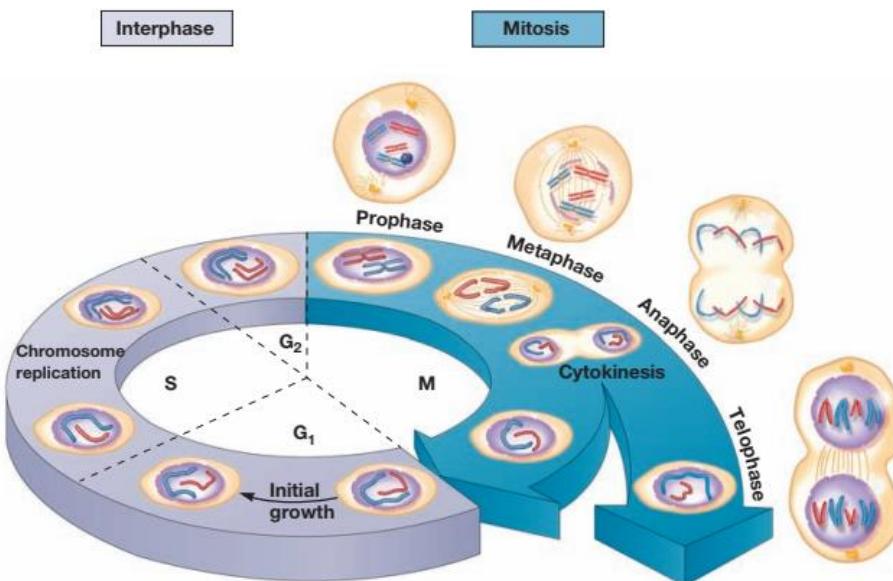


Figure 4.17 The Eukaryotic Cell Cycle. The length of the M period has been increased disproportionately in order to show the phases of mitosis. G₁ period: synthesis of mRNA, tRNA, ribosomes, and cytoplasmic constituents. Nucleolus grows rapidly. S period: rapid synthesis and doubling of nuclear DNA and histones. G₂ period: preparation for mitosis and cell division. M period: mitosis (prophase, metaphase, anaphase, telophase) and cytokinesis.

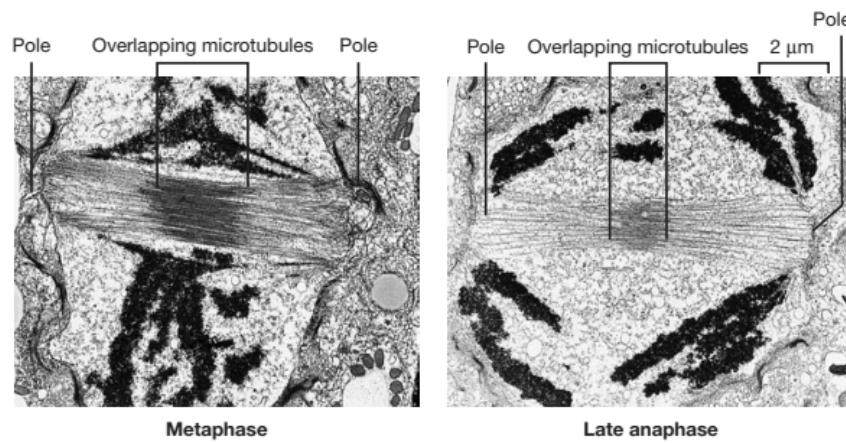


Figure 4.18 Mitosis. In these electron micrographs of dividing diatoms, the overlap of the microtubules lessens markedly during spindle elongation as the cell passes from metaphase to anaphase.

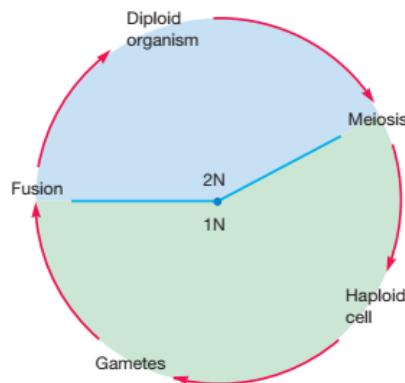


Figure 4.19 Generalized Eucaryotic Life Cycle.

by which the number of chromosomes is reduced in half with each daughter cell receiving one complete set of chromosomes is called **meiosis**. Life cycles can be quite complex in eucaryotic microorganisms and are discussed in more detail in chapters 25 and 26.

Meiosis is quite complex and involves two stages. The first stage differs markedly from mitosis. During prophase, homologous chromosomes come together and lie side-by-side, a process known as **synapsis**. The homologues move to opposite poles in anaphase, thus reducing the number of chromosomes by half. The second stage of meiosis is similar to mitosis in terms of mechanics, and chromatids of each chromosome are separated. After completion of meiosis I and meiosis II, the original diploid cell has been transformed into four haploid cells.

1. Describe the structure of the nucleus. What are euchromatin and heterochromatin? What is the role of the pores in the nuclear envelope?
2. Briefly discuss the structure and function of the nucleolus. What is the nucleolar organizer?

3. Describe the eucaryotic cell cycle, its periods, and the process of mitosis.
4. What is meiosis, how does it take place, and what is its role in the microbial life cycle?

4.9 EXTERNAL CELL COVERINGS

Eucaryotic microorganisms differ greatly from prokaryotes in the supporting or protective structures they have external to the plasma membrane. In contrast with most bacteria, many eucaryotes lack an external cell wall. The amoeba is an excellent example. Eucaryotic cell membranes, unlike most prokaryotic membranes, contain sterols such as cholesterol in their lipid bilayers, and this may make them mechanically stronger, thus reducing the need for external support. Of course many eucaryotes do have a rigid external **cell wall**. The cell walls of photosynthetic protists usually have a layered appearance and contain large quantities of polysaccharides such as cellulose and pectin. In addition, inorganic substances like silica (in diatoms) or calcium carbonate may be present. Fungal cell walls normally are rigid. Their exact composition varies with the organism; usually cellulose, chitin, or glucan (a glucose polymer different from cellulose) are present. Despite their nature the rigid materials in eucaryotic cell walls are chemically simpler than prokaryotic peptidoglycan. [The bacterial cell wall \(section 3.6\)](#)

Many protists have a different supportive mechanism, the **pellicle** (figure 4.14a). This is a relatively rigid layer of components just beneath the plasma membrane (sometimes the plasma membrane is also considered part of the pellicle). The pellicle may be fairly simple in structure. For example, *Euglena* has a series of overlapping strips with a ridge at the edge of each strip fitting into a groove on the adjacent one. In contrast, the pellicles of ciliate protozoa are exceptionally complex with two membranes and a variety of associated structures. Although pellicles are not as strong and rigid as cell walls, they give their possessors a characteristic shape.

4.10 CILIA AND FLAGELLA

Cilia (s., **cilium**) and **flagella** (s., **flagellum**) are the most prominent organelles associated with motility. Although both are whip-like and beat to move the microorganism along, they differ from one another in two ways. First, cilia are typically only 5 to 20 μm in length, whereas flagella are 100 to 200 μm long. Second, their patterns of movement are usually distinctive (figure 4.20). Flagella move in an undulating fashion and generate planar or helical waves originating at either the base or the tip. If the wave moves from base to tip, the cell is pushed along; a beat traveling from the tip toward the base pulls the cell through the water. Sometimes the flagellum will have lateral hairs called flimmer filaments (thicker, stiffer hairs are called **mastigonemes**). These filaments change flagellar action so that a wave moving down the filament toward the tip pulls the cell along instead of pushing it. Such a flagellum often is called a **tinsel flagellum**, whereas the naked flagellum is referred to as a **whiplash flagellum** (figure 4.21). Cilia, on the other hand, normally have a beat with two distinctive phases. In the effective stroke, the cilium strokes through the surrounding fluid like an oar, thereby propelling the organism along in the water. The cilium next bends along its length while it is pulled forward during the recovery stroke in preparation for another effective stroke. A ciliated microorganism actually coordinates the beats so that some of its cilia are in the

recovery phase while others are carrying out their effective stroke (figure 4.22). This coordination allows the organism to move smoothly through the water.

Despite their differences, cilia and flagella are very similar in ultrastructure. They are membrane-bound cylinders about 0.2 μm

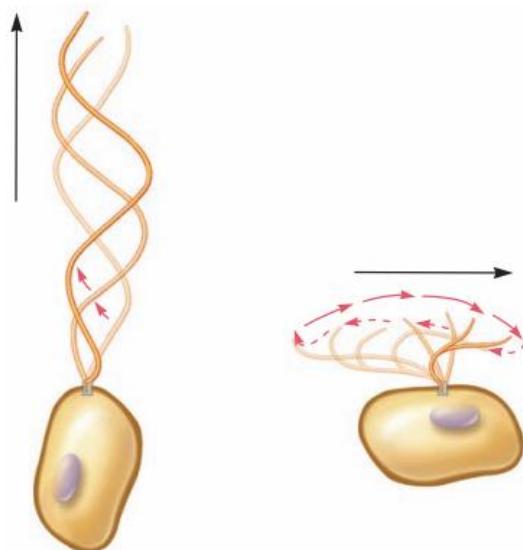


Figure 4.20 Patterns of Flagellar and Ciliary Movement. Flagellar and ciliary movement often takes the form of waves. Flagella (left illustration) move either from the base of the flagellum to its tip or in the opposite direction. The motion of these waves propels the organism along. The beat of a cilium (right illustration) may be divided into two phases. In the effective stroke, the cilium remains fairly stiff as it swings through the water. This is followed by a recovery stroke in which the cilium bends and returns to its initial position. The black arrows indicate the direction of water movement in these examples.

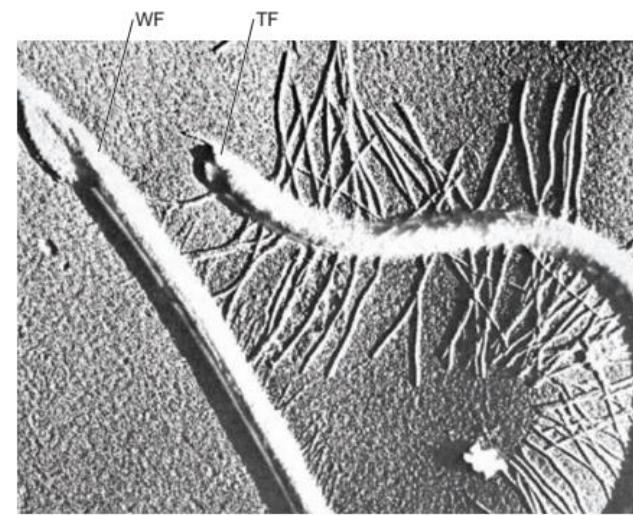


Figure 4.21 Whiplash and Tinsel Flagella. Transmission electron micrograph of a shadowed whiplash flagellum, WF, and a tinsel flagellum, TF, with mastigonemes.



Figure 4.22 Coordination of Ciliary Activity. A scanning electron micrograph of *Paramecium* showing cilia ($\times 1,500$). The ciliary beat is coordinated and moves in waves across the protozoan's surface, as can be seen in the photograph.

in diameter. Located in the matrix of the organelle is a complex, the **axoneme**, consisting of nine pairs of microtubule doublets arranged in a circle around two central tubules (figure 4.23). This is called the 9 + 2 pattern of microtubules. Each doublet also has pairs of arms projecting from subtube A (the complete microtubule) toward a neighboring doublet. A radial spoke extends from subtube A toward the internal pair of microtubules with their central sheath. These microtubules are similar to those found in the cytoplasm. Each is constructed of two types of tubulin subunits, α - and β -tubulins, that resemble the contractile protein actin in their composition.

Components external to the cell wall: Flagella and motility (section 3.9)

A **basal body** lies in the cytoplasm at the base of each cilium or flagellum. It is a short cylinder with nine microtubule triplets around its periphery (a 9 + 0 pattern) and is separated from the rest of the organelle by a basal plate. The basal body directs the construction of these organelles. Cilia and flagella appear to grow through the addition of preformed microtubule subunits at their tips.

Cilia and flagella bend because adjacent microtubule doublets slide along one another while maintaining their individual lengths. The doublet arms (figure 4.23), about 15 nm long, are made of the protein **dynein**. ATP powers the movement of cilia and flagella, and isolated dynein hydrolyzes ATP. It appears that dynein arms interact with the B subtubules of adjacent doublets to cause the sliding. The radial spokes also participate in this sliding motion.

Cilia and flagella beat at a rate of about 10 to 40 strokes or waves per second and propel microorganisms rapidly. The record

holder is the flagellate *Monas stigmatica*, which swims at a rate of 260 $\mu\text{m}/\text{second}$ (approximately 40 cell lengths per second); the common euglenoid flagellate, *Euglena gracilis*, travels at around 170 μm or 3 cell lengths per second. The ciliate protozoan *Paramecium caudatum* swims at about 2,700 $\mu\text{m}/\text{second}$ (12 lengths per second). Such speeds are equivalent to or much faster than those seen in higher animals, but not as fast as those in prokaryotes.

- How do eucaryotic microorganisms differ from prokaryotes with respect to supporting or protective structures external to the plasma membrane? Describe the pellicle and indicate which microorganisms have one.
- Prepare and label a diagram showing the detailed structure of a cilium or flagellum. How do cilia and flagella move, and what is dynein's role in the process? Contrast the ways in which flagella and cilia propel microorganisms through water.
- Compare the structure and mechanism of action of prokaryotic and eucaryotic flagella.

4.11 COMPARISON OF PROKARYOTIC AND EUKARYOTIC CELLS

A comparison of the cells in figure 4.24 demonstrates that there are many fundamental differences between eucaryotic and prokaryotic cells. **Eucaryotic cells** have a membrane-enclosed nucleus. In

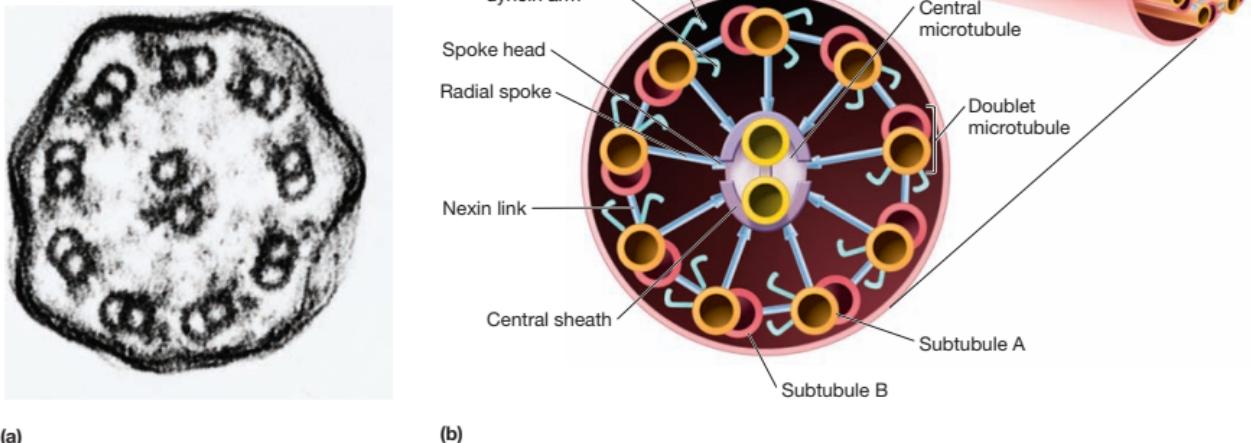


Figure 4.23 Cilia and Flagella Structure. (a) An electron micrograph of a cilium cross section. Note the two central microtubules surrounded by nine microtubule doublets ($\times 160,000$). (b) A diagram of cilia and flagella structure.

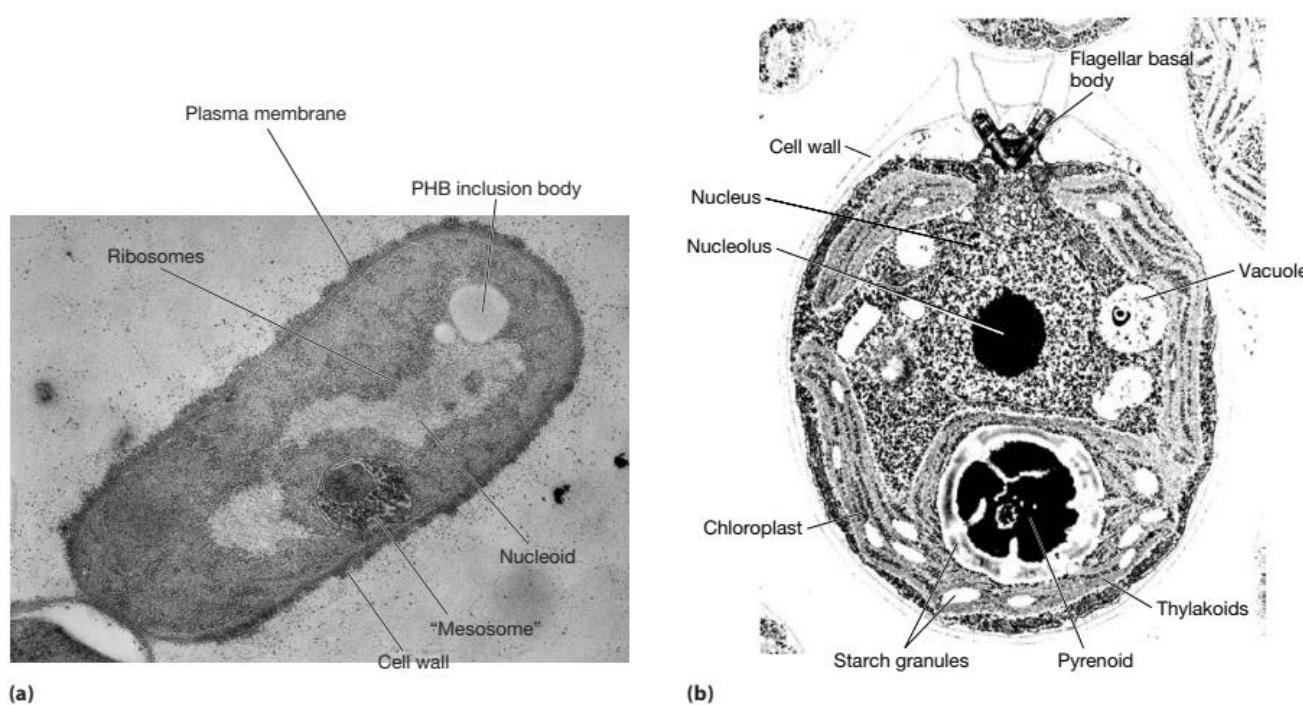


Figure 4.24 Comparison of Prokaryotic and Eucaryotic Cell Structure. (a) The prokaryote *Bacillus megaterium* ($\times 30,500$). (b) The eucaryotic alga *Chlamydomonas reinhardtii*, a deflagellated cell. Note the large chloroplast with its pyrenoid body ($\times 30,000$).

contrast, **prokaryotic cells** lack a true, membrane-delimited nucleus. *Bacteria* and *Archaea* are prokaryotes; all other organisms—fungi, protists, plants, and animals—are eucaryotic. Most prokaryotes are smaller than eucaryotic cells, often about the size of eucaryotic mitochondria and chloroplasts.

The presence of the eucaryotic nucleus is the most obvious difference between these two cell types, but many other major distinctions exist. It is clear from **table 4.2** that prokaryotic cells are much simpler structurally. In particular, an extensive and diverse collection of membrane-delimited organelles is missing. Furthermore, prokaryotes are simpler functionally in several ways. They lack mitosis and meiosis, and have a simpler genetic organization. Many complex eucaryotic processes are absent in prokaryotes: endocytosis, intracellular digestion, directed cytoplasmic streaming, and amoeboid movement, are just a few.

Despite the many significant differences between these two basic cell forms, they are remarkably similar on the biochemical level as we discuss in succeeding chapters. Prokaryotes and eucaryotes are composed of similar chemical constituents. With a few exceptions, the genetic code is the same in both, as is the way in which the genetic information in DNA is expressed. The principles underlying metabolic processes and many important metabolic pathways are identical. Thus beneath the profound structural and functional differences between prokaryotes and eucaryotes, there is an even more fundamental unity: a molecular unity that is basic to all known life processes.

1. Outline the major differences between prokaryotes and eucaryotes. How are they similar?
2. What characteristics make *Archaea* more like eucaryotes? What features make them more like *Bacteria*?

Comparison of Prokaryotic and Eucaryotic Cells			
Property	Bacteria	Prokaryotes	Eucaryotes
		Archaea	Eukarya
Organization of Genetic Material			
True membrane-bound nucleus	No	No	Yes
DNA complexed with histones	No	Some	Yes
Chromosomes	Usually one circular chromosome	Usually one circular chromosome	More than one; chromosomes are linear
Plasmids	Very common	Very common	Rare
Introns in genes	No	No	Yes
Nucleolus	No	No	Yes
Mitochondria			
Chloroplasts			
Plasma Membrane Lipids			
Flagella	Submicroscopic in size; composed of one protein fiber	Submicroscopic in size; composed of one protein fiber	Microscopic in size; membrane bound; usually 20 microtubules in 9 + 2 pattern
Endoplasmic Reticulum	No	No	Yes
Golgi Apparatus	No	No	Yes
Peptidoglycan in Cell Walls	Yes	No	No
Ribosome Size	70S	70S	80S
Lysosomes	No	No	Yes
Cytoskeleton	Rudimentary	Rudimentary	Yes
Gas Vesicles	Yes	Yes	No

Summary

4.1 An Overview of Eucaryotic Cell Structure

- a. The eucaryotic cell has a true, membrane-delimited nucleus and many membranous organelles (**table 4.1**; **figure 4.2**).
- b. The membranous organelles compartmentalize the cytoplasm of the cell. This allows the cell to carry out a variety of biochemical reactions simultaneously. It also provides more surface area for membrane-associated activities such as respiration.

4.2 The Plasma Membrane and Membrane Structure

- a. Eucaryotic membranes are similar in structure and function to those of bacteria. The two differ in terms of their lipid composition.
- b. Eucaryotic membranes contain microdomains called lipid rafts. They are enriched for certain lipids and proteins and participate in a variety of cellular processes.

4.3 The Cytoplasmic Matrix, Microfilaments, Intermediate Filaments, and Microtubules

- a. The cytoplasmic matrix contains microfilaments, intermediate filaments, and microtubules, small organelles partly responsible for cell structure and movement. These and other types of filaments are organized into a cytoskeleton (**figure 4.5**).
- b. Microfilaments and microtubules have been observed in eucaryotic microbes. Microfilaments are composed of actin proteins; microtubules are composed of α -tubulin and β -tubulin.
- c. Intermediate filaments are assembled from a heterogeneous family of proteins. They have not been identified or studied in eucaryotic microbes.

4.4 Organelles of the Biosynthetic-Secretory and Endocytic Pathways

- a. The cytoplasmic matrix is permeated with a complex of membranous organelles and vesicles. Some are involved in the synthesis and secretion of ma-

terials (biosynthetic-secretory pathway). Some are involved in the uptake of materials from the extracellular millieu (endocytic pathway).

- b. The endoplasmic reticulum (ER) is an irregular network of tubules and flattened sacs (cisternae). The ER may have attached ribosomes and may be active in protein synthesis (rough endoplasmic reticulum), or it may lack ribosomes (smooth ER) (**figure 4.7**).
- c. The ER can donate materials to the Golgi apparatus, an organelle composed of one or more stacks of cisternae (**figure 4.8**). This organelle prepares and packages cell products for secretion.
- d. The Golgi apparatus also buds off vesicles that deliver hydrolytic enzymes and other proteins to lysosomes. Lysosomes are organelles that contain digestive enzymes and aid in intracellular digestion of extracellular materials delivered to them by endocytosis (**figure 4.10**).
- e. Eucaryotes ingest materials using several kinds of endocytosis. These include phagocytosis, clathrin-dependent endocytosis, and caveolae-dependent endocytosis. Some macromolecules are bound to receptors prior to endocytosis in a process called receptor-mediated endocytosis.

4.5 Eucaryotic Ribosomes

- a. Eucaryotic ribosomes are either found free in the cytoplasmic matrix or bound to the ER.
- b. Eucaryotic ribosomes are 80S in size.

4.6 Mitochondria

- a. Mitochondria are organelles bounded by two membranes, with the inner membrane folded into cristae (**figure 4.11**).
- b. Mitochondria are responsible for energy generation by the tricarboxylic acid cycle, electron transport, and oxidative phosphorylation.

4.7 Chloroplasts

- a. Chloroplasts are pigment-containing organelles that serve as the site of photosynthesis (**figure 4.14**).
- b. The trapping of light energy takes place in the thylakoid membranes of the chloroplast, whereas CO₂ fixation occurs in the stroma.

Key Terms

autophagosome 88	clathrin-dependent endocytosis 86	intermediate filament 83	pellicle 94
autophagy 87	coated vesicles 87	interphase 92	phagocytosis 86
axoneme 96	cristae 89	late endosomes 87	phagosomes 86
basal body 96	cytoplasmic matrix 83	lipid raft 81	plastid 90
biosynthetic-secretory pathway 86	cytoskeleton 83	lysosome 86	procaryotic cells 97
caveolae 86	dictyosome 85	meiosis 94	pyrenoid 90
caveolae-dependent endocytosis 86	dynein 96	microfilament 83	receptor-mediated endocytosis 86
cell cycle 92	early endosome 87	microtubule 83	residual body 88
cell wall 94	endocytic pathway 86	mitochondrion 88	rough endoplasmic reticulum (RER) 85
chloroplast 90	endocytosis 86	mitosis 92	smooth endoplasmic reticulum (SER) 85
chromatin 91	endoplasmic reticulum (ER) 84	nuclear envelope 91	stroma 90
chromosome 91	eucaryotic cells 96	nuclear pores 91	thylakoid 90
cilia 95	flagella 95	nucleolus 91	26S proteasome 86
cisternae 84	Golgi apparatus 85	nucleus 91	
clathrin 86	grana 90	organelle 79	

Critical Thinking Question

1. Discuss the statement: "The most obvious difference between eucaryotic and prokaryotic cells is in their use of membranes." What general roles do membranes play in eucaryotic cells?

Learn more:

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