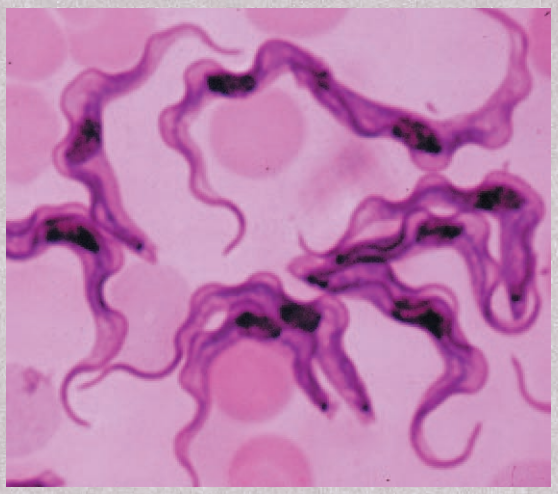
CHAPTER 4

Eucaryotic Cell Structure and Function



Often we exclusively emphasize procaryotes 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.

Outline

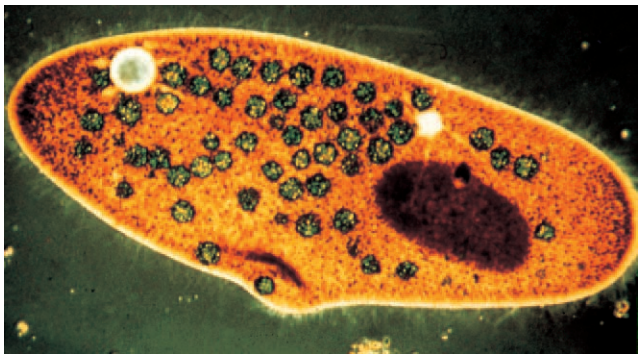
Concepts

1. Eucaryotic cells differ most obviously from procaryotic 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.
2. A cytoskeleton composed of microtubules, microfilaments, and intermediate filaments helps give eucaryotic cells shape; microtubules and microfilaments are also involved in cell movements and intracellular transport.
3. In eucaryotes, genetic material is distributed between cells by the highly organized, complex processes called mitosis and meiosis.
4. Despite great differences between eucaryotes and procaryotes with respect to such things as morphology, they are similar on the biochemical level.

The key to every biological problem must finally be sought in the cell.
—E. B. Wilson

In chapter 3 considerable attention is devoted to procaryotic cell structure and function because bacteria are immensely important in microbiology and have occupied a large portion of microbiologists' attention in the past. Nevertheless, eucaryotic algae, fungi, and protozoa also are microorganisms and have been extensively studied. These organisms often are extraordinarily complex, interesting in their own right, and prominent members of the ecosystem (**figure 4.1**). In addition, fungi (and to some extent, algae) are exceptionally useful in industrial microbiology. Many fungi and protozoa are also major human pathogens; one only need think of either malaria or African sleeping sickness (see chapter opener) to appreciate the significance of eucaryotes in pathogenic microbiology. So, although this text emphasizes bacteria, eucaryotic microorganisms are discussed at many points.

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, procaryotic and eucaryotic cells are compared in some depth.



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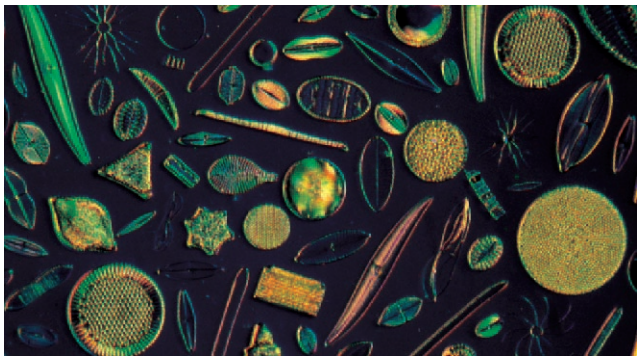

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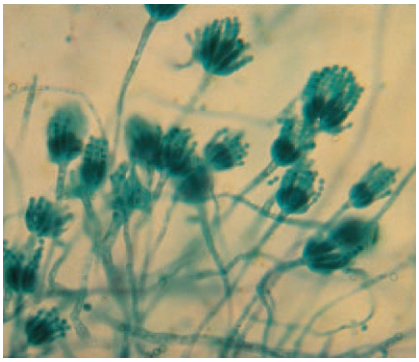

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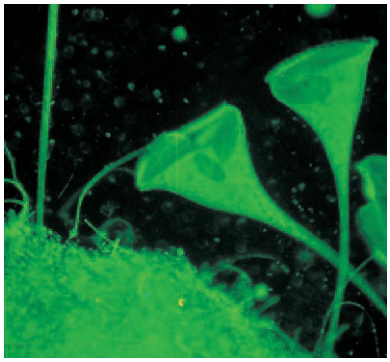

(e)

(f)

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

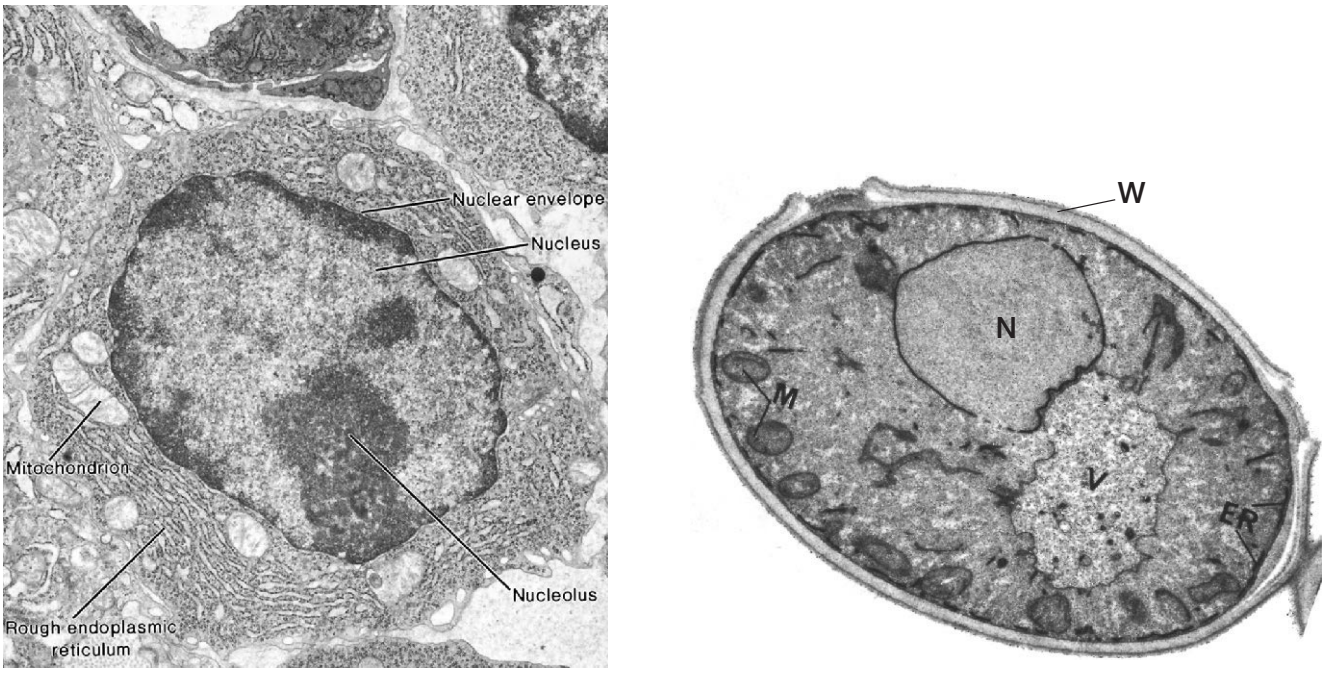

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Figure 4.2 **Eucaryotic Cell Ultrastructure.** (**a**) A lymphoblast in the rat lymph node (×17,500). (**b**) The yeast *Saccharomyces* (×7,200). Note the nucleus (n), mitochondrion (m), vacuole (v), endoplasmic reticulum (er), and cell wall (w).

4.1 An Overview of Eucaryotic Cell Structure

The most obvious difference between eucaryotic and procaryotic 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 figure 3.11 (*p. 51*) shows how much more 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 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, 4.3, and 4.26*b* provide generalized views of eucaryotic cell structure and illustrate most of the organelles to be discussed. **Table 4.1** briefly summarizes the functions of the major eucaryotic organelles. Those organelles lying inside the plasma membrane are first described, and then components outside the membrane are discussed.

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

When a eucaryotic cell is examined at low power with the electron microscope, its larger organelles are seen to lie in an apparently featureless, homogeneous substance called the **cytoplasmic matrix.** The matrix, although superficially uninteresting, is actually 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.

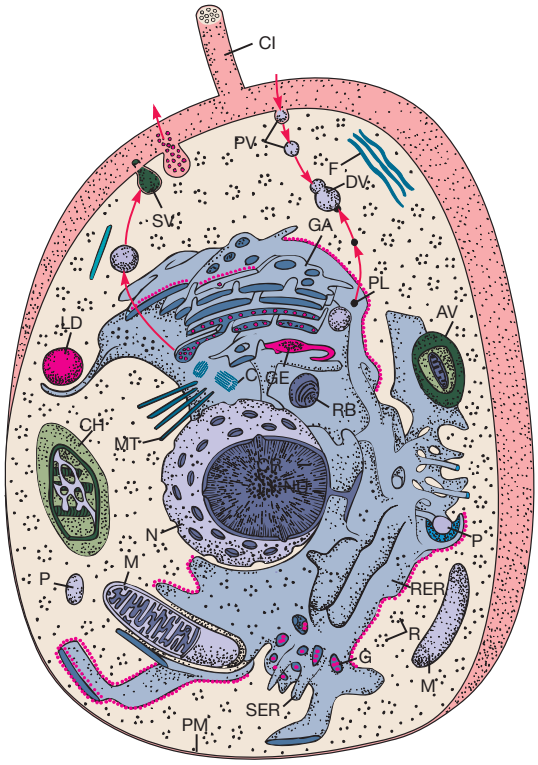


Figure 4.3 **Eucaryotic Cell Ultrastructure.** This is a schematic, three-dimensional diagram of a cell with the most important organelles identified in the illustration. AV, autophagic vacuole; C, centriole; CH, chloroplast; CI, cilium; CR, chromatin; DV, digestion vacuole; F, microfilaments; G, glycogen; GA, Golgi apparatus; GE, GERL; LD, lipid droplet; M, mitochondrion; MT, microtubules; N, nucleus; NU, nucleolus; P, peroxisome; PL, primary lysosome; PM, plasma membrane; PV, pinocytotic vesicle; R, ribosomes and polysomes; RB, residual body; RER, rough endoplasmic reticulum; SER, smooth endoplasmic reticulum; SV, secretion vacuole.

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)

Water constitutes about 70 to 85% by weight of a eucaryotic cell. Thus a large part of the cytoplasmic matrix is water. Cellular water can exist in two different forms. Some of it is bulk or free water; this is normal, osmotically active water. Osmosis, water activity, and growth (pp. 61, 121–23)

Water also can exist as bound water or water of hydration. This water is bound to the surface of proteins and other macromolecules and is osmotically inactive and more ordered than bulk water. There is some evidence that bound water is the site of many metabolic processes. The protein content of cells is so high that the cytoplasmic matrix often may be semicrystalline. Usually matrix pH is around neutrality, about pH 6.8 to 7.1, but can vary widely. For example, protozoan digestive vacuoles may reach pHs as low as 3 to 4.

Probably all eucaryotic cells have **microfilaments,** minute protein filaments, 4 to 7 nm in diameter, which may be either scattered within the cytoplasmic matrix or organized into networks and parallel arrays. Microfilaments are involved in cell motion and shape changes. Some examples of cellular movements associated with microfilament activity are the motion of pigment granules, amoeboid movement, and protoplasmic streaming in slime molds (*see chapter 25*).

The participation of microfilaments in cell movement is suggested by electron microscopic studies showing that they frequently are found at locations appropriate for such a role. For example, they are concentrated at the interface between stationary and flowing cytoplasm in plant cells and slime molds. Experiments using the drug cytochalasin B have provided additional

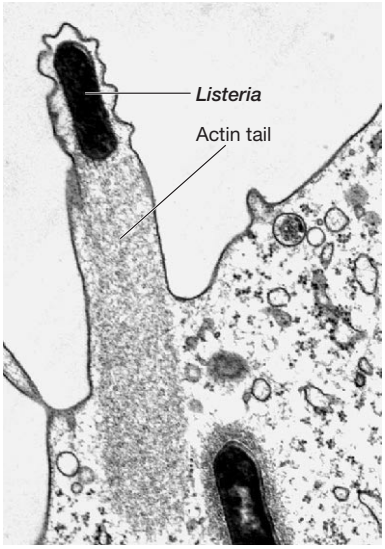


Figure 4.4 ***Listeria*** **Motility and Actin Filaments.** A *Listeria* cell is propelled through the cell surface by a bundle of actin filaments.

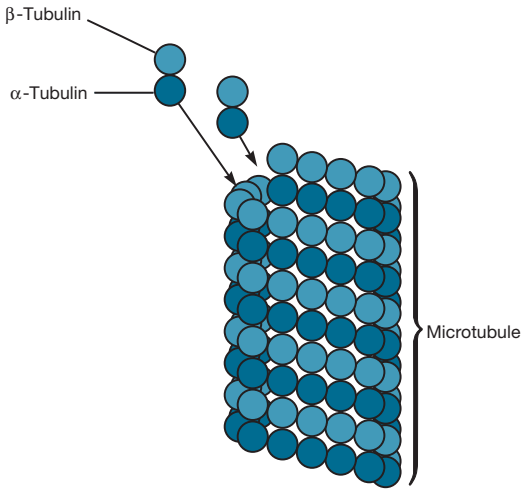


Figure 4.5 **Microtubule Structure.** The hollow cylinder, about 25 nm in diameter, is made of two kinds of protein subunits, α-tubulin and β-tubulin.

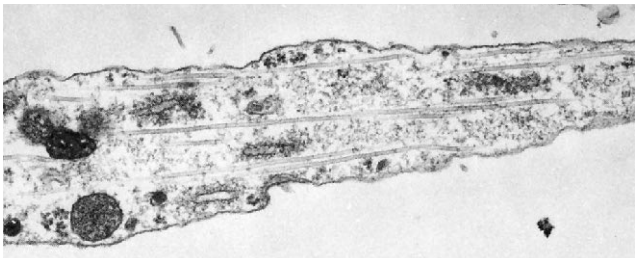
evidence. Cytochalasin B disrupts microfilament structure and often simultaneously inhibits cell movements. However, because the drug has additional effects in cells, a direct cause-and-effect interpretation of these experiments is sometimes difficult.

Microfilament protein has been isolated and analyzed chemically. It is an actin, very similar to the actin contractile protein of muscle tissue. This is further indirect evidence for microfilament involvement in cell movement.

Some pathogens such as *Listeria monocytogenes* make use of eucaryotic actin to move rapidly through the host cell. The ActA protein released by *Listeria* causes the polymerization of actin filaments at the end of the bacterium. A tail of actin is formed and trapped in the host cytoskeleton. Its continued elongation pushes the bacterium along at rates up to 11 μm/minute. The bacterium can even be propelled through the cell surface and into neighboring cells (**figure 4.4**).

A second type of small filamentous organelle in the cytoplasmic matrix is shaped like a thin cylinder about 25 nm in diameter. Because of its tubular nature this organelle is called a **microtubule.** Microtubules are complex structures constructed of two slightly different spherical protein subunits named tubulins, each of which 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. Evidence for a structural role comes from their intracellular distribution and studies on the effects of the drug colchicine. Long, thin cell structures requiring support such as the axopodia (long, slender, rigid pseudopodia) of protozoa contain microtubules (**figure 4.6**). When migrating embryonic nerve and



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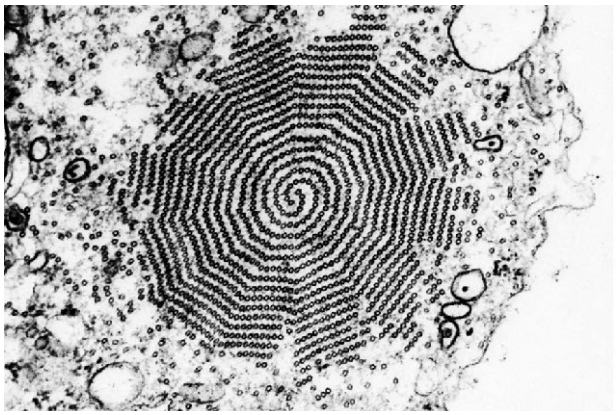

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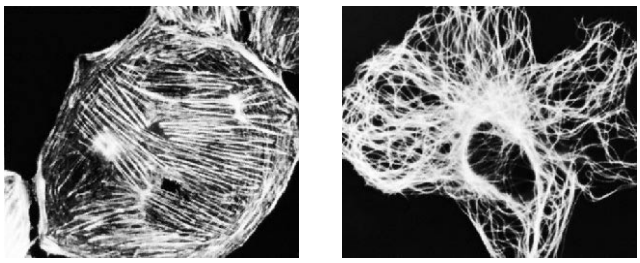
Figure 4.6 **Cytoplasmic Microtubules.** Electron micrographs of pseudopodia with microtubules. (**a**) Microtubules in a pseudopodium from the protozoan *Reticulomyxa* (×65,000). (**b**) A transverse section of a heliozoan axopodium (×48,000). Note the parallel array of microtubules organized in a spiral pattern.

heart cells are exposed to colchicine, they simultaneously lose their microtubules and their characteristic shapes. The shapeless cells seem to wander aimlessly as if incapable of directed movement without their normal form. Their microfilaments are still intact, but due to the disruption of their microtubules by colchicine, they no longer behave normally.

Microtubules also are present in structures that participate in cell or organelle movements—the mitotic spindle, cilia, and flagella. For example, the mitotic spindle is constructed of microtubules; when a dividing cell is treated with colchicine, the spindle is disrupted and chromosome separation blocked. Microtubules also are essential to the movement of eucaryotic cilia and flagella.

Other kinds of filamentous components also are present in the matrix, the most important of which are the **intermediate filaments** (about 8 to 10 nm in diameter). The microfilaments, microtubules, and intermediate filaments are major components of a vast, intricate network of interconnected filaments called the **cytoskeleton** (**figure 4.7**). As mentioned previously, the cytoskeleton plays a role in both cell shape and movement. Procaryotes lack a true, organized cytoskeleton and may not possess actinlike proteins.



(a) (b)

Figure 4.7 The Eucaryotic Cytoskeleton. (**a**) Antibody-stained microfilament system in a mammal cell (×400). (**b**) Antibody-stained microtubule system in a mammal cell (×1,000).

1. What is an organelle?
2. Define cytoplasmic matrix, bulk or free water, bound water, microfilament, microtubule, and tubulin. Discuss the roles of microfilaments, intermediate filaments, and microtubules.
3. Describe the cytoskeleton. What are its functions?

4.3 The Endoplasmic Reticulum

Besides the cytoskeleton, the cytoplasmic matrix is permeated with an irregular network of branching and fusing membranous tubules, around 40 to 70 nm in diameter, and many flattened sacs called **cisternae** (s., **cisterna**). This network of tubules and cisternae is the **endoplasmic reticulum** (**ER**) (figure 4.2*a* and **figure 4.8**). 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** or **granular endoplasmic reticulum** (**RER** or **GER**). Other cells, such as those producing large quantities of lipids, have ER that lacks ribosomes. This is **smooth** or **agranular ER** (**SER** or **AER**).

The endoplasmic reticulum has many important functions. It transports proteins, lipids, and probably other materials through the cell. 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.

New endoplasmic reticulum is produced through expansion of the old. Many biologists think the RER synthesizes new ER proteins and lipids. "Older" RER then loses its connected ribosomes and is modified to become SER. Not everyone agrees with this interpretation, and other mechanisms of growth of ER are possible.

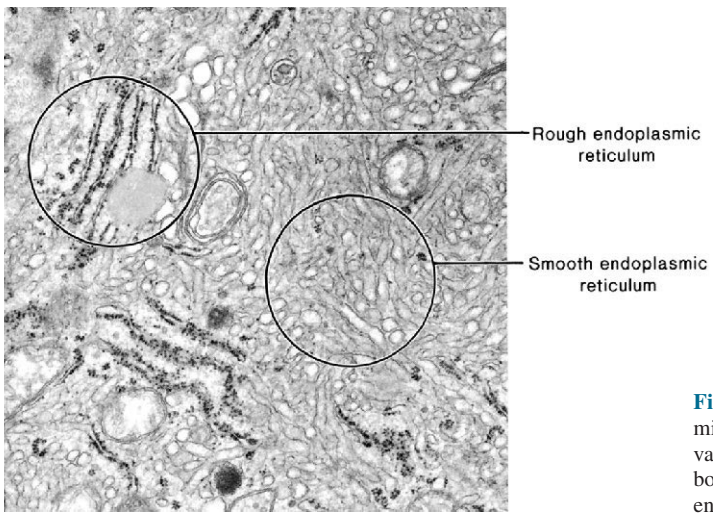
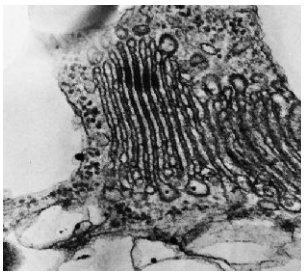


Figure 4.8 The Endoplasmic Reticulum. A transmission electron micrograph of the corpus luteum in a human ovary showing structural variations in eucaryotic endoplasmic reticulum. Note the presence of both rough endoplasmic reticulum lined with ribosomes and smooth endoplasmic reticulum without ribosomes (×26,500).



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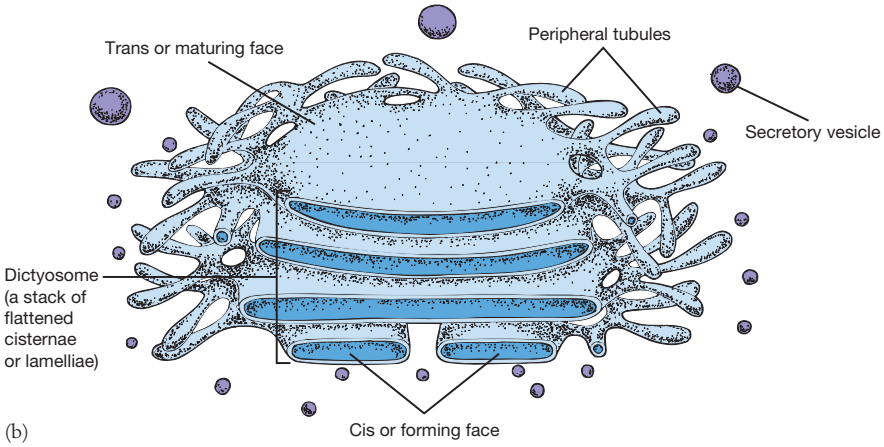

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Figure 4.9 Golgi Apparatus Structure. Golgi apparatus of *Euglena gracilis.* Cisternal stacks are shown in the electron micrograph (×165,000) in (**a**) and diagrammatically in (**b**).

4.4 The Golgi Apparatus

The **Golgi apparatus** is a membranous organelle composed of flattened, saclike cisternae stacked on each other (**figure 4.9**). These membranes, like the smooth ER, lack bound ribosomes. There are usually around 4 to 8 cisternae or sacs in a stack, although there may be many more. Each sac 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 ends or 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. It appears that material is transported from cis to trans cisternae by vesicles that bud off the cisternal edges and move to the next sac.

The Golgi apparatus is present in most eucaryotic cells, but many fungi and ciliate protozoa may lack a well-formed structure. Sometimes it 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.

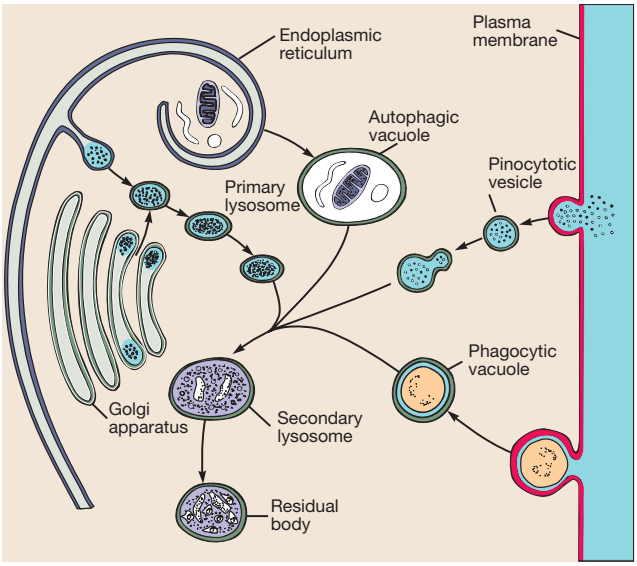
The Golgi apparatus packages materials and prepares them for secretion, the exact nature of its role varying with the organism. The surface scales of some flagellated algae and radiolarian protozoa appear to be constructed within the Golgi apparatus and then transported to the surface in vesicles. It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

In all these processes, materials move from the ER to the Golgi apparatus. Most often vesicles bud off the ER, travel to the Golgi apparatus, and fuse with the cis cisternae. Thus the Golgi apparatus is closely related to the ER in both a structural and a functional sense. Most proteins entering the Golgi apparatus from the ER are glycoproteins containing short carbohydrate chains. The Golgi apparatus frequently modifies proteins destined for different fates by adding specific groups and then sends the proteins on their way to the proper location (e.g., lysosomal proteins have phosphates added to their mannose sugars).

4.5 Lysosomes and Endocytosis

A very important function of the Golgi apparatus and endoplasmic reticulum is the synthesis of another organelle, the **lysosome.** This organelle (or a structure very much like it) is found in a variety of microorganisms—protozoa, some algae, and fungi—as well as in 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 acid conditions (usually around pH 3.5 to 5.0). Lysosomes maintain an acidic environment by pumping protons into their interior. Digestive enzymes are manufactured by the RER and packaged to form lysosomes by the Golgi apparatus. A segment of smooth ER near the Golgi apparatus also may bud off lysosomes.

Lysosomes are particularly important in those cells that obtain nutrients through **endocytosis.** In this process a cell takes up solutes or particles by enclosing them in vacuoles and vesicles pinched off from its plasma membrane. Vacuoles and vesicles are membrane-delimited cavities that contain fluid, and often solid material. Larger cavities will be called vacuoles, and smaller cavities, vesicles. There are two major forms of endocytosis: phagocytosis and pinocytosis. During **phagocytosis** large particles and even other microorganisms are enclosed in a phagocytic vacuole or phagosome and engulfed (**figure 4.10*a***). In **pinocytosis** small amounts of the surrounding liquid with its solute molecules are pinched off as tiny pinocytotic vesicles (also called pinocytic vesicles) or pinosomes. Often phagosomes and pinosomes are collectively called **endosomes** because they are formed by endocytosis. The type of pinocytosis, receptor-mediated endocytosis, that produces coated vesicles (*see p. 403*) is important in the entry of animal viruses into host cells.



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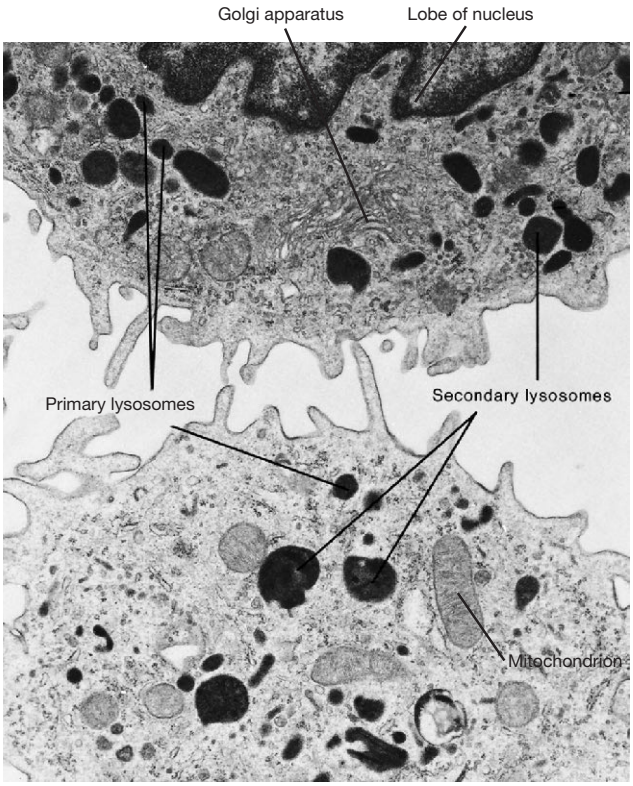

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Figure 4.10 **Lysosome Structure, Formation, and Function.** (**a**) A diagrammatic overview of lysosome formation and function. (**b**) Lysosomes in macrophages from the lung. Secondary lysosomes contain partially digested material and are formed by fusion of primary lysosomes and phagocytic vacuoles (×14,137).

Material in endosomes is digested with the aid of lysosomes. Newly formed lysosomes, or **primary lysosomes,** fuse with phagocytic vacuoles to yield **secondary lysosomes,** lysosomes with material being digested (figure 4.10). These phagocytic vacuoles or secondary lysosomes often are called food vacuoles. Digested nutrients then leave the secondary lysosome and enter the cytoplasm. When the lysosome has accumulated large quantities of indigestible material, it is known as a **residual body.**

Lysosomes join with phagosomes for defensive purposes as well as to acquire nutrients. Invading bacteria, ingested by a phagocytic cell, usually are destroyed when lysosomes fuse with the phagosome. This is commonly seen in leukocytes (white blood cells) of vertebrates. Phagocytosis and resistance to pathogens (pp. 718–20)

Cells can selectively digest portions of their own cytoplasm in a type of secondary lysosome called an **autophagic vacuole** (figure 4.10*a*). It is thought that these arise by lysosomal engulfment of a piece of cytoplasm (**figure 4.11**), or when the ER pinches off cytoplasm to form a vesicle that subsequently fuses with lysosomes. Autophagy probably plays a role in the normal turnover or recycling of cell constituents. A cell also can survive a period of starvation by selectively digesting portions of itself to remain alive. Following cell death, lysosomes aid in digestion and removal of cell debris.

A most remarkable thing about lysosomes is that they accomplish all these tasks without releasing their digestive enzymes into the cytoplasmic matrix, a catastrophe that would destroy the cell. The lysosomal membrane retains digestive enzymes and other macromolecules while allowing small digestion products to leave.

The intricate complex of membranous organelles composed of the Golgi apparatus, lysosomes, endosomes, and associated structures seems to operate as a coordinated whole whose main function is the import and export of materials (figure 4.11). Christian de Duve (Nobel Prize, 1974) has suggested that this complex be called the vacuome in recognition of its functional unity. The ER manufactures secretory proteins and membrane, and contributes these to the Golgi apparatus. The Golgi apparatus then forms secretory vesicles that fuse with the plasma membrane and release material to the outside. It also produces lysosomes that fuse with endosomes to digest material acquired through phagocytosis and pinocytosis. Membrane movement in the region of the vacuome lying between the Golgi apparatus and the plasma membrane is two-way. Empty vesicles often are recycled and returned to the Golgi apparatus and plasma membrane rather than being destroyed. These exchanges in the vacuome occur without membrane rupture so that vesicle contents never escape directly into the cytoplasmic matrix.

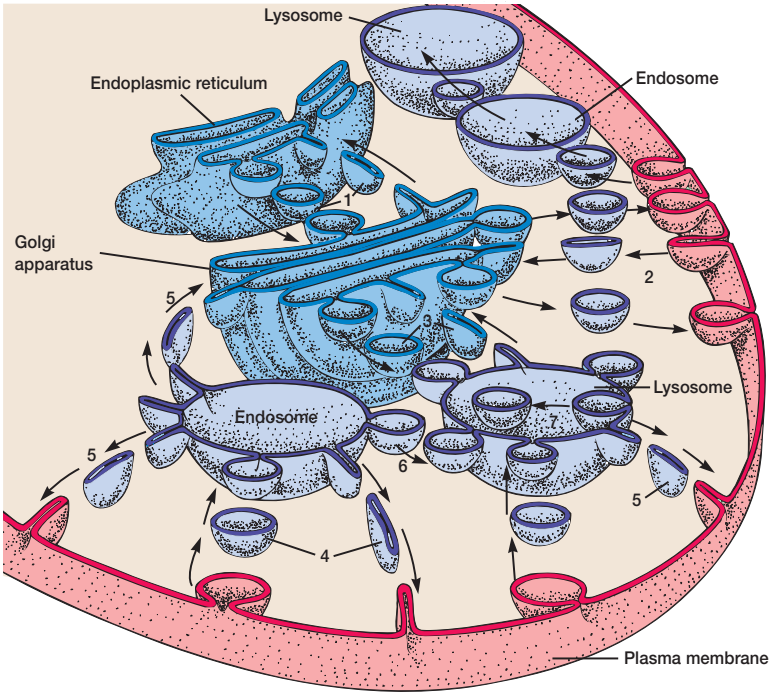


Figure 4.11 Membrane Flow in the Vacuome. The flow of material and membranes between organelles in a eucaryotic cell.
(*1*) Vesicles shuttling between the ER and Golgi apparatus.
(*2*) The Golgi–plasma membrane shuttle for secretion of materials.
(*3*) The Golgi-lysosome shuttle.
(*4*) The movement of material and membranes during endocytosis.
(*5*) Pathways of plasma membrane recovery from endosomes, lysosomes, and through the Golgi apparatus.
(*6*) Movement of vesicles from endosomes to lysosomes.
(*7*) Autophagy by a lysosome.

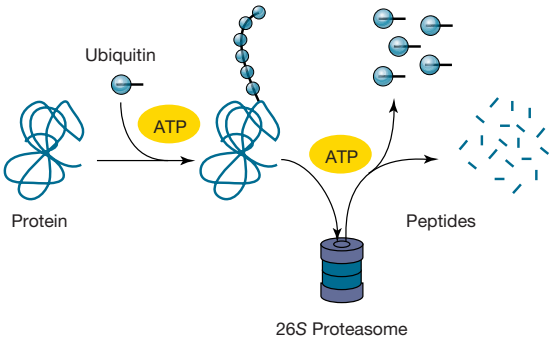


Figure 4.12 Proteasome Degradation of Proteins. See text for details.

More recently a nonlysosomal protein degradation system has been discovered in eucaryotic cells, a few bacteria, and many archaea. The majority of eucaryotic proteins may be degraded by this system. In eucaryotes, proteins are targeted for destruction by the attachment of several small ubiquitin polypeptides (**figure 4.12**). The marked protein then enters a huge cylindrical complex called a 26S **proteasome,** where it is degraded to peptides in an ATP-dependent process and the ubiquitins are released. The peptides may be hydrolyzed to amino acids. In this case the system is being used to recycle proteins. The proteasome also is involved in producing peptides for antigen presentation during many immunological responses (*see section 32.4*).

1. 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.
2. 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.
3. How are lysosomes formed? Describe the various forms of lysosomes and the way in which they participate in intracellular digestion. What is an autophagic vacuole? Define endocytosis, pinocytosis, and phagocytosis. What is a proteasome?

4.6 Eucaryotic Ribosomes

The eucaryotic ribosome can either be associated with the endoplasmic reticulum or be free in the cytoplasmic matrix and is larger than the bacterial 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. When bound to the endoplasmic reticulum to form rough ER, it is attached through its 60S subunit.

Both free and RER-bound ribosomes synthesize proteins. As mentioned earlier, proteins made on the ribosomes of the RER either enter its lumen for transport, and often for secretion, 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 12 (*see pp. 52, 272–74*), molecular chaperones aid the proper folding of proteins after synthesis. They also assist the transport of proteins into eucaryotic organelles such as mitochondria. Several ribosomes usually attach to a single messenger RNA and simultaneously translate its message into protein. These complexes of messenger RNA and ribosomes are called **polyribosomes** or **polysomes.** Ribosomal participation in protein synthesis is dealt with later. The role of ribosomes in protein synthesis (pp. 267–72)

1. Describe the structure of the eucaryotic 80S ribosome and contrast it with the procaryotic ribosome.
2. How do free ribosomes and those bound to the ER differ in function?

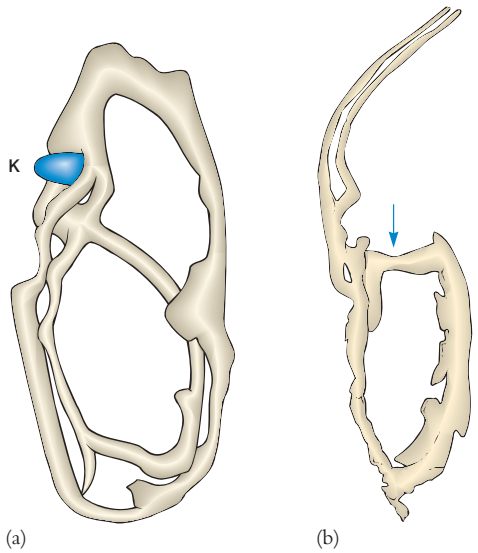


Figure 4.13 Trypanosome Mitochondria. The giant mitochondria from trypanosomes. (**a**) *Crithidia fasciculata* mitochondrion with kinetoplast, K. The kinetoplast contains DNA that codes for mitochondrial RNA and protein. (**b**) *Trypanosoma cruzi* mitochondrion with arrow indicating position of kinetoplast.

4.7 Mitochondria

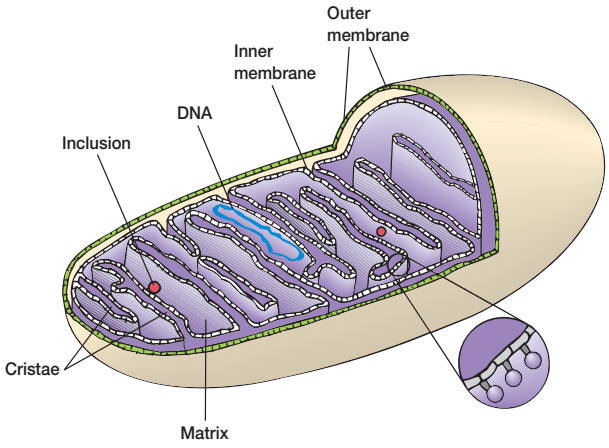
Found in most eucaryotic cells, **mitochondria** (s., **mitochondrion**) frequently are called the "powerhouses" of the cell. Tricarboxylic acid cycle activity and the generation of ATP by electron transport and oxidative phosphorylation take place here. In the transmission electron microscope, mitochondria 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 bacterial cells.) Although cells can possess as many as 1,000 or more mitochondria, at least a few cells (some yeasts, unicellular algae, and trypanosome protozoa) have a single giant tubular mitochondrion twisted into a continuous network permeating the cytoplasm (**figure 4.13**). The tricarboxylic acid cycle, electron transport, and oxidative phosphorylation (pp. 183–89)

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 4.14**). Special infoldings of the inner membrane, called **cristae** (s., **crista**), greatly increase its surface area. Their shape differs in mitochondria from various species. Fungi have platelike (laminar) cristae, whereas euglenoid flagellates may have cristae shaped like disks. Tubular cristae are found in a variety of eucaryotes; however, amoebae can possess mitochondria with cristae in the shape of vesicles (**figure 4.15**). 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. Mitochondrial DNA is a closed circle like bacterial DNA.

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 the β-oxidation pathway for fatty acids (*see chapter 9*) are located in the matrix.

The inner membrane of the mitochondrion has another distinctive structural feature related to its function. Many small spheres, about 8.5 nm diameter, are attached by stalks to its inner surface. The spheres are called **F_1 particles** and synthesize ATP during cellular respiration (*see pp. 187–89*).

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



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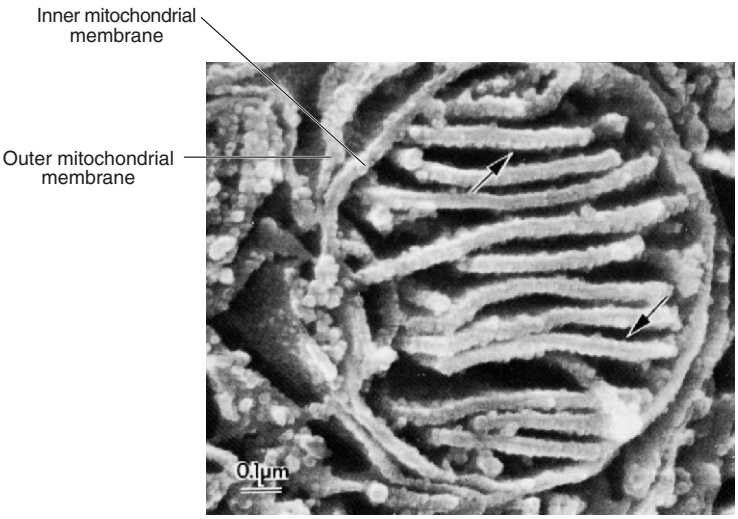

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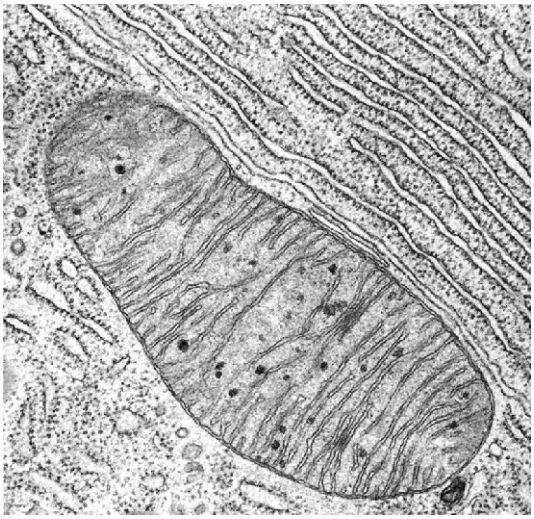
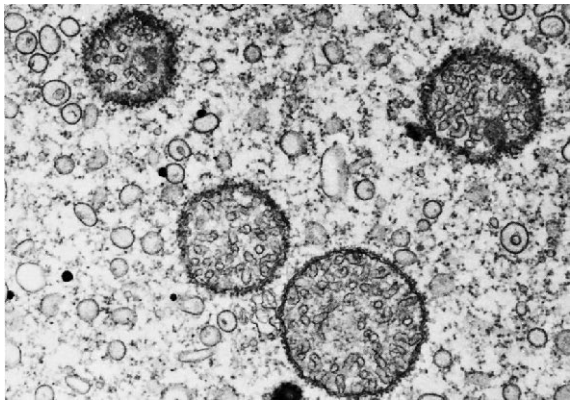


(c)

Figure 4.14 Mitochondrial Structure. (**a**) A diagram of mitochondrial structure. The insert shows F_1F_0 complexes lining the inner surface of the cristae. (**b**) Scanning electron micrograph (×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 (×85,000). Note outer and inner mitochondrial membranes, cristae, and inclusions in the matrix. The mitochondrion is surrounded by rough endoplasmic reticulum.



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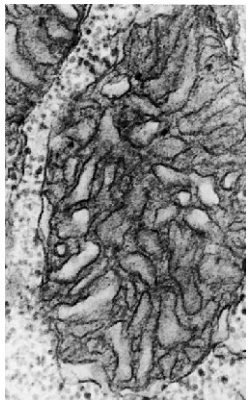


(b)

Figure 4.15 Mitochondrial Cristae. Mitochondria with a variety of cristae shapes. (**a**) Mitochondria from the protostelid slime mold *Schizoplasmodiopsis micropunctata.* Note the tubular cristae (×49,500). (**b**) The protozoan *Actinosphaerium* with vesicular cristae (×75,000).

Box 4.1

The Origin of the Eucaryotic Cell

The profound differences between eucaryotic and procaryotic cells have stimulated much discussion about how the more complex eucaryotic cell arose. Some biologists believe the original "protoeucaryote" was a large aerobic archaean 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 blue-green bacterium 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 procaryotic cell, which may have been an archaean, lost its cell wall and gained the ability to obtain nutrients by phagocytosing other procaryotes. When photosynthetic cyanobacteria arose, the environment slowly became aerobic. If an anaerobic, amoeboid, phagocytic procaryote—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 aerobic 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 procaryotic 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 procaryotic 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. Despite such evidence, the endosymbiotic theory still is somewhat speculative and the center of much continuing research and discussion.

the nucleus. Mitochondria reproduce by binary fission. Chloroplasts show similar partial independence and reproduction by binary fission. Because both organelles resemble bacteria to some extent, it has been suggested that these organelles arose from symbiotic associations between bacteria and larger cells (**Box 4.1**).

4.8 Chloroplasts

Plastids are cytoplasmic organelles of algae and higher 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 CO_2 and water to carbohydrates and O_2. That is, they are the site of photosynthesis.

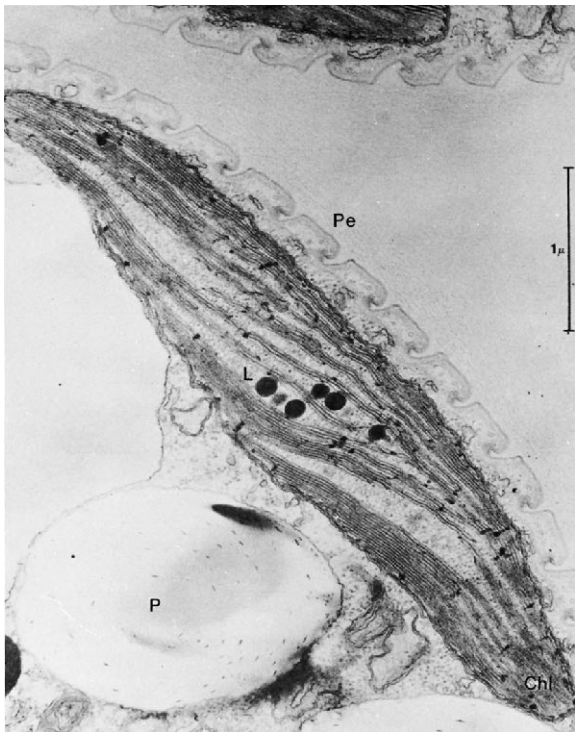
Although chloroplasts are quite variable in size and shape, they share many structural features. Most often they are oval with dimensions of 2 to 4 μm by 5 to 10 μm, but some algae possess one huge chloroplast that fills much of the cell. Like mitochondria, chloroplasts are encompassed by two membranes (**figure 4.16**). 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 4.16 and 4.25*b*). In some groups of algae, several disklike thylakoids are stacked on each other like coins to form **grana** (s., **granum**).

Photosynthetic reactions are separated structurally in the chloroplast just as electron transport and the tricarboxylic acid cycle are in the mitochondrion. The formation of carbohydrate from CO_2 and water, the dark reaction, takes place in the stroma. The trapping of light energy to generate ATP, NADPH, and O_2, the light reaction, is located in the thylakoid membranes, where chlorophyll and electron transport components are also found.

Photosynthesis (pp. 195–201)

The chloroplasts of many algae contain a **pyrenoid** (figure 4.25*b*), 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 F_1 particle, plastid, dark reaction, light reaction, and pyrenoid.
3. What is the role of mitochondrial DNA?



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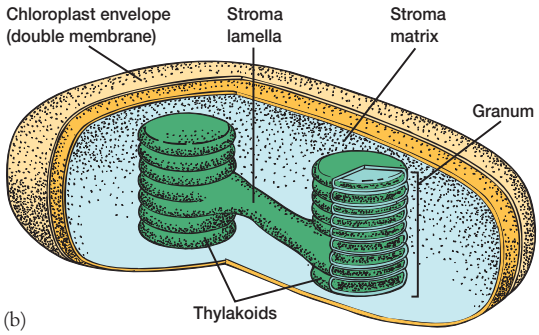


(b)

Figure 4.16 **Chloroplast Structure.** (**a**) The chloroplast (Chl), of the euglenoid flagellate *Colacium cyclopicolum.* 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 (×40,000). (**b**) A diagram of chloroplast structure.

4.9 The Nucleus and Cell Division

The cell **nucleus** is by far the most visually prominent organelle. 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.

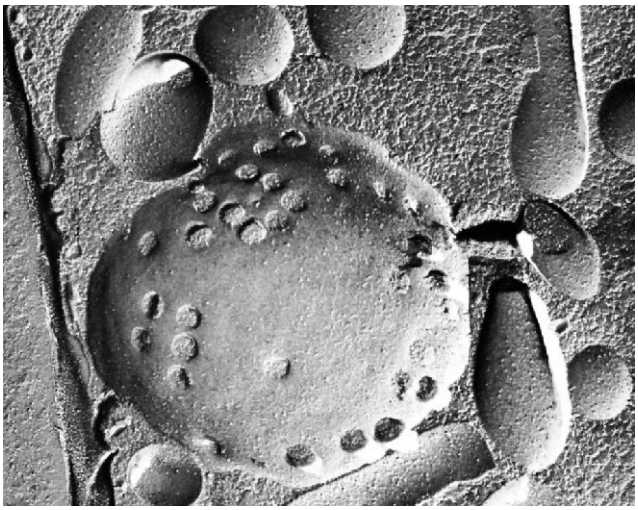


Figure 4.17 **The Nucleus.** A freeze-etch preparation of the conidium of the fungus *Geotrichum candidum* (×44,600). Note the large convex nuclear surface with nuclear pores scattered over it.

Nuclear Structure

Nuclei are membrane-delimited spherical bodies about 5 to 7 μm in diameter (figures 4.2 and 4.25*b*). 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 exists in a dispersed condition, but condenses during mitosis to become visible as **chromosomes.** Some nuclear chromatin, the euchromatin, is loosely organized and contains those genes that are expressing themselves actively. Heterochromatin is coiled more tightly, appears darker in the electron microscope, and is not genetically active most of the time. Organization of DNA in eucaryotic nuclei (pp. 234–35)

The nucleus is bounded by the **nuclear envelope** (figures 4.2 and 4.25*b*), 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, 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 4.17**), each pore 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.

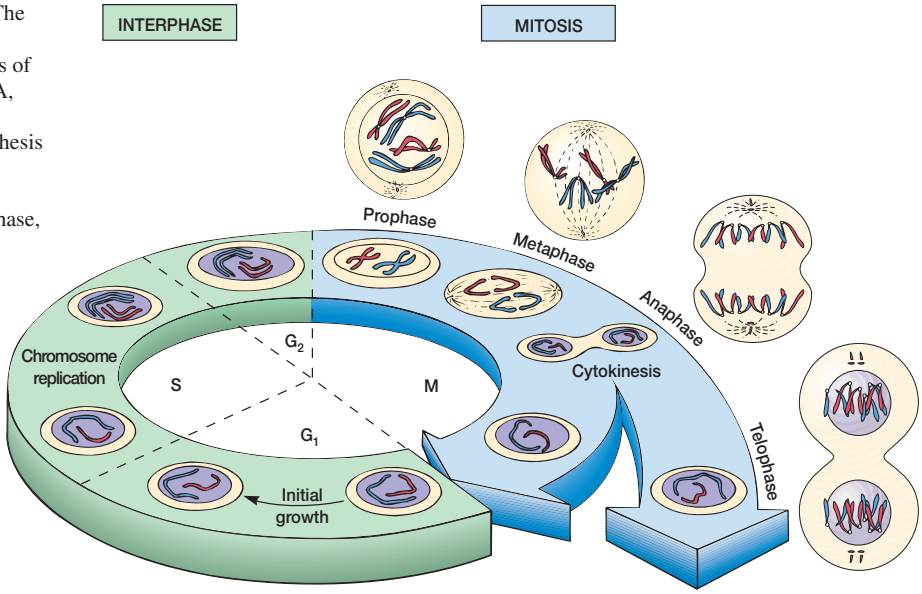


Figure 4.18 **The Eucaryotic Cell Cycle.** The length of the M period has been increased disproportionately in order to show the phases of mitosis. G_1 period: synthesis of mRNA, tRNA, ribosomes, and cytoplasmic constituents. Nucleolus grows rapidly. S period: rapid synthesis and doubling of nuclear DNA and histones. G_2 period: preparation for mitosis and cell division. M period: mitosis (prophase, metaphase, anaphase, telophase) and cytokinesis.

The Nucleolus

Often the most noticeable structure within the nucleus is the **nucleolus** (figures 4.2 and 4.25*b*). 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. 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 RNA (rRNA). This RNA is synthesized in a single long piece that then 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. RNA splicing (p. 264)

Mitosis and Meiosis

When a eucaryotic microorganism reproduces, 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 4.18**). 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 G_1 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 G_2 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 G_1.

Mitotic events are summarized in figure 4.18. During mitosis, the genetic material duplicated during the S period is distributed equally to the two new nuclei 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 has disappeared. During anaphase the chromatids in each chromosome separate and move toward the opposite poles of the spindle. 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.

Mitosis in eucaryotic microorganisms can differ from that pictured in figure 4.18. For example, the nuclear envelope does not disappear in many fungi and some protozoa and algae (**figure 4.19**). 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.

In mitosis the original number of chromosomes is the same after division and a diploid organism will remain diploid or 2N (i.e., it still has two copies of each chromosome). Frequently a microorganism reduces its chromosome number by half, from the diploid state to the haploid or 1N (a single copy of each chromosome).

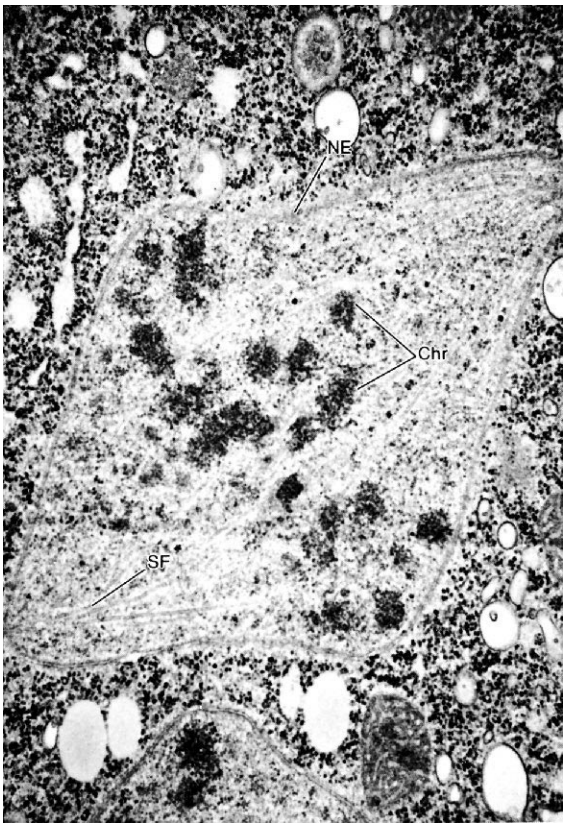


Figure 4.19 Mitosis with an Intact Nuclear Envelope. Mitosis in the slime mold *Physarum flavicomum.* The nuclear envelope, NE, remains intact, and the spindle is intranuclear. The process is at metaphase with the chromosomes, Chr, aligned in the center and attached to spindle fibers, SF (×15,000).

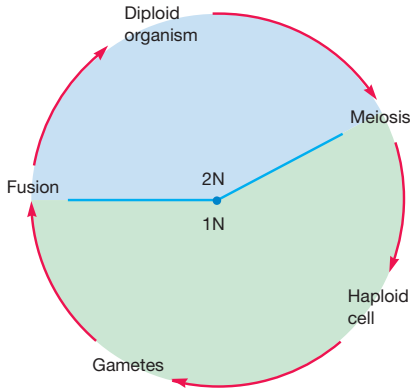


Figure 4.20 Generalized Eucaryotic Life Cycle.

Haploid cells may immediately act as gametes and fuse to reform diploid organisms or may form gametes only after a considerable delay (**figure 4.20**). The process 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; a classic example is the life cycle of *Plasmodium,* the cause of malaria (*see pp. 954–56*). Life cycles of eucaryotic microorganisms (chapters 25–27)

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. Then the double-stranded chromosomes from each homologous pair move to opposite poles in anaphase. In contrast, during mitotic anaphase the two strands of each chromosome separate and move to opposite poles. Consequently the number of chromosomes is halved in meiosis but not in mitosis. The second stage of meiosis is similar to mitosis in terms of mechanics, and single-stranded chromosomes 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. What is meiosis, how does it take place, and what is its role in the microbial life cycle?

4.10 External Cell Coverings

Eucaryotic microorganisms differ greatly from procaryotes 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 procaryotic membranes, contain sterols such as cholesterol in their lipid bilayers, and this may make them mechanically stronger, thus reducing the need for external support. (However, as mentioned on page 47, many procaryotic membranes are strengthened by hopanoids.) Of course many eucaryotes do have a rigid external **cell wall.** Algal cell walls 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 (some red algae) may be present. Fungal cell walls normally are rigid. Their exact composition varies with the organism; but usually, cellulose, chitin, or glucan (a glucose polymer different from cellulose) are present. Despite their nature the rigid materials in eucaryotic walls

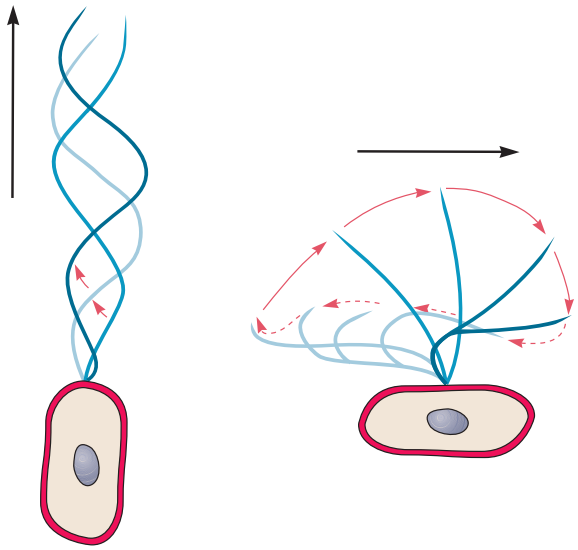


Figure 4.21 Patterns of Flagellar Movement. Flagellar movement (left illustration) often takes the form of waves that move either from the base of the flagellum to its tip or in the opposite direction. The motion of these waves propels the organism along. The beat of a cilium (right illustration) may 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.

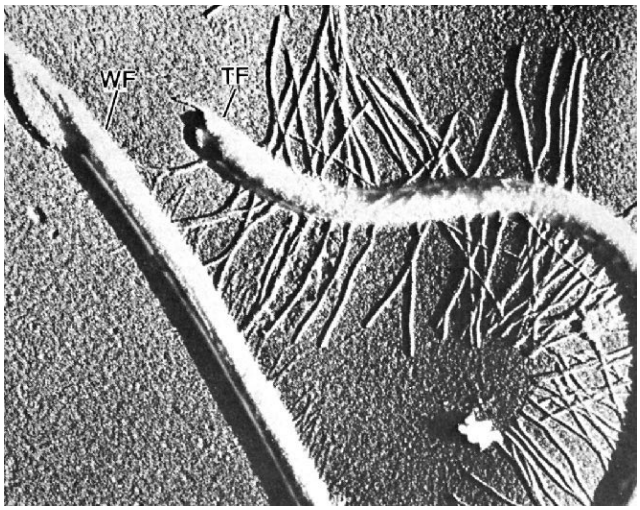


Figure 4.22 Whiplash and Tinsel Flagella. Transmission electron micrograph of a shadowed whiplash flagellum, WF, and a tinsel flagellum, TF, with mastigonemes.

are chemically simpler than procaryotic peptidoglycan. Bacterial cell wall structure and chemistry (pp. 55–60)

Many protozoa and some algae have a different external structure, the **pellicle** (figure 4.16*a*). 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, ciliate protozoan pellicles are exceptionally complex with two membranes and a variety of associated structures. Although pellicles are not as strong and rigid as cell walls, they do give their possessors a characteristic shape.

4.11 Cilia and Flagella

Cilia (s., **cilium**) and **flagella** (s., **flagellum**) are the most prominent organelles associated with motility. Although both are whiplike 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 4.21**). 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 4.22**). 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 4.23**). 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 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 4.24**). This is called the 9 + 2 pattern of microtubules. Each doublet also has pairs of arms projecting from subtubule A (the complete microtubule) toward a neighboring doublet. A radial spoke extends from subtubule 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

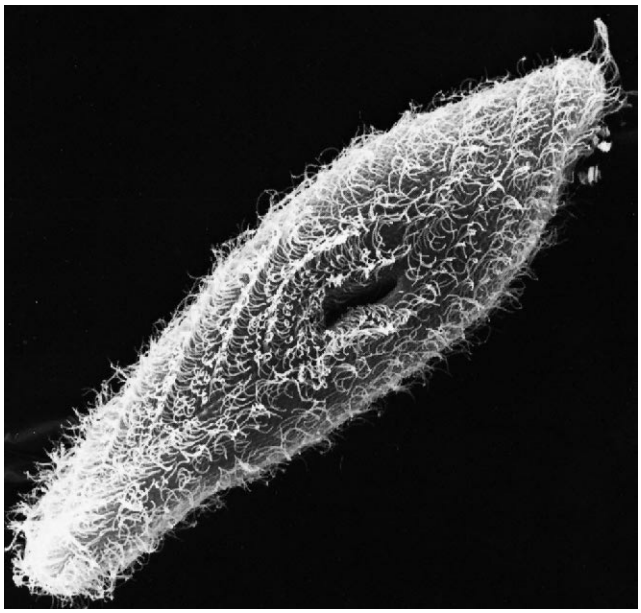


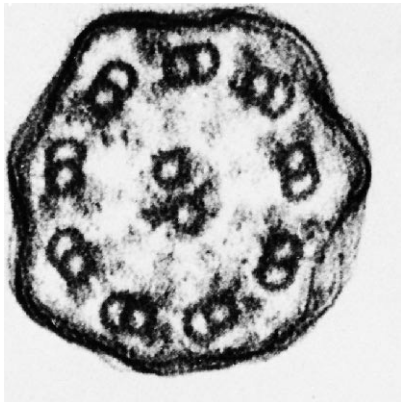
Figure 4.23 Coordination of Ciliary Activity. A scanning electron micrograph of *Paramecium* showing cilia (×1,500). The ciliary beat is coordinated and moves in waves across the protozoan's surface, as can be seen in the photograph.

of tubulin subunits, α- and β-tubulins, that resemble the contractile protein actin in their composition. Bacterial flagella and motility (pp. 63–66)

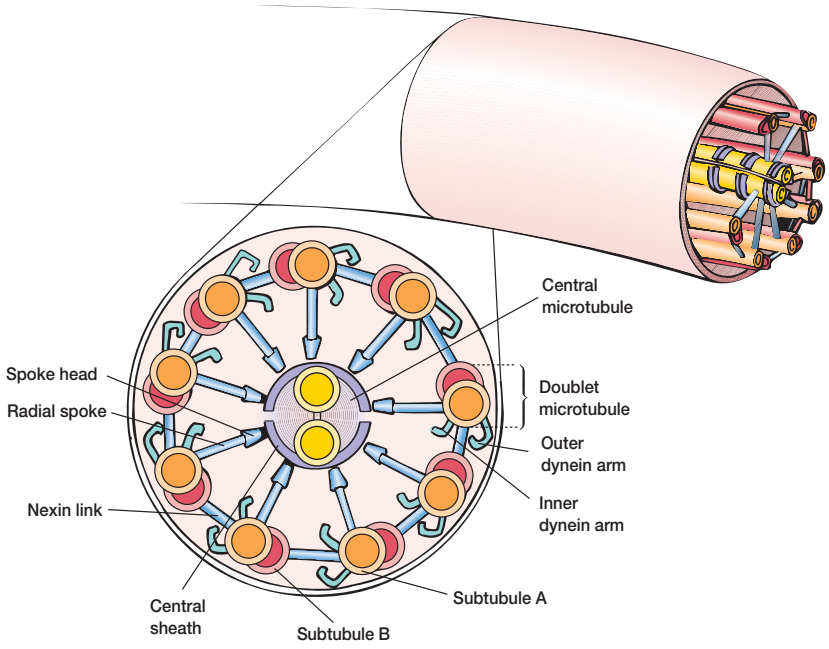
A **basal body** lies in the cytoplasm at the base of each cilium or flagellum. It is a short cylinder with nine microtubule triplets around its periphery (a 9 + 0 pattern) and is separated from the rest of the organelle by a basal plate. The basal body directs the construction of these organelles. Cilia 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 4.24), 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 μm/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 μm/second (12 lengths per second). Such speeds are equivalent to or much faster than those seen in higher animals.



(a)



(b)

Figure 4.24 Cilia and Flagella Structure. (**a**) An electron micrograph of a cilium cross section. Note the two central microtubules surrounded by nine microtubule doublets (×160,000). (**b**) A diagram of cilia and flagella structure with two doublets removed for sake of visibility.

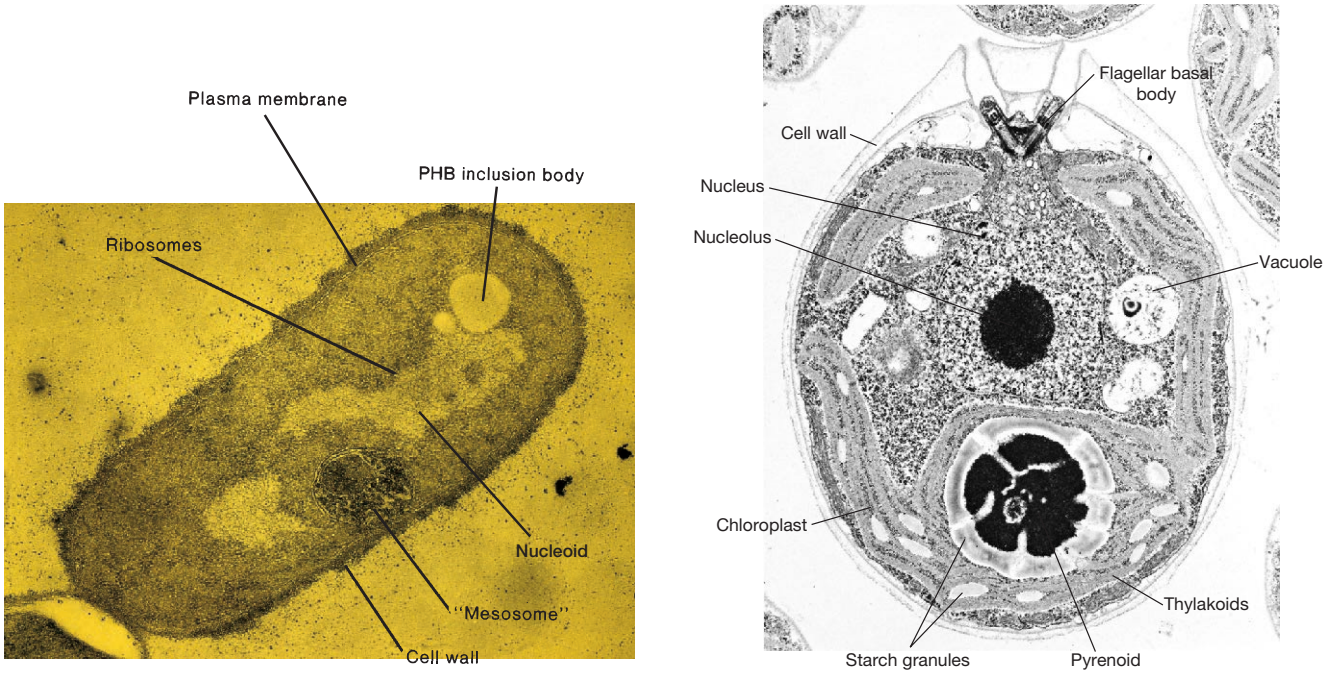


Figure 4.25 Comparison of Procaryotic and Eucaryotic Cell Structure. (**a**) The procaryote *Bacillus megaterium* (×30,500). (**b**) The eucaryotic alga *Chlamydomonas reinhardtii,* a deflagellated cell. Note the large chloroplast with its pyrenoid body (×30,000).

1. How do eucaryotic microorganisms differ from procaryotes with respect to supporting or protective structures external to the plasma membrane? Describe the pellicle and indicate which microorganisms have one.
2. 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?

4.12 Comparison of Procaryotic and Eucaryotic Cells

A comparison of the cells in **figure 4.25** demonstrates that there are many fundamental differences between eucaryotic and procaryotic cells. **Eucaryotic cells** have a membrane-enclosed nucleus. In contrast, **procaryotic cells** lack a true, membrane-delimited nucleus. Bacteria and Archaea are procaryotes; all other organisms—algae, fungi, protozoa, higher plants, and animals—are eucaryotic. Procaryotes normally 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 several other major distinctions should be noted. It is clear from **table 4.2** that procaryotic cells are much simpler structurally. In particular, an extensive and diverse collection of membrane-delimited organelles is missing. Furthermore, procaryotes are simpler functionally in several ways. They lack mitosis and meiosis, and have a simpler genetic organization. Many complex eucaryotic processes are absent in procaryotes: phagocytosis and pinocytosis, intracellular digestion, directed cytoplasmic streaming, ameboid movement, and others.

Despite the many significant differences between these two basic cell forms, they are remarkably similar on the biochemical level as will be discussed in succeeding chapters. Procaryotes 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 most of the more important metabolic pathways are identical. Thus beneath the profound structural and functional differences between procaryotes and eucaryotes, there is an even more fundamental unity: a molecular unity that is basic to all known life processes.

Table 4.2 Comparison of Procaryotic and Eucaryotic Cells

Property	Procaryotes	Eucaryotes
Organization of Genetic Material		
True membrane-bound nucleus	Absent	Present
DNA complexed with histones	No	Yes
Number of chromosomes	One[a]	More than one
Introns in genes	Rare	Common
Nucleolus	Absent	Present
Mitosis occurs	No	Yes
Genetic Recombination	Partial, unidirectional transfer of DNA	Meiosis and fusion of gametes
Mitochondria	Absent	Present
Chloroplasts	Absent	Present
Plasma Membrane with Sterols	Usually no[b]	Yes
Flagella	Submicrosopic in size; composed of one fiber	Microscopic in size; membrane bound; usually 20 microtubules in 9 + 2 pattern
Endoplasmic Reticulum	Absent	Present
Golgi Apparatus	Absent	Present
Cell Walls	Usually chemically complex with peptidoglycan[c]	Chemically simpler and lacking peptidoglycan
Differences in Simpler Organelles		
Ribosomes	70S	80S (except in mitochondria and chloroplasts)
Lysosomes and peroxisomes	Absent	Present
Microtubules	Absent or rare	Present
Cytoskeleton	May be absent	Present
Differentiation	Rudimentary	Tissues and organs

[a]Plasmids may provide additional genetic information.
[b]Only the mycoplasmas and methanotrophs (methane utilizers) contain sterols. The mycoplasmas cannot synthesize sterols and require them preformed. Many procaryotes contain hopanoids.
[c]The mycoplasmas and Archaea do not have peptidoglycan cell walls.

Summary

1. The eucaryotic cell has a true, membrane-delimited nucleus and many membranous organelles (**table 4.1**).
2. 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.
3. The matrix is permeated by an irregular network of tubules and flattened sacs or cisternae known as the endoplasmic reticulum (ER). The ER may have attached ribosomes and be active in protein synthesis (rough or granular endoplasmic reticulum) or lack ribosomes (smooth or agranular ER).
4. The ER can donate materials to the Golgi apparatus, an organelle composed of one or more stacks of cisternae (**figure 4.9**). This organelle prepares and packages cell products for secretion.
5. The Golgi apparatus also forms lysosomes (**figures 4.10** and **4.11**). These organelles contain digestive enzymes and aid in intracellular digestion of materials, including those taken up by endocytosis.
6. Eucaryotic ribosomes found free in the cytoplasmic matrix or bound to the ER are 80S ribosomes. Several may be attached to the same messenger RNA forming polyribosomes or polysomes.
7. Mitochondria are organelles bounded by two membranes, with the inner membrane folded into cristae, and are responsible for energy generation by the tricarboxylic acid cycle, electron transport, and oxidative phosphorylation (**figure 4.14**).
8. Chloroplasts are the site of photosynthesis. The trapping of light energy takes place in the thylakoid membranes, whereas CO_2 incorporation is located in the stroma (**figure 4.16**).
9. The nucleus is a large organelle containing the cell's chromosomes. It is bounded by a complex, double-membrane envelope perforated by pores through which materials can move.
10. The nucleolus lies within the nucleus and participates in the synthesis of ribosomal RNA and ribosomal subunits.
11. Eucaryotic chromosomes are distributed to daughter cells during regular cell division by mitosis (**figure 4.18**). Meiosis is used to halve the chromosome number during sexual reproduction.
12. When a cell wall is present, it is constructed from polysaccharides, like cellulose, that are chemically simpler than procaryotic peptidoglycan. Many protozoa have a pellicle rather than a cell wall.
13. Many eucaryotic cells are motile because of cilia and flagella, membrane-delimited organelles with nine microtubule doublets surrounding two central microtubules (**figure 4.24**). The doublets slide along each other to bend the cilium or flagellum.
14. Despite the fact that eucaryotes and procaryotes differ in many ways (**table 4.2**), they are quite similar metabolically.

Key Terms

autophagic vacuole *81*
axoneme *89*
basal body *90*
cell cycle *87*
cell wall *88*
chloroplast *85*
chromatin *86*
chromosome *86*
cilia *89*
cisternae *79*
cristae *83*
cytoplasmic matrix *76*
cytoskeleton *79*
dictyosome *80*
dynein *90*
endocytosis *80*
endoplasmic reticulum (ER) *79*
endosome *80*
endosymbiotic theory *85*
eucaryotic cells *91*
F_1 particle *83*
flagella *89*
Golgi apparatus *80*
grana *85*
intermediate filament *79*
interphase *87*
lysosome *80*
meiosis *88*
microfilament *77*
microtubule *78*
mitochondrion *83*
mitosis *87*
nuclear envelope *86*
nuclear pores *86*
nucleolus *87*
nucleus *86*
organelle *76*
pellicle *89*
phagocytosis *80*
pinocytosis *80*
plastid *85*
polyribosomes *83*
polysomes *83*
primary lysosomes *81*
procaryotic cells *91*
proteasome *82*
pyrenoid *85*
residual body *81*
rough or granular ER (RER or GER) *79*
secondary lysosomes *81*
smooth or agranular ER (SER or AER) *79*
stroma *85*
thylakoid *85*

Questions for Thought and Review

1. Describe the structure and function of every eucaryotic organelle discussed in the chapter.
2. Discuss the statement: "The most obvious difference between eucaryotic and procaryotic cells is in their use of membranes." What general roles do membranes play in eucaryotic cells?
3. Describe how the Golgi apparatus distributes proteins it receives from the ER to different organelles.
4. Briefly discuss how the complex of membranous organelles that de Duve calls the "vacuome" functions as a coordinated whole. What is its function?
5. Describe and contrast the ways in which flagella and cilia propel microorganisms through the water.
6. Outline the major differences between procaryotes and eucaryotes. How are they similar?

Critical Thinking Questions

1. *Giardia lamblia* is an example of eucaryotes that contain nuclei, but no mitochondria. How does the existence of *Giardia* affect the endosymbiosis theory? How do you think *Giardia* obtains its energy? Would your answer change if you learned that *Giardia* is parasitic?
2. Would you expect to find organisms with mitochondria, but without nuclei? Why or why not? Support your answer with literature sources.

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