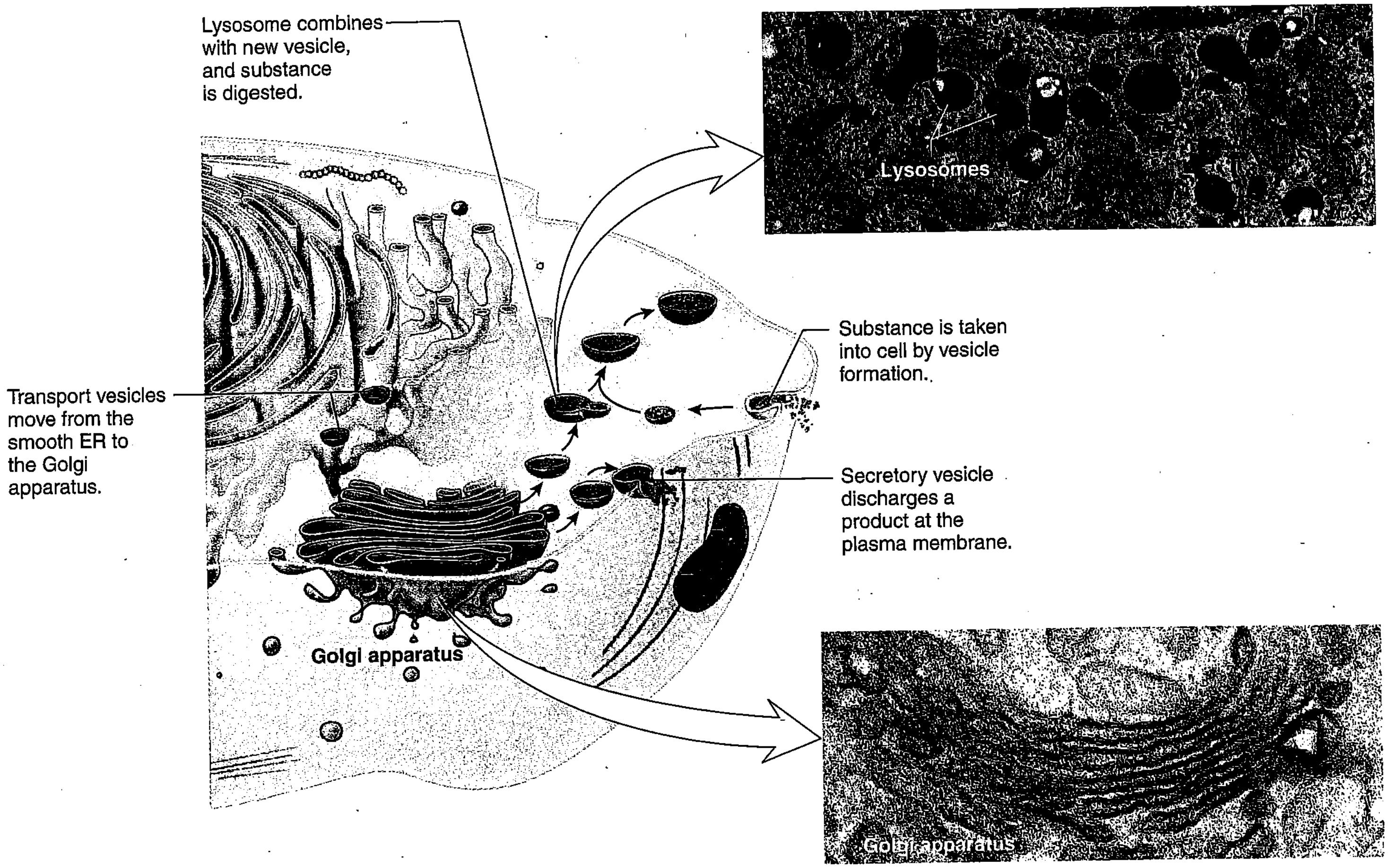


Figure 3.6 **The Golgi apparatus.**
The Golgi apparatus receives transport vesicles containing proteins from smooth ER. After modifying the proteins, it repackages them in either secretory vesicles or lysosomes. When lysosomes combine with newly formed vesicles, their contents are digested. Lysosomes also break down cellular components.

The Golgi Apparatus

The **Golgi apparatus** is named for Camillo Golgi, who discovered its presence in cells in 1898. The Golgi apparatus consists of a stack of three to twenty slightly curved saccules whose appearance can be compared to a stack of pancakes (Fig. 3.6). In animal cells, one side of the stack (the inner face) is directed toward the ER, and the other side of the stack (the outer face) is directed toward the plasma membrane. Vesicles can frequently be seen at the edges of the saccules.

The Golgi apparatus receives protein and also lipid-filled vesicles that bud from the smooth ER. These molecules then move through the Golgi from the inner face to the outer face. How this occurs is still being debated. According to the maturation saccule model, the vesicles fuse to form an inner face saccule, which matures as it gradually becomes a saccule at the outer face. According to the stationary saccule model, the molecules move through stable saccules from the inner face to the outer face by shuttle vesicles. It is likely that both models apply, depending on the organism and the type of cell.

During their passage through the Golgi apparatus, glycoproteins have their sugar chains modified before they are repackaged in secretory vesicles. Secretory vesicles proceed to the plasma membrane, where they discharge their contents. Because this is **secretion**, the Golgi apparatus is said to be involved in processing, packaging, and secretion.

The Golgi apparatus is also involved in the formation of lysosomes, vesicles that contain proteins and remain within the cell. How does the Golgi apparatus direct traffic—in other words, what makes it direct the flow of proteins to different destinations? It now seems that proteins made at the rough ER have specific molecular tags that serve as "zip codes" to tell the Golgi apparatus whether they belong in a lysosome or secretary vesicle. The final sugar chain serves as a tag that directs proteins to their final destination.

The Golgi apparatus processes, packages, and distributes molecules about or from the cell. It is also said to be involved in secretion.

Lysosomes

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

Sometimes macromolecules are brought into a cell by vesicle formation at the plasma membrane (Fig. 3.6). When a lysosome fuses with such a vesicle, its contents are digested by lysosomal enzymes into simpler subunits that then enter the cytoplasm. For example, some white blood cells defend the body by engulfing pathogens that are then enclosed within vesicles. When lysosomes fuse with these vesicles, the bacteria are digested. It should come as no surprise then, that even parts of a cell are digested by its own lysosomes (called autodigestion). Normal cell rejuvenation takes place in this manner.

Lysosomes contain many enzymes for digesting all sorts of molecules. The absence or malfunction of one of these results in a so-called lysosomal storage disease. Instead of being degraded, the molecule accumulates inside lysosomes, and illness develops when they swell and crowd the other organelles. Occasionally, a child inherits the inability to make a lysosomal enzyme, and therefore has a lysosomal storage disease. In Tay Sachs disease, the cells that surround nerve cells cannot break down a particular lipid, and the nervous system is affected. At about six months, the infant can no longer see, and then gradually also loses hearing and even the ability to move. Death follows at about three years of age.

Lysosomes are produced by a Golgi apparatus, and their hydrolytic enzymes digest macromolecules from various sources.

Vacuoles

A **vacuole** is a large membranous sac. A vesicle is smaller than a vacuole. Animal cells have vacuoles, but they are much more prominent in plant cells. Typically, plant cells have a large central vacuole so filled with a watery fluid that it gives added support to the cell (see Fig. 3.3).

Vacuoles store substances. Plant vacuoles contain not only water, sugars, and salts but also pigments and toxic molecules. The pigments are responsible for many of the red, blue, or purple colors of flowers and some leaves. The toxic substances help protect a plant from herbivorous animals. The vacuoles present in unicellular protozoans are quite specialized, and they include contractile vacuoles for ridding the cell of excess water and digestive vacuoles for breaking down nutrients.

The endomembrane system contains the endoplasmic reticulum (rough and smooth), Golgi apparatus, lysosomes, and vacuoles.

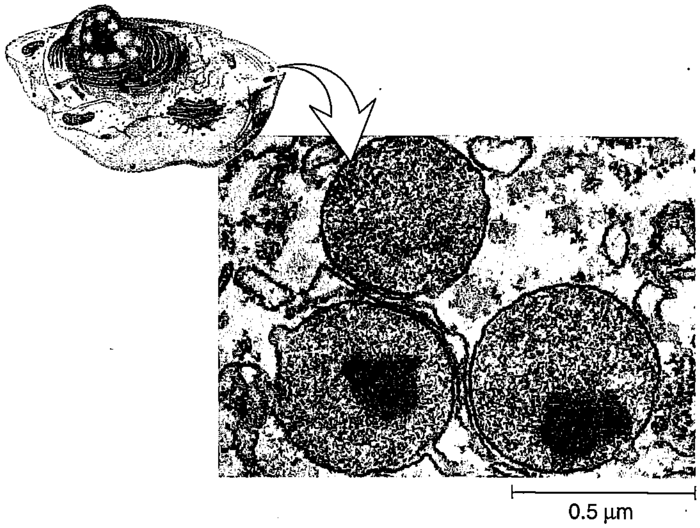


Figure 3.7 **Peroxisomes.**
Peroxisomes are vesicles that oxidize organic substances with a resulting buildup of hydrogen peroxide. Peroxisomes contain the enzyme catalase, which breaks down hydrogen peroxide (H_2O_2) to water and oxygen.

Peroxisomes

Peroxisomes, similar to lysosomes, are membrane-bounded vesicles that enclose enzymes (Fig. 3.7). However, the enzymes in peroxisomes are synthesized by free ribosomes and transported into a peroxisome from the cytoplasm. All peroxisomes contain enzymes whose action results in hydrogen peroxide (H_2O_2):

$$RH_2 + O_2 \rightarrow R + H_2O_2$$

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

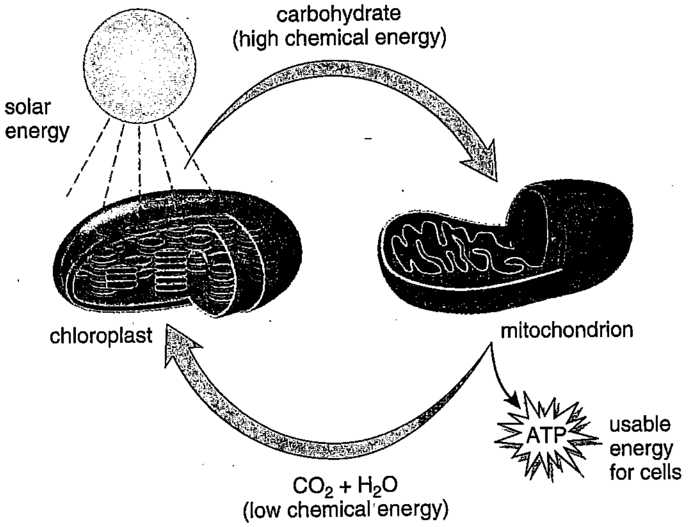
The enzymes in a peroxisome depend on the function of a particular cell. However, peroxisomes are especially prevalent in cells that are synthesizing and breaking down fats. In the liver, some peroxisomes produce bile salts from cholesterol, and others break down fats. In the movie *Lorenzo's Oil*, a boy's cells lacked a carrier protein to transport a specific enzyme into peroxisomes, and he died because a type of lipid accumulated in his cells.

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

The enzymes in peroxisomes produce hydrogen peroxide because they use oxygen to break down molecules.

Energy-Related Organelles

Life is possible only because of a constant input of energy used for maintenance and growth. Chloroplasts and mitochondria are the two eukaryotic membranous organelles that specialize in converting energy to a form that can be used by the cell. **Chloroplasts** use solar energy to synthesize carbohydrates, and carbohydrate-derived products are broken down in mitochondria (sing., **mitochondrion**) to produce ATP molecules, as shown in the following diagram:



Trace the cyclic path of carbon and the noncyclic flow of energy in this diagram.

Photosynthesis takes place in chloroplasts. During photosynthesis, solar energy is converted to chemical energy within carbohydrates. The process can be represented by this equation:

solar energy + carbon dioxide + water ⟶ carbohydrate + oxygen

Only plants, algae, and cyanobacteria are capable of carrying on photosynthesis in this manner. Solar energy is the ultimate source of energy for cells because nearly all organisms, either directly or indirectly, use the carbohydrates produced by photosynthesizers as an energy source.

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

carbohydrate + oxygen ⟶ carbon dioxide + water + energy

Here *energy* is in the form of ATP molecules. When a cell needs energy, ATP supplies it. The energy of ATP is used for synthetic reactions, active transport, and all energy-requiring processes in cells. All organisms carry on cellular respiration, and all organisms except bacteria complete the process in mitochondria.

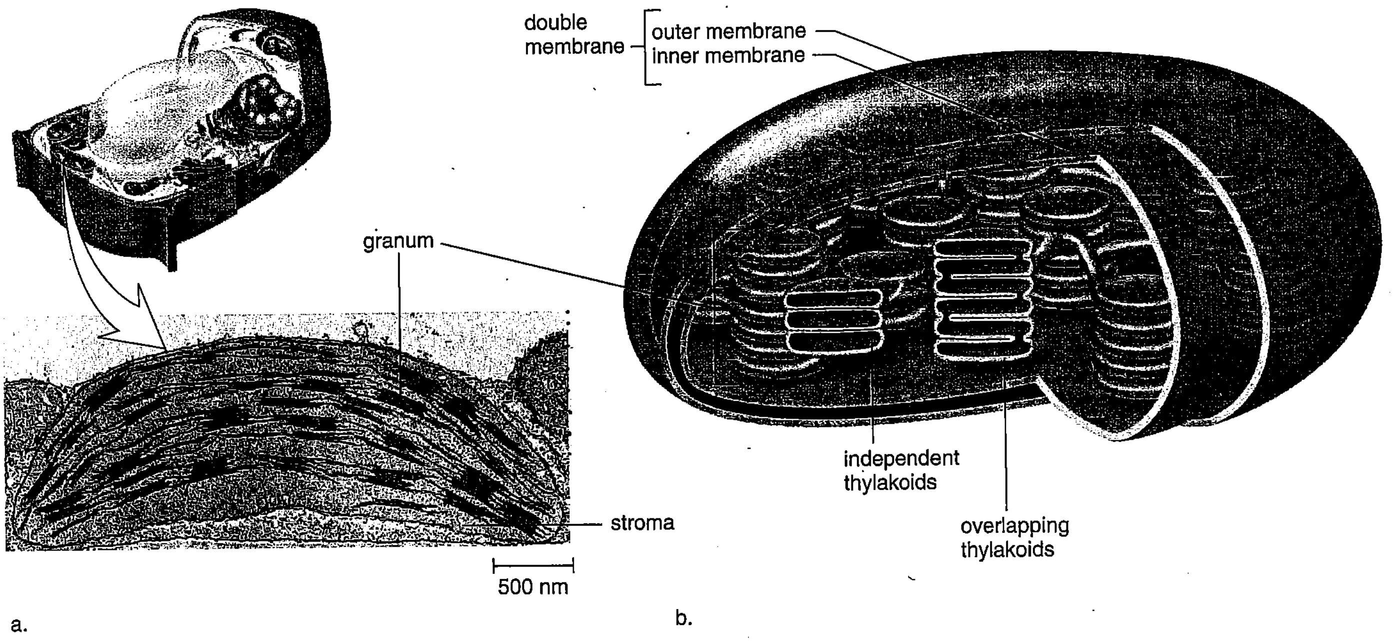


Figure 3.8 Chloroplast structure.
a. Electron micrograph. **b.** Generalized drawing in which the outer and inner membranes have been cut away to reveal the grana.

Chloroplasts

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

A chloroplast is bounded by two membranes that enclose a fluid-filled space called the **stroma.** A membrane system within the stroma is organized into interconnected flattened sacs called **thylakoids.** In certain regions, the thylakoids are stacked up in structures called grana (sing., **granum**). There can be hundreds of grana within a single chloroplast (Fig. 3.8). Chlorophyll, which is located within the thylakoid membranes of grana, captures the solar energy needed to enable chloroplasts to produce carbohydrates. The stroma also contains DNA, ribosomes, and enzymes that synthesize carbohydrates from carbon dioxide and water.

Mitochondria

All eukaryotic cells, including plant cells, contain mitochondria. This means that plant cells contain both chloroplasts and mitochondria. Most mitochondria are usually 0.5–1.0 μm in diameter and 2–5 μm in length.

Mitochondria, like chloroplasts, are bounded by a double membrane (Fig. 3.9). In mitochondria, the inner fluid-filled space is called the **matrix.** The matrix contains DNA, ribosomes, and enzymes that break down carbohydrate products, releasing energy to be used for ATP production.

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

Mitochondria and chloroplasts are able to make some proteins, but others are imported from the cytoplasm.

Chloroplasts and mitochondria are membranous organelles whose structures lend themselves to the energy transfers that occur within them.

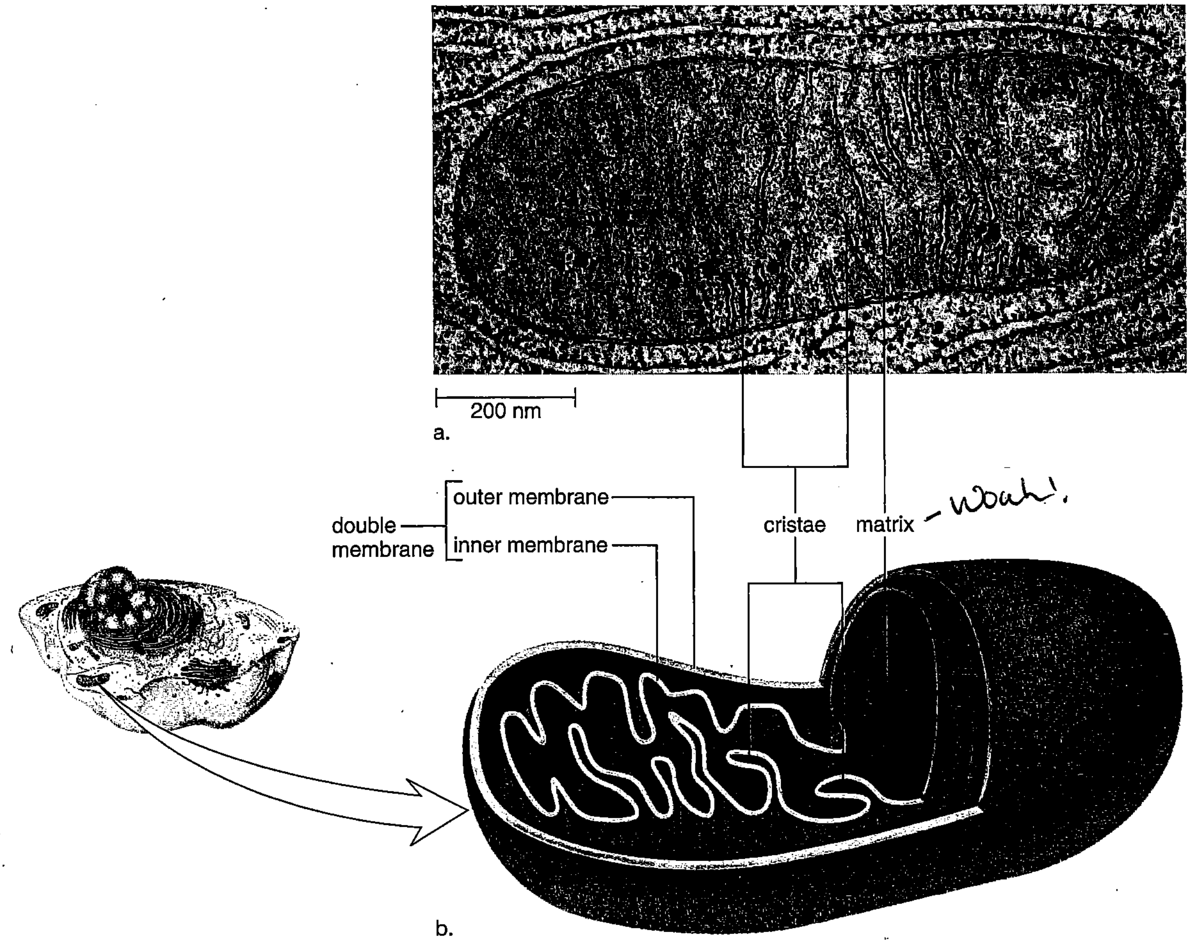


Figure 3.9 **Mitochondrion structure.**
a. Electron micrograph. **b.** Generalized drawing in which the outer membrane and portions of the inner membrane have been cut away to reveal the cristae.

The Cytoskeleton

The **cytoskeleton** is a network of interconnected filaments and tubules that extends from the nucleus to the plasma membrane in eukaryotic cells. Prior to the 1970s, it was believed that the cytoplasm was an unorganized mixture of organic molecules. Then, high-voltage electron microscopes, which can penetrate thicker specimens, showed that the cytoplasm is instead highly organized. The technique of immunofluorescence microscopy identified the makeup of specific protein fibers within the cytoskeletal network (Fig. 3.10).

The name *cytoskeleton* is convenient in that it compares the cytoskeleton to the bones and muscles of an animal. Bones and muscles give an animal structure and produce movement. Similarly, the elements of the cytoskeleton maintain cell shape and cause the cell and its organelles to move. The cytoskeleton is dynamic; elements undergo rapid assembly and disassembly by monomers continuously entering or leaving the polymer. These changes occur at rates that are measured in seconds and minutes. The entire cytoskeletal network can even disappear and reappear at various times in the life of a cell. Before a cell divides, for instance, the elements disassemble and then reassemble into a structure called a spindle that distributes chromosomes in an orderly manner. At the end of cell division, the spindle disassembles, and the elements reassemble once again into their former array.

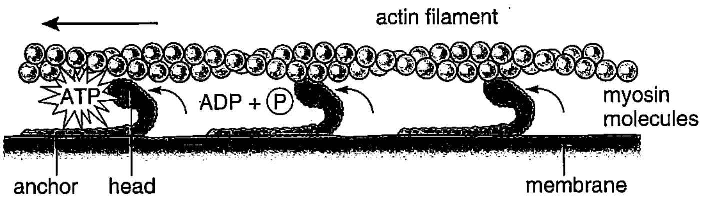
The cytoskeleton contains three types of elements that are responsible for cell shape and movement: actin filaments, microtubules, and intermediate filaments.

Actin Filaments

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

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

How are actin filaments involved in the movement of the cell and its organelles? They interact with **motor molecules,** which are proteins that move along either actin filaments or microtubules. These motor molecules accomplish this by attaching, detaching, and reattaching farther along the actin filament or microtubule. In the presence of ATP, the motor molecule myosin attaches, detaches, and reattaches to actin filaments. Myosin has both a head and a tail. In muscle cells, the tails of several muscle myosin molecules are joined to form a thick filament. In nonmuscle cells, cytoplasmic myosin tails are bound to membranes, but the heads still interact with actin.



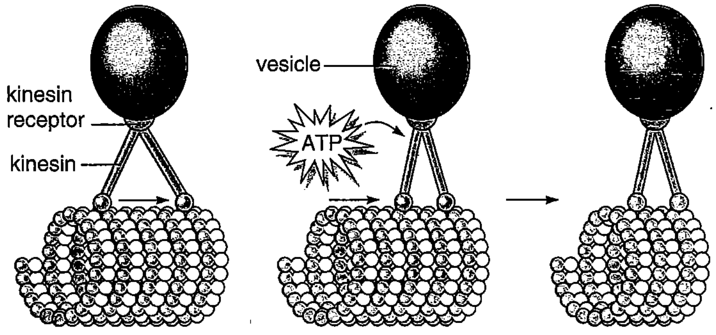
During animal cell division, the two new cells form when actin, in conjunction with myosin, pinches off the cells from one another.

Microtubules

Microtubules are small, hollow cylinders about 25 nm in diameter and from 0.2 to 25 μm in length.

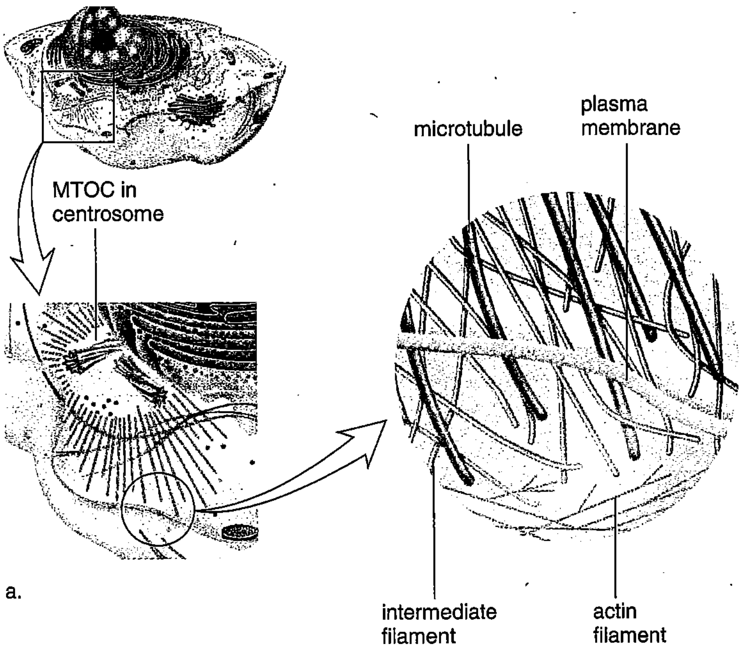
Microtubules are made of a globular protein called tubulin. When microtubules assemble, tubulin molecules come together as dimers, and the dimers arrange themselves in rows. Microtubules have 13 rows of tubulin dimers surrounding what appears in electron micrographs to be an empty central core.

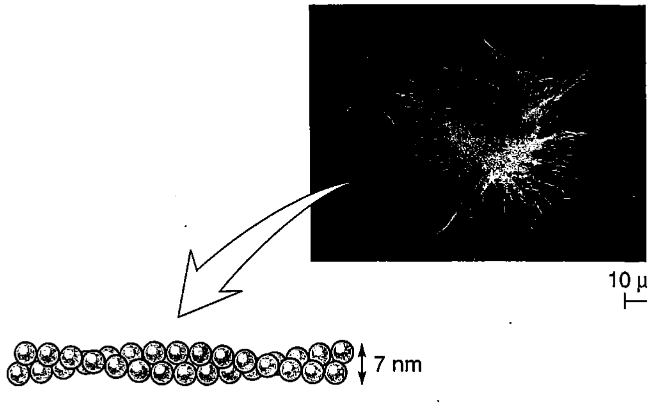
In many cells, microtubule assembly is under the control of a microtubule organizing center, called the **centrosome,** which lies near the nucleus. Microtubules help maintain the shape of the cell and act as tracks along which organelles can move. Whereas the motor molecule myosin is associated with actin filaments, the motor molecules kinesin and dynein move along microtubules. One type of kinesin is responsible for moving vesicles along microtubules, including those that arise from the ER.



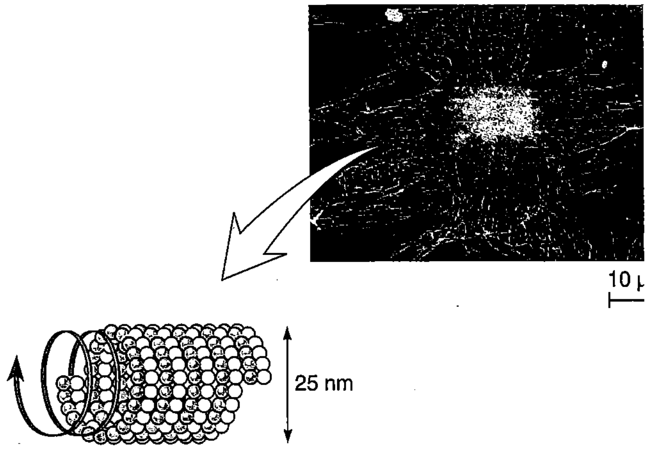
vesicle moves, not microtubule

There are different types of kinesin proteins, each specialized to move one kind of vesicle or cellular organelle. One

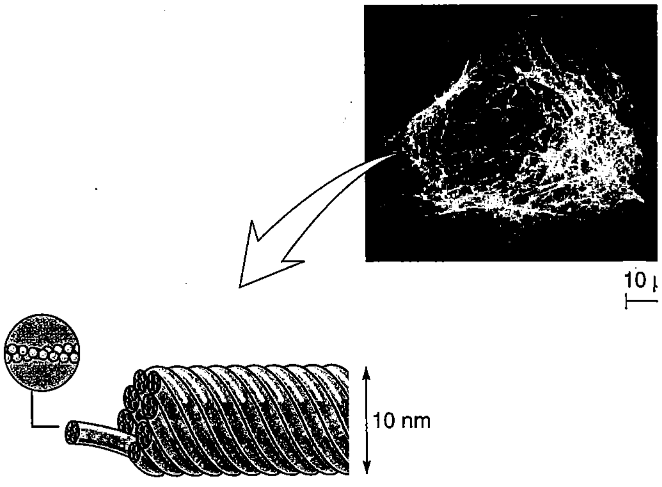




b. Actin filament



c. Microtubule



d. Intermediate filament

Figure 3.10 **The cytoskeleton.**
a. Diagram comparing the size relationship of actin filaments, intermediate filaments, and microtubules. **b.** Actin filaments as they appear in the cell and in diagram. **c.** Microtubules as they appear in the cell and in diagram. The filaments and tubules are visible following immunofluorescence, a technique that binds fluorescent antibodies to specific proteins in cells. **d.** Intermediate filaments as they appear in the cell and in diagram.

type of dynein molecule, called cytoplasmic dynein, is closely related to the dynein found in flagella (see Fig. 3.12).

Intermediate Filaments

Intermediate filaments (8–11 nm in diameter) are intermediate in size between actin filaments and microtubules. They are ropelike assemblies of fibrous polypeptides that support the nuclear envelope and the plasma membrane. In the skin, intermediate filaments made of the protein keratin give great mechanical strength to skin cells. Recent work has shown intermediate filaments to be highly dynamic. They also are able to assemble and disassemble in the same manner as actin filaments and microtubules.

The cytoskeleton contains actin filaments, microtubules and intermediate filaments. These maintain cell shape and allow organelles to move within the cytoplasm. Sometimes they are also involved in movement of the cell itself.

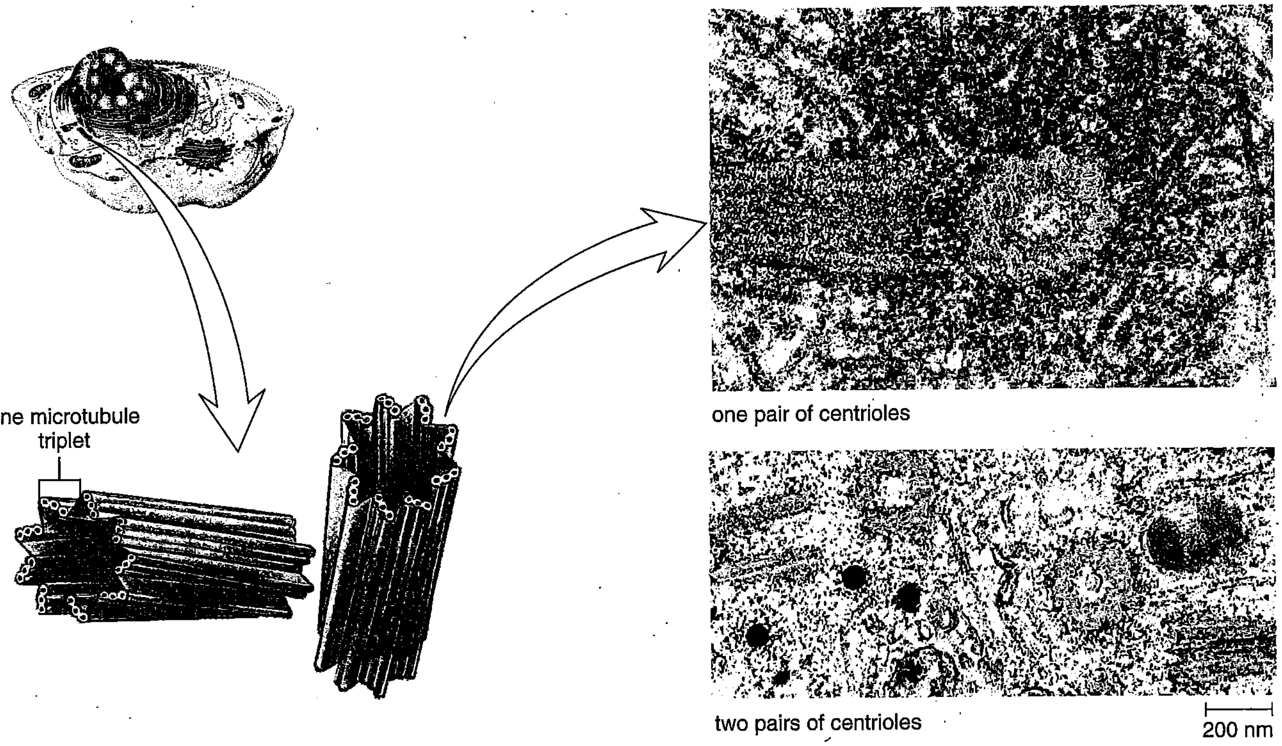


Figure 3.11 Centrioles.
Top, right: A nondividing cell contains a pair of centrioles in a centrosome outside the nucleus. *Left and top right:* Just before a cell divides, the centrosome divides so that there are two pairs of centrioles (*Bottom, right*). During cell division, the centrosomes separate so that each new cell has one pair of centrioles.

Centrioles

Centrioles are short cylinders with a 9 + 0 pattern of microtubule triplets—that is, a ring having nine sets of triplets with none in the middle (Fig. 3.11). In animal cells, a centrosome contains two centrioles lying at right angles to each other. The centrosome is the major microtubule organizing center for the cell, and centrioles may be involved in the process of microtubule assembly and disassembly.

Before an animal cell divides, the centrioles replicate, and the members of each pair are at right angles to one another (Fig. 3.11). Then, each pair becomes part of a separate centrosome. During cell division, the centrosomes move apart and may function to organize the mitotic spindle. Plant cells have the equivalent of a centrosome, but it does not contain centrioles, suggesting that centrioles are not necessary to the assembly of cytoplasmic microtubules.

Centrioles are believed to give rise to basal bodies that direct the organization of microtubules within cilia and flagella. In other words, a basal body does for a cilium (or flagellum) what the centrosome does for the cell.

Centrioles, which are short cylinders with a 9 + 0 pattern of microtubule triplets, may be involved in microtubule formation and in the organization of cilia and flagella.

Cilia and Flagella

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

In eukaryotic cells, cilia are much shorter than flagella, but they have a similar construction. Both are membrane-bounded cylinders enclosing a matrix area. In the matrix are nine microtubule doublets arranged in a circle around two central microtubules. Therefore, they have a 9 + 2 pattern of microtubules. Cilia and flagella move when the microtubule doublets slide past one another (Fig. 3.12).

As mentioned, each cilium and flagellum has a basal body lying in the cytoplasm at its base. Basal bodies have the same circular arrangement of microtubule triplets as centrioles and are believed to be derived from them. The basal body initiates polymerization of the nine outer doublets of a cilium or flagellum

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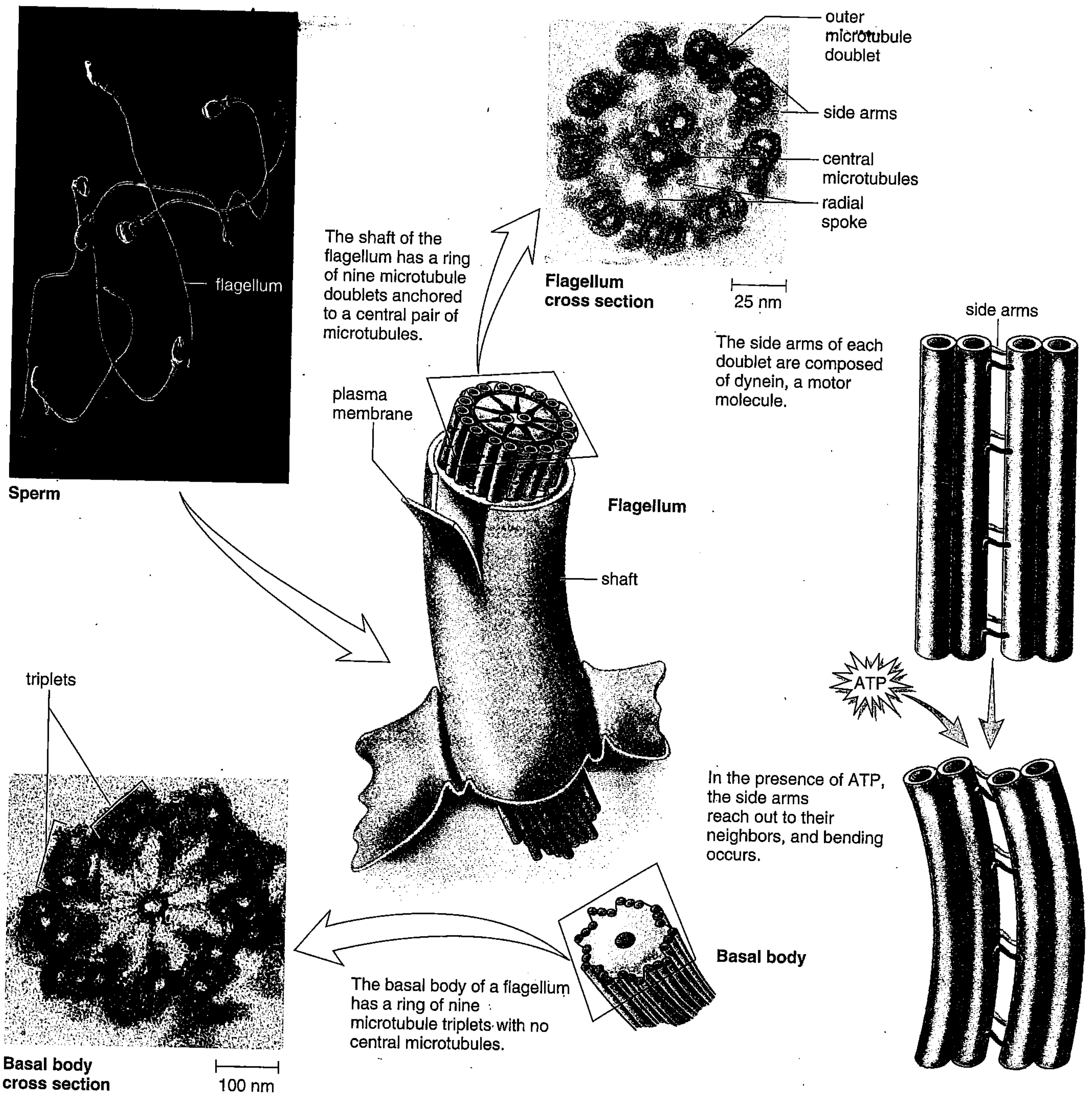
Cilia and flagella, which have a 9 + 2 pattern of microtubules, enable some cells to move.

Visual Focus



The shaft of the flagellum has a ring of nine microtubule doublets anchored to a central pair of microtubules.

The side arms of each doublet are composed of dynein, a motor molecule.

In the presence of ATP, the side arms reach out to their neighbors, and bending occurs.

The basal body of a flagellum has a ring of nine microtubule triplets with no central microtubules.

Figure 3.12 **Structure of a flagellum or cilium.**
A basal body derived from a centriole is at the base of a flagellum or cilium. The shaft of a flagellum (or cilium) contains microtubule doublets whose side arms are motor molecules that cause the flagellum (such as those of sperm) to move. Without the ability of sperm to move to the egg human reproduction would not be possible.